

Pat Vickers Rich



DEPARTMENT OF NATIONAL DEVELOPMENT
BUREAU OF NATIONAL RESOURCES, GEOLOGY AND GEOPHYSICS

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**The Dromornithidae, an extinct
family of large ground birds
endemic to Australia**

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ABSTRACT

Many of Australia's birds are unique to this continent, but none are more impressive than a group of giant ground birds, the Dromornithidae, one member of which may have exceeded in volume and weight any bird that has ever trod the surface of the earth. Although first discovered in the early 19th century, only two genera (*Genyornis* and *Dromornis*), both monotypic, had been recognized when work beginning in the 1950's in central Australia brought to light at least six new forms including three new genera (*Barawertornis*, *Bullockornis*, and *Ilbandornis*), described for the first time in this paper. Based almost entirely on post-cranial material, the Dromornithidae appear to be most closely related to the Casuariidae, the only other Australian ratite group, but before a satisfactory higher taxonomic allocation can be made, good cranial material is needed. Unfortunately, the maximum age of known dromornithid fossils is about 15-20 million years, and from that first record to the last in the late Pleistocene, only minor evolutionary changes are known to have occurred, namely: reduction of the forelimb, reduction of the medial digit of the foot, and development of hoof-like ungual phalanges on the foot. A much more fascinating evolutionary picture of this diverse group awaits future palaeontological discoveries.

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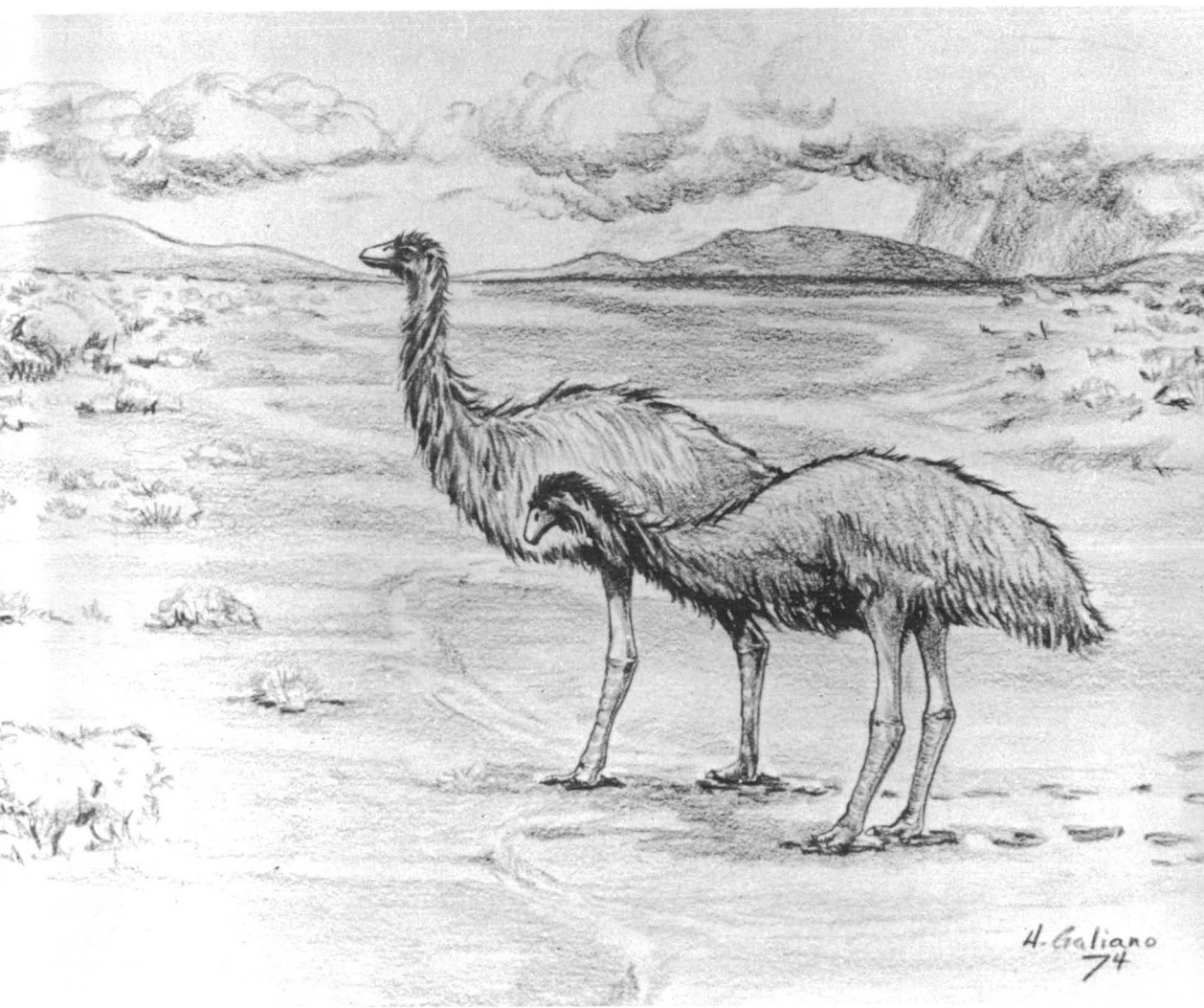
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Back Cover: Giant ground bird and Quinkin from the Cape York Peninsula, Queensland thought by some to represent *Genyornis*. Found by Percy Trezise and photographed by Xenia Dennett.

Front Cover: Restoration of *Genyornis newtoni*, restricted to the Pleistocene of Australia.



Frontispiece: Restoration of two *Genyornis newtoni*, Lake Callabonna, Pleistocene of Australia by Henry Galiano, 1974, about 2 metres in height.

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INTRODUCTION AND HISTORY OF PREVIOUS WORK ON THE DROMORNITHIDAE

Perhaps the first allusion to birds in the family Dromornithidae was made by Aborigines in Australia, for Tindale (1951) and Hall et al. (1951) have noted traditions among the Tjapwurong tribe in western Victoria concerning 'mihirung parimjal' or giant emus that lived 'long ago when the volcanic hills of the Western districts of Victoria were in a state of eruption' (some flows as young as 8000 B.P.; Gill, 1972, R. H. Tedford, pers. comm., 1973). Based on that legend, the common name 'Mihirung Birds' is here given to this group, referring to their gargantuan proportions. Aboriginal rock carvings of 'giant bird tracks' accompanying recognisable emu tracks at Pimba also may represent dromornithids, most probably *Genyornis*.

The first convincing evidence of the former presence of giant ground birds in Australia resulted from Major T. L. Mitchell's exploration and survey work in the 'heights beyond Wellington Valley' in 1830 (Mitchell, 1839, p. 359). There he investigated several limestone caverns and collected the first bones of dromornithids along with a number of other birds and marsupials. The find was fortuitous at best, for as Mitchell explains, 'The pit had been first entered only a short time before I examined it, by Mr Rankin, to whose assistance in these researches, I am much indebted. He went down, by means of a rope, to one landing place, and then fixing the rope to what seemed a projecting portion of rock, he let himself down to another stage, where he discovered, on the fragment giving way, that the rope had been fastened to a very large bone, and thus these fossils were discovered' (Mitchell, 1839, p. 362). Mitchell illustrated this large bone on plate 51¹ (1839, figures 12, 13) noting that it was from the upper part of the reddish breccia in the cave but made no further mention of its identity. Although the illustration shows only two views of this large femur (@18 inches or 460 mm in length), it appears to be avian and most likely a dromornithid as suggested by size alone. According to a letter written by Owen to Mitchell (Mitchell, 1839, p. 365) the bone collected by the latter had been deposited in the Museum of the Geological Society (? of London), but at present it cannot be located.

The account of Mitchell's discovery, as well as all of those as late as 1900, are quite well detailed in two papers: Etheridge (1889) and Stirling and Zietz (1900). Thus, the following account of that period will be brief.

No further additions to Mitchell's discovery were made until the Reverend J. E. T. Woods discovered and excavated 'two tibias and two tarso-metatarsal bones of some extinct and very large bird' on 25 April 1866. In his first report he noted that the bones were found 'in sinking a well on the edge of a swamp fourteen miles north-northwest of Penola (Woods, 1866, p. 7). He further noted that the giant bird 'appears to have been contemporaneous with the natives, for these bones are marked with old scars, one of which must certainly have been inflicted by a sharper instrument than any in possession of the natives at present; there were, however, fragments of flint buried with the bones, and a native well about fifty yards away' (Ibid., p. 7). In his report, Woods proposed the name *Dromaius australis* for the bird bones but neither figured the specimens nor sufficiently diagnosed or described the new taxon to validate such a name, which therefore must be considered a *nomen nudum*. In a later publication, Woods (1882) further noted that the avian bones were found in 'one of the kitchen-middens of the natives of South Australia'. Surprisingly, Etheridge (1889) did not report Woods' discovery in his summary of previous work on the dromornithids. Stirling and Zietz (1900) implied that there were a number of contradictions in Woods' locality description of the Penola dromornithid remains. I can find no fault with Woods' locality descriptions, however. Stirling and Zietz (1900) state 'There is further discrepancy in Mr Woods' notices of the discovery in respect of the position in which the bones were found, for, in one place he states that they were found "in sinking a well" and, in another, that they were found "near a native well"'. In fact, both statements were made by Woods but are not contradictory. Unfortunately these specimens, which at present might provide the only convincing support for temporal overlap of aboriginal man and the dromornithids, could not be located when Stirling and Zietz sought them in the early twentieth century and are

¹ Plate cited incorrectly by Lambrecht (1931) and later writers as Plate 32.

still lost, despite an intensive search for them in the Penola Institute, the major Australian museums, the Hunterian Museum in Glasgow, and the British Museum of Natural History.

Somewhat later, in 1869, the Reverend W. B. Clarke, government geologist for the province of New South Wales, reported that a large bird had been recovered from a well dug in the Peak Downs of Queensland between Lord's Table Mountain and the head of Theresa Creek, near the track from Clermont to Broad Sound. From Clarke's description it appears that the femur (AM F10950) came from a depth of 180 feet² or 55 metres from a stratum of 'drift pebbles and boulders'. Clarke and Gerard Krefft, Curator at the Australian Museum, came to the conclusion that the femur was closely allied to that of the New Zealand moa genus *Dinornis*. Sir Richard Owen, however, prepared a memoir in 1872 describing in detail Clarke's femur on the basis of a cast and photographs (Owen, 1874), designating it a new genus and species, *Dromornis australis*. His paper was mentioned briefly in the *Proceedings of the Royal Society of London* in 1872, but his text was not actually published until 1874 in the *Transactions* of that same society. Owen pointed out characters that clearly distinguished the Peak Downs femur from that of *Dinornis* and closely allied it with the living emu and cassowary.

In 1876-77 Clarke sent Owen a fragmentary synsacrum (BM(NH) 49160) of yet another large bird, which had been recovered by a Mr Dietz during mining activities at a depth of 200 feet or 61 metres in the Canadian Gold Lead mine near Mudgee, Gulgong mining district, New South Wales. The specimen, along with the 'lower portion of a tibia, found in a cave in the Gambier Range' (Clarke, 1877; Stirling and Zietz, 1900) of South Australia, was described by Owen (1879b). Owen believed that both the pelvis and the tibia were from a bird of a size similar to that producing the type femur of *Dromornis australis*. The synsacrum is too fragmentary to identify any more precisely than Dromornithidae, gen. et sp. indet. A femur fragment (BM(NH) 49160a) also known from Canadian Lead and reported in Lydekker (1891) is dromornithid, but not *Genyornis*. The Mt Gambier tibiotarsal fragment (BM(NH) 44011), referred to *Dro-*

mornis by Owen, is most probably, as suggested by Stirling and Zietz (1900), *Genyornis newtoni*, a taxon not recognized until the late nineteenth century.

R. M. Robertson discovered a number of fragmentary hind limb elements (SAM Nos. 17098-17100C) of a dromornithid, probably *Genyornis*, in the stream bed of Salt Creek near Normanville, South Australia. This material was deposited in the South Australian Museum and never described or measured, being only briefly mentioned in Stirling and Zietz (1900, p. 45).

In 1884, DeVis (1884, 1891) reported on a fragmentary femur presented to the Queensland Museum by J. Daniels and supposedly from King's Creek, Darling Downs, Queensland, which he called *Dinornis*, thus allying it with the New Zealand moas. Scarlett (1969), however, correctly pointed out that the preservation of the *Dinornis* specimen was radically different from other fossils collected along King's Creek, that the femoral fragment had a similar preservation, and that it was morphologically indistinguishable from the New Zealand *Pachyornis elephantopus*, known only from South Island.

In 1889 near Cainwarra Station at Thorbindah (= ?Thorlindah on the Paroo River) a fragmentary tibiotarsus (cast AM L529; actual specimen now lost) was recovered from a shallow well sunk at an old spring and was sent to A. S. Cotter, then government geologist. Etheridge (1889) described the tibiotarsus as well as an accompanying 'fibula', which he assigned to *Dromornis australis*. The ?fibula is definitely not avian and the cast of the tibiotarsus so fragmentary that assignment beyond Dromornithidae, gen. et sp. indet., is not warranted even though Stirling and Zietz assigned it to *Genyornis newtoni*.

In the same year A. Zietz recovered a fragmentary femur (SAM P17102) of cf. *Genyornis newtoni* from Baldina Creek, near Burra, South Australia, which was only briefly mentioned by Stirling and Zietz (1900) in their monograph on *Genyornis*.

By far the most significant discovery, however, occurred at Lake Callabonna in 1892 when an Aboriginal reported the occurrence of giant bones to F. B. Raglass, who in turn visited the site. J. Meldrum, an employee of Raglass, also visited the locality at Lake Calla-

² Clarke stated that 'the well passed through 30 feet of black trappean alluvial soil, so common in Australia, which rested on 150 feet of drift pebbles and boulders, on one of which (at that depth) rested a short thick femur . . .'. Later (1877, p. 41) Clarke clarified this depth as 180 feet.

bonna and took a number of fragments to the South Australian Museum in Adelaide. This whetted the interest of members of the museum staff, who then employed H. Hurst to oversee an expedition to Callabonna that left Adelaide in January, 1893. Work carried out by this party produced the material that led to A. Newton's announcement in April 1893 of a 'large Struthious bird' in *Nature*. Zietz, and for a short time, Stirling, replaced Hurst in August of 1893 and continued to collect material of *Genyornis*, *Dromaius*, and several different genera of marsupials. The *Genyornis* material was later described in detail in a number of papers by Stirling (1896) and Stirling and Zietz (1896, 1900, 1905, 1913) where the name *Genyornis newtoni* was proposed (see figure 1). In these papers a total of 6 femora (only 3 in good condition), 21 tibiotarsi-tarsometatarsi-feet, 1 sternum, a partial skull and parts of a second with a lower jaw, 1 complete wing and fragments of several others, 1 complete set of caudal vertebrae, parts of three synsacra, and several isolated vertebrae were reported (see Stirling and Zietz, 1900, in particular). Some elements were associated, but most of the associations have been lost over the years, and thus further recovery of partially or completely associated individuals would be an important addition to present information available on dromornithid morphology.

No significant additional work was carried out at Lake Callabonna after the South Australian Museum expedition in the late 19th century until R. A. Stirton and his associates returned during the 1950s. Their collections mainly emphasized the marsupial fauna, in particular *Diprotodon*, but a little dromornithid material was recovered. In 1970, a joint American Museum of Natural History (New York), Smithsonian Institution (Washington, D.C.), South Australian Museum expedition spent three months excavating during the austral winter. A large sample of *Genyornis* was recovered, which included a number of elements not well preserved or lacking in the early South Australian Museum collections. Much of the material has yet to be prepared but is presently being cleaned and studied by P. Rich.

In the first decade of the 20th century, J. W. Gregory and a number of his students discovered several new localities and made significant collections in the Great Artesian Basin

of South Australia. Some dromornithid material, not previously reported, was among the material collected by this expedition.³ Gregory's Emu Camp and Lower Cooper Locality 2 produced a tarsometatarsus (HM B774) and vertebrae (HM Nos. B768, B769, B968) fragments that are presently housed in the Hunterian Museum in Glasgow, Scotland.

The first report of fauna found in Mammoth Cave in Western Australia appeared in 1910 and was followed later by a number of papers published by Glauert (1910, 1914, 1948), concerning additions to that fauna. Among material from the cave, but unreported until now, was a single sacral vertebra of a dromornithid, gen. et sp. indet. (WAM 65.4.152).

Anderson and Fletcher (1934) later reported on a large bone concentration in fluvial sediments at Cuddie Springs near Brewarrina on Gelgoine Station in New South Wales. The dromornithid material, including several hind limb fragments (AM F33402, F33405-6, F33408-9, MM F16777), can all be included in *Genyornis newtoni*.

1954 was a most significant year in the gradual elucidation of dromornithid history in Australia. R. A. Stirton and associates discovered Tertiary fossil-bearing terrestrial sediments in the Lake Eyre Basin of South Australia. At one of the localities (Lawson Quarry), along the western side of Lake Palankarina a fragmentary synsacrum (UCMP 60613) of a dromornithid, gen. et sp. indet., was recovered (see Miller, 1963a).

Throughout the 1950s a number of Pleistocene localities (see stratigraphic section of this paper) were found by joint South Australian Museum-University of California parties along the Warburton River and Cooper's Creek. These were discovered in the following sequence:

- 1953 Pirranna Soakage (= Tilla Tilla Waterhole)
- Cooper's Creek Site 6 (= Markoni Locality)
- 1955 Cassidy Locality
- 1958 Cooper's Creek Sites 5, 8
- Cooper's Creek Site 9 (= Katipiri or Kuttipirra Waterhole)

In 1962 the Leaf Locality was discovered at Lake Ngapakaldi in northern South Australia and produced several bones (UCMP Nos.

³ DeVis (in Gregory, 1906) identified some of the material that Gregory collected and appended a faunal list to Gregory's *The Dead Heart of Australia*. He did not, however, report on the "larger birds' bones" (Ibid, p. 353).

88186, 88188, 88335, 109180 and 114732) including phalanges and a synsacral fragment that could be assigned to Dromornithidae, gen. et sp. indet.

During that same year, Charles H. Taylor of Pioneer, Tasmania while supervising sluicing operations at the Old Endurance Tin Mine at South Mount Cameron found a number of trackways in mid-Tertiary sediments at that locality. The tracks were apparently produced by dromornithids (Rich and Green, 1974), but again genus and species are undetermined.

Although bones had been reported from the Carl Creek Limestone in western Queensland as early as 1901, R. H. Tedford and A. R. Lloyd (see Tedford, 1968) were the first to discover dromornithids at the Riversleigh locality in 1963. *Barawertornis tedfordi*, n. gen. et n. sp. was proposed for the first taxonomically useful Tertiary dromornithid material (CPC Nos. 7341, 7346-8) found since the Peak Downs femur (*Dromornis australis*) was recovered at the end of the previous century.

In the years that followed a number of other Tertiary localities were discovered in relatively rapid succession. A large and generically diverse (*Dromornis*, *Ilbandornis*) sample of dromornithids was collected from the late Miocene or early Pliocene Waite Formation on Alcoota Homestead, Northern Territory during 1962-1963. Although local pastoralists and Aborigines had long been aware of deposits in the area, not until R. Gorey notified the resident geologist at Alice Springs and in turn A. E. Newsome and K. A. Rochow had notified R. A. Stirton of the find, was any scientific investigation of the site undertaken. In 1962, Stirton and Tedford, along with Newsome and Rochow, visited the site and made the first collections there. They were followed in 1963 by M. O. Woodburne, J. E. Mawby, and J. E. Ferguson, who carried out the major collection

of vertebrates at Alcoota (see Woodburne, 1967).

Yet another Tertiary (mid-Miocene) locality was reported in 1968 by Plane and Gatehouse. The Camfield Beds near Bullock Creek in the northern part of the Northern Territory produced two species of dromornithids, probably both in the same genus, *Bullockornis* (*B. planei* and *B. sp.*). While *B. sp.* is represented only by a tarsometatarsus fragment (CPC 13849), several hind limb elements as well as vertebrae and ribs are known of the second species, *B. planei*.

In 1969 Butler briefly mentioned the discovery of an enormous egg in dune deposits south of the Scott River in Western Australia. The egg had been found several years earlier by an amateur and was 'lodged in the Western Australian Museum' (see also Anon., 1962; Edwards, 1962a, b; Hyslop, 1967). At present (see later section for more detailed discussion) the egg is tentatively assigned to the Dromornithidae, but its taxonomic position is open to question pending further studies when permitted.

Further evidence of oological remains was recovered in 1972-73 by M. O. Woodburne and M. Archer from a unit seemingly contemporaneous with the mid-Tertiary Etadunna Formation. The Snake Dam Locality in northern South Australia produced an egg shell fragment, which is much too thick to belong to *Dromaius* and is probably dromornithid.

Only two additional localities, one at Brother's Island in western South Australia and a second specified only as Diamantina (could be in either South Australia or Queensland, but probably the former), have produced dromornithid remains represented in collections of the South Australian Museum. The history of discovery of bones, probably representing *Genyornis*, at these two localities is at present unknown.

ABBREVIATIONS

AM, Australian Museum, Sydney	MM, Geological and Mining Museum, Sydney
AMNH, American Museum of Natural History, Department of Vertebrate Paleontology, New York.	NMV, National Museum of Victoria, Melbourne
AMNH, B, American Museum of Natural History, Department of Ornithology	QM, Queensland Museum, Brisbane
BM(NH), British Museum of Natural History, London	QVM, Queen Victoria Museum and Art Gallery, Launceston
BMR, Bureau of Mineral Resources, Canberra	SAM, South Australian Museum, Adelaide
CPC, Commonwealth Paleontological Collections, Bureau of Mineral Resources, Canberra, type and figured specimens	SIAM, Smithsonian Institution, American Museum of Natural History Expedition, at respective Institutions in Washington and New York
CSIRO, Commonwealth Scientific and Industrial Research Organization, Wildlife, Canberra	TM, Tasmanian Museum, Hobart
F, Fossil Collection, Bureau of Mineral Resources, Canberra	UCMP, University of California, Museum of Paleontology, Berkeley
HM, Hunterian Museum, Glasgow	USNM, United States National Museum of Natural History, Washington
HMCZ, Harvard Museum of Comparative Zoology, Cambridge	WAM, Western Australian Museum, Perth
KU, University of Kansas, Lawrence	@, Approximately
	>, Greater than
	<, Less than

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SYSTEMATICS

Diagnoses and Descriptions

In the following paper *diagnoses* are used to distinguish the taxon under discussion from other closely related taxa of the same taxonomic rank and within the same higher category. Thus, species within the same genus are diagnosed with respect to one another, genera within the same family, etc. The standard diagnoses include comparisons with other taxa; synoptic diagnoses, on the other hand, are only a listing of character-states (without comparisons) that are diagnostic for the taxon under consideration. Where possible, as an aid in the *description*, tables and photographs are used. Not all characters used in the generic diagnoses are mentioned in each diagnosis; however, tables 6-8 summarize the character-state of every character used in any generic diagnosis for each genus of Dromornithidae and thus should be referred to if the information required is not present in a given diagnosis. Characters previously mentioned in the diagnoses, tables, and illustrated in figures are not mentioned in the descriptions unless requiring further elaboration. If several specimens of one element of a single taxon are represented, descriptions are always composite and are never detailed descriptions of individual specimens. Preserved condition of individual specimens, if known, is described when such specimens are first listed under the headings 'Type Specimen' or 'Referred Specimens'. In cases where specimens or taxa have been described in previous publications, references to text and figures are given and only characters not previously discussed are evaluated in the present text.

In all descriptions, width refers to medio-lateral dimensions, length to proximo-distal dimensions, and depth to anteroposterior (or palmoanconal in the case of the forelimb) dimensions. On the synsacrum and vertebrae length refers to anteroposterior, width to mediolateral, and depth to dorsoventral dimensions. Np. in descriptions and diagnoses is an abbreviation for 'not preserved'.

Characters Used in Diagnoses and Descriptions

Characters on each of the hind limb elements are mentioned in the diagnoses and descriptions with respect to six orientations of individual bones: proximal, anterior, medial, posterior, lateral, and distal views. As the character-states are described, indication of the viewing orientation is made.

In the diagnoses only those characters that are useful in distinguishing a particular taxon from closely related forms of the same taxonomic rank are mentioned. Thus, particular characters will not necessarily be evaluated for each taxon under consideration in the text. Tables are provided, however, which do evaluate for each taxon under consideration in this paper those characters used in the diagnoses. In both the text and the tables each character is numbered or lettered, to allow easy reference from diagnoses of one taxon to the next. For each element (humerus, radius, ulna, etc.) the numbering system begins with 1 or a.

Characters used in the descriptions are consistently evaluated for each taxon considered, and each character is numbered, continuing from the numbering system in the diagnoses for any particular element. Thus, if the reader wishes to check the character-state of any particular character, he needs simply refer to the appropriate number under the description for that taxon. Characters discussed in some, but not all, diagnoses are not usually mentioned in the description except in cases where the tabularized character-states are not sufficiently explanatory and the character-state is not mentioned in particular diagnoses due to its lack of uniqueness for certain taxa.

Characters Used in the Diagnosis of the Dromornithidae from Other Palaeognath Groups

The following characters were employed in the diagnosis of the Dromornithidae:

VERTEBRAE

Anterior view

- a. presence/absence of vertebral arterial canals
- b. depth, breadth of atlas vertebra

Dorsal view

- c. orientation of dorsal surface of neural arch

STERNUM

Proximal view

- a. outline of sternum
- b. comparative length and breadth of sternum
- c. nature of sternocoracoidal processes
- d. shape of anterior border of sternum
- e. number of intercostal spaces (larger sample needed for meaningful study)
- f. length of costal margin with respect to length of lateral margins of sternum

- g. presence/absence of sternal notches
- h. shape of posterior sternal margin

Ventral view

- i. presence/absence of carina (keel)
- j. nature of ventral surface of sternum

Anterior view

- k. depth, size, and location of coracoidal sulci

SCAPULOCORACOID (= CORACO-SCAPULA)

Anterior view

- a. shape of coracoid
- b. orientation of glenoid facet
- c. presence/absence of groove mediad of glenoid facet
- d. nature of anterior surface between glenoid facet
- e. shape of scapular blade

Lateral view

- f. shape of scapulocoracoid

HUMERUS

- a. general proportions of humerus

Proximal view

- b. nature of ligamental furrow

Anconal view

- c. presence/absence of pneumatic fossa
- d. degree of internal projection of internal tuberosity
- e. relative proximal protrusion of head and internal tuberosity
- f. location of head on proximal end

Ventral view

- g. presence/absence of ligamental attachment at proximodistal midpoint of ventral surface of shaft

Palmar view

- h. depth and size of brachial depression
- i. presence/absence of ridge trending from base of deltoid crest to dorsal margin of shaft
- j. development of ectepicondylar prominence

Distal view

- k. degree of definition of articular surfaces
- l. cross-sectional outline of shaft
- m. shape of distal end
- n. degree of development of olecranal fossa

ULNA-RADIUS

Proximal view

- a. nature of proximal articular surface
- b. nature of olecranon
- c. depth of proximal end

Anconal view

- d. degree of fusion of radius-ulna-carpometacarpus
- e. comparative widths of radius-ulna
- f. comparative widths of proximal and distal ends of radius
- g. comparative lengths of radius-ulna and humerus

CARPOMETACARPUS

Proximal view

- a. degree of flattening of carpal trochlea

Medial view

- b. presence/absence of phalangeal articulation on metacarpal I
- c. degree of fusion of metacarpals II and III
- d. distinctness of metacarpal I from remainder of carpometacarpus
- e. comparative depths of distal and proximal ends of carpometacarpus
- f. breadth of metacarpal II

Distal view

- g. number of metacarpals with phalangeal articulations

SYNSACRUM

Dorsal view

- a. nature of dorsal surface of synsacrum posteriad of antitrochanter
- b. width of dorsal surface of synsacrum posteriad of antitrochanter
- c. presence/absence of canals in anterior end of ilium
- d. fore-aft location of antitrochanter
- e. relative posterior protrusion of ilium, ischium, pubis

Lateral view

- f. pubes fused/unfused along midline posteriorly
- g. pubes fused/unfused with ischium, ischium with ilium
- h. ischia fused/unfused along midline
- i. caudal vertebrae fused/unfused to ischia
- j. depth of ilium dorsad of acetabulum
- k. nature of pectinal process
- l. depth (dorsoventral) of pubic and ischial bars

FEMUR

Proximal view

- a. shape of posterior margin of proximal articular surface

Anterior view

- b. comparative proximal extension of trochanter and head

- c. orientation of long axes of condyles with respect to long axis of shaft
- d. comparative distal extension of internal and external condyles
- e. comparative degree of inflation of external and internal condyles

Lateral view

- f. shape of dorsal margin of external condyle
- g. comparative lengths of fibular and external condyles
- h. degree of posterior extension of external condyle beyond shaft

Posterior view

- i. shape of internal margin of trochanter
- j. presence/absence of muscle scar near proximointernal region of popliteal area
- k. shape and extent of popliteal area
- l. comparative breadths of fibular and external condyles

Medial view

- m. location of distalmost extension of internal condyle with respect to remainder of distal end of femur
- n. shape of internal condyle; angle major axis of internal condyle forms with posterior margin of shaft
- o. shape of shaft distal end
- p. shape of posterior margin of internal condyle; location of posteriormost extension of internal condyle

Distal view

- q. comparative depths of internal and external condyles
- r. comparative breadth and depth of distal end
- s. shape of internal margin of internal condyle

TIBIOTARSUS

Proximal view

- a. degree of mediolateral compression of cnemial crests
- b. comparative depths of inner cnemial crest and remaining proximal articular surface
- c. degree of proximal extension of inner cnemial crest
- d. degree of lateral protrusion of external articular surface; shape of margin between outer cnemial crest and external articular surface
- e. angle formed between inner cnemial crest and medial margin of internal articular surface
- f. angle formed by projection of internal

margin of inner cnemial crest and another line passing through anteriormost extensions of condyles

- g. degree of channelling of interarticular area
- h. presence/absence of intercondylar eminence
- i. breadth of internal and external articular surfaces

Anterior view

- j. location of inner cnemial crest with respect to midline of shaft
- k. presence/absence of supratendinal bridge
- l. location of tendinal canal on shaft with respect to midline
- m. presence/absence of ridge extending laterad from distal border of supratendinal bridge
- n. shape of proximal margin of condyles

Lateral view

- o. degree of posterior extension of posterior surface of shaft in vicinity of fibular crest
- p. outline of anterior and distal margins of external condyle
- q. position along external condyle of antermost projection
- r. degree of posterior extension of external condyle beyond shaft
- s. presence/absence of deep excavation near anterior end of external condyle
- t. presence/absence of knob extending far laterad near anteroposterior midpoint of external condyle

Medial view

- u. depth and length of internal condyle
- v. shape of proximal margin of internal condyle

Distal view

- w. comparative depths of internal and external condyles
- x. shape of condylar fossa
- y. shape of anterior margin of internal condyle

TARSOMETATARSUS

Proximal view

- a. shape of hypotarsus; number of calcaneal canals
- b. shape of internal border of proximal end
- c. comparative proximal extension of hypotarsus and intercotylar prominence
- d. presence/absence of marked depression between intercotylar area and hypotarsus
- e. presence/absence of ridge projecting ex-

ternally from lateral margin of cotylar surface

- f. shape of proximal articular surface; comparative depths of internal and external cotyla

Anterior view

- g. depth of metatarsal canal

Posterior view

- h. number and length of subhypotarsal ridge(s)
- i. degree of grooving of posterior shaft surface
- j. presence/absence of metatarsal I articulation
- k. presence/absence of distal foramen
- l. number of trochleae present
- m. degree of grooving of distal margin, trochlea III
- n. comparative distal extensions of trochlea IV and II
- o. degree of distal extension of trochlea III beyond II and IV

Distal view

- p. depth of trochleae
- q. relationship of medial and lateral margins of trochlea III, parallel or divergent

PES

- a. phalangeal count for digits II, III, IV
- b. total number of digits present
- c. comparative lengths of digits

Dorsal view

- d. shape of proximal margins of many phalanges (2, digit II; 3, digit III; 2, 3, digit IV)

Phalanx 1, Digit II

- e. shape of phalanx
- f. presence/absence of deep indentation in ventral margin of proximal articular surface
- g. degree of mediolateral compression and depth of proximal articular surface

Phalanx 2, Digit II

- h. degree of excavation of proximal articular surface; degree of development of dorsoventrally oriented median ridge

Phalanx 1, Digit III

- i. location of greatest depth of proximal articular surface
- j. presence/absence of two distinct processes on ventral margin of proximal articular surface
- k. in distal view, relationship of internal and external margins of condyles, parallel or divergent ventrally

Phalanx 2, Digit III

- l. shape and depth of proximal articular surface
- m. degree of excavation of proximal articular surface; presence/absence of median ridge
- n. comparative depths of proximal and distal ends of phalanx
- o. in distal view, relationship of medial and lateral margins of condyles, parallel, divergent ventrally

Phalanx 3, Digit III

- p. comparison of length, width, depth of phalanx

Phalanx 1, Digit IV

- q. shape of ventral margin of proximal articular surface
- r. presence/absence of process extending proximad from medioventral corner of phalanx
- s. relationship of internal and external margins of condyles, parallel, convergent or divergent ventrally

Phalanx 2, Digit IV

- t. presence/absence of central ridge (oriented dorsoventrally) bisecting proximal articular surface
- u. relationship of internal and external margins of condyles, parallel, divergent ventrally
- v. degree of dorsoventral compression of proximal articular surface
- w. comparative length and width of phalanx

Phalanx 3, Digit IV

- x. comparative length and width of phalanx

Terminal Phalanges

- y. shape of phalanx, spade-shaped or claw-shaped

Characters used in Diagnoses and Descriptions of the Dromornithidae

The following characters were employed in the diagnoses of taxa within the Dromornithidae:

VERTEBRAE

Axis

- 1. degree of inflation of vertebra, neural arch in particular
- 2. direction of tilt of prezygapophyses
- 3. shape of prezygapophyses
- 4. degree of anterior protrusion of odontoid process
- 5. nature of dorsal surface of neural arch between neural spine and prezygapophyses

Anterior cervical

1. shape and orientation of prezygapophyses
2. shape of lateral margin of neural arch
3. presence/absence of foramina in surface of neural arch laterad of neural spine
4. location of foramina on lateral surface of centrum
5. length of lateral arch; location of narrowest part
6. area of greatest depth of depression on ventral surface, anterior half of centrum
7. nature of ventral surface of centrum
8. shape of posterior articular surface of centrum
9. comparative diameters of vertebral canal and neural canal
10. area of maximum breadth of vertebra

STERNUM

Dorsal view

1. nature of sternocoracoid processes
2. orientation of lateral margins of sternum with respect to one another

Anterior view

3. shape of anterodorsal margin of sternum
4. presence or absence of subcarinate ridge

SCAPULOCORACOID (= CORACOSCAPULA)

Anterior view

1. degree of medial extension of ventromedial corner of coracoid
2. shape of ventral margin of coracoid
3. relationship of minimum width of coracoid and length of coracoid
4. comparative lengths of medial and lateral margins of coracoid

Lateral view

5. depth of coracoid

Posterior view

6. nature of surface between glenoid facet and medial margin of scapulocoracoid
7. presence/absence of ridge near ventral part of coracoid
8. degree of inflation of scapulocoracoid
9. nature of ventromedial corner of coracoid

CARPOMETACARPUS

1. presence/absence of metacarpal space between metacarpals I and II

FEMUR

Proximal view

1. degree of posterior expansion of trochanter; depth

2. outline of posterior border of proximal articular surface
3. degree of narrowing at neck, with respect to head and trochanter
4. conformation of the proximal articular surface on internal side of trochanter

Anterior view

5. degree of neck elongation
6. degree of slenderness/robustness of shaft with respect to length
7. shape of internal margin of shaft
8. location along long axis of shaft of its minimum width

Lateral view

9. degree of anterior extension of trochanter
10. degree of anteroposterior compression of shaft
11. size of angle formed between anteroposterior axis of fibular condyle and long axis of shaft
12. prominence of obturator ridge

Posterior view

13. prominence of posterior intermuscular line
14. depth of popliteal area
15. degree of external protrusion of fibular condyle
16. angle the proximodistal axis of the external condyle forms with long axis of shaft
17. degree of development of depression at proximoexternal base of fibular condyle

Medial view

18. shape of internal condyle
19. nature of distal one fourth of internal surface of shaft and internal condyle

Distal view

20. cross-sectional shape of shaft
21. degree of anteroposterior compression of condyles with respect to width of distal end
22. comparative width of external condyle with respect to internal condyle
23. comparative depths of internal and external condyles
24. degree of anterior or posterior convergence/divergence of long axes of condyles
25. shape of internal condyle's internal margin
26. position of posterior margin of fibular condyle with respect to posterior margin of internal condyle

TIBIOTARSUS

Proximal view

1. shape of lateral margin of proximal articular surface and degree of lateral protrusion of external articular surface
2. depth of external articular surface
3. width of interarticular surface between cnemial crests and articular surfaces

Anterior view

4. width of condyles with respect to width of shaft near distal end

Lateral view

5. size of angle formed by intersection of anterior and posterior shaft surfaces laterally along fibular crest

Posterior view

6. conformation of lateral margin of shaft between fibular crest and proximal articular surface

Medial view

7. degree of anterior extension of internal condyle

Distal view

8. depth of condyles

TARSOMETATARSUS

Proximal view

1. depth of proximal end

Anterior view

2. width of intertrochlear space between trochleae III and IV

Medial view

3. depth of shaft
4. width of subhypotarsal ridge
5. prominence of subhypotarsal ridge

Posterior view

6. width of shaft with respect to width of distal end
7. degree of flare of distal and proximal ends
8. nature of lateral and medial shaft margins
9. comparative extension distad of trochleae II and IV

Lateral view

10. posterior extension of posteroproximal margin of trochlea IV
- 10A. nature of lateral and medial shaft surfaces on proximal half of shaft

Distal view

11. reduction of trochlea II with respect to III and IV
12. relation (parallel, divergent?) of medial and lateral margins of trochlea II

13. depth of trochlear groove on posterior surface of trochlea III
14. comparative widths of posterior and anterior 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

PES

Phalanx 1, Digit II

1. depth of condyles
2. degree of divergence ventrally of condylar margins; comparative depths of long axes of external and internal condyles

Phalanx 2, Digit II

1. comparative length and width of phalanx
2. in dorsal view shape of proximal margin of phalanx

Phalanx 2, Digit IV

1. shape of internal margin of internal condyle

Phalanx 3, Digit III

1. comparative length and width of phalanx

A number of additional characters not found particularly useful in the diagnoses are evaluated in the descriptions. These include:

STERNUM

Dorsal view

5. radius of curvature of internal sternal surface from front to back
6. angle formed by intercostal spaces and lateral wall of internal sternal surface
7. shape of internal sternal surface over anterior half of sternum

Anterior view

8. nature of medial surfaces of sternocoracoid processes
9. nature of external sternal surface between sternocoracoid process and coracoid sulcus

Lateral view

10. location of most dorsoventrally elongate intercostal space
11. degree of curvature of ventral border of sternum along mediolateral midline

SCAPULOCORACOID (= CORACOSCAPULA)

Anterior view

10. location and size of foramina on anterior surface

Posterior view

11. location and size of foramina on posterior surface
12. nature of medial margin of scapula

HUMERUS

Proximal view

1. comparative widths of head, internal and external tuberosities
2. distinctness of head from remainder of proximal end

Anconal view

3. presence/absence of pneumatic fossa
4. abruptness of projection of head from region of external tuberosity
5. shape of shaft
6. presence/absence of prominent ridge on proximal half of anconal surface

Palmar view

7. presence/absence of distinct ectepicondylar prominence

FEMUR

Proximal view

27. shape of the posterior margin of the trochanter

Anterior view

28. degree of curvature of proximal articular surface
29. comparative proximal extensions of trochanter and head
30. comparative internal and external extension of internal and external condyles respectively

Lateral view

31. nature of external shaft surface near proximal end
32. shape of trochanter
33. comparative anterior and posterior extension of external condyle from shaft
34. shape of anterior and posterior shaft margins
35. conformation of shaft's lateral surface
36. shape of external condyle
37. shape of fibular condyle
38. depth of fibular condyle with respect to external condyle

Posterior view

39. length of obturator ridge with respect to total length of shaft
40. degree of mediolateral expansion of femur's proximal and distal ends with respect to one another; distal expansion with respect to minimum width of shaft
41. conformation of posterior shaft surface
42. angle formed by proximal margin of ex-

ternal condyle with posterior margin of shaft;

43. shape of margin of external condyle
44. shape of margin of internal condyle
45. depth and conformation of rotular groove
46. conformation of medial shaft surface
47. comparative anterior and posterior extension of internal condyle from shaft

Distal view

48. shape of external and fibular condyles
49. shape and depth of intercondylar fossa
50. shape and depth of rotular groove
51. orientation of posterior margin of internal condyle with respect to mediolateral axis of distal end

TIBIOTARSUS

Proximal view

9. shape of external articular surface
10. location of intercondylar eminence
11. nature of proximal articular surface excluding external articular surface and intercondylar eminence
12. nature of surface between external articular surface and intercondylar eminence
13. nature and orientation of interarticular area between cnemial crests and proximal articular surface
14. outline of proximal end

Anterior view

15. relationship of margins of inner and outer cnemial crests
16. shape of inner and outer cnemial crests
17. nature of anterior shaft surface
18. location of intermuscular line
19. nature of shaft surface over proximal half between intermuscular line and internal margin of shaft
20. location of muscle scars on distal end
21. comparative lengths of condyles
22. angle that supratendinal bridge forms with long axis of shaft
23. nature of surfaces of condyles
24. shape of proximal margins of internal and external condyles
25. shape of distal margins of condyles and sulcus between

Lateral view

26. nature of shaft surfaces near distal end
27. comparative anterior and posterior extension of external condyle
28. position of distal-most extension of external condyle
29. location of ridge dividing anterior and posterior shaft surfaces

Posterior view

30. nature of posterior shaft surface
31. nature of lateral and medial margins respectively of internal and external condyles
32. comparative internal extension of internal condyle and internal ligamental prominence
33. degree of curvature of shaft

Medial view

34. nature of medial shaft surface
35. orientation of proximal articular surface
36. orientation of posterior margin of inner cnemial crest
37. shape of distal margin of internal condyle
38. shape of posterior margin of internal condyle

Distal view

39. shape and orientation of medial and lateral margins of condyles

TARSOMETATARSUS

Proximal view

18. comparative excavation of cotyla
19. angle external cotyla forms with horizontal plane
20. nature of margins of proximal end
21. nature of depression between hypotarsus and intercotylar prominence on proximal surface
22. type of triangular figure formed by hypotarsus
23. nature of hypotarsus (bulbous, slender?)
24. point of proximal-most projection of hypotarsus

Anterior view

25. nature of proximal ligamental attachment
26. depth of proximal end of metatarsal canal
27. nature of attachment for external ligament
28. nature of surface between external ligamental attachment and lateral ligamental attachment
29. location of metatarsal canal
30. nature of surface of distal half of shaft
31. anterior projection of trochlea III with respect to that of trochleae II and IV

32. relationship of central axis of trochlea III to that of central axis of shaft
33. nature of surfaces (articular) of trochleae

Lateral view

34. shape of hypotarsus
35. nature of external cotyla
36. nature of lateral shaft surface
37. comparative depth of shaft over entire length of tarsometatarsus
38. shape of trochlea IV
39. nature of depression in lateral surface of trochlea IV
40. shape of external margin of trochlea III

Posterior view

41. position of subhypotarsal ridge
42. distance that subhypotarsal ridge extends along shaft in comparison to total shaft length
43. nature of cross-sectional shape of shaft
44. comparative proximal extensions of intertrochlear spaces and proximal surfaces within spaces
45. presence/absence of distal foramen

Medial view

46. expansion of internal cotyla and hypotarsus beyond shaft margins
47. shape of trochlea II
48. shape of trochlea III
49. comparative extension of anterior and posterior margins of trochlea III beyond shaft
50. depth of excavation on medial side of trochlea II

Distal view

51. nature of margins and surface of trochleae IV
52. comparative depths anteriorly and posteriorly of trochlear groove on trochlea III
53. nature of medial margin of trochlea IV and lateral margin of trochlea II

Variability observed within a sample of extinct *Dromaius minor* (King Island Emu) was used in conjunction with other published variability studies in determining species limits within the Dromornithidae (see tables 30, 33, and 36).

Class: **AVES**

Family: **DROMORNITHIDAE** Furbringer,
1888

Included Genera: *Barawertornis*, *Bullockornis*,
Ilbandornis, *Dromornis*, and *Genyornis*.

Distribution: Australia (including Tasmania).

Range: Mid-Tertiary to Pleistocene.

Etymology: *Dromos*, G., a running, race; *ornitho*, G., bird.

Common Name: Mihirung Bird, to distinguish this group of birds from *Emus*. Previous references have, unfortunately, termed the group 'Giant Emus', which is misleading. The name *Mihirung* is derived from the phrase 'mihirun parimjal' used by the western Victorian Tjapwurong Aborigines in a tradition concerning the occurrence of giant birds in that area when the 'volcanic hills (of the western districts of Victoria) were in the state of eruption' (Tindale, 1951).

Synoptic Diagnosis: Large, cursorial to probably graviportal birds, the smallest being intermediate in size between the ostrich (*Struthio camelus*) and the emu (*Dromaius novaehollandiae*), the largest species equalling or exceeding the volume and weight (but not the total height) attained by any previously reported bird, including *Aepyornis maximus*.

Atlas vertebra lacks lateral arches or even lateral processes and thus vertebrarterial canals. *Sternum* longer than broad with straight lateral margins; sternocoracoidal processes protrude anteriorly, not dorsally; coracoidal sulci shallow and restricted to either side of central, anteriorly concave section of sternal margin, thus not overlapping one another along midline; area of attachment for costal ribs occupies over 60% of lateral margin; no sternal notches present and sternum with broadly convex posterior margin; no carina present. *Scapulocoracoid* a single element, not two; coracoidal section broadest at sternal end, narrowest near fusion with scapula, lacking any medial process in area near glenoid facet; glenoid facet well developed and directed laterad, not dorsolaterad; scapular blade concave medially; in lateral view, scapula and coracoid meet one another at large obtuse angle. *Humerus* short, deep, reduced, and lacks well defined articular surfaces and ligamental furrow, but with shallow pneumatic fossa, short internal tuberosity (not extending any further proximad than head, if that far), a brachial depression of moderate depth and size, a marked olecranal fossa, and of about equal depth over entire distal width. *Ulna-radius* with broad olecranon, deep proximal end; both elements often fused and carpometacarpus fused in turn to both; radius and ulna of similar width

and depth with radius tapering to rounded (in cross-section) distal articulation. *Carpometacarpus* with carpal trochlea nearly planar, not highly convex proximally, and lacks well defined central groove; articulation for only one digit (II) indicated; in adults, metacarpals II and III fused over entire length; carpometacarpus deep palmoanconally. *Synsacrum* of moderate width posteriad of antitrochanter, neither broad nor extremely narrow, neither decreasing or increasing in width posteriad of antitrochanter; pubis and ischium do not extend far posteriad of ilium; pubes not fused with one another posteriorly along midline; ischium, ilium, and pubis all fused to one another posteriorly with ischio-pubic fenestra decidedly more elongate than ilio-ischiatic fenestra; ischial and pubic bars of subequal depths; ischia not fused with one another and caudal vertebrae along midline; ilium not deep dorsad of acetabulum. *Femur* with nearly straight posterior margin of proximal articular end; trochanter extending about same distance proximad as head or moderately further than head; trochanter not recurved over articular surface; long axes of condyles not parallel to long axis of shaft; external condyle not bulbous and extends somewhat beyond but not far distad of internal; dorsal margin of external condyle straight or only slightly concave proximally; external condyle extends far posteriad of shaft and is decidedly deeper than fibular condyle; proximomedial corner of popliteal area lacks any large muscle scar; popliteal excavation extends from base of external condyle to medio-lateral midpoint of internal condyle; fibular condyle narrower than external condyle; in medial view, outline of internal condyle not semicircular but elliptical in shape; distalmost point on internal condyle shifted anteriorly of condylar midpoint; posterior margin of internal condyle smoothly rounded with posteriormost projection occurring near proximodistal midpoint of condyle; internal and external condyles of nearly equal depth, not with external condyle decidedly deeper than internal; distal end broader than deep. *Tibiotarsus* with cnemial crests moderately, but not extremely, compressed mediolaterally; inner cnemial crest of subequal depth with remaining proximal articular surface, crest extending far proximad of articular surface; lateral margin of articular surface between outer cnemial crest and external articular surface deeply concave externally; long axis of inner cnemial crest not parallel to medial margin of internal articular surface but forming moderate obtuse angle with it; internal and external articular surface broad, not mediolaterally compressed; in anterior view, inner cnemial crest lies approximately on midline of shaft; supratendinal bridge present partially covering centrally located tendinal canal; shaft lacks any ridge extending laterad from

distal border of supratendinal bridge; in lateral view, external condyle does not extend far posterior of shaft, and highly curved anterior margin whose anteriormost extension occurs near proximodistal midpoint of condyle; anterior half of lateral surface of external condyle not deeply excavated; internal condyle of moderate depth and length, not deep and shortened; in distal view, internal condyle deeper than external; condylar fossa of moderate depth, neither shallow nor deeply excavated. *Tarsometatarsus* with three trochlea, not two, and no indication of a metatarsal facet for metatarsal I; hyotarsus broad and triangular in outline, incised by two shallow hypotarsal canals, one on either side of the central apex of the hypotarsus; hypotarsus projects slightly to decidedly further proximad of cotylar surface than intercotylar prominence; internal margin of proximal end projects far proximad of cotylar surface; marked excavation present in intercotylar area between intercotylar prominence and hypotarsus; margins of proximal articular surface rounded, not angular; metatarsal canal of moderate depth, not deep; posterior shaft surface smooth, ungrooved; distal foramen present; trochlea III extends furthest distad followed by IV and II; trochlea III does not extend far distad of other trochleae; trochleae deep, and in distal view trochlea III narrow with parallel external and internal margins. *Pes.* Phalangeal count for digits II, III, and IV is 3-4-4, not 3-4-5; in several genera (*Genyornis*, *Ilbandornis*) terminal phalanges spade-shaped, "hoof-shaped", not claw-shaped.

Diagnosis:

VERTEBRAE. *Atlas. Anterior view.* (a) No vertebrarterial canals or bounding lateral arches present as in adult Dinornithidae, Emeidae, nor even lateral protuberances as in Casuariidae, Aepyornithidae; (b) atlas deep and narrow unlike shallow, broad vertebra in Dinornithidae, Casuariidae, Apterygidae. *Dorsal view.* (c) Dorsal surface of neural arch tilted anteroventrally, not nearly horizontal as in Dinornithidae, Emeidae, Casuariidae, Apterygidae, Aepyornithidae.

STERNUM. *Dorsal view.* (a) Lateral margins straight over most of length, not concave laterally as in Struthionidae, Casuariidae, Dinornithidae, Emeidae, Tinamidae (convex laterally over posterior three-fourths of lateral margins); not as decidedly convergent posteriorly as in Rheidae; not decidedly divergent with two striking concavities in lateral margin as in Aepyornithidae; (b) sternum longer than wide unlike the short, broad sternum in Aepyornithidae or the nearly square sternum in Apterygidae; (c) sternocoracoidal processes (= costal processes) directed anteriorly, not dor-

sally as in Casuariidae, Struthionidae; not laterodorsally as in Emeidae, Dinornithidae, Apterygidae; not anterodorsally as in Rheidae; nor short as in Casuariidae, Struthionidae, or Aepyornithidae; (d) anterior border of sternum concave anteriorly in central half and straight on either side to bases of sternocoracoidal processes, not straight overall as in Emeidae, Dinornithidae, or concave anteriorly overall as in Apterygidae, Aepyornithidae; not convex anteriorly over most of anterior margin with small concavities on either side as in Struthionidae; (e) sternum with five, well-defined intercostal spaces, not four as in Tinamidae, Rheidae, Apterygidae, Emeidae, or Dinornithidae; (f) costal margin comprises approximately 60% of lateral margin of sternum unlike that in Tinamidae where it comprises only 10%, in Struthionidae 40%, in Rheidae less than 30%, or in Dinornithidae, Emeidae about 20%; (g) sternal notches entirely lacking, unlike in Struthionidae with four shallow notches, Tinamidae with two deep notches, Emeidae-Dinornithidae-Apterygidae with two notches of moderate depth, Aepyornithidae with two shallow notches; (h) posterior sternal margin broadly convex posteriorly, not concave posteriorly as in Rheidae, Struthionidae. *Ventral view.* (i) True carina not present but low, broad, slightly indicated subcarinate ridge may be present (in *Genyornis*, but not *Dromornis*), unlike in Tinamidae where narrow, deep keel present; (j) ventral surface of sternum moderately convex ventrally, smoothly rounded throughout, not highly curved and with broad well defined central ridge (anteroposteriorly directed) as in Rheidae or with median flattened area on posterior half of sternum as in Struthionidae; not as flattened as in Dinornithidae, Emeidae, Apterygidae, Aepyornithidae. *Anterior view.* (k) Coracoidal sulci shallow and restricted to lateral one-quarter of anterior margin of sternum, not meeting centrally as in Struthionidae where sulci deep, nearly meeting centrally; not as in Rheidae where of moderate depth, occupying at least lateral thirds of sternum; not as in Casuariidae where of moderate depth, meeting centrally (and not as in the case of *Casuarius*, with a rounded process just ventral to central fusion that is perforated by enlarged pneumatic foramen); not as in Emeidae, Dinornithidae, Apterygidae where sulci shallow to deep but restricted to small area (about one-sixth of anterior margin) far laterad of sternal midpoint (mediolateral).

SCAPULOCORACOID (CORACO - SCAPULA). Scapula and coracoid fused, not separate elements as in Tinamidae. *Anterior view*. (a) Coracoid broadest at sternal end, narrowest near fusion with scapula, just sternad (ventrad) of glenoid facet, lacking any medial process mediad of that facet unlike in Apterygidae, Dinornithidae, Emeidae where coracoid about same width throughout with distinct foramen slightly mediad of midpoint between medial and lateral margins; unlike in Casuariidae with large process extending mediad of glenoid facet; unlike in Rheidae, Struthionidae where ventromedially directed process fuses with coracoid mediad of glenoid facet leaving a moderate to large foramen between main body of coracoid and process; (b) glenoid facet directed laterad, not dorsolaterad as in Rheidae, Struthionidae; not extremely reduced or absent as in Dinornithidae, Emeidae; (c) groove of moderate depth present near internal border of scapulocoracoid, just mediad of glenoid facet unlike in *Dromaius* or Rheidae, where groove not present and much narrower than that in Struthionidae; (d) scapulocoracoidal surface between glenoid facet and medial margin of scapulocoracoid smooth, lacking distinct, anteriorly directed knob that is present in Struthionidae, Rheidae, and lacking a distinct ridge trending ventromedially from ventral border of glenoid facet present in Apterygidae; (e) blade of scapula concave medially unlike that in Apterygidae, Dinornithidae (and probably Emeidae), Rheidae, Struthionidae, Aepyornithidae, and to some extent *Dromaius* where blade concave externally. *Lateral view*. (f) Scapulocoracoid only moderately curved (concave dorsally) with coracoid forming large obtuse angle with scapula unlike that in Dinornithidae (? Emeidae also) which is straight, or that in Casuariidae, Rheidae, and Apterygidae with moderate to small obtuse angles between scapula and coracoid, and that in Struthionidae, Aepyornithidae with moderate obtuse angles.

HUMERUS. (a) Humerus short and deep, reduced, not slender and elongate as in Struthionidae, Rheidae, but present unlike in Dinornithidae, Emeidae where unknown. *Proximal view*. (b) No well defined ligamental furrow present as in Tinamidae. *Anconal view*. (c) Shallow pneumatic fossa developed in adult unlike deep fossa in *Casuaris* and unlike in Struthionidae, Rheidae, Apterygidae,

Aepyornithidae where totally absent; (d) internal tuberosity not projecting far internally as that in *Casuaris*; (e) head projects as far as or further proximad than internal tuberosity unlike in Struthionidae, Rheidae, Apterygidae where internal tuberosity extends further proximad than head; (f) head located in middle (dorsoventral) of proximal end, not shifted towards ventral border as in Aepyornithidae. *Ventral view* (no ventral view of Aepyornithidae humerus available). (g) Large ligamental scar near proximodistal midpoint of shaft unlike in Casuariidae, Struthionidae, Rheidae, Tinamidae, where absent. *Palmar view*. (h) Brachial depression of moderate depth and size, not shallow and small or lacking as in Apterygidae, Casuariidae, Tinamidae, Struthionidae, Rheidae; (i) no prominent ridge trending from base of deltoid crest to dorsal margin of shaft as in Aepyornithidae; (j) ectepicondylar prominence well developed, unlike in Apterygidae, Casuariidae where only slightly indicated. *Distal view*. (k) Articular surfaces on distal end neither well defined nor distinct from one another as in Tinamidae, Struthionidae, Rheidae; (l) shaft elliptical in cross-section, not circular as in Casuariidae or triangular as in Struthionidae, Rheidae; (m) distal end about same depth over entire width, not decidedly narrower in area of ectepicondyle as in Struthionidae, Rheidae and not inflated with highly arched palmar margin as in Apterygidae; (n) olecranal fossa well developed, whereas not evident in Casuariidae, Apterygidae, and probably not in Aepyornithidae. **ULNA-RADIUS**. *Proximal view*. (a) Articular surface covers entire proximal end, smooth, lacking distinct cotyla as in Struthionidae, Rheidae, Tinamidae; (b) no distinct, narrow olecranon present as in Tinamidae, Struthionidae, Rheidae; (c) proximal end deep, not shallow as in Casuariidae, Apterygidae. *Anconal view*. (d) In adults fusion commonly occurs between radius, ulna, and carpometacarpus, but radius and ulna remain distinguishable as separate units unlike in Aepyornithidae where almost totally fused over entire length; bones unfused in Struthionidae, Rheidae, Apterygidae, Tinamidae⁴; (e) radius and ulna of nearly same width, ulna not decidedly broader and deeper as in Tinamidae, Struthionidae, *Casuaris*; (f) radius tapers to rounded articulation, almost semicircular to circular in distal view, not widening distally and not terminating

⁴ This, however, needs further verification as available sample was small and many of the specimens were of immature individuals.

in flattened, elliptical articulation as in Tinamidae, *Casuarii*; (g) radius and ulna longer than or subequal in length to humerus instead of shorter as in Casuariidae, Apterygidae, Aepyornithidae, Rheidae, Struthionidae.

CARPOMETACARPUS. Proximal view. (a) Carpal trochlea almost planar, not highly curved (convex proximally) as in Struthionidae, Rheidae, Tinamidae; trochlea lacking central groove that is well developed in Tinamidae, moderately developed in Rheidae. **Internal view.** (b) No distinct articulation for phalanx present on metacarpal I as in Tinamidae, Struthionidae, Rheidae; (c) in adults, metacarpals II and III apparently fused over most of length, unlike in Struthionidae, Rheidae, Tinamidae where two metacarpals separated by large intermetacarpal space; (d) distinct metacarpal I present and fused to dorsal margin of metacarpal II, unlike in Aepyornithidae where not discernable probably due to such complete fusion; (e) proximal end decidedly deeper (dorsoventrally) than distal end, unlike nearly subequal depths in Apterygidae, Rheidae, Struthionidae or in Tinamidae, Aepyornithidae where proximal end only slightly shallower than distal; (f) metacarpal II deep palmoanconally, not compressed as in Struthionidae, Rheidae, Casuariidae, Apterygidae, Aepyornithidae. **Distal view.** (g) Only one articulation indicated distally for phalanges (on metacarpal II), unlike in Struthionidae, Rheidae, Tinamidae where metacarpals I, II, and III have facets for phalangeal articulation.

SYNSACRUM. Dorsal view. (a) Synsacrum of moderate width posteriad of antitrochanter unlike that in Struthionidae, Casuariidae, and in particular in Apterygidae and Rheidae, where narrow ridge defines dorsal surface but not as broad as in Tinamidae, Dinornithidae, Emeidae, Aepyornithidae; (b) dorsal surface of synsacrum posteriad of antitrochanter remains about same width, not decreasing posteriorly as in Tinamidae, Dinornithidae, Emeidae, decidedly so as in Apterygidae, Rheidae, Struthionidae; (c) lacks distinct canals at anterior end of synsacrum on either side of vertebrae that open dorsally on synsacrum anterior to shield and anteriorly at front end of synsacrum that are present in Tinamidae; (d) antitrochanter located about midway between front and back of synsacrum, not decidedly posterior of midpoint as in Tinamidae, Apterygidae, and not anterior of midpoint as in

Struthionidae; (e) pubis and ischium do not extend far posteriad of ilium in contrast to those in Tinamidae, Rheidae. **Lateral view.** (f) Pubes not fused along midline near posterior end of pelvis as in Struthionidae; (g) in adults, pubis fused posteriorly with ischium and ischium with ilium forming two enclosed fenestrae on either side of the synsacrum, the ischio-pubic fenestra being decidedly more elongate than ilio-ischiatic unlike in Casuariidae where fenestrae of nearly equal length unlike in Tinamidae, Apterygidae, Dinornithidae, Emeidae, Struthionidae where ischium is not fused to ilium; (h) ischia not fused or closely apposed along midline as in Rheidae; (i) no caudal vertebrae fused to ischia as in Rheidae; (j) ilium not deep above acetabulum unlike in Casuariidae where about 3 acetabular diameters is minimum depth from acetabulum to dorsal margin, in Dromornithidae about 1-1.5; (k) no elongate, slender pectinal process as in Struthionidae, nor a more broad, elongate one as in Tinamidae, nor a moderate, elongate one as in Apterygidae; (l) ischial and pubic bars of about equal dorsoventral depth unlike in Tinamidae, Casuariidae, Apterygidae where pubis decidedly shallower than ischium. **FEMUR. Proximal view.** (a) Posterior margin nearly straight or only slightly indented⁵, not strongly concave anteriorly as in Tinamidae, Casuariidae, Aepyornithidae, or moderately concave as in Rheidae and Struthionidae. **Anterior view.** (b) Trochanter extends about same distance proximad as head or moderately proximad of head (as in *Bullockornis*) but not as in Aepyornithidae where it extends about one head length (proximodistal length) beyond head nor as in Struthionidae where head extends proximad of trochanter; (c) long axes of condyles do not closely parallel long axis of shaft as in Aepyornithidae, Tinamidae; (d) external condyle extends further distad than internal condyle but not as disproportionately as in Struthionidae and Rheidae and not of equal distance as in Tinamidae and Apterygidae; (e) external condyle neither bulbous nor extremely elongate on anterior surface with respect to internal condyle as in the Struthionidae. **Lateral view.** (f) Dorsal margin of external condyle that merges with posterior margin of shaft nearly straight or only slightly concave proximally, not U-shaped as in Casuariidae (highly concave proximally), Rheidae, Struthionidae; (g) fibular condyle not as elon-

⁵ True in all dromornithid species except *Dromornis australis* where posterior projection in margin near trochanter interrupts an otherwise slightly curved margin.

gate proximodistally as external condyle (generally 1/2-2/3 that of external), not closely approximating or exceeding the depth of external condyle as in Tinamidae, Dinornithidae, Emeidae, Struthionidae, Aepyornithidae; (h) external condyle extends far posterior of shaft surface unlike shorter condyle in Aepyornithidae, Dinornithidae, Emeidae. *Posterior view*. (i) Internal margin of trochanter nearly (if not) straight, not U-shaped, concave internally, and thus not recurving over proximal articular surface as in Tinamidae; (j) no marked muscle scar near proximointernal region of popliteal area as in Dinornithidae, Emeidae, Aepyornithidae; (k) popliteal area elliptical in shape and extends from external condyle internally to about mediolateral midpoint of internal condyle, not restricted to small area at proximal base of internal condyle as in Struthionidae, but also not totally lacking excavation in this area as in Tinamidae; (l) fibular condyle not broader than external condyle unlike that in the Dinornithidae, Emeidae. *Medial view*. (m) Distal-most extension of internal condyle occurs anterior of anteroposterior midpoint of condyle unlike that in Casuariidae, Dinornithidae, Emeidae, which occurs near or at midpoint; (n) internal condyle approaching elliptical shape with major axis forming acute angle with posterior margin of shaft, not semicircular as in *Dromaius*, Dinornithidae, Emeidae, Aepyornithidae, nor flattened distally as in Rheidae, Struthionidae; (o) near distal end, shaft highly concave internally near point of merger with internal condyle, not flattened and uncurved as in Aepyornithidae, Struthionidae, Dinornithidae, Emeidae; (p) posterior margin of internal condyle smoothly rounded with posteriormost point of projection near proximodistal midpoint of condyle unlike in Dinornithidae, Emeidae, Apterygidae, Tinamidae, and *Casuarius* where distalmost point lies decidedly proximad of midpoint unlike in Aepyornithidae where posterior margin nearly straight. *Distal view*. (q) Internal and external condyles of nearly equal depth, not with external condyle deeper than internal as in Casuariidae, Dinornithidae, Emeidae, Rheidae, Struthionidae, Tinamidae; (r) distal end always broader than deep (even in *Bullockornis*) thus differing from Struthionidae where the two nearly subequal; (s) internal margin of internal condyle straight over most of its length or only slightly convex internally, not highly convex as in Aepyornithidae, Dinornithidae, Emeidae.

TIBIOTARSUS. Proximal view. (a) Cnemial crests not as mediolaterally compressed (except perhaps in *Ibandornis*) as in Struthionidae, Rheidae, Aepyornithidae, but more so than in Casuariidae, Apterygidae, Tinamidae, Dinornithidae, Emeidae; (b) inner cnemial crest of approximately equal depth with remainder of articular surface unlike that in Struthionidae, Rheidae, Casuariidae where inner cnemial crest deeper than remaining articular surface and unlike that in Aepyornithidae that is decidedly shorter; (c) inner cnemial crest extends far proximad of articular surface unlike those in Struthionidae, Rheidae, Aepyornithidae that either do not extend proximad of surface or extend only slightly beyond it, and somewhat further than those in Dinornithidae, Emeidae, Apterygidae, Tinamidae that protrude only moderately proximad of proximal articular surface; (d) external articular surface protrudes far laterad and margin between it and outer cnemial crest deeply concave externally unlike slightly to moderately protruding articular surfaces in Apterygidae, Emeidae, Dinornithidae, Rheidae, Struthionidae, Tinamidae, some with shallow concavities between external articular surface and outer cnemial crest (Apterygidae, Dinornithidae, Emeidae, Tinamidae) and others with a margin that is concave laterally near its anterior border but convex near its posterior extension (Struthionidae, Rheidae); (e) angle formed between inner cnemial crest and medial margin of internal articular surface approximating 130° unlike that in Aepyornithidae, which exceeds 150°, unlike in Dinornithidae, Emeidae, Apterygidae, Tinamidae, Casuariidae that approximates 180°; (f) in projection, line parallel to and extending distad of internal margin of the inner cnemial crest forms approximately a right angle with another line passing between anteriormost extensions of condyles unlike that in Aepyornithidae where angle only moderately obtuse; (g) no distinct channelling of interarticular area between internal-external articular surfaces and cnemial crests that is present in Dinornithidae, Emeidae, Apterygidae, Tinamidae; (h) inner articular surface with knob-like projection (= intercondylar eminence, Stirling and Zietz, 1900) extending further proximad than external articular which is opposite the case in Aepyornithidae, Rheidae and also differs from Apterygidae, Casuariidae where no distinct internal knob is present, and other ratites where inner and outer surfaces extend nearly equal dis-

tances proximad; (i) internal and external articular surfaces broad, not mediolaterally compressed as in Dinornithidae, Emeidae, Casuariidae, Rheidae. *Anterior view*. (j) Inner cnemial crest located on midline of shaft near proximal end, not displaced far laterad as in Aepyornithidae or mediad as in *Dromaius*; supratendinal bridge present as in Dinornithidae, Emeidae, and Tinamidae but differing from all other ratites, where not present; (l) tendinal canal centrally located, not displaced far mediad as in Tinamidae, Dinornithidae, Emeidae; (m) no distinct ridge extending laterad from distal border of supratendinal bridge as in Dinornithidae and Emeidae; (n) proximal margin of condyles moderately concave proximally, not straight over much of width as in Aepyornithidae. *Lateral view*. (o) Posterior surface of shaft just posterior to fibular crest extends further posteriad of crest than that in Aepyornithidae where entire shaft is anteroposteriorly compressed; (p) anterior border of external condyle rounded, highly curved, and together with anterior half of distal border semicircular in outline, not with large radius of curvature (and ovaloid together with distal margin) as in Aepyornithidae; (q) anteriormost projection of external condyle near or slightly distad of the proximodistal midpoint of the condyle unlike that in Struthionidae, Rheidae which lies decidedly proximad of midpoint; (r) external condyle not extending far posteriad of shaft as that in Rheidae, Struthionidae; (s) external condyle lacks deep excavation near anterior end of external condyle that is present in Aepyornithidae, Struthionidae, Rheidae, or moderately deep excavation as in Dinornithidae, Emeidae, Apterygidae, Casuariidae; (t) external condyle lacks knob that extends far laterad at about anteroposterior midpoint of external condyle as in Aepyornithidae. *Medial view*. (u) Internal condyle of moderate depth and length, not deep and proximodistally compressed as in Aepyornithidae, Rheidae, Struthionidae; (v) proximal margin of internal condyle anterior of shaft nearly straight or only slightly concave proximad unlike the U-shaped (highly concave proximally) margins in Aepyornithidae or those in which a prominent process projects decidedly anteriad as in Dinornithidae, Emeidae, Casuariidae. *Distal view*. (w) Internal condyle deeper than external unlike condyles of subequal depth in Rheidae, Struthionidae and nearly subequal ones in Casuariidae, Tinamidae; (x) distinct condylar fossa present,

U-shaped, not as in Aepyornithidae where only slightly indicated, broad and extremely shallow but also not as deep and narrow as in Tinamidae, Apterygidae; (y) anterior border of internal condyle medially convex anteriad, then more laterally composed of a straight section forming a 30-40° angle with main mediolateral axis of condyles, lateralmost section also straight and forming large acute angle with mediolateral axis of shaft unlike the slightly anteriorly convex internal condyle in Aepyornithidae; unlike the smoothly curved, more highly anteriorly convex condyles in other ratites, which may have in addition a straight, lateral segment but lack the change in angulation of that segment characteristic of Dromornithidae.

TARSOMETATARSUS. Proximal view. (a) Hypotarsus broad, triangular in outline with two shallow hypotarsal canals near medial and lateral boundaries of hypotarsus respectively, thus differing from that in Dinornithidae-Emeidae-Apterygidae where deep calcaneal canal bisects hypotarsus resulting in two distinct hypotarsal ridges on either side of median canal; in Struthionidae-Rheidae which is narrow and laterally offset; in Tinamidae which is rectangular, laterally offset with deep lateral-facing canal and two shallow posteriorly directed canals producing three low calcaneal ridges; and in Casuariidae which is narrow-based though centrally located; (b) internal border of proximal end formed by narrow anteroposteriorly directed ridge that projects far proximad of cotylar surface (as far proximad as intercotylar prominence) much as in the Tinamidae but differs from all other ratites in which such a ridge is low or non-existent; (c) hypotarsus projects slightly to decidedly further proximad of cotylar surface than intercotylar prominence as in Casuariidae but unlike that in Struthionidae-Rheidae-Apterygidae, which is subequal in proximad projection with that of intercotylar prominence; that in Aepyornithidae which lacks intercotylar prominence; unlike that in Dinornithidae-Emeidae-Tinamidae, which does not extend as far proximad as intercotylar prominence; (d) marked depression in intercotylar area between intercotylar prominence and hypotarsus that is lacking in Aepyornithidae-Struthionidae-Dinornithidae-Emeidae and only slightly indicated in Casuariidae; (e) prominent narrow ridge (anteriad to midpoint of external border) projects laterally from cotylar surface that is low and broad or lacking in all other ratites, in

some (Apterygidae) located near posterior margin of cotylar surface; (f) shape of proximal articular surface trapezoidal (but closely approaches rectangular) in shape with internal cotyla moderately deeper than external and margins rounded, not angular, thus differing from Dinornithidae - Emeidae - Apterygidae, which have greater differential between cotyla and latter two with highly angular margins; differing from Aepyornithidae, which have an external cotyla that is much deeper than internal; differing from Struthionidae-Rheidae, which have cotyla of nearly subequal depth and decided posterior expansion of internal cotyla. *Anterior view.* (g) Moderately deep metatarsal canal present on proximal half of tarsometatarsus differing from that in Dinornithidae - Emeidae - Apterygidae where only slightly indicated or absent and that in Casuariidae, which is deeper and extends almost entire length of shaft. *Posterior view.* (h) Subhypotarsal ridge single, elongate, broadest slightly distad of proximal end differing from the short double ridge in Dinornithidae-Emeidae-Apterygidae; the short, broadly divergent (proximally) triple ridge in the Tinamidae; the short, narrow ridge in Rheidae-Struthionidae; and not distally convergent on a prominent lateral ridge as in Casuariidae; (i) posterior shaft surface not deeply grooved as in Casuariidae-Rheidae or even slightly grooved as in Struthionidae; (j) no indication of a metatarsal I articulation in contrast to the Tinamidae-Apterygidae—some Dinornithidae-Emeidae⁶; (k) distal foramen present on posterior surface of shaft differing from Dinornithidae-Emeidae-Aepyornithidae where absent; (l) three trochleae present differing from Struthionidae with only two; (m) distal margin of external trochlea (IV) ungrooved and forms acute angle closely approaching 45° with distal margin of median trochlea (III) differing from much smaller acute angle and grooved trochlea IV in Aepyornithidae; much smaller angle in Dinornithidae; and the grooved trochlea IV in Tinamidae-Casuariidae-Rheidae; (n) trochlea IV extends slightly further distad than trochlea II, not decidedly further as in Dinornithidae-Emeidae-Tinamidae; (o) trochlea III does not extend far distad to II and IV in contrast to that in Tinamidae-Apterygidae-Rheidae. *Distal view.* (p) Trochleae deep, not anteroposteriorly flattened as in Casuariidae-Dinornithidae; (q) trochlea III narrow with margins

convergent posteriorly; not parallel-sided as in Rheidae-Struthionidae-Casuariidae; not parallel-sided as in Emeidae-Apterygidae; nor convergent anteriorly as in Tinamidae; more abruptly convergent posteriorly than that in Dinornithidae.

PES. (a) Phalangeal count for digits II, III, and IV, 3-4-4 respectively, not 3-4-5 as in Tinamidae, Casuariidae, Rheidae, Apterygidae, Dinornithidae, some Emeidae (not in *Emeus* or *Euryapteryx* where count is 3-4-4); (b) three digits (II, III, IV) present, not two as in Struthionidae (III, IV) or four as in Apterygidae, Dinornithidae, and Emeidae; (c) based on *Genyornis newtoni* alone (only taxon within the Dromornithidae with articulated feet known) of the three proximalmost phalanges of each digit, that of digit II longest, and of IV shortest unlike in Dinornithidae, Emeidae, Apterygidae where that of III longest and that of II shortest; unlike in Aepyornithidae where those of III and IV subequal in length but both more elongate than that in II; unlike in Struthionidae where that in II shorter than in III; and unlike in Tinamidae where that in III and II subequal and both more elongate than that in IV. *Dorsal view.* (d) Proximal margins of many of phalanges (2, Digit II; 3, Digit III; 2, 3, Digit IV) straight, not deeply V-shaped (V opening distally) as in Tinamidae, Casuariidae, Struthionidae (no digit IV), Rheidae, Apterygidae, Dinornithidae, Emeidae, nor broadly V-shaped as in Aepyornithidae. *Phalanx 1, Digit II.* (e) Phalanx slender and elongate, not broad as in Apterygidae, Dinornithidae, Emeidae, Aepyornithidae, or Rheidae. *Proximal view.* (f) Proximal articular surface lacking deep indentation in ventral margin as in Dinornithidae, Apterygidae, Casuariidae, Aepyornithidae; (g) proximal articular surface compressed medio-laterally, decidedly deeper (dorsoventrally) than wide unlike broad, shallow proximal articular surfaces in *Casuarius*, Apterygidae, Emeidae, Dinornithidae, Aepyornithidae. *Phalanx 2, Digit II.* (h) Proximal articular surface flattened, slightly concave proximally, not deeply biconcave proximally with concavities separated by well-defined median ridge as in Casuariidae, Dinornithidae, Emeidae, Apterygidae, Rheidae, Tinamidae, Aepyornithidae. *Phalanx 1, Digit III. Proximal view.* (i) Proximal articular surface deepest along internal margin unlike in Tinamidae, Aepyornithidae,

⁶ Although the first digit is present in all moas, the metatarsal articulation is often not clearly defined on the tarsometatarsus.

Dinornithidae, Apterygidae, Rheidae where greatest depth occurs near mediolateral midpoint; (j) ventral margin of proximal articular surface nearly straight, may be slightly concave ventrally, but totally lacking two distinct processes, one on either side of mediolateral midpoint of proximal end as in Tinamidae, Casuariidae, Aepyornithidae, only slightly developed in Dinornithidae, Emeidae, Rheidae due to moderately ventrally concave margin at midpoint. *Distal view.* (k) External and internal condylar margins parallel, not divergent ventrally as in Tinamidae, Casuariidae, Apterygidae, nor slightly divergent as in Dinornithidae, Struthionidae, Emeidae. *Phalanx 2, Digit III. Proximal view.* (l) Proximal articular surface elliptical in outline with long axis oriented lateromedially, not triangular, yet dorsoventrally compressed as in Casuariidae; not triangular and deep as in Tinamidae, Dinornithidae, Emeidae, Apterygidae, Struthionidae, Rheidae; (m) proximal articular surface nearly planar, lacking marked central ridge dividing medial and lateral segments of surface unlike that in Apterygidae, Dinornithidae, Emeidae, and probably Aepyornithidae where distinct median ridge present. *Lateral or Medial view.* (n) Proximal end decidedly deeper than condyles on distal end unlike in Dinornithidae where nearly subequal in depth. *Distal view.* (o) Medial and lateral margins of condyles nearly parallel or only slightly divergent posteriorly, not broadly divergent ventrally as in Dinornithidae, Emeidae, Struthionidae, Rheidae, Casuariidae. *Phalanx 3, Digit III.* (p) Phalanx decidedly short anteroposteriorly, broad, and highly dorsoventrally flattened unlike the deep, longer than broad (or at least as long as broad) phalanges (III, 3) in Tinamidae, Apterygidae, Dinornithidae, Emeidae, Rheidae, and unlike the more elongate than broad, moderately deep phalanges in Casuariidae. *Phalanx 1, Digit IV. Proximal view.* (q) Ventral margin of proximal articular surface slightly convex ventrally, not deeply incised ventrally by medially placed canal as in Tinamidae, Casuariidae, Dinornithidae, Emeidae, Apterygidae, Aepyornithidae; (r) lacking process that extends proximad from medioventral corner of phalanx as in Casuariidae, Apterygidae, Rheidae. *Distal view.* (s) Internal and external margins of condyles nearly parallel or slightly convergent ventrally, not divergent ventrally as in the Tinamidae, Casuariidae, Rheidae, Aepyornithidae, and Dinornithidae. *Phalanx 2, Digit IV. Proximal view/*

distal view. (t) As in phalanx 2, digit III central ridge lacking on proximal articular surface; (u) condylar margins nearly, if not, parallel, not strongly divergent ventrally; (v) proximal articular surface dorsoventrally compressed, not deep (see diagnosis for 2, III for comparisons). *Dorsal view.* (w) Phalanx more elongate than broad or of subequal breadth and length, differing from that in Dinornithidae, Emeidae, Aepyornithidae, Rheidae where broader than long. *Phalanx 3, Digit IV.* Diagnosis as that for phalanx 2, digit IV except that (x) phalanx shorter than broad unlike in the Tinamidae, Casuariidae, Apterygidae where longer than broad. *Terminal phalanges.* (y) In some dromornithids (*Ilbandornis*, *Genyornis* at least) three terminal phalanges of digits II, III, IV broad, shallow, spade-shaped ('hoof-like') unlike claw-like structures with triangular cross-section characteristic of Tinamidae, Struthionidae, Rheidae, Aepyornithidae, Casuariidae, Apterygidae, Dinornithidae, and Emeidae.

Genus *Barawertornis*, n. gen.

Type species: Barawertornis tedfordi Rich, n. sp.

Distribution: Riversleigh Homestead, North-western Queensland, Australia.

Range: Medial Miocene.

Etymology: *Barawerti*, Aboriginal word for ground; *ornis*, G., bird.

Synoptic Diagnosis: Smallest of known dromornithids with slender, yet anteroposteriorly compressed limb elements. *Femur* with posteriorly concave posterior margin of proximal articular surface; neck elongate and distinctly shallower than head or trochanter; shaft shallow and slender with moderately medially concave internal margin; minimum width of shaft proximad of shaft's midpoint; posterior intermuscular line a prominent ridge, not a small tubercle; popliteal area deeply excavated; proximodistal axis of external condyle forms approximately 155° angle with long axis of shaft; ligamental depression at proximal end of fibular condyle well developed; in medial view, internal condyle approaching circular outline with most distally projecting point occurring near or at anteroposterior midpoint of condyle; condyles of moderate depth, not deep; external condyle about one-third the width of internal condyle. *Tarso-metatarsus* with narrow intertrochlear space between trochleae III and IV; shaft narrow with respect to width of distal end and lateral/medial margins parallel over much of shaft's length; trochlea II not decidedly reduced with medial and lateral margins divergent posteriorly; grooving on posterior surface of trochlea III shallow.

Diagnosis:

FEMUR. Proximal view. (2) Posterior margin of articular surface not straight as in *Genyornis* and *Bullockornis* but concave posteriorly over internal one-half more like *Dromornis*; (3) neck distinctly shallower than head or trochanter differing from *Ilbandornis* and *Genyornis*. **Anterior view.** (5) Neck elongate unlike in *Ilbandornis* and *Dromornis*; (6) shaft slender, not broadened as in *Ilbandornis*, *Dromornis*, and *Genyornis*; (7) internal margin of shaft moderately concave internally, more highly curved than in *Ilbandornis* but not as highly curved as in *Bullockornis* and *Genyornis*; (8) minimum width of shaft proximad of midpoint unlike that in *Bullockornis*, *Ilbandornis*, and *Genyornis*. **Lateral view.** (10) Shaft shallow, not as deep as that in *Genyornis*, *Ilbandornis*, and *Bullockornis*. **Posterior view.** (13) Posterior intermuscular line a prominent ridge, not small tubercle as in *Bullockornis*, *Dromornis* and *Genyornis* and totally absent in *Ilbandornis*; (14) popliteal area deeper with regard to total depth of shaft than in any other dromornithid; (16) proximodistal axis of external condyle twisted about 25° off main axis of shaft, a maximum displacement for the dromornithids, differing from much smaller angle in *Bullockornis*; (17) ligamental depression at proximal end of fibular condyle well developed unlike that in *Dromornis*. **Medial view.** (18) Internal condyle approaching circular shape with most distally projecting point at about anteroposterior midpoint of condyle, differing from other dromornithids where distalmost point offset anteriorly and condylar margin decidedly ovoid; (19) internal surface of shaft near distal end smooth and not ridged unlike *Ilbandornis* and most *Dromornis*, certainly differing from *Genyornis* where most distal part extends abruptly mediad of shaft surface. **Distal view.** (21) Condyles moderately compressed anteroposteriorly, not deep as in *Bullockornis* or highly compressed as in *Genyornis*; (22) external condyle broad, about one-third width of internal condyle, not as narrow as that in *Bullockornis* (about one-fourth the width of internal condyle) but not as broad as in *Genyornis* where external condyle two-fifths to one-half width of internal condyle; (25) internal margin of internal condyle a straight line, not markedly convex internally as in *Dromornis*; (26) posterior margin of fibular condyle located anterior to posterior margin of internal condyle, intermediate between *Bullockornis* on the one hand

and *Ilbandornis-Dromornis-Genyornis* on the other.

TARSOMETATARSUS. Anterior view. (2) Intertrochlear space between trochleae III and IV narrow, not broad as in *Bullockornis*. **Medial view.** (3) Shaft of moderate depth, not deep as in *Bullockornis* or shallow as in *Ilbandornis* and *Dromornis*; (4-5) subhypotarsal ridge low, not prominent and narrow as in *Bullockornis*. **Posterior view.** (6) Shaft narrow with respect to width of distal end unlike that of moderate width in *Ilbandornis*, *Dromornis*, *Genyornis*; (7) flare of distal end broad, not moderate as in *Ilbandornis*, *Dromornis*, *Genyornis*; (8) lateral and medial shaft margins parallel over much of length, not proximally divergent over much of length as in *Ilbandornis*, *Dromornis*, *Genyornis*; (9) trochleae II and IV extend almost equal distances distad unlike in *Bullockornis* where II extends decidedly distad of IV. **Lateral view.** Posteroproximal margin of trochlea IV extends far posteriad, not short as in *Dromornis* and *Genyornis*. **Distal view.** (11) Trochlea II not extremely reduced as in *Genyornis*; (12) medial and lateral margins of trochlea II not parallel, in contrast to *Genyornis*, but divergent posteriorly; (13) groove on posterior surface of trochlea III shallow, unlike moderate to deep grooves in *Ilbandornis*, *Dromornis*, *Bullockornis*, *Genyornis*; (14) width of posterior margin of trochlea II nearly twice that of anterior margin, unlike more nearly subequal margins in *Dromornis*, *Ilbandornis*, *Genyornis*; (15) trochlea III of moderate depth, not deep as in *Bullockornis*.

***Barawertornis tedfordi*, n. sp.**

(Figures 2, 7-11, 15-20)

Type: CPC 7341, left femur lacking trochanter and lateral part of shaft on proximal half of femur.

Referred material: CPC 7347, distal end, right femur lacking external and fibular condyles; CPC 7346, distal end and shaft fragment, left tarsometatarsus lacking distal ends of trochlea II and III; CPC 7348, dorsal vertebra (nearly complete but in need of extensive preparation before full description can be completed).

Type locality: Four miles north of Riversleigh Homestead, northwestern Queensland, Australia, between the Gregory River and Verdon Creek (Camooweal and Lawn 4-mile sheets); BMR Locality 103D (see Tedford, 1968).

Lithic unit and temporal range: Carl Creek

Limestone, above basal conglomerate; medial Miocene.

Fauna: Riversleigh.

Etymology: Named for Richard H. Tedford, who collected the Riversleigh material and a vast amount of other Tertiary avian material known from Australia.

Diagnosis: See generic diagnosis; only species in genus.

Measurements: See tables 19, 31, 37.

Description:

FEMUR. *Proximal view.* (27) Np. *Anterior view.* (28) Np; (29) np; (30) condyles moderately separated, external and fibular condyles protrude further externally than internal condyle protrudes internally. *Lateral view.* (31) Np; (32) np; (33) external condyle extends far posteriad, only slightly anteriad; (34) over the distal half that is preserved, anterior and posterior shaft margins nearly parallel, interrupted only by slight bulge of posterior intermuscular line from posterior margin; (35) lateral shaft surface nearly planar over distal half that is preserved, smoothly grading into anterior and posterior shaft surfaces that lie at approximately 90° angles to lateral surface; (36) proximal margin of external condyle straight, posterior margin smoothly rounded, semicircular in outline; distal margin broadly convex distally with depression for *tibialis anterior* ligament located slightly anteriad of the anteroposterior midpoint, anterior margin only slightly convex anteriorly-almost straight; (37) fibular condyle narrowest posteriorly with distal and proximal margins diverging anteriorly; distal margin of condyle forms approximately 90° angle with shaft's long axis while proximal margin forms about 130° angle; (38) at a maximum, fibular condyle slightly more than 75% length of external condyle. *Posterior view.* (39) Np; (40) comparison of proximal and distal expansion cannot be made due to incompleteness of proximal end; minimum shaft width about 40% of width of distal end; (41) posterior surface of shaft nearly planar with rounded margins internally and externally, interrupted only by a proximointernally trending posterior intermuscular line that forms approximately a 20-25° angle with the shaft's long axis; (42) angle formed between proximal margin of external condyle and posterior shaft margin, approximately 115°; (43) much of distal margin of external condyle is straight forming approximately a 135° angle with the shaft's long axis but near external part margin highly convex

distally, V-shaped; (44) internal margin of internal condyle slightly convex internally, distal margin straight; (45) rotular groove of moderate depth and can be angular to gently rounded; (46) medial shaft surface nearly planar along posterior one-half of surface but rounded to meet anterior shaft surface over anterior one-half of medial surface; distinct ridge on proximal one-fourth of medial surface originating along posterior margin of shaft and trending anteroproximally, turning 90° near base of head and then trending nearly directly posteriorly until it terminates near the anteroposterior midpoint of shaft; (47) posterior margin of internal condyle protrudes further from shaft than does anterior but neither as far as posterior margin of external condyle. *Distal view.* (48) See figure 11; (49) intercondylar fossa moderately deep and broadly U-shaped where parallel sides of U form approximately 90° angle with mediolateral axis of distal end; (50) rotular groove of moderate depth, broadly U-shaped, broader than intercondylar fossa, and midpoint offset medially from that of intercondylar fossa; (51) posterior margin of internal condyle forming approximately 25° angle with mediolateral axis of distal end.

TARSOMETATARSUS. Only distal end is preserved. *Proximal view.* (18-24) Np. *Anterior view.* (25-28) Np; (29) metatarsal canal in middle of shaft on distal half of tarso-metatarsus, trends somewhat laterally near distal extension, terminating before reaching trochleae; (30) distal half of shaft slightly concave anteriorly over proximal half (due to presence of metatarsal canal) and moderately convex anteriorly over distal half with medial section having shorter radius of curvature than lateral; (31) trochlea III projects moderately beyond other trochleae; (32) central axis of shaft lies laterad of main axis of trochlea III, the former, if extended, passing approximately along the medial margin of trochlea III; (33) trochlea II not well preserved; trochlea III grooved, thus concave anteriorly; trochlea IV nearly planar with plane tilted posteriorly towards lateral border at large obtuse angle with anterior shaft surface. *Lateral view.* (34-35) Np; (36) lateral shaft surface over distal part planar, forming approximately 90° with anterior shaft surface; near far distal end, lateral part of shaft narrower and convex laterally; (37) preserved shaft shallow near distal end, gradually increasing in depth proximally; (38) anterior, distal, and posterior

margins of trochlea IV forms semielliptical outline; posterior margin's most posterior projection somewhat distad of proximal end of that margin; (39) depression in lateral surface of trochlea IV deep; (40) np. *Posterior view*. (41) Np; (42) subhypotarsal ridge extends almost to trochleae; (43) shaft trapezoidal in shape with base formed by anterior surface of shaft; (44) intertrochlear space between trochleae III and IV extends far proximad of trochleae II and III; surface within intertrochlear space between trochleae II and III slopes gradually to a shelf about midway between anterior and posterior shaft surfaces; thus excavation for space extends almost to shaft's midline; (45) distal foramen present. *Medial view*. (46-48) Np; (49) posterior margin of trochlea III extends further beyond shaft than anterior margin of trochlea; (50) np. *Distal view*. (51) Anterior and posterior margins of trochlea IV convergent laterally; medial margin slightly convex medially; posterior margin slightly concave posteriorly; lateral margin highly concave laterally; trochlear surface ungrooved; (52) trochlear groove on trochlea III decidedly deeper anteriorly than posteriorly; (53) medial margin of trochlea IV and lateral margin of trochlea II convergent posteriorly; medial margin of trochlea IV forms approximately 90° angle with anterior shaft surface.

Genus *Bullockornis*, n. gen.

Type species: Bullockornis planei Rich, n. sp.

Distribution: Bullock Creek, Northern Territory, Australia.

Range: Medial Miocene (see Stirton et al., 1968).

Etymology: *Bullock*, part of place name where specimens collected, Bullock Creek; *ornis*, G., bird. Common name: Bull bird.

Synoptic Diagnosis: Large dromornithids, most strikingly different from other members of the family in having extremely deep (with respect to overall length) and slender elements in the limb.

Femur with deep trochanter having little if any expansion beyond straight posterior margin of proximal articular surface; neck distinctly shallower than head and elongate; shaft slender with highly curved (internally concave) medial margin; minimum width of shaft near midpoint of shaft; marked obturator ridge present; small tubercle represents posterior intermuscular line; in medial view, internal condyle ovoid in shape with distalmost point occurring distinctly anterior of anteroposterior midpoint of condyle; additionally, medial surface of internal condyle smooth, lacking ridging; condyles deep and subequal in depth;

external condyle exceedingly narrow; in distal view, condyles converge both anteriorly and posteriorly; distal end broadest in midsection (viewed distally). *Tarsometatarsus* with broad intertrochlear space between trochleae III and IV; subhypotarsal ridge narrow; shaft slender with broad flare at both proximal and distal ends; trochlea II extending decidedly further distad than trochlea IV; trochlea II not markedly reduced.

Diagnosis:

FEMUR. Proximal view. (1) Trochanter deep; little or no posterior expansion of trochanter beyond posterior shaft surface; (2) posterior margin of proximal articular surface straight, differing from *Barawertornis* and *Dromornis*; (3) neck distinctly shallower than head differing from *Ilbandornis* and *Genyornis* where both of nearly equal depth. *Anterior view*. (5) Neck elongate unlike that in *Ilbandornis* and *Dromornis*, somewhat more elongate than that even in *Barawertornis*; (6) shaft slender, differing from more robust shafts in *Ilbandornis*, *Dromornis*, and *Genyornis*; (7) internal margin of shaft not as highly curved as that in *Genyornis* but more so than in other dromornithids; (8) minimum width of shaft near its proximodistal midpoint. *Lateral view*. (9) Trochanter extends far forward unlike that in *Dromornis* and *Genyornis*, which extends only slightly anterior of shaft; (10) shaft deep, not anteroposteriorly compressed as in other dromornithids. *Posterior view*. (12) No distant obturator ridge present unlike in *Barawertornis*; (13) no elongate posterior intermuscular line present unlike the condition in *Barawertornis*, instead small tubercle along internal border of posterior shaft surface just proximad of internal condyle; (16) proximodistal long axis of external condyle nearly parallel with long axis of shaft, forming only 5-10° angle with shaft's axis in contrast to significantly larger angles in other dromornithids. *Medial view*. (18) Internal condyle ovoid in shape with distalmost point distinctly anterior of the condyle's anteroposterior midpoint unlike that in *Barawertornis* and *Genyornis* that are situated nearer midpoint; (19) medial surface near distal end smooth, not ridged, grading gradually into internal condyle, differing from ridged surfaces in *Ilbandornis*, *Dromornis*, and *Genyornis*. *Distal view*. (20) Shaft trapezoidal, very nearly triangular in cross section (with the posterior shaft surface forming the base) differing from remaining dromornithids where broader trapezoidal form approaches rectangular shape; (21) condyles deep, differing from the much more anteroposteriorly compressed

condition of other dromornithids; (22) external condyle extremely narrow, being approximately one-fourth the width of the internal condyle, thus differing from other dromornithids where external condyle is much wider; (23) internal and external condyles nearly subequal in depth unlike in the remaining dromornithids where external condyle is distinctly deeper than internal; (24) condyles converge both anteriorly and posteriorly, diverging in between, differing from *Barawertornis* and *Dromornis* where convergence occurs only anteriorly and from *Genyornis* where condyles are nearly parallel or only slight divergent anteriorly; (25) internal margin of internal condyle convex internally unlike straight margins in *Barawertornis* and *Ilbandornis* or markedly convex margins in *Dromornis*; (26) posterior margin of fibular condyle far anterior of the internal condyle's posterior margin, in contrast to *Ilbandornis*, *Dromornis* and *Genyornis* where the two margins about same level and to *Barawertornis* where posterior margin of fibular condyle situated only slightly anterior of internal condyle's posterior margin.

TARSOMETATARSUS. *Proximal view.* (1) Maximum depth across intercotylar prominence and hypotarsus proportional to width of proximal end decidedly greater than that in *Genyornis*, *Ilbandornis*, and probably *Dromornis* (i.e. proximal end deep). *Anterior view.* (2) Intertrochlear space broad between trochleae III and IV, not narrow as in all other dromornithids. *Medial view.* (3) Shaft deeper than that in *Barawertornis*, *Ilbandornis*, *Dromornis*, but quite similar to that in *Genyornis* except near proximal end where *Bullockornis* deeper, resulting from exaggerated posterior extension of hypotarsus; (4-5) subhypotarsal ridge narrow, extends nearly entire length of shaft as prominent, narrow ridge in contrast to proximally broader, lower ridge in *Barawertornis*, *Ilbandornis*, *Dromornis*, *Genyornis*. *Posterior view.* (6) Shaft narrower with respect to width of distal end than in *Ilbandornis*, *Dromornis*, *Genyornis*; (7) distal and proximal ends flare more broadly from shaft than those in *Ilbandornis*, *Dromornis*, *Genyornis*; (8) lateral and medial shaft margins parallel over much of shaft length unlike curved, proximally divergent margins in *Ilbandornis*, *Dromornis*, *Genyornis*; (9) internal trochlea (II) extends decidedly further distad than external trochlea (IV) unlike in other dromornithids where the two trochleae extend

nearly the same distance distad. *Lateral view.* (10) Trochlea IV with decidedly more elongate posteroproximal border than that in *Dromornis*, *Genyornis*; (10A) lateral surface and lateral segment of posterior shaft surface merge indistinguishably and form moderately acute angle with anterior shaft surface, unlike the smaller angle characteristic of *Dromornis*, *Ilbandornis* and unlike the distinct lateral surface forming 90° angle with anterior surface of shaft in *Genyornis*. *Distal view.* (11) Trochlea II not reduced as in *Genyornis*, *Ilbandornis*; (12) medial and lateral margins of trochlea II divergent posteriorly, not parallel as in *Genyornis*; (13) trochlear groove on posterior surface of trochlea III of moderate depth, not shallow as in *Barawertornis*; (14) posterior margin of trochlea II nearly twice the width of anterior margin, not subequal to it as in *Ilbandornis*, *Dromornis*, *Genyornis*; (15) trochlea III deep, not of moderate depth as in all other dromornithids; (16) trochlea III narrow (with respect to width of trochlea IV), deep, neither broad and of moderate depth as in *Genyornis* nor of moderate depth as in *Barawertornis*, *Ilbandornis*, *Dromornis*; (17) lateral and medial margins of trochlea III moderately convergent posteriorly, not parallel as in *Genyornis*.

***Bullockornis planei*, n. sp.**

(Figures 2, 7-11, 15-20, 31)

Type: CPC 13844, right femur.

Referred Material: CPC 13846, 13847, dorsal vertebrae; CPC 13845, right femur; F23013 J, cf. costal rib; CPC 13848, right tarsometatarsus.

Type locality: Bullock Creek, Northern Territory, Australia. Low limestone hill one-half mile east of type section of Camfield Beds, 131°31'20"E, 17°07'S, Wave Hill (1:250 000), SE 52-8.

Lithic unit and temporal range: Camfield Beds; medial to late Miocene.

Fauna: Bullock Creek.

Etymology: Named for Michael Plane who collected the vertebrate material from Bullock Creek. Common name: Plane's Bull Bird.

Diagnosis: See generic diagnosis; largest species of genus. Differs from *B. sp.* in having a narrower hypotarsus and a more highly convex internal margin of the proximal articular surface.

Measurements: See tables 19, 31, 37.

Description:

VERTEBRAE. *Cervico-Dorsal.* See Figure 31 and discussion of similar vertebrae of *Dromornis*, *Genyornis*.

FEMUR. *Proximal view.* (27) Posterior margin of trochanter not smoothly curved but meets lateral margin at nearly a 90° angle; (28) highly curved proximal articular surface, narrowly U-shaped; (29) trochanter extends much further proximad than head; (30) internal and external condyles protrude internally and externally about the same distances. *Lateral view.* (31) External shaft surface near proximal end convex; entire surface laterad of trochanter curved, not planar; posterior margin of shaft concave posteriorly with only slight curvature posteriad near proximal end while anterior margin broadly splayed anteriorly; (32) anterior margin of trochanter and proximal one-fourth of shaft margin describe a semi-circle; proximal margin of trochanter slightly convex proximally with flattened midsection, most highly curved posteriorly; (33) external condyle extends much further posteriad than anteriorly; anterior margin only very slightly convex anteriorly, extending only a short distance anteriorly of anterior shaft surface; (34) posterior margin of shaft nearly straight, curving slightly posteriad only near proximal end; anterior margin slightly concave anteriorly over much of its length, then markedly curved anteriorly over proximal one-fourth of shaft to accommodate deep trochanter; (35) shaft surface convex externally as far distally as midpoint; distad of midpoint shaft nearly planar (except for far posterior surface that is convex posteroexternally); shaft lateral to condyles concave externally; (36) proximal margin of external condyle straight, posterior margin rounded, semicircular in outline, distal and anterior margins nearly straight and oriented at an angle slightly greater than 90° to one another; depression for *tibialis anterior* ligament located near anterior margin of external condyle; (37) fibular condyle narrowest posteriorly with distal and proximal margins diverging anteriorly; distal margin forms about 100° angle with shaft's long axis, proximal margin about 125° angle; (38) fibular condyle about 75% the depth of external condyle. *Posterior view.* (39) Obturator ridge not present; (40) mediolateral expansion of proximal and distal ends of about equal magnitude, the width of the distal end exceeding that of the proximal somewhat; minimum shaft width about 50% of width of distal end; (41) posterior surface

nearly planar over most of its length, with plane forming nearly a 90° angle with the medial shaft surface near its distal end and a gradually decreasing acute angle proximally; external half of surface rounded, convex posteroexternally; (42) angle formed by proximal margin of external condyle and posterior margin of shaft approximately 105°; (43) much of distal margin of external condyle straight, forming approximately a 135° angle with shaft's long axis, near external one-fourth highly convex distally, U-shaped; (44) internal margin of internal condyle highly convex medially, nearly a straight line distally; (45) rotular groove of moderate depth, broad and rounded. *Medial view.* (46) Medial shaft surface planar over distal one-fourth, midshaft convex anteromedially, and proximal half concave anteromedially; (47) posterior margin of internal condyle protrudes much further from shaft than anterior margin. *Distal view.* (48) See Figure 11; (49) intercondylar fossa deep to moderate and narrowly U-shaped, where nearly parallel sides of U forming about 45-65° angle with mediolateral axis of distal end; (50) rotular groove of moderate depth, broadly U-shaped, much broader than intercondylar fossa (even more so than in *Barawertornis*); (51) posterior margin of internal condyle forming approximately 45° angle with mediolateral axis of distal end.

TARSOMETATARSUS. *Proximal view.* (18) Internal cotyla concave proximally, not deeply excavated, but more so than external cotyla whose surface nearly flat; (19) external cotyla forms small acute angle with horizontal plane, sloping downward externally; (20) anterior border straight over much of its length; broad, rounded anteriorly projecting processes near external margin; external margin convex externally, extending furthest externad near anterior end; internal margin likewise convex but its medialmost extension occurs slightly forward of anteroposterior midpoint of internal cotyla; medial margin curves smoothly to meet hypotarsus; part of posterior margin internal to hypotarsus straight; (21) U-shaped depression (opening posteriorly) on proximal surface lateral to intercotylar area deep (although some of this depth may be due to overpreparation); (22) hypotarsus triangular (scalene) with external side more elongate than internal and base being longest of all; (23) hypotarsus bulbous, not with sharply defined ridge; (24) point of proximalmost projection of hypotarsus near anterior

margin of that structure. *Anterior view.* (25) Proximal ligamental attachment low, rounded knob midway between internal shaft margin and metatarsal groove, originating near proximal extension of that groove; (26) proximal end of metatarsal canal deepest part of canal, ellipsoid, deep; only low, indistinct ridge for attachment of *tibialis anticus*; no nutrient foramen evident; (27) external ligamental attachment a low, rounded ridge, though not knob-like as internal ligamental attachment; (28) surface between external and lateral ligamental attachments forms small obtuse angle with anterior shaft surface; (29) metatarsal canal located slightly mediad of shaft centre proximally but centrally located over much of its length; canal narrow over entire length; (30) surface of distal half of shaft planar and tilted slightly posteriorly towards lateral border; (31) trochlea III projects far anterior of other two trochleae; (32) central axis of shaft lies laterad of central axis of trochlea III, the former extending only slightly mediad of external border of trochlea III; (33) trochlea II slightly convex anteriorly; trochlea III concave anteriorly due to centrally located trochlear groove; trochlea IV nearly planar with plane tilted posteriorly towards lateral border, thus forming moderately obtuse angle with anterior border of shaft of tarsometatarsus. *Lateral view.* (34) Hypotarsus deepest about midway between proximal and distal ends, not near proximal end, with deepest part located somewhat distad of surface of external cotyla; (35) articular surface of external cotyla nearly planar, forming approximately a right angle with long axis of shaft; (36) lateral shaft surface slightly concave lateroposteriorly over proximal half of tarsometatarsus; shallow groove present near base of hypotarsus trending proximodistally; area where outer proximal foramen might open, crushed; over distal half, nearly planar and tilted medially towards posterior border; (37) shaft shallowest near distal end; gradually increasing in depth until deepest at point of maximum hypotarsal depth about two and one-half times distal depth; (38) anterior, distal, and posterior margins of trochlea IV form semicircle; proximal border (posterior to shaft) slightly concave proximally, joining posterior margin at angle only slightly greater than 90°; posteriormost projection of trochlea IV at proximal end of posterior margin; (39) depression in lateral surface of trochlea IV deep; (40) external margin of trochlea III semicircular (anterior, distal, posterior seg-

ments); anterior margin grades smoothly into shaft; posterior margin forms approximately 90° angle with proximal margin (posterior to shaft) that is slightly concave proximally. *Posterior view.* (41) Subhypotarsal ridge located slightly mediad of shaft's midline, curving slightly more mediad near proximal end; (42) subhypotarsal ridge extends nearly entire length of shaft, terminating slightly proximad of shaft's distal flare towards trochleae; (43) most of shaft triangular in cross-section with apex formed by subhypotarsal ridge; apical angle moderately acute, approximately 45°; far distal end near trochleae elliptical in cross-section with mediolaterally oriented major axis; (44) intertrochlear space between trochleae II and III does not extend as far proximad as that between III and IV; surface within intertrochlear space between trochleae II and III nearly perpendicular to plane passing through long axis of shaft except for narrow, distally protruding shelf at about level of anterior shaft surface; excavation does not extend far laterad; (45) distal foramen apparently not present (preparation of specimen makes evaluation of this area difficult to interpret). *Medial view.* (46) Anterior margin of internal cotyla and hypotarsus bulge decidedly anteriorly and posteriorly (respectively) beyond shaft margins; (47) anterior margin of trochlea II slightly convex anteriorly; distal and posterior margins smoothly rounded, approaching semicircular shape; more proximal part of posterior margin concave posteriorly; anterior margin grades smoothly into shaft as a straight line; (48) posteroproximal border of trochlea II nearly straight, grading into shaft at moderately obtuse angle; posterodistal border nearly straight, again forming moderately obtuse angle with posteroproximal margin; posterior margin intersects nearly straight posterior border at an angle approaching 90°; anterior border convex anteriorly, grading into shaft at large obtuse angle; (49) trochlea III extends about equal distances anterior and posterior of shaft; (50) excavation on medial side of trochlea II of moderate depth. *Distal view.* (51) Anterior and posterior margins of trochlea IV convergent laterally; medial and posterior margins slightly convex medially and posteriorly, anterior margin nearly straight; lateral margin concave externally; trochlear surface ungrooved; (52) trochlear groove on trochlea III more deeply excavated anteriorly than posteriorly; (53) medial margin of trochlea IV and lateral margin of trochlea II conver-

gent posteriorly; medial margin of trochlea IV forms approximately 90° angle with anterior shaft surface.

?Bullockornis sp.

(Figures 16, 18)

Referred material and locality: CPC 13849, proximal end, left tarsometatarsus. Bullock Creek, Northern Territory, Australia.

Lithic unit and temporal range: Camfield Beds, medial to late Miocene.

Fauna: Bullock Creek.

Diagnosis: Smallest species of genus. See diagnosis for *B. planei*.

Measurements: See table 37.

Description:

TARSOMETATARSUS. Proximal end only preserved; only those characters that differ from or are not preserved in *B. planei* are described below. *Proximal view.* (23) Hypotarsus bulbous with well defined channel dissecting medial wall. *Lateral view.* (36) Shallow groove near base of hypotarsus terminates just distad of and posterior to opening for outer proximal foramen.

Genus *Dromornis* Owen, 1872

Type species: *Dromornis australis* Owen, 1872.

Distribution: Queensland and Northern Territory.

Range: Late Miocene-Pliocene.

Synoptic Diagnosis: Medium-sized to very large-massive dromornithids with decidedly anteroposteriorly flattened, broad hind limb elements.

Sternum with moderately broad, elongate sternocoracoidal processes that extend beyond anterior margin of sternum; lateral margins slightly divergent posteriorly; no indication of subcarinate ridge.

Scapulocoracoid with straight, not concave ventral margin; coracoid near glenoid facet narrow; medial and lateral margins of coracoid more nearly subequal in length; coracoid neither deep nor inflated; ventromedial corner of coracoid extends posteriorly. *Carpometacarpus* with metacarpal space separating metacarpals I and II.

Femur with trochanter extending a moderate distance antiad, not extremely far; posterior margin of proximal articular surface concave; neck distinctly shallower than head and of moderate length, not elongate; shaft robust, broad with moderately curved (concave internally) medial margin; trochanter extends only slightly antiad of shaft; angle formed by long axes of fibular condyle and long axis of shaft 115-120°; neither obturator ridge nor posterior intermuscular line developed; in medial view, internal condyle semi-ovoid in shape with distalmost point lying antiad

of condylar midpoint; also in medial view, medial surface of internal condyle smooth, lacking any ridging; condyles moderately compressed anteroposteriorly; external condyle broad; in distal view, medial margin of internal condyle highly convex internally. *Tibiotarsus* with condyles only slightly broader than shaft; angle formed laterally between anterior and posterior shaft surfaces moderately obtuse; in medial view, internal condyle extends far antiad. *Tarsometatarsus* with shallow internal cotyla; intertrochlear space between trochleae III and IV narrow; shaft broad and shallow; subhypotarsal ridge broad and low; flare of proximal and distal ends moderate; over most of shaft, margins divergent proximally, not parallel; trochlea II extending only slightly further distad than trochlea IV; trochlea IV shallow; trochlea II not markedly reduced, with medial and lateral margins divergent posteriorly; groove on posterior surface of trochlea III of moderate depth to deep; in distal view, trochlea III of moderate depth, not narrow, with medial and lateral margins slightly convergent posteriorly. *Pes.* Condyles of phalanx 1, digit II shallow and highly divergent ventrally; internal margin of phalanx 2, digit IV highly concave mediadorsally.

Diagnosis:

VERTEBRAE. *Atlas.* Shows some differences from adult specimens of *Genyornis newtoni* but this may be correlated more with age of the individual (?juvenile) under consideration than with morphologic difference between genera. *Anterior view.* (1) Lateral walls of centrum parallel, not diverging posteriorly as in *Genyornis* and *Ilbandornis*; (2) no indication of a hypapophysial spine; (3) neural canal ellipsoid in outline with major axis parallel to horizontal; (4) lateral arches diverge from one another at angle approximating 45°. *Dorsal view.* (5) Posterior margin of neural arch V-shaped with a rounded apex, approximating a 90° angle, concave posteriorly; (6) anapophyses broad. *Lateral view.* (7) Lateral walls of neural arches elongate (anteroposteriorly), approaching that of the centrum in length, not short as in *Genyornis*, *Ilbandornis*; (8) centrum short (anteroposteriorly), not elongate as in *Genyornis* and some *Ilbandornis*. *Posterior view.* (9) Posterior articular surface of centrum lacks distinct groove along ventral half and pronounced lip extending posteriorly from ventral margin that is present in *Genyornis* and in some (?adult) *Ilbandornis* specimens. *Cervico-Dorsals/Dorsals.* Vertebrae in this series of *Dromornis* and *Genyornis* are not complete enough to allow many meaningful comparisons. In those few characters present in both genera, the two compare closely. Due to the lack of a complete series of vertebrae

from one individual dromornithid, it is impossible at this time to ascertain that comparisons of homologous vertebrae are being made. It seems best at present to await the discovery of a complete vertebral series of any dromornithid (most probably *Genyornis*) before detailed comparisons of individual vertebral elements are made. *Caudal. ?Anteriormost caudal. Anterior view.* (1) Centrum more dorsoventrally compressed than that in *Genyornis*; (2) excavation in anterior half of dorsal surface of neural arch extends to dorsalmost extension of arch, not interrupted by a medio-laterally trending ridge near dorsalmost margin of arch as in *Genyornis*; (3) ventral surface of centrum flattened over only small area along midline (laterolateral) of centrum; (4) lateral processes of neural arch do not extend as far laterad as those in *Genyornis*. *Lateral view.* (5) Large foramen on either side of centrum located slightly posteriad of midpoint, just dorsal to transverse process, not present in *Genyornis*; (6) anterior and posterior margins of centrum parallel, not dorsally divergent as in *Genyornis*; (7) lateral surface of transverse process primarily concave laterally except for central area that protrudes laterally, thus convex externally.

STERNUM. *Dorsal view.* (1) Sternocoracoidal processes of moderate width and elongate, extending forward of anterior margin of main body of sternum unlike in *Genyornis* where processes short, broad, not extending beyond anterior margin; (2) lateral margins of sternum slightly divergent posteriorly, nearly parallel, not convergent posteriorly as in *Genyornis*. *Anterior view.* (3) Outline of anterodorsal margin semielliptical, broadly U-shaped, not semicircular as in *Genyornis*; in essence, sternum not as deep dorsoventrally as that in *Genyornis*; (4) no indication of a subcarinate ridge as in *Genyornis*.

SCAPULOCORACOID (= CORACO-SCAPULA). *Anterior view.* (1) Ventromedial corner of coracoid not extending as far medially as that in *Genyornis*; (2) ventral (= sternal) margin of coracoid straight, not concave ventrally as in *Genyornis*; (3) width of coracoid near glenoid facet decidedly narrower with respect to coracoidal length than that in *Genyornis* (1:4 in comparison to 1:5); (4) medial and lateral margins of coracoid more nearly the same length than in *Genyornis* where medial margin decidedly shorter. *Lateral view.* (5) Coracoid not deep and about same depth over entire length, unlike in *Genyornis*

where coracoid quite deep slightly sternal of dorsoventral midpoint and shallower both dorsal and ventral to that area. *Posterior view.* (6) Surface between glenoid facet and medial margin of scapulocoracoid flattened, not domed (convex posteriorly) as in *Genyornis*; (7) no distinct ridge trending dorsolaterally from ventromedial edge of coracoid as in *Genyornis*; (8) entire scapulocoracoid quite anteroposteriorly flattened, not inflated overall as in *Genyornis*; (9) ventromedial corner of coracoid extends posteriorly unlike in *Genyornis* where this area flattened with no posterior extension.

CARPOMETACARPUS. (1) Metacarpal space separates metacarpals I and II unlike in *Genyornis* where the two metacarpals completely fused.

FEMUR. *Proximal view.* (1) Trochanter extends only slightly posteriad; (2) posterior margin of proximal articular surface concave posteriorly unlike the straight margins in *Bullockornis* and *Genyornis*; (3) neck distinctly shallower than head and trochanter differing from *Ilbandornis* and to a lesser degree *Genyornis*. *Anterior view.* (5) Neck of moderate length, not elongate as in *Barawertornis*, *Bullockornis*, and *Genyornis*; (6) shaft robust, broad with respect to those of *Barawertornis* and *Bullockornis*; (7) internal margin of shaft moderately curved, more so than in *Ilbandornis* but less so than in *Bullockornis* and *Genyornis*; (8) minimum width of shaft at or somewhat proximad of anteroposterior midpoint unlike *Ilbandornis* where it lies distinctly distad of midpoint. *Lateral view.* (9) Trochanter extends only slightly anteriad of main shaft; (10) shaft of moderate to shallow depth, unlike the much deeper shaft in *Bullockornis*; (11) angle formed between anteroposterior axis of fibular condyle and long axis of shaft between 115-120°, smallest of all the dromornithids. *Posterior view.* (12) No continuous obturator ridge is present, unlike in *Ilbandornis*; (13) unlike that in *Barawertornis*, posterior intermuscular line not developed; (17) depression at proximoexternal base of fibular condyle only slightly indicated, if at all, not well developed as in *Barawertornis* and *Genyornis*. *Medial view.* (18) Internal condyle semi-ovoid in shape with distalmost point anterior of anteroposterior midpoint, unlike *Barawertornis* and *Genyornis*; (19) internal surface of femur's distal one-fourth either completely smooth or with only low, short ridge near posterior margin and nearly parallel to distal mar-

gin of internal condyle, differing from *Genyornis* where medial shaft surface adjacent to internal condyle elevated medially from internal shaft surface. *Distal view*. (21) Condyles moderately anteroposteriorly compressed, more so than in *Genyornis* but less so than in *Bullockornis*; (22) external condyl wide, one-third to one-fifth the width of the internal condyle, not as broad as in most *Genyornis* but decidedly broader than that in *Bullockornis*; (25) internal condyle's medial margin much more highly convex internally than in any other dromornithids; (26) posterior margin of fibular condyle about same position or only slightly anterior of internal condyle's posterior margin.

TIBIOTARSUS. *Anterior view*. (4) Condyles somewhat, but not greatly, broader than shaft near distal end, unlike those in *Genyornis* that are decidedly broader than shaft. *Lateral view*. (5) Angle formed laterally by intersection of anterior and posterior shaft surfaces a moderately obtuse angle, not small obtuse or moderate acute angle as in *Ilbandornis* and *Genyornis* respectively. *Medial view*. (7) Internal condyle extends far anteriorly, not a moderate distance as in *Ilbandornis*.

TARSOMETATARSUS. *Proximal view*. (1) Internal cotyla shallow, not deep as in *Bullockornis*. *Anterior view*. (2) Intertrochlear space between trochleae III and IV decidedly narrower than that in *Bullockornis*. *Medial view*. (3) Shaft shallow unlike deep shaft in *Bullockornis* and moderately deep shaft in *Barawertornis*; (4-5) subhypotarsal ridge broad and low, unlike prominent, narrow ridge in *Bullockornis*. *Posterior view*. (6) Shaft broad with respect to width of distal end in contrast to *Bullockornis* in which the shaft is narrow; (7) flare or expansion of proximal and distal ends moderate, not broad as in *Barawertornis* and *Bullockornis*; (8) over most of length shaft margins divergent proximally rather than parallel as in *Bullockornis* and *Barawertornis*; (9) trochlea II extends only slightly further distad than trochlea IV, unlike decidedly greater extension of II in *Bullockornis*. *Lateral view*. (10) Posteroproximal margin of trochlea IV does not extend far posteriorly, i.e. trochlea IV shallow unlike deeper trochlea in *Barawertornis*, *Bullockornis*, *Ilbandornis*; (10A) lateral shaft surface and lateral segment of posterior surface merge indistinguishably, forming small acute angle with anterior shaft surface unlike in *Bullockornis* where angle larger and in *Genyornis* where distinct lateral surface present

that forms a 90° angle with anterior shaft surface. *Distal view*. (11) Trochlea II not markedly reduced as in *Genyornis* or *Ilbandornis* but with trochlea II and IV nearly subequal in size; (12) medial and lateral margins of trochlea II divergent posteriorly, not parallel as in *Genyornis*; trochlear groove on posterior surface of trochlea III of moderate depth to deep, not shallow as in *Barawertornis*; (14) posterior and anterior margins of trochlea II nearly subequal, not as in *Barawertornis* and *Bullockornis* where posterior margin nearly twice the width of anterior; (15) trochlea III of moderate depth, not extremely deep as that in *Bullockornis*; (16) width of trochlea III with respect to that of trochlea IV (at their anteroposterior midpoints) only moderately broader, not as narrow proportionally as that in *Ilbandornis* or many *Genyornis*; (17) lateral and medial margins of trochlea III moderately convergent posteriorly, not parallel or only slightly divergent as in *Ilbandornis*, *Genyornis*. **PES. Phalanx 1, Digit II.** *Distal view*. (1) Condyles decidedly shallower than those in *Genyornis*, *Ilbandornis*; (2) internal and external margins of condyles highly divergent ventrally with internal margin of internal condyle decidedly more elongate than external margin of external condyle unlike in *Genyornis* and *Ilbandornis* where condyles nearly parallel or only slightly divergent ventrally and margins of nearly equal depth. **Phalanx 2, Digit IV.** *Distal view*. Internal margin of internal condyle highly concave internodorsally unlike that in *Genyornis*, which is straight.

Dromornis australis Owen, 1872

(Figures 2-6, 11)

Type: AM F10950, right femur lacking much of trochanter and anterior parts of the condyles; shaft crushed on anterior surface near proximal and distal ends.

Referred material: None.

Type locality: Well at Peak Downs in Queensland. At about latitude 22°40'S between Lord's Table Mountain and the head of Theresa Creek, 3 miles east of Leichart's Peak (tag accompanying specimen in Australian Museum), near the track from Clermont to Broad Sound (Clarke, 1869), central Queensland.

Lithic unit and temporal range: From ?180 feet down in well (tag in Australian Museum accompanying specimen states 188 feet below the ground surface). Upper 30 feet, 'black trappean alluvial soil' overlying 150 feet of

'drift pebbles and boulders' (Clarke, 1869, p. 383); femur resting on a 'block of granite' (Clarke, 1877) in the 'superficial beds'. Probably Pliocene.

Diagnosis: Smallest species of genus; about three-quarters the size of *D. stirtoni*; further differs from *D. stirtoni* in that:

FEMUR. Anterior view. (6) Shaft broader with respect to total femoral length; (7) internal margin of shaft straight over much of its length, not continuously curved. **Lateral view.** (19) Distal one-fourth of internal surface of shaft proximad of internal condyle planar, not convex (i.e. not curved). Additionally, pit for posterior cruciate ligament much deeper (perhaps due to *overenthusiastic* laboratory preparation) than in *D. stirtoni*, as well as that in all other dromornithids.

Measurements: See table 31.

Description: Same as for *D. stirtoni* in all parts preserved except for those characters discussed in the diagnosis and the following characters whose significance is difficult to evaluate: (32) posterior shaft margin moderately concave posteriorly, not nearly straight as in *D. stirtoni*; anterior shaft margin moderately convex anteriorly (possibly due to crushing of distal end), not straight as in *D. stirtoni*—nonetheless, margins parallel except near distal and proximal ends as in *D. stirtoni*.

***Dromornis stirtoni*, n. sp.**

(Figures 2-6, 8, 12-22, 24, 27, 29, 35-36, 38)

Type: CPC 13851, right femur lacking part of trochanter and anterior part of internal condyle.

Referred material: *Paine Quarry.* (UCMP Loc. V-6345). *Femur:* UCMP 70112, left; UCMP 70114, right; UCMP 70115, right; UCMP 70648, right. *Tibiotarsus:* UCMP 71415, left with proximalmost part of articular end and posterior segment of condyles broken away.

Tarsometatarsus: UCMP 108608, trochlea II only; UCMP 70106, left with external part of proximal end lacking; UCMP 70652, right with proximal end destroyed; UCMP 70117, left lacking proximal end; UCMP 70647, right lacking proximal end; UCMP 70656, left lacking proximal end. *Vertebrae:* Atlas. UCMP 111306, lacking both postzygapophyses. Cervical or Cervico-Dorsal. UCMP 109206 lacking right prezygapophyses and parts of postzygapophyses; UCMP 70657, lacking part of left prezygapophysis and left lateral arch. Cervico-Dorsal. UCMP Nos. 66973, lacking postzyga-

pophyses and posteriormost part of centrum; 70108, lacking parts of pre- and postzygapophyses, anterior part of centrum. Caudal. UCMP 113047, complete. *Sternum:* UCMP 113049, complete. *Scapulocoracoid:* UCMP 113050, nearly complete missing only dorsal tip of scapula. *Carpometacarpus:* UCMP 70996, right, cf. *D. stirtoni*. *Phalanges of Pes:* Phalanx 1, Digit II. UCMP 66234, left. Phalanx 1, Digit III. UCMP Nos. 70084, right; 70085, right; 70086, left with external condyle broken ventrally; 70087, left, with internal margin of proximal articular surface damaged; UCMP 70995. Phalanx 3, Digit III. UCMP 67094, articular surfaces, both proximal and distal, damaged. Phalanx 1, Digit IV. UCMP Nos. 111304, right; 70093, right, distal condyles damaged; 70654, left, internal condyle missing; 70088, distal and proximal articular surfaces damaged; 70090, right, internal margin of proximal articular surface damaged. Phalanx 2, Digit IV. UCMP Nos. 67031, right, heavily eroded, lacking much of distal end; 67072, left; 70593, left. Terminal Phalanx. UCMP 70626. *Newsome Quarry or Locality.* (UCMP Loc. V-6346). *Tarsometatarsus.* UCMP 108608, central trochlea only. Phalanx 1, Digit III, UCMP 119210, distal end only.

Type locality: *Paine Quarry*, Alcoota Homestead, Northern Territory, Australia; UCMP Loc. V-6345; 3.6 miles map distance (Alcoota 4-mile sheet; Quinlan, 1962) or 4.9 statute miles, SW of Alcoota Station homestead west of Waite Creek, on 'low northeast trending rise about 1000' west of the conspicuous, pointed, red erosional remnant' (M. Woodburne, UCMP Locality card). Sediments composed of green siltstone (see Woodburne, 1967).

Other localities: *Newsome Locality (Quarry)*, Alcoota Homestead, Northern Territory, Australia; UCMP Loc. V-6346, about 40 feet north of Paine Quarry (UCMP Loc. V-6345) in the red siltstone that overlies the green lacustrine beds found in the latter quarry.

Lithic unit and temporal range: Waite Fm., late Miocene or early Pliocene.

Fauna: Alcoota.

Etymology: Named for Dr Ruben A. Stirton.

Diagnosis: Largest species of genus. See diagnosis for *D. australis*.

Measurements: See tables 6-7, 12-13, 18, 20-27, 29, 31, 34, 37.

Description:

VERTEBRAE. See figures 27, 29, 35.

SCAPULOCORACOID. Anterior view. (10) No foramina readily apparent, but bone sur-

face highly fractured and may camouflage foramina. *Posterior view.* (11) Same as for 10; (12) no notch present in medial margin of scapula dorsal to glenoid facet.

STERNUM. *Dorsal view.* (5) Sternum most highly concave dorsally near anterior end, gradually increasing in radius of curvature posteriorly; (6) intercostal spaces forming small acute angle ($30-35^\circ$) with internal wall of sternum; (7) internal sternal surface broadly U-shaped over anterior half of sternum with dorsal parts of lateral walls approximating 90° or small obtuse angle with ventral border. *Anterior view.* (8) Medial surfaces of sternocoracoid processes decidedly concave medially; (9) external sternal surface between sternocoracoid process and coracoid sulcus concave lateroventrally. *Lateral view.* (10) Most dorsoventrally elongate intercostal space is medial (or 3rd) space; (11) ventral border of sternum along mediolateral midline most highly curved near posterior end.

FEMUR. *Proximal view.* (27) Posterior margin of trochanter smoothly curved to join lateral margin. *Anterior view.* (28) Proximal articular surface moderately to highly curved; (29) trochanter can extend about same distance proximad as head; (30) in some individuals internal and external condyles extend about equal distances internally and externally from shaft while in others internal extension of internal condyle decidedly greater. *Lateral view.* (31) External shaft surface near proximal end nearly planar except immediately near proximal margin of trochanter where surface is convex laterally; (32) anterior margin of trochanter and proximal one-fourth of shaft margin describe part of a circular outline not projecting as far anteriad as in *Bullockornis*, however; proximal margin of trochanter moderately convex proximally with flattened midsection, posterior end not preserved; (33) external condyle extends much further posteriorly than anteriad; anterior margin only slightly convex anteriorly, extending only a short distance anteriad of anterior shaft surface; (34) margins of shaft slightly convergent at midshaft or parallel over much of length with anterior and posterior margins prescribing straight lines or only slightly anteroposteriorly concave anterior and posterior margins respectively; only slight to moderate divergences of margins to accommodate trochanter and external condyle; (35) lateral shaft surface tends to be planar near proximal and distal ends and convex laterad over its midsection, although

midsection can approach planar condition in some individuals; (36) proximal margin of external condyle straight, posterior margin rounded, semicircular in outline, distal and anterior margins convex distally and anteriorly respectively with smoothly rounded connection between the two, no angular connection between the two margins; indentation for *tibialis anterior* ligament located near anterior margin, far anteriad of anteroposterior midpoint; (37) fibular condyle narrowest posteriorly, in some individuals not much narrower with distal and proximal margins diverging anteriorly; distal margin forms approximately $105-125^\circ$ angle with long axis of shaft, proximal margin $115-130^\circ$ angle; (38) fibular condyle about 75-77% of depth of external condyle. *Posterior view.* (39) Distinct obturator ridge not present; (40) mediolateral expansion of distal end distinctly greater than that of proximal end; minimum width of shaft 43-45% that of width of distal end; (41) posterior shaft surface planar over most of its length, forming nearly 90° angle with medial surface over proximal half; as distal end approached intersection between posterior and lateral surfaces occurs at an increasingly larger obtuse angle; in some individuals this lateral surface forms planar, broad area, lying at large obtuse angle to posterior surface, not nearly at 90° to it as in most other dromornithids and not convex externally as in many dromornithids; if not planar, the lateral surface is slightly concave externally; (42) proximal margin of external condyle forms $135-140^\circ$ angle with posterior margin of shaft; (43) distal margin of external condyle nearly straight with slight indentation just mediad of main condylar ridge; most lateral part of margin, V-shaped; (44) medial margin of internal condyle slightly to highly convex internally; distal margin slightly concave distally to straight; (45) rotular groove of shallow to moderate depth, broad to very broad and evenly rounded. *Medial view.* (46) Shaft planar or convex internally over distal one-third and is convex internally over remainder; (47) posterior margin of internal condyle protrudes moderately further from shaft than anterior margin. *Distal view.* (48) See figure 2; (49) intercondylar fossa of moderate depth, broadly V-shaped, smoothly rounded instead of angular; internal part of margin forms lower angle with mediolateral axis of distal end than external; internal angle varies from approximately $35-50^\circ$, external from $70-90^\circ$; (50) rotular groove shallow, extremely broadly

U-shaped, much broader than intercondylar fossa, midpoint offset medially from that of intercondylar fossa; (51) external part of internal condyle's posterior margin forming low angle (10-20°) with mediolateral axis of distal end; posterior margin can be straight or convex posteriorly.

TIBIOTARSUS. *Proximal view.* (9-14) Np. *Anterior view.* (15-16) Np; (17) although shaft extremely broken into many tiny pieces, in general most of anterior shaft surface flattened or only slightly convex anteriorly; over proximal half of shaft, flattened surface tilted posteriorly towards medial margin; (18) only most distal segment of intermuscular line preserved, intersecting medial margin somewhat distad of proximodistal midpoint of shaft; (19) surface between intermuscular line and medial margin of shaft flattened or somewhat convex anteromedially; (20-21) np; (22) supratendinal bridge forms large acute angle, closely approaching 90°, with long axis of shaft; (23) external condyle relatively flattened to only slightly convex distoanteriorly; internal condyle anteriorly and anterodistally convex with smaller radius of curvature than that of external condyle; (24) np; (25) distal margins of both internal and external condyles slightly convex distally; sulcus between a broad swail, concave distally, not reaching an apex and thus not V-shaped. *Lateral view.* (26) Shaft surface near distal end flattened or slightly concave laterally; posterior surface not preserved; (27) posterior part of external condyle not preserved; (28) np; (29) shaft surface so broken up that it is impossible to determine the position of lateral ridge. *Posterior view.* (30) Posterior shaft surface nearly flattened near proximal end but slightly convex posteriorly over most of shaft; (31) np; (32) anteroproximal segment of external condyle not preserved; (33) shaft slightly, not moderately, curved, not straight with internal margin being more highly curved than external. *Medial view.* (34) Shaft moderately to highly convex medially over proximal half, becoming less so over distal half; far distal end of shaft flattened and tilted laterally toward posterior part of shaft; only far anterior part of shaft convex anteromedially; (35-36) np; (37) distal margin of internal shaft surface straight where preserved, with anterior segment gently curving to meet anterior surface; posterior segment np; (38) np. *Distal view.* (39) Np.

TARSOMETATARSUS. *Proximal view.* (18) Np; (19) np; (20) internal margin convex

internally, most highly curved anteriorly; internalmost projection of internal margin far anterior of anteroposterior midpoint of cotyla (21-24) np. *Anterior view.* (25) Proximal ligamental attachment extremely low, rounded knob displaced medially from midpoint between metatarsal groove and medial margin of shaft; (26) proximal end of metatarsal canal of moderate depth, not extremely deep; low, elongate, distinct ridge to only slightly indicated ridge for *tibialis anticus*; no nutrient foramen indicated; (27-28), np; (29) proximally, metatarsal canal displaced medially somewhat but over distal two-thirds of shaft canal lies along midline of shaft; canal narrow proximally but broadens distally to include much of the anterior shaft surface; (30) distal half of shaft slightly concave anteriorly; (31) trochlea III projects far anterior of other trochleae; (32) line passing through main axis of shaft when projected distally beyond shaft nearly passes through that of trochlea III or falls slightly laterad of it; medial margin of trochlea III projects into or slightly mediad of internal margin of shaft; (33) trochlea II flattened anteriorly, ungrooved; trochlea III centrally concave distally, convex medially and laterally due to centrally placed trochlear groove; trochlea IV nearly planar with plane tilted posteriorly towards lateral margin and forming moderately obtuse angle with anterior border of shaft. *Lateral view.* (34-35) Np; (36) lateroposterior surface of shaft contains opening for outer proximal foramen; (37) shaft relatively shallow over its entire length but shallowest near distal end just proximad of trochleae; proximal end depth about twice that of distal end; (38) anterior and distal margins of trochlea IV semielliptical in outline with long axis trending anteroproximally; although not angular, outline of condyle changes abruptly more posteriorly with posterior and distal margins forming a large acute angle with one another; posterior margin convex posteriorly, grading smoothly into shaft; (39) depression in lateral surface of trochlea IV shallow; (40) external margin of trochlea III U-shaped (anterior, distal, and posterior margins); both anterior and posterior margins grade gradually into shaft surfaces at large obtuse angles. *Posterior view.* (41) Subhypotarsal ridge mediad of shaft midline, slightly concave medially; (42) subhypotarsal ridge extends almost entire length of shaft, terminating slightly proximad of trochleae; (43) shaft an irregular polygon in cross-sectional shape; distally ellipsoid; further proximad

anterior margin flattened as is lateral margin, both of which meet in a 90° angle; antero-lateral margin forming moderately obtuse angle with posterolateral surface; posterior and medial margins meet at apex of subhypotarsal ridge forming small obtuse angle to a right angle; near anterior end medial surface becoming noticeably convex internally, thus forming approximately a 90° angle with anterior surface of shaft; (44) intertrochlear space between trochlea III and IV may extend only slightly or far proximad of space between trochleae II and III; surface within spaces forming approximately 90° angle with anterior and posterior shaft surfaces; narrow shelf near anterior extent present in medial intertrochlear space; (45) distal foramen present or absent. *Medial view.* (46) Anterior margin of internal cotyla bulges decidedly anterior of shaft; hypotarsus np; (47) posterior and distal margins semielliptical in outline with long axis trending posteroproximally; anterodistal margins convex anterodistally but with much larger radius of curvature than other margins; proximal margin, posterior to shaft, concave posteroproximally; trochlea II extending moderately to far posteriad of posterior shaft surface; (48) trochlea III U-shaped; (49) posterior margin extending further from shaft surface than anterior margin; both margins, however, grading gradually into shaft; (50) excavation on medial side of trochlea II shallow. *Distal view.* (51) Anterior margin not well preserved; posterior margin either slightly concave posteriorly, flattened, or convex posteriorly; medial margin slightly concave internally; lateral margin slightly concave laterally over anterior two-thirds, convex laterally over posterior one-third; (52) trochlear groove either of subequal depth both anteriorly and posteriorly or deepest posteriorly; (53) medial margin of trochlea IV and lateral margin of trochlea II slightly to decidedly convergent posteriorly. PES. See diagnosis for *Dromornis* and figures 8, 36, and 38. A few large, recurved ungual phalanges (see figure 40) with triangular cross-section recovered from the Waite Formation on Alcoota Homestead may represent this species, but association with the rest of the foot is absolutely necessary if this is to be verified.

***Ilbandornis*, n. gen.**

Type species: *Ilbandornis woodburnei* Rich, n. sp.

Distribution: Alcoota Homestead, Northern Territory, Australia.

Range: Late Miocene or Early Pliocene.

Etymology: *Ilbanda*, Aboriginal word for ground; *Ornis*, G., bird.

Synoptic Diagnosis: Medium-sized dromornithids with hind limbs of moderate width and moderate depth, neither extremely deep as in *Bullockornis* or highly compressed as in *Dromornis*. *Femur* with straight posterior margin of proximal end; neck and head of approximately the same depth and neck of moderate length, not elongate; shaft of moderate width, not slender with slightly curved medial margin; minimum width of shaft distad of midpoint; shaft moderately compressed antero-posteriorly; prominent obturator ridge; internal condyle semiovoid in shape with distalmost extension occurring anteriad of midpoint; in medial view, medial surface of internal condyle smooth, lacking any ridging; condyles moderately antero-posteriorly compressed, neither deep nor shallow; external condyle of moderate width. *Tibiotarsus* with lateral margin of external articular surface broadly convex laterally, not protruding far beyond shaft; external articular surface deep; inter-articular surface between articular surfaces and cnemial crests narrow; small obtuse angle formed laterally by intersection of anterior and posterior surfaces; lateral margin between shaft and fibular crest and proximal articular surface only slightly curved; internal condyle extends a moderate distance anteriad, not far; condyles shallow to moderate in depth. *Tarsometatarsus* with shallow proximal end; intertrochlear space narrow between trochlea III and IV; shaft of moderate width, shallow; subhypotarsal ridge of moderate width, low; moderate degree of flare at proximal and distal ends of tarsometatarsus; lateral and medial margins of shaft divergent proximally over most of length; trochlea II moderately reduced; in distal view, medial and lateral margins of trochlea II divergent posteriorly; trochlear groove on posterior surface of trochlea III of moderate depth to deep; trochlea III of moderate depth; trochlea III decidedly broader than trochlea IV; in distal view, lateral and medial margins of trochlea III parallel or only slightly convergent posteriorly. *Pes.* Condyles of phalanx 1, digit II of moderate depth, not shallow; internal and external margins of condyles nearly parallel or only slightly divergent ventrally; phalanx 2, digit II decidedly shorter than broad; in dorsal view, proximal margin of phalanx convex proximally, not straight; phalanx 3, digit III slightly shorter than broad; phalanx 2, digit IV with straight medial margin of internal condyle.

Diagnosis:

VERTEBRAE. *Atlas.* See description for *Genyornis newtoni*; vertebrae assigned to *Ilbandornis* quite variable morphologically, which is probably directly associated with age of individuals concerned; all vertebrae assigned to *Ilbandornis* somewhat smaller than those of *G. newtoni* (see table 13). *Dorsal.* See figure 32. FEMUR. *Proximal view.* (2) Posterior margin

of proximal end straight, not concave posteriorly as in *Barawertornis* and *Dromornis*, joining a straight segment of the trochanter just laterad of the mediolateral midpoint at 140° angle; (3) no shallowing of proximal surface at neck unlike *Barawertornis*, *Bullockornis*, and *Dromornis*. *Anterior view*. (5) Neck of moderate length, not elongate as in *Barawertornis*, *Bullockornis*, and *Genyornis*; (6) shaft of moderate width, not slender as in *Barawertornis* and *Bullockornis*; (7) internal margin of shaft only slightly concave internally, not moderately to highly curved as in *Barawertornis*, *Bullockornis*, *Dromornis*, or *Genyornis*; (8) minimum width lies distad of proximodistal midpoint unlike that in *Barawertornis* and *Dromornis* where it lies at or proximad of midpoint. *Lateral view*. (10) Anteroposterior compression of shaft moderate, shaft not deep as in *Bullockornis*. *Posterior view*. (12) Obturator ridge prominent, extending over one-third of the shaft's length, unlike in *Bullockornis* and *Dromornis* where it is not present and in *Genyornis* where a hardly perceptible ridge is present only in some individuals. *Medial view*. (18) Internal condyle semiovoid in shape with distalmost point anteriad of anteroposterior midpoint of condyle, unlike *Barawertornis* and *Genyornis*; (19) medial surface near distal end smooth except for short, low ridge near proximoposterior end of internal condyle differing from unridged condition in *Barawertornis* and *Bullockornis* and extreme condition where entire internal condyle is abruptly raised medially from shaft surface. *Distal view*. (21) Condyles moderately anteroposteriorly compressed, neither deep as in *Bullockornis* nor extremely shallow as in *Genyornis*; (22) external condyle moderately wide, about one-third width of internal condyle, not narrow as in *Bullockornis* nor very wide as in *Genyornis*; (25) internal margin of internal condyle forms straight line, not markedly convex internally as in *Dromornis*; (26) posterior margin of fibular condyle and posterior margin of internal condyle extends about same distance posteriad of shaft. **TIBIOTARSUS. Proximal view**. (1) External articular surface with lateral margin broadly convex externally, protruding only slightly laterad, not far laterad as in *Genyornis*; (2) external articular surface deep anteroposteriorly, unlike shallow surface as in *Genyornis*; (3) interarticular surface between articular surfaces and cnemial crests narrow, not moderately broad as in *Genyornis*. *Lateral view*. (5) Angle formed by intersection of

anterior and posterior shaft surfaces laterally, small obtuse angle, not moderate obtuse angle as in *Dromornis* or moderate acute angle as in *Genyornis*. *Posterior view*. (6) Lateral margin of shaft between fibular crest and proximal articular surface only slightly curved, not highly curved as in *Genyornis*. *Medial view*. (7) Internal condyle extends moderate distance anteriad, not far anteriad as in *Dromornis* and *Genyornis*. *Distal view*. (8) Condyles of moderate to shallow depth, not deep as in *Genyornis*.

TARSOMETATARSUS. Proximal view. (1) Proximal end shallow, not deep as in *Bullockornis*. *Anterior view*. (2) Intertrochlear space between trochleae III and IV narrow, not broad as in *Bullockornis*. *Medial view*. (3) Shaft shallow, not deep as in *Bullockornis* or even of moderate depth as in *Barawertornis* and *Genyornis*; (4-5) subhypotarsal ridge of moderate width and low, not narrow and prominent as in *Bullockornis*. *Posterior view*. (6) Shaft of moderate width with respect to width of distal end, not narrow as in *Bullockornis*; (7) moderate degree of flare of proximal and distal ends with respect to width of shaft, unlike the broad flare in *Barawertornis* (at least distal end) and *Bullockornis*; (8) lateral and medial margins of shaft proximally divergent over most of length, not parallel as in *Barawertornis* and *Bullockornis*; (9) trochlea II and IV extend distally about same distance unlike those in *Bullockornis* where II extends decidedly distad of IV. *Lateral view*. (10) Posteroproximal margin of trochlea IV moderately elongate, not short as in *Dromornis* and *Genyornis*, nor as elongate as in *Barawertornis* and *Bullockornis*; (10A) lateral shaft surface and lateral part of posterior surface merge indistinguishably, forming small acute angle with anterior shaft surface unlike larger angle in *Bullockornis* and distinct lateral surface forming 90° angle with anterior shaft surface in *Genyornis*. *Distal view*. (11) Trochlea II moderately reduced, not as highly reduced as in *Genyornis*, but more reduced than that in *Barawertornis*, *Bullockornis*, and *Dromornis*; (12) medial and lateral margins of trochlea II divergent posteriorly, not parallel as in *Genyornis*; (13) trochlear groove on posterior surface of trochlea III of moderate depth to deep, not shallow as in *Barawertornis*; (14) posterior and anterior margins of trochlea II of nearly subequal widths, not as in *Barawertornis* and *Bullockornis* where posterior margin twice the width of anterior; (15) trochlea III of

moderate depth, but not deep as in *Bullockornis*; (16) trochlea III decidedly broader than trochlea IV unlike in *Bullockornis* where trochlea III only slightly broader; (17) lateral and medial margins of trochlea III parallel or only slightly convergent posteriorly unlike the moderately convergent margins in *Bullockornis* and *Dromornis*.

PES. Phalanx 1, Digit II. Distal view. Condyles decidedly deeper than those in *Dromornis*; internal and external margins of condyles nearly parallel or only slightly divergent ventrally and of nearly equal depth unlike in *Dromornis* where highly divergent ventrally with internal margin of internal condyle more elongate than external margin of external condyle. **Phalanx 2, Digit II.** Identification of this element in *Ibandornis* not certain at present, but if element correctly identified (1) that in *Ibandornis* decidedly shorter than wide unlike that in *Genyornis* where it is more elongate than broad. **Dorsal view.** (2) Proximal margin of phalanx convex proximally, not straight as in *Genyornis*. **Phalanx 3, Digit III.** Phalanx slightly shorter than broad, not decidedly broader than long as in *Genyornis*. **Phalanx 2, Digit IV. Distal view.** Medial margin of internal condyle straight, unlike highly concave (mediolaterally) margin as in *Dromornis*.

***Ibandornis woodburnei*, n. sp.**

(Figures 2-6, 15-20, 28, 32, 37, 39)

Type: CPC 13850, right femur with anterior part of trochanter broken off.

Referred material: Paine Quarry (UCMP Loc. V-6345). UCMP 67465, right tarsometatarsus.

Type locality: Paine Quarry, Alcoota Homestead, Northern Territory, Australia; UCMP Loc. V-6345; 4.9 miles southwest of Alcoota Station Homestead; see type locality discussion for *Dromornis stirtoni*.

Lithic unit and temporal range: Waite Fm., late Miocene or early Pliocene.

Etymology: Named for Michael O. Woodburne, who in conjunction with John E. Mawby and J. E. Ferguson excavated the bird material at Alcoota Homestead.

Diagnosis:

FEMUR. See generic diagnosis, as element not preserved in other species of genus, *I. lawsoni*. **TARSOMETATARSUS.** Differs from *I. lawsoni* in that tarsometatarsus shorter with respect to width of distal end (ratio of total length to width of trochlea III approximately 1 in contrast to greater than 1.25 in *I. lawsoni*). **Anterior view.** Medial and lateral margins of shaft

divergent proximally over much of length, not parallel; intercotylar prominence low, not prominent; trochleae flare more broadly from distal end of shaft.

Measurements: See tables 31, 37.

Description:

FEMUR. Proximal view. (27) Posterior margin of trochanter smoothly curved to join lateral margin. **Anterior view.** (28) Proximal articular surface moderately curved; (29) head and trochanter extend approximately an equal distance proximad; (30) internal condyle extends further internally than external extends externally. **Lateral view.** (31) External surface of shaft near proximal end convex externoposteriorly, but anterior part np; (32) posterior margin of trochanter slightly convex distally, but proximal and anterior margins np; (33) external condyle extends much further posteriad of shaft than anteriad; (34) anterior and posterior shaft margins straight and parallel over most of their length except for bulge of obturator ridge on posterior margin about two-fifths the shaft length from the proximal end; slight divergence at proximal and distal ends; (35) shaft's lateral surface convex externally over much of its length except near far distal end where anterior half is planar, becoming somewhat concave externally near distal end; (36) proximal and posterior margins of external condyle np; distal margin slightly convex distally with major indentation for *tibialis anterior* ligament not far anteriad of anteroposterior midpoint of condyle; anterior margin not well preserved; (37) fibular condyle decidedly narrower posteriorly, with proximal and distal margins diverging anteriorly; distal margin forms approximately 90° angle with shaft's long axis; (38) since posterior margin external condyle not preserved, cannot judge comparative depths of external and fibular condyles. **Posterior view.** (39) Obturator ridge about two-fifths total length of shaft, most prominent near its distal end; (40) distal end more broadly expanded than proximal end; distal end about 50% wider than shaft at proximodistal midpoint; (41) posterior shaft surface nearly planar over proximal one-half while convex posteriorly over distal half; (42) approximately 145° angle formed between proximal margin of external condyle and posterior margin of shaft; (43) distal margin of external condyle straight with slight indentation just mediad of condylar ridge; condylar ridge more nearly U-shaped with slightly diverging sides (diverg-

ing proximally); (44) internal margin of internal condyle moderately convex internally, distal margin slightly concave distally; (45) rotular shallow, formed by the straight distal margins of the internal and external condyles intersecting at an angle of approximately 130°. *Medial view.* (46) Medial shaft surface planar over distal one-fourth becoming highly convex posteriorly, planar anteriorly further proximad; over proximal three-fourths of shaft anterior part grades imperceptibly into planar anterior shaft surface giving rise to an ovoid shaft cross-section that is trapezoidal further distally; (47) internal condyle extends decidedly further posteriad than anteriad. *Distal view.* (48) See figure 11; (49) intercondylar fossa shallow, but external margin not sufficiently preserved to allow determination of shape; (50) rotular groove deep, U-shaped, broader than intercondylar fossa, and its midpoint displaced mediad of intercondylar groove's; posterior margin of internal condyle forms approximately 15° angle with mediolateral axis of condyles.

TARSOMETATARSUS. *Proximal view.* (18) Internal cotyla concave proximally, external flattened, slightly concave near posterior part of cotyla; (19) external cotyla parallel to horizontal plane; (20) anterior border mostly straight with posterior indentation slightly laterad of intercotylar prominence (accentuated by crushing); lateral margin basically convex externally with prominent ridge located slightly anteriad of anteroposterior midpoint; medial margin moderately convex internally with medialmost extension far anteriad of anteroposterior midpoint; posterior margin on either side of hypotarsus straight; (21) np; (22-24) not well preserved. *Anterior view.* (25) Proximal ligamental attachment quite low, rounded knob displaced medially from midpoint between metatarsal canal and medial border of shaft; (26) crushed, np; (27-28) np; (29) appears to be displaced somewhat laterad of shaft's midline over entire length although crushing makes such evaluation tentative at best; (30) distal half of shaft crushed but apparently planar over much of length; (31) trochlea III projects moderately anteriad of trochlea IV; trochlea II not preserved; (32) central axis of shaft can be projected approximately through central axis of trochlea III, medial shaft margin can be projected into medial margin of trochlea III; (33) trochlea II np; trochlea III centrally grooved, thus concave anteriorly along midline, convex anteriorly, both medially and laterally; trochlea IV planar, tilted posteriorly towards lateral

border forming large obtuse angle with anterior surface of shaft. *Lateral view.* (34) Np; (35) articular surface of external cotyla nearly planar, tilted slightly distad anteriorly, thus forming small acute angle with long axis of shaft; (36) not well preserved; lateral and posterior surfaces merge indistinguishably, forming small acute angle with anterior shaft surface unlike in *Genyornis*; (37) quite shallow distally, increasing in depth proximally; no accurate comparisons of the depths of distal and proximal segments of shaft possible; (38) anterior part np; posterior and distal margins semielliptical in outline with major axis trending posteroproximally; proximal margin posterior to shaft slightly concave proximoposteriorly; posteriormost projection of trochlea IV somewhat proximad of proximodistal midpoint of trochlea IV; (39) np; (40) posterior and distal parts of external margin semicircular in outline; anterior margin with much greater radius of curvature, though certainly convex anteriorly; anterior part of margin projects only slightly anteriad. *Posterior view.* (41) Np; (42) not well preserved; (43) shaft triangular in cross-section over most of length, apex of triangle being the subhypotarsal ridge, with anterior surface of shaft concave proximally; apical angle probably small obtuse angle, though difficult to estimate due to some crushing of bone; distal third of shaft elliptical; (44) lateral intertrochlear space extending further proximad than medial space; proximal surfaces within intertrochlear spaces form angles approaching 90° with posterior and anterior shaft surfaces; (45) np. *Medial view.* (46) Internal cotyla extends moderately anteriad of shaft; hypotarsus bulging decidedly posteriad of main body of shaft; (47) np; (48) trochlea III U-shaped; (49) anterior border of trochlea III protruding only slightly anteriad of shaft, posterior border extending decidedly further from shaft (posteriad); (50) np. *Distal view.* (51) Anterior and posterior margins of trochlea IV convergent laterally at large acute angle; medial and lateral margins not well preserved; posterior margin straight over much of width but convex posteriorly near lateral border; anterior border slightly concave anteriorly; (52) trochlear groove about same depth anteriorly and posteriorly, perhaps slightly deeper posteriorly; (53) np.

***Ibandornis? lawsoni*, n. sp.**

(Figures 12, 20)

Type: CPC 13852, right tarsometatarsus, proximal articular surfaces broken off.

Referred material: Paine Quarry (UCMP Loc. V-6345). UCMP 70118, left tibiotarsus lacking internal half of internal articular surface and both anterior and proximal part of cnemial crests.

Type locality: Newsome Locality (UCMP Loc. V-6346), Alcoota Homestead, Northern Territory, Australia; approximately 200 feet northwest of Paine Quarry (UCMP Loc. V-6345) and about 4.9 miles southwest of Alcoota Station Homestead.

Lithic unit and temporal range: Waite Fm., late Miocene or early Pliocene.

Fauna: Alcoota.

Etymology: Named for Paul F. Lawson, coordinator extraordinaire of many of the American-Australian expeditions investigating Tertiary sediments in Australia since the early 1950s.

Diagnosis: See diagnosis for *I. woodburnei*.

Measurements: See tables 34, 37.

Description:

TIBIOTARSUS. *Proximal view.* (9) External articular surface elliptical in outline with major axis trending posteromedially; (10) np (i.e. internal margin of proximal articular surface not preserved and thus estimate of position of intercotyler eminence not possible; (11-14) np. *Anterior view.* (15-18) np; (19) shaft surface between intermuscular line and medial margin of shaft highly concave anteromedially; (20-21) np; (22) supratendinal bridge forming varied angles with long axis of shaft, moderate to large acute; (23) external condyle relatively flat over proximal half, distally becoming more distoanteriorly convex; internal condyle convex anteriorly over proximal half and slightly convex distally or flattened except near internal border; (24) proximal margins of internal and external condyles U-shaped (opening distally) with internal condyle being by far the broadest; margin between two condyles nearly straight or slightly concave proximally, forming large acute angle with long axis of shaft; (25) both condyles convex distally; sulcus between broadly V-shaped. *Lateral view.* (26) Moderate depression of lateral shaft surface present near posterior border just proximad of external condyle; (27) external condyle extends only short distance posteriad of shaft but a decided distance anteriorly; tuberosity just proximad of external condyle on anterior surface rises gradually, not abruptly from shaft surface; (28) distalmost extension of external condyle near or anteriorly of anteroposterior

midpoint of external condyle; (29) ridge dividing anterior and posterior shaft surfaces proximally far posteriad of anteroposterior midpoint of shaft; ridge trends closer to anterior shaft margin distally (distal one-quarter of shaft not well preserved). *Posterior view.* (30) Most of posterior shaft surface flattened or only slightly convex posteriorly; distinct canal just mediad of fibular crest passing into distinct foramen at distal end of fibular crest; (31) np; (32) anterior part of internal condyle extends further internally than low, rounded internal ligamental prominence; (33) shaft straight, particularly external border; internal shaft margin straight over middle half but concave medially both distally and proximally, decidedly more so than external margin. *Medial view.* (34) Not well preserved; (35-36) np; (37) posterior part not preserved, but anterior half of distal margin slightly convex distally with slight indentation (concave distally) near anteroposterior midpoint of internal condyle; (38) np. *Distal view.* (39) Np.

TARSOMETATARSUS. Only those characters differing from those in *I. woodburnei* or those preserved in *I. lawsoni* and not in *I. woodburnei* are mentioned below. *Proximal view.* (18-24) np. *Anterior view.* (25) Np; (26) proximal end of metatarsal canal shallow; distinct, elongate ridge present for *tibialis anticus* ligament; no nutrient foramen indicated; (27-28) np; (30) approximately half of distal half of shaft deeply incised by metatarsal canal, which gradually shallows proximally; distal half either flattened or convex anteriorly with radius of curvature decreasing distally; (31) trochlea III projects only moderately anteriorly of other trochleae; (33) trochlea II with slightly distally convex distal margin, straight lateral margin, other margins not complete. *Lateral view.* (34-35) Np; (36) although not well preserved, apparently convex laterally over proximal half and near distal end; between these two sections, shaft flattened with lateral surface forming 90° angle with anterior surface of shaft; (38) trochlea IV semicircular in outline (anterior, distal, posterior margins) with proximally concave margins grading into shaft, the posteroproximal border extending further from the shaft than the anteroproximal. *Posterior view.* (42) Subhypotarsal ridge extends approximately two thirds of the shaft's total length from the proximal end; (44) internal and external intertrochlear spaces extend about equal distances proximad; (45) distal foramen present. *Medial view.* (46) Np; (47) anterior margin moderately convex anteriorly, distal

and anterior margins semielliptical in outline with major axis trending anteroproximally; posteroproximal margin slightly concave posteroproximally; posterior margin broken off; (50) not prepared. *Distal view.* (53) Medial margin of trochlea IV and lateral margin of trochlea II nearly parallel, only very slightly convergent posteriorly.

Specimens assigned to *Ilbandornis*
species, indet.

(Figures 12-14, 21, 28, 32, 37, 39)

Measurements: See tables 13, 20-21, 25-26, 34, 37.

VERTEBRAE. *Paine Quarry* (UCMP Loc. V-6345). UCMP 113048, atlas lacking neural arch; UCMP 119207, atlas lacking neural arch; UCMP 70861, atlas lacking most of neural arch; UCMP 111305, cervico-dorsal, lacking left prezygapophysis.

Rochow Locality (UCMP Loc. V-6349). UCMP Nos. 108609-610, two atlas vertebrae lacking neural arches.

TIBIOTARSUS. *Paine Quarry* (UCMP Loc. V-6345). UCMP 70649, right, distal end only, probably *I. woodburnei*.

Newsome Locality (UCMP Loc. V-6346). UCMP 108606, left, distal end only; UCMP 108603, left, distal end only.

TARSOMETATARSUS. *Paine Quarry* (UCMP Loc. V-6345). UCMP Nos. 70094, right, distal end only; 70095, left, distal end only; 70096, left, distal end only; 70653, right, distal end only.

Newsome Locality (UCMP Loc. V-6346). UCMP 108600, left, distal end only; UCMP 108604, right, proximal end only; UCMP 108605, left, distal segment with trochlea and lengthy section of shaft, juvenile; UCMP 108601, left, distal end only; UCMP 108602, distal end only.

PES. *Paine Quarry* (UCMP Loc. V-6345). *Phalanx 1, Digit II.* UCMP Nos. 66233, right; 70102, right; 70804, right, with both distal and proximal articular surfaces damaged; 71019, right, lateral margin of proximal articular surface lacking. *?Phalanx 2, Digit II.* UCMP Nos. 66628, ?right; 70679, ?left. *Phalanx 3, Digit II.* UCMP Nos. 66618, 119212, ?right. *Phalanx 1, Digit III.* UCMP Nos. 66203a, right, lacking significant parts of proximal articular surface; 67039, right, lacking lateral half of proximal articular surface; 70087, left; 70098, right; 70655, cf. right, lacking much of proximal articular surfaces and section of mid-

shaft; 71016, left; ?71017, ?right; 71018, right, lacking distal half of phalanx; 71021, left, lacking margins of proximal articular surface; 71024, left; 71025, right; 71026, right, lacking external segments of both distal and proximal articular surfaces; 71027, left. *Phalanx 2, Digit III.* UCMP Nos. 66125, ?right; 66203b, right; 67017, ?left; 109179; 67080, ?left; 67089, lacking parts of both distal and proximal articulations; 67090, left; 70590, right; 70591, right; 70592, right; 70594, 70595, left; 70646, ?right. *?Phalanx 3, Digit III.* UCMP Nos. 70599; 70601; 70602; 70627. *?Phalanx 4, Digit III.* UCMP Nos. 67038; 70630. *Phalanx 1, Digit IV.* UCMP Nos. 67042, left; 66203c, right; ?70099, right, distal articular surface damaged; 70100, left, proximal end only; 70101, distal two-thirds only and lacking fragments of condyles; 70103, right; 70104, left; 70105, right; 71020, right; 71023, right, distal end only. *Phalanx 2, Digit IV.* UCMP Nos. 108613, 108615, both right; UCMP Nos. 67010; 67037, right; 67093, right; 70596, ?right; 70597, left; 70600, ?right.

Newsome Locality (UCMP Loc. V-6346). *Phalanx 1, Digit III.* UCMP 108607, right, lacking parts of both proximal and distal articular surfaces.

Rochow Locality (UCMP Loc. V-6349). *Phalanx 1, Digit II.* UCMP 108612, left. *Phalanx 2, Digit III.* UCMP 108611, lacking part of proximal articular surface.

Genus **Genyornis** Stirling and Zietz, 1896

Type species: *Genyornis newtoni* Stirling and Zietz, 1896.

Distribution: South Australia, New South Wales, Queensland and possibly Western Australia.

Range: Pleistocene.

Synoptic Diagnosis: *Sternum* with broad, short sternocoracoidal processes; lateral margins of sternum convergent posteriorly; low, distinct subcarinate ridge present. *Scapulocoracoid* with coracoidal segment that has ventromedial corner extending far internally; ventral margin of coracoid concave ventrally, not straight; coracoid broad near glenoid; medial margin of coracoid decidedly shorter than lateral margin; coracoid inflated and deep, not dorsoventrally compressed; surface between glenoid facet and medial margin domed; ventromedial corner of coracoid flattened with no posterior projections. *Carpometacarpus* lacks metacarpal space separating metacarpals I and II. *Femur* with straight posterior border of proximal articular surface; neck of about equal depth with head and elongate; shaft of moderate

breadth, not slender; internal margin of shaft highly concave medially; minimum width of shaft occurs near or distad of midpoint of shaft; trochanter extends only a short distance anteriorly of shaft, not far; shaft moderately compressed anteroposteriorly, but not shallow or deep; obturator ridge low or absent; internal condyle extends abruptly medially of distal shaft surface, not grading evenly into shaft, and thus internal surface of distal end ridged, not smooth; condyles shallow, highly compressed anteroposteriorly; external condyle broad; in distal view, condyles parallel or only slightly convergent anteriorly. *Tibiotarsus* with U-shaped lateral margin of articular surface (convex externally), protruding far beyond shaft; external articular surface shallow; interarticular surface between articular surfaces and cnemial crests moderately broad; angle formed at lateral confluence of anterior and posterior shaft surfaces, moderately acute, not obtuse; lateral shaft margin between fibular crest and proximal articular surface highly curved (concave externally); internal condyle extends far anteriorly; condyles deep. *Tarso-metatarsus* with shallow proximal end; intertrochlear space between trochleae III and IV narrow; shaft of moderate depth and width; subhypotarsal ridge low, of moderate width; distal and proximal flare of shaft moderate; lateral and medial shaft margins divergent proximally over most of length; trochlea II and IV extend nearly same distance distad; lateral shaft surface distinct from posterior, forming 90° angle with anterior shaft surface; trochlea II small, greatly reduced; in distal view, medial and lateral margins of trochlea II parallel; groove on posterior surface of trochlea III of moderate depth to deep; trochlea III of moderate depth to deep; trochlea III moderately to decidedly broader than trochlea IV; in distal view, lateral and medial margins of trochlea III parallel or only slightly convergent posteriorly. *Pes*. Phalanx 1, digit II with deep condyles; internal and external margins of condyles nearly parallel or only slightly divergent ventrally and of nearly equal depth; phalanx 3, digit III decidedly broader than long; phalanx 2, digit IV, when viewed distally, with straight medial margin of internal condyle.

Diagnosis:

STERNUM. *Dorsal view.* (1) Sternocoracoid processes broad and short, not extending beyond anterior margin of main body of sternum unlike elongate, more narrow processes in *Dromornis* that extend beyond anterior sternal margin; (2) lateral margins convergent posteriorly unlike those in *Dromornis* that are slightly divergent posteriorly. *Anterior view.* (3) Outline of anterodorsal margin semicircular, not semielliptical, more dorsoventrally compressed as in *Dromornis*; (4) low, but distinct, subcarinate ridge present that is not present in *Dromornis*.

SCAPULOCORACOID (= CORACO-SCAPULA). *Anterior view.* (1) Ventromedial corner of coracoid extending far medially, decidedly further than that in *Dromornis*; (2) ventral margin of coracoid concave ventrally, not straight as in *Dromornis*; (3) width of coracoid near glenoid facet broader with respect to coracoidal length than that in *Dromornis* (1:5 vs. 1:4); (4) medial margin of coracoid decidedly shorter than lateral margin, unlike that in *Dromornis* that is nearly subequal with lateral margin. *Lateral view.* (5) Coracoid deep midway between dorsal and ventral margins, not shallow throughout as in *Dromornis*. *Posterior view.* (6) Surface between glenoid facet and medial margin of scapulocoracoid domed, not flattened as in *Dromornis*; (7) distinct ridge trending dorso-laterally from ventromedial edge of coracoid unlike unridged surface in *Dromornis*; (8) entire scapulocoracoid inflated, not anteroposteriorly flattened as in *Dromornis*; (9) ventromedial corner of coracoid flattened, not projecting posteriorly as in *Dromornis*.

CARPOMETACARPUS. (1) No metacarpal space separating metacarpals I and II unlike in *Dromornis* where space present.

FEMUR. *Proximal view.* (1) Trochanter does not extend posteriorly of shaft; (2) posterior border of proximal articular surface straight, not indented at neck as in *Barawertornis* and *Dromornis*; (3) neck almost same depth as head, in some individuals only slight concavity in anterior margin, unlike distinct narrowing at neck in *Barawertornis*, *Bullockornis*, and *Dromornis*. *Anterior view.* (5) Neck elongate, not of moderate length as in *Ilbandornis* and *Dromornis*; (6) shaft moderately broad, not slender as in *Barawertornis* and *Bullockornis*; (7) internal margin of shaft highly concave internally, more highly curved than in any other dromornithids; (8) minimum width of shaft at or distad of midpoint unlike in *Barawertornis* where the minimum width lies proximad of the midpoint. *Lateral view.* (9) Trochanter extends only slightly anteriorly of shaft margin unlike great extension in *Bullockornis*; (10) shaft moderately anteroposteriorly compressed, not shallow as in *Barawertornis* or deep as in *Bullockornis*. *Posterior view.* (12) Obturator ridge quite low if present at all, extending about one-half length of shaft, unlike prominent ridge in *Ilbandornis*; (15) fibular condyle extends far externally, much further proportional to width of distal end than in any other dromornithids; (17) depression at

proximoexternal base of fibular condyle quite well developed unlike slight depression seen in *Dromornis*. *Medial view*. (18) Internal condyle semiovoid in outline with distalmost extension slightly anteriad of midpoint; (19) internal condyle abruptly extended mediad of distal shaft surface, thus differing from continuous gradation of shaft and condylar surfaces in all other dromornithids. *Distal view*. (21) Condyles highly compressed anteroposteriorly, neither moderately so as in *Dromornis*, *Ilbandornis*, and *Barawertornis* nor deep as in *Bullockornis*; (22) external condyle very wide, two-fifths to one-half width of internal condyle, unlike the narrower external condyles in *Barawertornis* and *Bullockornis*; (24) condyles parallel or only slightly convergent anteriorly unlike the greater convergence anteriorly seen in *Ilbandornis* or the anterior and posterior convergence seen in *Bullockornis*; (25) internal condyle's internal margin straight or only slightly convex internally, not markedly convex internally as in *Dromornis*; (26) fibular and internal condyles extend nearly an equal distance posteriad unlike in *Barawertornis* and *Bullockornis* where internal condyle extends further.

TIBIOTARSUS. *Proximal view*. (1) External articular surface with lateral margin U-shaped, protruding far laterad, not broadly convex externally and protruding only slightly laterad as in *Ilbandornis*; (2) external articular surface not deep anteroposteriorly, unlike deep surface in *Ilbandornis*; (3) interarticular surface between articular surfaces and cnemial crests moderately broad, not as narrow as in *Ilbandornis*. *Anterior view*. (4) Condyles broader with respect to shaft width near distal end (resulting in internal margin being more highly curved) than that in *Dromornis*. *Lateral view*. (5) Angle formed by intersection of anterior and posterior shaft surfaces laterally moderate acute angle, unlike small obtuse angle in *Ilbandornis* or moderate obtuse angle in *Dromornis*. *Posterior view*. (6) Lateral margin of shaft between fibular crest and proximal articular surface highly curved (with small radius of curvature) near proximal end, concave externally, unlike that in *Ilbandornis* in which margin only slightly concave externally. *Medial view*. (7) Internal condyle extends far anteriad, not a moderate distance as in *Ilbandornis*. *Distal view*. (8) Condyles deep, not moderate to shallow as in *Dromornis* and *Ilbandornis*.

TARSOMETATARSUS. *Proximal view*. (1) Proximal end shallow, not deep as in *Bullock-*

ornis. *Anterior view*. Intertrochlear space between trochleae III and IV narrow, not broad as in *Bullockornis*. *Medial view*. (3) Shaft of moderate depth, not extremely shallow as in *Dromornis* and *Ilbandornis* and not deep as in *Bullockornis*; (4-5) subhypotarsal ridge low and of moderate width, not prominent and narrow as in *Bullockornis*. *Posterior view*. (6) Shaft of moderate width with respect to width of distal end, not narrow as in *Barawertornis* and *Bullockornis*; (7) distal and proximal ends flared moderately, not broadly as in *Barawertornis* and *Bullockornis*; (8) lateral and medial margins of shaft proximally divergent over most of length, not parallel as in *Barawertornis* and *Bullockornis*; (9) trochlea II and IV extend same distance distad, trochlea II not extending decidedly further distad than IV as in *Bullockornis*. *Lateral view*. (10) Posterior extension of posteroproximal margin of trochlea IV short, not elongate as in *Barawertornis* and *Bullockornis* or even moderately elongate as in *Ilbandornis*; (10A) lateral shaft surface distinct from posterior surface and forms 90° angle with anterior shaft surface. *Distal view*. (11) Trochlea II highly reduced, not well developed as in *Barawertornis*, *Bullockornis*, and *Dromornis* or only moderately reduced as in *Ilbandornis*; (12) medial and lateral margins of trochlea II parallel, not divergent posteriorly as in all other dromornithids; (13) trochlear groove on posterior surface of trochlea III moderate to deep, not shallow as in *Barawertornis*; (14) anterior and posterior margins of trochlea II equal in width unlike those in *Barawertornis* and *Bullockornis* where anterior margin about half as wide as posterior; (15) trochlea III of moderate depth, not deep as in *Bullockornis*; (16) trochlea III moderately to decidedly broader than trochlea IV, unlike that in *Bullockornis* where trochlea III only slightly broader than trochlea IV; (17) lateral and medial margins of trochlea III parallel or only slightly convergent posteriorly, not moderately convergent posteriorly as in *Bullockornis* and *Dromornis*.

PES. *Phalanx 1, Digit II. Distal view*. (1) Condyles decidedly deeper than those in *Dromornis*; (2) internal and external margins of condyles nearly parallel or only slightly divergent ventrally and of nearly equal depth unlike those in *Dromornis* that are highly divergent ventrally with internal margin of internal condyle decidedly deeper than external margin of external condyle. *Phalanx 2, Digit II*. Identification of this element in *Ilbandornis* not cer-

tain at present, but if element correctly identified that in *Ibandornis* decidedly shorter than wide unlike that in *Genyornis* that is more elongate than broad. *Dorsal view*. Proximal margin of phalanx straight, not convex proximally as in *Ibandornis*. *Phalanx 3, Digit III*. Phalanx decidedly broader than long unlike in *Ibandornis* where only slightly shorter than broad. *Phalanx 2, Digit IV*. *Distal view*. Medial margin of internal condyle straight unlike highly concave (mediodorsally) margin in *Dromornis*.

***Genyornis newtoni* Stirling and Zietz, 1896**
(Figures 1, 23, 26, 30, 33-34)

Type: Lectotype. SAM P17001, left femur (see Stirling and Zietz, 1900, p. 57).

Referred material: *Lake Callabonna*, South Australia. *Femur*: SAM Nos. P13864, right; P13878, left; P17001, left (see Stirling and Zietz, 1900, Pl. XIX); P17002, right; P17003, right; P17004, left; P17005, left; P17006, right; P17007, right; P17008, right; P17009, right; P17010, left; P17011, P17012, P17043, all right. *Tibiotarsus*: BM(NH) 36217, distal end, right, lacking supratendinal bridge; AMNH 2649, right, lacking parts of proximal end; SAM Nos. P13866, right; P13927, right; P17026, left; P17027, right; (see Stirling and Zietz, 1900, Pls. XX, XXI, Figs. 1-3 in both) P17028, left; P17029, right; P17030, left; P17031, left; P17032, right; P17033, left. *Tarsometatarsus*: AM F4486, left; SAM Nos. P17013, left; P17014, left; P17015, right; P17016, left; P17017, left; P17018, left; P17019, left; P17020, right; P17021, right; P17022, right; P17023, left; P17024, right (see Stirling and Zietz, 1900, Pl. XXII, Figs. 1-2) P17025, left; P17036, right; P13865, right; AMNH 2645, right, SIAM 58, right; SIAM 85, left. *Vertebrae*: Figured in Stirling and Zietz, 1905, where indicated. *Atlas*. SAM Nos. P13928, missing neural arch (Pl. XXV, Figs. 3-4); P13929 (Pl. XXV, Figs. 1-2), missing most of neural arch; P17134, missing neural arch. *Axis*. SIAM 51, missing fragments of left postzygapophysis and most of centrum. *Middle Cervical*. SAM Nos. P13935A, P13935B, nearly complete (Pl. XXV, Figs. 8-11; Pl. XXVI, Figs. 1-5); SIAM 51, missing most of prezygapophyses and anterior part of centrum; SAM Nos. P17078, lacking right and part of left prezygapophyses and left lateral arch; P17079, lacking prezygapophyses, lateral arches, and right postzygapophysis; P17080, lacking left prezygapophysis, anterior part of centrum, and lateral arches; P17081, lacking

pre- and postzygapophyses, lateral arches; P17086, lacking pre- and postzygapophyses, anterior part of centrum, and lateral arches; P17087, complete. *Posterior Cervical*. SAM Nos. P13935C (Pl. XXVII, Figs. 1-5), lacking most of prezygapophyses, lateral arches, and left interzygapophysial bar; P13935D (Pl. XXVIII, Figs. 1-5), lacking right lateral arch; P13935E (Pl. XXIX, Figs. 1-5), lacking right prezygapophysis, lateral arches; P17091, lacking lateral and interzygapophysial bars. *Cervical*. SAM Nos. ?P17084, very fragmentary vertebra lacking anterior part of centrum, most of neural arch, and lateral arches; P17089, lacking most of right half of vertebra and posterior part of centrum. *Cervico-Dorsal*. SAM Nos. P13935F (Pl. XXX, Figs. 1-5), lacking pre- and postzygapophyses; P13935G (Pl. XXXI, Figs. 1-5), lacking prezygapophyses; P17083, lacking prezygapophyses; P17085, lacking hypapophysis and most of neural arch; P17088, lacking left prezygapophysis and hypapophysis; P17090, lacking part of right prezygapophysis and parts of centrum both anterior and posterior. *Cervico-Dorsal or Dorsal*. SAM P13935H (Pl. XXXIII, Figs. 1-4; Pl. XXXIV, Fig. 1), lacking left prezygapophysis and anterior right segment of centrum; P13935I; P17082, lacking anterior part of hypapophysis and most of neural arch. *Dorsal*. SAM Nos. P13935J (Pl. XXXIV, Figs. 2-5), lacking much of neural arch; P13935L (Pl. XXII, Figs. 5-8), centrum only; P17092, lacking dorsal part of neural spine, most of right prezygapophysis; P17093-7, centrum only; SIAM 51, posterior segment of centrum only; SIAM 58, lacking much of neural arch; SIAM 61; UCMP 56336, lacking much of neural arch. *Vertebra*. SAM P17134, fragmentary with only left pre- and postzygapophyses and fragments of centrum. *Sternum*: Unnumbered SAM (see Stirling and Zietz, 1900, Pl. XXXIII). *Scapulocoracoid*: SAM P13872a, b (see Stirling and Zietz, 1900, Pl. XXIV, Figs. 1-2 and 3 respectively); SIAM Nos. 51, right, nearly complete, lacking tip of scapula only; 61, left, fragmentary with glenoid facet and part of sternal (ventral) end only. *Synsacrum*: SAM Nos. P17041, fragmentary with partial ilium and all vertebrae anterior of acetabulum, partial ilium posterior of acetabulum, fragments of pubes, ischia (see Stirling and Zietz, 1913, Pl. XXXIX, Fig. 1); P17048, ischial and pubic fragment plus some ilium anterior of acetabulum (Ibid., Pl. XXXIX, Fig. 3); P17049, nearly complete synsacrum lacking only some anteriormost parts (Ibid., Pl.

XXXVIII, Fig. 1); P17050, right pubis fragment; P17051, right pubis fragment with ascending connection to ischium; P17052, ?left pubis fragment. *Humerus*: SAM Nos. P13871, right (see Stirling and Zietz, 1900, Pl. XXIV, Figs. 4-6); P17065, right, lacking part of head and internal tuberosity; P17066, distal end right; P17068, distal end, left; SIAM Nos. 51A, left, missing distal end, part of head, and internal tuberosity; 61, proximal three-quarters, right humerus. *Radius*: SAM Nos. P13873, left (see Stirling and Zietz, 1900, Pl. XXIV, Fig. 7); P17069, left; P17070, ?right, proximal end only; P17071, ?right, proximal end only; P17123, fragments (2); SIAM Nos. 51, left (2) (ulna and carpometacarpus fused in both cases); 58, right and left, both fused to ulnae. *Ulna*: SAM P13873, left (see Stirling and Zietz, 1900, Pl. XXIV, Fig. 8); P17123, right, four ulna fragments, ulna fused to radius and carpometacarpus; SIAM Nos. 51, left (see radius above); 58, right and left, fused to radii and carpometacarpus. *Carpometacarpus*: SAM Nos. P13875, left (see Stirling and Zietz, 1900, Pl. XXIV, Fig. 9); P17072, left, missing proximal and distal articular ends. SIAM 51, left (2) (ulna and radius fused); 58, right (fused to ulna). *Pes*: AMNH Nos. 2646, right digit III, complete; 2647, right digit II, complete; 2648, right digit IV, phalanges 1-3, lacking terminal phalanx 4; SAM Nos. P13868, left digit II, phalanges 1-2; P13869, right digit III, complete; P13870A, ?left, digit IV, phalanx 1, proximal end lacking but restored in plaster; P13870B, digit IV, terminal (4) phalanx; P13870C, right, digit IV, phalanx 2; P17044, left, complete pes (see Stirling and Zietz, 1900, Pl. XXII, Figs. 1-2, 5-6); P17045, left, complete but some articulation between phalanges not good suggesting all elements may not be naturally associated; P17057K, ?right, digit III, phalanx 2; SIAM Nos. 47, right, complete pes; 51A, right complete pes with associated distal end tarsometatarsus; 51B, left, lacking terminal phalanx, digit IV, otherwise complete; 51C, phalanx 1, digit III; 58, right, complete pes, phalanges 2-3 of digit II and arthritic as is distal end phalanx 1, digit II; 85, left, complete.

Baldina Creek, South Australia. SAM 17102, fragmentary femur, cf. *G. newtoni*.

Mt Gambier, South Australia. BM(NH) 44011, distal tibiotarsus fragment, cf. *G. newtoni*.

Naracoorte, Big Cave, South Australia. SAM P17320, anterior cervical vertebra, fragment-

ary, left side missing, probably *Genyornis newtoni*.

Port Lincoln, Brothers Island, South Australia. SAM P17104, proximal two-thirds of femur in highly indurated matrix.

Salt Creek (Normanville), South Australia. SAM P17099, tibiotarsus, right, midshaft fragment only, probably *G. newtoni*; SAM Nos. P17098, P17100A-C, hind limb fragments, cf. *G. newtoni*.

Cuddie Springs, New South Wales. *Tibiotarsus*. AM 33402, right, distal end only; AM 35405, right, distal end only, cf. *G. newtoni*. *Tarsometatarsus*. AM Nos. 33406, left; 33408, left, distal end only lacking trochlea II; 33409, right, distal end only, lacking trochlea IV; MM F16777, right, distal end only, lacking trochleae II and IV.

Type locality: Lake Callabonna, central eastern South Australia.

Lithic unit and temporal range: From the basal sands and overlying gypsiferous laminated clays of an unnamed formation; Pleistocene.

Diagnosis: Only species in genus, see generic diagnosis.

Measurements: See Stirling and Zietz, 1900, 1905, 1913 and tables 6-19, 28, 32, 35, 38.

Description:

VERTEBRAE. See figures 30, 33-34. *Atlas*. See Stirling and Zietz, 1905, pp. 81-83. *Axis*. (1) Entire vertebra inflated when compared to those of Casuariidae. *Anterior view*. (1A) Neural arch bulbous, not slender, gradually merging into anapophyses laterally and posteriorly; (2) prezygapophyses tilted ventrally outward and anteriorward; (3) prezygapophyses elliptical in shape, with major axis oriented posterolaterally, forming moderately acute angle with long axis of vertebra; (4) odontoid process protrudes far forward of neural canal; (5) a pair of marked depressions (one on either side of vertebra) occur between neural spine and prezygapophyses, on dorsal surface of neural arch. *Anterior Cervical*. Neural arch greatly inflated. *Anterior view*. (1) Prezygapophysis nearly square in outline, dipping ventrad anteriorly. *Dorsal view*. (2) Lateral margin of neural arch not decidedly concave externally but nearly straight; (3) dorsal surface of neural arch laterad of neural spine interrupted by a number of large and small foramina. *Lateral view*. (4) Dorsal part of lateral surface of centrum interrupted by two large foramina, separated by a narrow, deep bridge; (5) lateral arch elongate, narrow-

est near junction with posterior process. *Ventral view*. (6) Depression on anterior half of centrum deep, deepest near anteriormost extension; (7) ventral surface of centrum smooth, lacking any distinct ridge. *Posterior view*. (8) Posterior articular surface of centrum nearly square in outline, with ventral margin projecting further posteriad than remainder; (9) vertebral canal with decidedly greater diameter than that of neural canal, both nearly circular in outline; (10) vertebra broadest slightly ventrad of dorsoventral midpoint of vertebra. Considering entire morphology, vertebra most similar to third cervical when compared to those of *Casuariidae*. *Middle-Posterior Cervicals*, *Cervico-Dorsals*, *Dorsals*. See Stirling and Zietz, 1905, pp. 83-110, pls. XXV-XXXV. *Dorsals*. Two vertebrae either better preserved than or not represented in the collection described by Stirling and Zietz are illustrated in figures 33-34. Further discussion and comparison of these vertebrae will be attempted when a more complete series from one individual *Genyornis* is known. See discussion of homology problem in comparisons in the description of *Dromornis* vertebrae.

STERNUM. (5-11) See Stirling and Zietz, 1900, Pl. XXIII and pp. 72-74; further examination and description needed.

HUMERUS. See Stirling and Zietz, 1900, pp. 76-77, Pl. XXIV, Figs. 4-6.

RADIUS. See Stirling and Zietz, 1900, pp. 77-78, Pl. XXIV, Fig. 7.

ULNA. See Stirling and Zietz, 1900, p. 78, Pl. XXIV, Fig. 8.

CARPOMETACARPUS. See Stirling and Zietz, 1900, p. 79, Pl. XXIV, Fig. 9.

CARPAL PHALANGES. See Stirling and Zietz, 1900, p. 79.

COMMENTS ON THE FRONT LIMB. Elements in the forelimb are characterized by much greater morphologic variability than those of the hind limb. Shapes of articular surfaces, in particular on the proximal ends of the humerus and radius are highly variable as is the degree of fusion between the radius-ulna-carpometacarpus. The latter may be entirely related to the age of the individuals concerned. All three distal forelimb elements may be entirely separate from one another, all three fused, or the carpometacarpus-ulna fused and the radius free. No unfused carpals have been recognized. The carpometacarpus is also highly variable in form. In SAM P13875 figured by Stirling and Zietz (1900, Pl. XXIV,

Fig. 9), metacarpals II and III are separated by an intermetacarpal space over much of their length but are almost completely fused in SIAM 51 and 58. Metacarpal II in all of these specimens is by far the largest, forming a deep, distinct ridge in those completely fused. Metacarpal I is only a short segment of bone fused to the dorsal margin of the carpometacarpus and not separated from metacarpal II by any intermetacarpal space. A small articular surface on the distal end of metacarpal II indicates that at least one phalanx was present in the front limb, and Stirling and Zietz (1900, p. 79) mentioned a 'wedge-shaped nodule' which was found in situ with an otherwise complete forelimb that may represent this element, whether the terminal element or not. (*Casuarius* has 1, *Dromaius* 3, Apterygidae 2, Rheidae 2, Struthionidae 3 phalanges in digit II; in addition Rheidae possess 2 phalanges in digit 1 and 1 in digit 3, Struthionidae 2 in both digits I and III.)

SCAPULOCORACOID. See Stirling and Zietz, 1900, p. 76, Pl. XXIV. Muscle scars quite prominent, indicating that the only nearly complete specimen known may be an old adult. *Anterior view* (based solely on SIAM 51). (10) Small foramen 5.2 mm from medial border of scapula, 44.5 mm dorsomedial of dorsolateral corner of glenoid facet. *Posterior view*. (11) Medium-sized foramen 7.1 mm laterad of medial border of scapula and 42.8 mm dorsomedial of dorsolateral corner of glenoid facet; (12) foramen lies at dorsal end and lateral to distinct notch in medial margin of scapula.

HUMERUS. See Stirling and Zietz, 1900, pp. 76-77, Pl. XXIV. *Proximal view*. (1) Proximal end varies from being of nearly equal width throughout to being decidedly broader (palmo-anconally) in region of internal tuberosity; (2) head may be quite distinct from surrounding articular surface or merge indistinguishably with it. *Anconal view*. (3) Pneumatic fossa present or absent (probably in juveniles); (4) head can project abruptly proximad of external tuberosity or gradually merge with it; (5) shaft may be broad and stout or quite slender near its midpoint; (6) marked ridge may or may not be present between proximal end and shaft's midpoint, trending proximodistally and situated slightly ventrad of dorsoventral midpoint when present. *Palmar view*. (7) Marked ectepicondylar prominence may or may not be present.

FEMUR. See Stirling and Zietz, 1900, pp. 50, 57-60, Pl. XIX. *Lateral view.* (31) External shaft surface over proximal half almost all planar except on anterior part over proximal one-fourth where trochanteric ridge convex externally, on very proximal end which curves medially to join proximalmost extension of trochanter, and posterior half of surface over proximal one-fourth of shaft which is convex externoposteriorly, joining external planar surface at an oblique angle; (32) anterior margin of trochanter only slightly convex anteriorly and extending only slightly anterior of shaft; proximal margin of trochanter nearly a straight line, sloping distad posteriorly; posterior margin slightly convex posteriorly; (33) posterior margin of external condyle extends far posteriorly whereas anterior margin extends only slightly anterior of shaft surface; (34) anterior and posterior shaft margins parallel or only slightly convergent near the proximodistal midpoint of shaft; margins smooth throughout; (35) external shaft surface moderate convex externally over distal one-half, nearly planar over much of proximal one-half except as described under character 31; (36) proximal margin of external condyle straight, posterior margin semicircular, distal margin slightly convex distally and interrupted by depression for *tibialis anterior* ligament situated about midway between anterior margin and anteroposterior midpoint of condyle, anterior margin only very slightly convex anteriorly to straight; (37) fibular condyle slightly broader anteriorly but proximal and distal margins not widely divergent; distal margin forms angle of approximately 100° with long axis of shaft; (38) fibular condyle about 86% length of external condyle. *Medial view.* (46) Medial shaft surface planar near distal end but increasingly highly convex internally proximad of this; (47) internal condyle extension anterior and posterior of shaft about equal.

TIBIOTARSUS. See Stirling and Zietz, 1900, pp. 60-65, Pls. XX-XXI. *Proximal view.* (9) External articular surface elliptical in outline with major axis oriented at small acute angle to posterior shaft surface, posteromedially; (10) intercondylar eminence located mediad of lateromedial midpoint of proximal articular surface; (11) excepting external articular surface and intercondylar eminence remaining articular surface nearly flat or only slightly concave proximally; (12) shallow postero-internally directed channel separates external articular surface and intercondylar eminence; (13) interarticular area between cnemial crests

and proximal articular surface concave proximolaterally and entire surface slants distolaterally; (14) see Plate XX, fig. 3 in Stirling and Zietz, 1900; internal half of posterior margin medial margin and much of anterior margin semicircular in outline; medial margin of cnemial crest straight; anterior margin of cnemial crests form a sigmoid curve; lateral margin of proximal end anteriorly highly concave laterally, then deeply convex externally, and most posteromedially broadly concave posteriorly. *Anterior view.* (15) Inner and outer cnemial crests convergent at small acute angle distally; (16) outer cnemial crest concave laterally; inner cnemial crest nearly straight, only slightly concave internally, particularly near distal end near proximodistal midpoint of shaft; (17) over proximal two-thirds, shaft convex anteriorly; distal one-third, surface flat over lateral two-thirds, but slightly convex anteromedially over medial one-third and forming most proximally a 90° angle with the lateral part of the shaft, an angle that gradually increases to a large obtuse angle near distal end; (18) anterior intermuscular line trends distointernally from base of inner cnemial crest, intersecting the internal margin of shaft about midway between proximal and distal ends; (19) shaft surface between intermuscular line and medial margin of shaft slightly concave anteromedially, distinct ridge originates at proximal end, continues along medial margin, terminating in distinct internally convex protuberance just distad of the level that inner cnemial crest extends to; (20) marked tuberosity at proximal base of external condyle and laterad of tendinal bridge; (21) internal condyle more elongate, extending further proximad than external; (22) supratendinal bridge forming varied angles with long axis of shaft, moderate to large acute; (23) external condyle relatively flat over proximal half, distally becoming more distoanteriorly convex; internal condyle anteriorly convex over most of surface; (24) proximal margins of internal and external condyles U-shaped (opening distally) with internal being broadest; margin between two condyles nearly straight or slightly concave proximally forming large acute angle with long axis of shaft; (25) both condyles convex distally; sulcus between broadly V-shaped. *Lateral view.* (26) Moderate depression on lateral shaft surface present near posterior border just proximad of external condyle; (27) external condyle extending only short distance posterior of shaft but a decided distance anterior; marked extension anterior of shaft

of tuberosity just proximad of condyle along anterior border of shaft; (28) distalmost extension of external condyle at or anterior to anteroposterior midpoint of condyle; (29) ridge dividing anterior and posterior shaft surfaces proximally slightly posterior to anteroposterior midpoint of shaft; ridge trending closer to anterior shaft margin distally. *Posterior view.* (30) Posterior shaft surface nearly flat or only slightly convex anteriorly over much of its length; distinct canal just mediad to most of length of fibular crest; (31) lateral margin of external condyle straight and projecting evenly into most distal part of shaft's lateral margin; medial margin of internal condyle straight over most of length, forming small acute (or large obtuse) angle with shaft's long axis; near proximalmost end, margin convex internally; (32) anterior part of internal condyle extending further internally than low, rounded internal ligamental prominence; (33) shaft moderately curved over entire length, not straight with internal margin being more highly curved than external. *Medial view.* (34) Shaft moderately to highly convex internally over approximately proximal half, nearly planar over most of remaining shaft except near distal end where moderately convex internally; (35) proximal articular surface slopes distad at a small angle posteriad; (36) posterior margin of inner cnemial crest forming moderately obtuse (about 140°) angle with internal articular surface; (37) distal margin of internal condyle slightly convex distally over anterior half, indented (concave distally) near anteroposterior midpoint and nearly straight over remaining posterior segment; (38) proximal half of posterior margin of internal condyle slightly convex posteriorly, concave posterodistally over remaining length. *Distal view.* (39) Medial and lateral margins of condyles straight over much of length and nearly parallel, converging only slightly posteriad; posterior third of internal margin of internal condyle straight, but forming large obtuse (150°-160°) angle with anterior segment.

TARSOMETATARSUS. See Stirling and Zietz, 1900, pp. 66-69, Pl. XXII. *Proximal view.* (18) Internal cotyla slightly to moderately excavated, concave proximally; external cotyla flattened and (19) nearly horizontally oriented, dipping slightly distad towards anterior and lateral margins; (20) anterior margin convex anteriorly over internal two-thirds with distinct posterior indentation laterad of this and remaining margin strongly convex anteriad; medial margin nearly straight to

moderately convex internally; lateral margin convex laterally, more highly curved anteriorly and interrupted somewhat anterior of midpoint by narrow ridge protruding laterad; posterior margin internal to hypotarsus either concave or convex posteriorly; lateral to hypotarsus concave posteriorly; (21) depression shallow posteriorly, deepening into distinct pit about midway between intercotylar prominence and hypotarsus; (22) hypotarsus forming scalene triangle with large acute angle at apex slightly less than 90°; internal margin shortest, anterior base longest; one tendonal groove occurring on either side of hypotarsus; (23) hypotarsus bulbous; (24) point of proximalmost extension of hypotarsus near anterior end. *Anterior view.* (25) Proximal ligamental attachment very low knob sometimes with narrow ridge extending distad from it; in some specimens, no ridge or knob present; (26) proximal end of metatarsal canal a deep nearly circular pit; slightly broad, remaining shallow but narrowing over remaining two-thirds of shaft; attachment for *tibialis anticus* ligament distinct as elongate ridge along medial side of canal just distad of circular pit; large nutrient foramen opens at distal end of ligamental attachment; (27) attachment for external ligament a rounded ridge of moderate height; (28) surface between external and lateral ligamental attachments forms moderately obtuse angle with anterior shaft surface; (29) metatarsal canal centrally located to slightly laterally offset over three-fifths to two-thirds of shaft; (30) distal half of shaft concave anteriorly over proximal third, flattened over medial third and convex anteriorly over distal third, being most highly curved internally; (31) trochlea III projects moderately anteriad of other trochleae; (32) central axis of shaft projects laterad of central axis of trochlea III; medial margin of trochlea III projects mediad of shaft's internal margin; (33) lateral margin of trochlea II straight, distal margin straight forming 90° angle with lateral margin, medial margin convex internally; medial and lateral margins of trochlea III approximately parallel with internal margin straight and lateral margin slightly convex externally; distal margin concave distally along midline while mediad and laterad of midline margin either straight or slightly convex distally; medial margin of trochlea IV straight, distal margin slightly concave distally, lateral margin convex laterally. *Lateral view.* (34) Hypotarsus deepest distad of proximal articular surface, not at far proximal end, but deepest proximad of lateral opening of outer

proximal foramen; in some specimens hypotarsus grades evenly into hypotarsal ridge but in some distinct break occurs between the two; in latter case, greatest depth occurs about midway between proximal and distal ends of hypotarsus; (35) surface of external cotyla planar, tilting slightly distad anteriorly thus forming large acute angle with long axis of shaft; (36) on proximal end, near distal end of hypotarsus, outer proximal foramen opens slightly posteriad of shaft's midline; distinct groove in hypotarsus has distal termination just posteriad of foramen; (37) depth of shaft increases from proximally to about two and one-half times distal depth; (38) posterior margin of trochlea IV semicircular; distal margin nearly flat, in some specimens slightly concave distally; distoanterior margin slightly convex anterodistally, with much greater radius of curvature than posterior surface; (39) depression on lateral surface of trochlea IV shallow to deep; (40) posterior and most of distal margins semicircular in outline; anterior margin smoothly rounded but with greater radius of curvature than other margins; anterior margin extends only slightly anterior of shaft; posterior margin extends decided distance posteriad of shaft. *Posterior view.* (41) Subhypotarsal ridge displaced somewhat laterad of shaft's midline, most highly displaced near proximal end; (42) subhypotarsal ridge extends almost entire length of shaft, terminating near bases of trochleae; (43) shaft triangular in cross-section except near far distal end where elliptical; apex of triangle is hypotarsal ridge with apical angle approaching 90°; base of triangle anterior shaft surface, which is concave anteriorly; (44) lateral intertrochlear space extends moderately proximad of medial space; proximal surface within lateral space forming approximately 90° angle with anterior and posterior shaft surfaces; proximal wall of medial space forms moderate to large obtuse angle with posterior shaft surface forming shelf that occurs approximately midway between anterior and posterior shaft surfaces; (45) distal foramen present. *Medial view.* (46) Internal cotyla and hypotarsus bulge only moderately anteriorly and posteriorly beyond shaft respectively; (47) anterior margin convex only slightly anteriorly; distal margin may be semicircular and smoothly rounded or flattened as may be the posterior margin; anterior margin grades gradually into shaft being

slightly concave anteriorly; posterior margin arises more abruptly, concave posteriorly with small radius of curvature; (48) internal margin of trochlea III U-shaped with main axis tilted anteroproximally; (49) anterior margin of trochlea III level with anterior shaft margin or rises only slightly anteriorly; posterior margin extends further beyond shaft but can arise either gradually or somewhat abruptly from shaft; (50) excavation on medial side of trochlea II shallow to deep. *Distal view.* (51) Anterior and posterior margins of trochlea IV convergent laterally; anterior margin straight, posterior margin slightly concave posteriorly; medial margin moderately concave medially over anterior three-fourths; distal fourth slightly convex medially; lateral margin slightly concave laterally; (52) trochlear groove on trochlea III deepest anteriorly; (53) medial margin of trochlea IV convergent at small acute angle posteriorly.

PES. See Stirling and Zietz, 1900, pp. 69-72, Pl. XXII, Figs. 1-2, 5-6.

Other Material

In addition to the osteological remains described, the Dromornithidae are probably represented in Australia by two other kinds of evidence: ichnites (footprints) and possibly one complete egg as well as an eggshell fragment.

Footprints

Several hundred three-toed footprints (see Figure 41) possibly produced by members of the Dromornithidae were found by Mr Charles H. Taylor in a seam of white pipe clay overlain by ten to twenty feet of overburden at the Old Endurance Tin Mine pit near South Mount Cameron (Spry and Banks, 1962, p. 240) about five miles north of Pioneer, northeastern Tasmania⁷ (Rich and Green, 1974). These same clays have produced a pollen flora (Harris, 1968) that dates the deposit as mid-Tertiary, thus militating against a dinosaurian origin of the prints. No large, three-toed mammals, reptiles, or amphibians are presently known from the Cenozoic of Australia, and thus birds appear to be the most probable producers of such trackways. Among those birds known from Australia, only the ratites (including cassowaries, emus, and the extinct dromornithids) produce or could have produced three-toed tracks that approach the dimensions of those found in the old Endurance pit.

⁷ Footprints were found during sluicing operations to remove overburden above pipe clay being mined for use in paper manufacture (see Alexander, 1947).

The trackways from the Endurance mine are of large (147-240 mm in length; A), three-toed prints that definitely lack a hind or first digit common to many birds including the New Zealand moas. The three digits are nearly evenly spaced, broadly splayed with the middle digit being longest and the two side toes varying from nearly subequal to differing as much as 40 mm in length (see Table 39). Size of prints varies considerably (147-245 mm, length of middle toe (A); 194-270 mm, maximum width across toes (D); see Table 39). Impressions of the digits are broad, not slender (width of base of middle, side digits: 45-70 mm (A); 50-75 mm (B); 55-75 mm (C); see Table 39). Contours of the prints are generally rounded; no narrow terminal phalanges (claws) indicated but instead broader, more distally rounded phalanges suggested. The distance between prints averaged about 380 mm, and thus stride (distance from heel to heel) would have approximated 520-625 mm, certainly within the range of a stride length of a 'walking emu' (see Table 41). Impressions of tracks in the clay are about 25 mm deep and were filled in the field with fine gravel and sand that had apparently washed into the tracks before they were further buried under clay. Such a filling was most probably responsible for preserving the tracks in the well defined condition in which they were found.

As mentioned above, of all the birds known to occur in Australia during the Cenozoic, only the ratites have large and robust enough feet to have produced trackways akin to those known from the Endurance pit. In an attempt to determine which of the known ratite groups (Casuariidae, Dromornithidae) most likely produced the Endurance tracks, trackways of the living Australian ratites (cassowaries and emus) were studied at the Bronx Zoo in New York City⁸. Emus and cassowaries share a number of similarities (i.e. slender, elongate digits), but cassowaries are distinctive in possessing an elongate distal phalanx on the internal digit (II). This is mirrored in their footprints and is not indicated on the Endurance pit

prints. Tracks of the living emu, on the other hand, are similar in many respects to those from northeastern Tasmania. Tables 39 and 40 summarize measurements of tracks of *Dromaius novaehollandiae* and of the Endurance pit forms. Although the sizes of these prints overlap, there are some differences that distinguish the Endurance prints from those of the living emu:

1. the side digits are more elongate with respect to the mid-toe (see tables 30 and 40);
2. the foot is broader with respect to mid-toe length (see tables 39 and 40);
3. the breadth of the side digit is greater with respect to length of mid-toe (see tables 39 and 40) and width of foot (see Rich and Green, 1974);
4. the maximum angles between digits are greater⁹.

Additionally, if the Endurance tracks are compared to those that could have been produced by the contemporaneous mid-Tertiary *Dromaius* (presently being described by P. V. Rich and about four-fifths the size of the living emu), they are found to be decidedly larger.

Thus, at present, though admittedly based on a small sample of both recent and fossil material, tentative assignment of the Endurance Tin Mine tracks to birds in the family Dromornithidae seems most reasonable.

Eggs, Eggshell

Both an eggshell fragment and a complete egg from Australia may have been produced by members of the Dromornithidae.

Dr Michael Archer recovered the 'fragment of a very large bird egg' (Archer, pers. comm. 1973) from the Snake Dam Locality on Muloorina Station, north of Maree, South Australia, in a unit lithologically similar to and possibly contemporaneous with the Etadunna Formation of mid-Miocene age. To date I have been unable to examine this material, but if in fact it is too thick for and does possess a microstructure distinct from that of the emu and/or cassowary, it would represent possibly the

⁸ The sample footprints measured and photographed were made by six emus (*Dromaius novaehollandiae*), four of which were between 3 and 4 years of age and two of which were approximately 7 years old. All of the stride measurements were made on trackways produced by the two older emus (listed in tables 39 and 40 as Individuals 1. and 2.) as they were the most cooperative at moving through the mud runway used for recording tracks.

⁹ Although this angle could be dependent on the substrate in which the prints were made, the Bronx Zoo survey suggests such is not the case for *D. novaehollandiae*. Tracks of varying depth (10-65 mm) made in varying substrates (firm soil to very soft mud) were measured with no indication that angles between toes were dependent on substrate firmness. Width of individual toes changed somewhat (often somewhat wider in softer mud), but those measurements were included in the modern emu sample summarized on table 40.

earliest record of the Dromornithidae in Australia.

In addition, a complete egg (see Figure 41) of large dimensions (maximum length, @ 276 mm; maximum width, @ 207 mm) and exceedingly thick (3-4 mm) was found by Mr V. C. Roberts in coastal dunes south of Scott River, southwestern Western Australia (Butler, 1969; Anon., 1962; Edwards, 1962a-b; Hyslop, 1967) on the property of Mr G. Dunnett (34°20'S, 115°25'E). About 20 acres surrounding the locality where the complete egg was found have produced a varied fauna containing mainly forms conspecific with living taxa (see Stratigraphic and Geographic Distribution section of this paper). *Sarcophilus*, now restricted to Tasmania, is the only form in the fauna not presently occurring on mainland Australia. The fauna appears to be a mixed Pleistocene-Recent one, and thus dating any one element is impossible presently.

The Scott River Egg has an extremely porous, porcellaneous surface structure, probably heavily pitted by the sandblasting that has occurred in the dune environment. The number of pore openings per 5.0 mm² averages 21 (based on a count of 50 mm²). The egg's shape is distinctly ovaloid, not closely approaching a spheroid. Based on Amadon's formula for calculating volume and weight of a bird egg, which has a specific gravity approximating 1 ($W \text{ (or V)} = 0.5 LB^2$ where W is weight in grams, V is volume in cubic centimetres, L is length of egg in centimetres, and B is breadth or width of egg in centimetres; Amadon, 1943, 1947), the Scott River Egg (when fresh) probably weighed approximately 5.9 kg (13 pounds) and displaced about 5.9 litres (about 6.2 quarts).

Identity of the Scott River Egg remains in question at present. An obvious comparison that needs to be carried out is between it and eggs of *Aepyornis*, the elephant bird, from Madagascar, the only other bird known that could have produced an egg of comparable size (Amadon, 1947; Lambrecht, 1933; Wetmore, 1967). Measurements on twenty such eggs presented by Lambrecht (1933) ranged from 215 to 351 mm in length, 199 to 247 mm in width, and 1.33 to 3.65 mm in thickness. Moa eggs, even those of *Dinornis* and *Pachyornis*, are of smaller dimensions (Oliver, 1949; Archey, 1941); the largest reported egg of a moa (from Kaikoua, South Island) measures 253 mm in length, 178 mm in width, tentatively assigned to *Dinornis maximus* (Oliver, 1949). Comparisons of the microstructure of

the eggshell of both *Aepyornis* (see Sauer, 1972) and the Scott River form would be most significant but unfortunately cannot be carried out at present (D. Ride, pers. comm., 1972). Although the Scott River Egg could easily have been produced by one of the dromornithids endemic to Australia, because *Aepyornis* eggs were traded around the world particularly in the late nineteenth and early twentieth centuries, it is not totally impossible that such a treasure could have made its way into Australia from Madagascar whether by shipwreck or trade. Thus until further examination can be carried out on the Western Australian egg, its taxonomic position among birds must remain questionable.

Specimens Identified to

Family Level Only:

Dromornithidae gen. et sp. indet.

(see figures 25, 41)

Limb fragments

1. Well worn limb fragments of 'giant ground birds' (Woodburne, 1967, p. 13); Alcoota Homestead, Northern Territory; UCMP Loc. V-6347; Mio-Pliocene.

Vertebrae

2. Fragment of a sacral vertebra (WAM 65.4.152), Mammoth Cave, 4 miles southwest of Witchcliffe, southwestern Western Australia; Pleistocene (37 000; 31 500 yrs. BP).

3. Fragments of three vertebrae: ?sacral fragment, posterior cervical (lacking part of neural arch), sacral fragment (HM Nos. B768, B769, B968, respectively), Malkuni Fauna, Lower Cooper Creek Loc. 2 of Gregory, South Australia; Pleistocene. (See also 23.)

4. Fragmentary vertebra, centrum only (UCMP 56331), Malkuni Fauna, Cooper's Creek Site 8 (UCMP Loc. V-5860), South Australia; Pleistocene.

5. Dorsal vertebra fragment (lacking neural arch and parts of transverse processes) (UCMP 56336), Malkuni Fauna, Katipiri Waterhole (= Cooper Creek Site 9).

6. Vertebra, posterior cervical (UCMP 56376), Malkuni Fauna, Cooper Creek Site 6 (UCMP Loc. V-5382) (= Malkuni Loc., = Markoni Loc.), South Australia; Pleistocene.

Femur

7. Right femur (UCMP 70116), Alcoota Fauna, Alcoota Homestead, Northern Territory; UCMP Loc. V-6345 (Paine Quarry); Mio-Pliocene.

8. Proximal end of femur, head (HM B1138), from Gregory Collection, no locality information but probably from northern South Australia; ?Pleistocene.

9. Midshaft of femur, lacking articular ends (UCMP 56332), Alcoota Fauna, Alcoota Homestead, Northern Territory; UCMP Loc. V-6345 (Paine Quarry); Mio-Pliocene.

10. Midshaft of femur (SAM P17098), cf. *Genyornis*, Salt Creek, Normanville, South Australia; Pleistocene.

11. Fragment of internal condyle, right femur (BM 49160a)¹⁰, not *Genyornis*, Gulgong Fauna, Canadian Gold Lead near Gulgong and Mudgee, County Phillip, New South Wales; Pleistocene. Comment: internal surface of internal condyle lacks elongate, raised ridge that occurs on all *Genyornis* specimens examined. (See also 31.)

12. Right femur with proximal end and most of distal condylar surface broken away (SAM P17102), cf. *Genyornis newtoni*, Baldina Creek, South Australia; Pleistocene.

13. Left femur with trochanter and distal articular surfaces (condyles) broken away (UCMP 102525), Alcoota Fauna, Alcoota Homestead, Northern Territory; UCMP Loc. V-6346; Mio-Pliocene.

14. Left femur, specimen lost, originally reported by Mitchell (1839; see pl. 51, figs. 12-13), 'breccia cave', Wellington Valley, New South Wales; Pleistocene.

Tibiotarsus

15. Distal eight inches of right tibiotarsus lacking supratendinal bridge (AM L529 cast), specimen lost, fluvialite deposits, Thorbindah, Paroo River, New South Wales; Pleistocene. Comment: originally identified as *Dromornis australis*.

16. Two tibiotarsi (now lost), reported on by Woods (1866), 14 miles NNW of Penola, South Australia; Pleistocene. (See also 22.)

17. Tibiotarsus fragment (right), internal condyle only (SAM 17136), Malkuni Fauna, Warburton River, South Australia; Pleistocene. (See also 20.)

17a. Tibiotarsus, internal condyle fragment, right (SAM P17136), Diamantina, Queensland or South Australia; ?Pleistocene.

Tarsometatarsus

18. Trochlea III, right tarsometatarsus (UCMP 102525), Alcoota Fauna, Alcoota

Homestead, Northern Territory; UCMP Loc. V-6346 (Newsome Locality); Pleistocene.

19. Left tarsometatarsus, distal fragment with only trochleae III and IV (HM B1011), Cooper's Creek, South Australia; Gregory's Emu Camp (= Malkuni Waterhole, UCMP Loc. V-5382); Pleistocene.

20. Tarsometatarsus fragment, trochlea III only (SAM 17135), ?Malkuni Fauna, Warburton River, South Australia; Pleistocene. (See also 17.)

21. Right tarsometatarsus fragment, distal end, with trochleae II and IV broken off near bases (UCMP 119353), Malkuni or Unnamed Fauna, Warburton River, South Australia; Cassidy Locality (UCMP Loc. V-5539); Pleistocene.

22. Two tarsometatarsii (now lost), reported on by Woods (1866), 14 miles NNW of Penola, South Australia; Pleistocene. (See also 16.)

23. Trochlea III of tarsometatarsus (HM B774), Malkuni Fauna, Lower Cooper Creek Loc. 2 of Gregory, South Australia; Pleistocene. (See also 3.)

24. Fragment of tarsometatarsus, trochlea III only (UCMP 108602), cf. *Ibandornis*, Alcoota Fauna, Alcoota Homestead, Northern Territory; Newsome Locality (UCMP Loc. V-6346); Mio-Pliocene.

25. Fragment of left tarsometatarsus, trochleae II and III only (UCMP 108601), cf. *Ibandornis*, Alcoota Fauna, Alcoota Homestead, Northern Territory; Newsome Locality (UCMP Loc. V-6346); Mio-Pliocene.

25a. Fragment of trochlea III, tarsometatarsus (SAM P17135), Diamantina (River?), Queensland or South Australia; ?Pleistocene.

25b. Distal trochleae, left tarsometatarsus (NMV P41827), Lancefield, Victoria; Pleistocene.

Phalanges

26. Phalanx 2, digit III (right) (UCMP 47918), Malkuni Fauna, Cooper Creek Site 5 (UCMP Loc. V-5831), South Australia; Pleistocene.

26a. Phalanx 1, digit III (UCMP 47957), ?Malkuni Fauna, Warburton River near Lake Miamiana (UCMP Loc. V-5539), South Australia; Pleistocene. (See also 21.)

27. Four phalanges (UCMP 88186, 88188, 88335, 114732), Kutjamarpu Fauna, Lake

¹⁰ Perhaps the same specimen Owen (1879a, b) mentions from Goree (= Geurie), N.S.W. If not, this latter specimen is an additional occurrence of the *Dromornithidae*.

Ngapakaldi, South Australia; Leaf Locality (UCMP Loc. V-6213); Miocene. (See also 29.)

28. Four phalanges (SAM Nos. P17137-8; phalanx 2, digit III, left; phalanx 1, digit III, left; P17135-6), Diamantina (?River), Queensland or South Australia; ?Pleistocene.

28a. Phalanx (UCMP 108614), ?digit IV, phalanx 2 (right), Alcoota Fauna, Alcoota Homestead, Northern Territory; Rochow Locality (UCMP Loc. V-6349); Mio-Pliocene.

Synsacrum

29. Synsacral fragment, right side, part of pubis and small segment of ischium posteroventral to acetabulum (UCMP 109180), Kutjamarpu Fauna, Lake Ngapakaldi, South Australia; Leaf Locality (UCMP Loc. V-6213); Miocene. (See also 27.)

30. Synsacral fragment, left side at least, very crushed and distorted, UCMP 119211, Alcoota Fauna, Alcoota Homestead, Northern Territory; Paine Quarry (UCMP Loc. V-6345); Mio-Pliocene.

31. Synsacral fragment (fused vertebrae only), UCMP 70107, Alcoota Fauna, Alcoota Homestead, Northern Territory; Red Hill Site (UCMP Loc. V-6347), Mio-Pliocene.

32. Synsacral fragment (fused vertebrae only) medium sized Dromornithidae, UCMP 70111, Alcoota Fauna, Alcoota Homestead, Northern Territory; Paine Quarry (UCMP Loc. V-6345), Mio-Pliocene.

33. Internal cast of neural canal of fused vertebrae in synsacrum, medium sized Dromornithidae, UCMP 70109, Alcoota Fauna, Alcoota Homestead, Northern Territory; Paine Quarry (UCMP Loc. V-6345), Mio-Pliocene.

34. Synsacral fragment, right side with parts of pubis, ischium posterior and posteroventral to acetabulum (UCMP 60613), Palankarinna Fauna, Lake Palankarinna, South Australia; Lawson Quarry (UCMP Loc. V-5769); Pliocene.

35. Synsacral fragment, including ilium, acetabulum (right only) and proximal fragments of pubis and ischium (right only) (BM(NH) 49160), Gulgong Fauna, Canadian Gold Lead, near Gulgong and Mudgee, New South Wales; Plio-Pleistocene. (See also 11.)

36. Synsacral fragments (2; fused vertebrae only), HM Nos. B768, B968, Malkuni Fauna, Katipiri Sands, South Australia; Kalamurina (Lower Cooper Locality 2 of Gregory).

Egg

37. Eggshell fragment, Snake Dam Locality, ?Etadunna Fm. equivalent, Muloorina Station north of Maree, South Australia; Miocene.

38. Complete egg, between Scott River and the South Indian Ocean, 34°20'S, 115°25'E, Western Australia; ?Pleistocene.

Trackways

39. Several hundred footprints, a few of which are preserved in the Queen Victoria Museum and Art Gallery (QVM 1972/39/1-8), Endurance Tin Mine pit, 5 miles north of Pioneer, northeastern Tasmania; mid-Tertiary.

Stratigraphic and Geographic Distribution of the Dromornithidae (Figure 42)

Tertiary (pre-Pleistocene)

Only a few pre-Pleistocene localities in Australia have produced specimens that can be referred to the family Dromornithidae, none probably older than early to mid-Miocene (R. H. Tedford, M. Plane, W. K. Harris, pers. comm., 1972-3).

An unnamed unit of green and green-gray claystone with patchy limonitic staining, lithologically similar to and possibly contemporaneous with the Etadunna Formation at the Snake Dam Locality on Muloorina Station north of Maree, South Australia has produced a fragment of a 'very large bird egg' (M. Woodburne and M. Archer, pers. comm., 1973). The locality lies west of the easternmost of three tracks north of Snake Dam, near the Clayton-Muloorina fence, Clayton Creek, Maree 4-mile Sheet. At present Dr Michael Woodburne at the University of California at Riverside is preparing this material and outlining the stratigraphic situation at the Snake Dam Locality; further comment will await the results of this study. If, in fact, the Snake Dam sediments were deposited contemporaneously with the Etadunna Formation, the eggshell fragment would represent the earliest known occurrence of the Dromornithidae in Australia with the possible exception of a number of trackways found at the Endurance Tin Mine in northern Tasmania.

At the Endurance Tin Mine pit near South Mount Cameron, five miles north of Pioneer, northeastern Tasmania, an unnamed white pipe clay overlain by ten to twenty feet of overburden including a recent soil horizon has yielded a number of trackways, most probably produced by dromornithids. Harris (1968) has

dated these same clays at the Endurance pit as mid-Tertiary based on the contained pollen flora. Harris noted that a limit to the age of the unit cannot be given but that comparison with floral assemblages from mid-Miocene sediments (e.g. Muddy Creek Marl from western Victoria, Munno Para Clay and Port Willunga Beds of the St Vincent Basin of South Australia) suggest the Endurance clays are older than these sediments.

The Carl Creek Limestone (containing the Riversleigh fauna¹¹) has produced a vertebra and hind limb remains (CPC 7341, 7346, 7347, 7348) of the dromornithid *Barawertornis tedfordi* n. gen. et n. sp. (identified as close to '*Dromiceius*' in Tedford, 1968) at a locality between the Gregory River and Verdon Creek (Camooweal and Lawn Hill 4-mile sheets), 4 miles north of Riversleigh Station homestead, northwestern Queensland (see Tedford, 1968; Stirton et al., 1968). Avian as well as most of the other vertebrate remains were recovered from the upper member of the Carl Creek Limestone, a 'thick-bedded to massive clastic arenaceous limestone composed of sub-angular to subrounded pebbles of Tertiary limestone and rarer grey Thornton limestone pebbles set in an arenaceous limestone matrix' (Tedford, 1968, p. 221). In addition to the avian material, a number of aquatic and terrestrial invertebrates and vertebrates were recovered including: gastropods (*Thersites forsteriana* and *Isidora*); lower vertebrates (teleost and possibly *Neoceratodus* (Whitehouse, 1940)); Crocodylia, possibly *Crocodylus*; and aquatic turtles (Tedford, 1968); and a number of marsupials (Palorchestinae gen. et sp. indet., *Zygomaturinae* gen. et sp. indet., and a nototheriine, *Bematherium angulum*). Tedford (1968) believed that the palorchestine in the Riversleigh fauna was not so primitive as either of the two diprotodonts (*Ngapakaldia* and *Pitikantia*), both palorchestines, from the Etadunna Formation, yet retained a primitive palorchestine molar dentition; in addition, the upper premolar of the Riversleigh form closely approximated the 'stage of development of the quadritubercular upper premolars of the primitive zygomaturine diprotodonts such as *Neohelos* Stirton (1967) from the Wipajiri Formation, which unconformably overlies the Etadunna Formation in the eastern Lake Eyre Basin, South Australia'

(Tedford, 1968, p. 225). Based on that evidence Tedford suggested an age equivalent or slightly younger than the Ngapakaldi fauna (Etadunna Formation) but older than the Kutjamarpu fauna (Wipajiri Formation) for the Riversleigh fauna. The zygomaturine and nototheriine diprotodonts are also more primitive in known structure than any previously described forms, further supporting a pre-Kutjamarpu age. At present, however, it is not possible to assign a date to the Carl Creek Limestone and the contained Riversleigh fauna in terms of the standard geochronological scale (in Lyellian epochs), although it is definitely older than the marine Cheltenhamian Stage (late Miocene). *Zygomaturus gilli*, found at Beaumaris, Victoria and associated with marine invertebrates of Cheltenhamian age, is more advanced than the Riversleigh zygomaturine (Stirton et al., 1967; Tedford, 1968; Woodburne, 1969).

The Leaf Locality (UCMP V-6213; Stirton et al., 1967, p. 430, 432) on the eastern shore of Lake Ngapakaldi in the eastern Lake Eyre Basin between the Birdsville Track and the shore of Lake Eyre and between Cooper Creek and the Warburton River (about 1835 feet north of Ngapakaldi Quarry V-5858; Grid Coord. 642-488, Grid Zone 5, Maree Sheet, 1:506880, Aust. Army H.Q. Cartograph. Co., 1942) has produced dromornithid remains: a synsacral fragment (UCMP 109180) and several phalanges (UCMP 88186, 88188, 88335, and 119212) Stirton et al., 1967). Sediments producing these remains (Wipajiri Formation, containing the Kutjamarpu fauna) are ferruginous, conglomeratic sandstone interbedded with dark green claystone that is poorly indurated, channeled into the Etadunna Formation, and overlain by recent dune sand. Associated with the dromornithid remains are *Dromaius*, dipnoans, teleosts, cheliid turtles, crocodilians, squamates, *Ektopodon* (Phalangeridae?, Woodburne, pers. comm., 1973), a dasyurid, peramelids, *Litokoala*, phalangerids, *Rhizophascolonus*, a macropodid, a potorine, and the diprotodontid *Neohelos*. Stirton et al. (1968, p. 10) pointed out that the peramelids, phascolarctids, and potorines in the Kutjamarpu fauna 'have closest affinities with forms in the Ngapakaldi fauna'. The wombat is more primitive than any Pleistocene or living form; the diprotodontid *Neohelos tirarensis* is more

¹¹ The term "fauna" is used in the sense defined by Tedford (1969): "the maximum geographic and temporal limits of a group of organisms sharing a suite of common species" and includes or may include a number of local faunas.

primitive than the related *Zygomaturus keani* from the Palankarinna fauna, as well as *Z. gilli* from the Sandringham Sands (Beaumaris fauna) of Cheltenhamian age, and more primitive than *Kolopsis torus* from the Waite Formation (Alcoota fauna) (Stirton et al., 1968). Thus the best temporal estimate at present for the Kutjamarpu fauna is a post Ngapakaldi-pre-Beaumaris (or mid to late Miocene) age. Furthermore, the Kutjamarpu fauna is older (see below) than the Bullock Creek fauna (Camfield Beds) of the Northern Territory (Plane and Gatehouse, 1968).

Several specimens representing two species of *Bullockornis* n. gen. (*B. planei* n. gen. et sp. and *B.* n. sp.) have been recovered from the upper 35 feet in the exposed section of the Camfield Beds (Bullock Creek fauna), a light coloured calcareous siltstone, sandstone, and limestone unit. Fossil producing localities in this unit occur 16 miles southeast of Camfield homestead (Wave Hill Sheet, 1:250 000, SE 53-8, 131°31'-1/3'E, 17°07'S) in the north-central Northern Territory (Plane and Gatehouse, 1968; Stirton et al., 1968). Fossils exclusive of birds also collected from the Camfield Beds include high and low-spined helicoid freshwater gastropods, dipnoans, turtles, crocodilians, as well as two marsupials, a thylacoleonid and a zygomaturine diprotodont, *Neohelos*. The Bullock Creek *Neohelos* is larger than *N. tirarensis* from the Kutjamarpu fauna of the Lake Eyre Basin and shares many characters with *Kolopsis* known from the Alcoota fauna of central Australia, perhaps being 'ancestral to that genus' (Plane and Gatehouse, 1968). Plane and Gatehouse (1968) assigned a pre-Alcoota, post-Kutjamarpu age to the Bullock Creek fauna, placing it most probably within the Miocene, definitely pre-Cheltenhamian (see previous paragraphs).

The Waite Formation (containing the Alcoota fauna) that crops out on Alcoota homestead, central Northern Territory approximately 75 miles northeast of Alice Springs has produced many skeletal elements of two genera and three species of Dromornithidae, *Dromornis stirtoni* n. sp., *Ilbandornis woodburnei* n. gen. et n. sp., and *Ilbandornis? law-*

soni n. gen. et n. sp., as well as a member of the Accipitridae. The formation is composed of at least two subunits, a lower lacustrine sequence of evenly bedded, light green siltstone and limestone, and an upper fluvial sequence of poorly bedded, lenticular, coarse red sandstones and conglomerates. Both subunits have produced both genera and all three species of dromornithids. In addition to the birds, the Waite Formation has yielded a variety of other vertebrates (Woodburne, 1967; Stirton et al., 1968) including *Crocodylus* and a number of marsupials: *Thylacinus potens*, ?Vombatidae, macropodids (*Dorcopsoides fossilis*, *Hadronomas puckridgi*, ?protemnodont), and diprotodontids (*Kolopsis torus*, *Plaisiodon centralis*, *Pyramios alcootense*, *Palorchestes painei*). The age of the Waite Formation is not narrowly bracketed at present. The thylacines and macropodids are thought to be more primitive than Pleistocene forms most closely related to them (Stirton et al., 1968). *Palorchestes painei* is known both in the Waite Formation and perhaps in the Kalimnan (early Pliocene in Lyellian terms; Berggren, 1969, 1971) Grange Burn Formation (Hamilton fauna) that is capped by a basalt dated at 4.35 ± 0.1 million years BP (Turnbull, Lundelius, and McDougall, 1965; Turnbull and Lundelius, 1970).¹² This species is more primitive than *P. azael* (Pleistocene) and probably *P. parvus* (Chinchilla fauna) and is more similar to those forms than to others in the Ngapakaldi fauna. The Alcoota *Dorcopsoides* is quite similar to the Hamilton *Dorcopsis* (Turnbull and Lundelius, 1970). Furthermore, the nototheriine *Pyramios alcootense* appears to represent a 'stage of evolution' (Stirton et al., 1968) intermediate between the Riversleigh notothere and those of the Awe (with an age of younger than 3.1 to 3.5 but possibly as great as 7.6¹³ million years BP, mid to late Pliocene (or possibly late Miocene)) and Palankarinna faunas. The zygomaturine *Plaisiodon centralis* is more advanced than *Neohelos tirarensis* (Kutjamarpu fauna), but the lineage ends with the Alcoota form. Stirton et al. (1968) believed that *Kolopsis torus* was 'rather closely aligned in an ancestor-descendent relationship with *N.*

¹² Recognition of *P. painei* at Hamilton is based on a single isolated molar. M. Woodburne (pers. comm., 1973) rightfully cautions the use of such a limited sample for correlation, citing the difficulty he has had in distinguishing *P. painei* (Alcoota) and the later Chinchilla *P. parvus* on the basis of isolated teeth. Thus such a correlation should remain tentative at best until additional fossil material is found.

¹³ Dates provided by Evernden et al. (1964) and Plane (1972) ranging from 3.9-7.6 million years BP have recently been questioned by Page and McDougall (1972), who suggested that all the earlier dates were based on plagioclase dating and are excessively old. Page and McDougall's dates were based on biotite samples and suggest an age of <3.1 to 3.5 million years BP.

tirarensis on the one hand and with *Zygomaturus gilli* Beaumaris fauna, Cheltenhamian, late Miocene on the other. *K. torus* is also more primitive than *K. rotundus* (Awe fauna). On the above basis Stirton et al. (1968) concluded that the Alcoota fauna was post-Kutjamarpu, pre-Beaumaris in age. Since Stirton et al.'s (1968) paper, *Kolopsis*-like forms have been recognized in faunas as young as the Chinchilla, perhaps even as late as the 'early Pleistocene' fauna from Portland, Victoria (R. H. Tedford, L. Marshall, pers. comm., 1973). Thus, not surprisingly, primitive forms may have existed contemporaneously with advanced forms, and thus a reappraisal of the stratigraphic distribution of *Kolopsis* at the *specific* level is necessitated before biostratigraphic interpretations based on such forms at individual localities can be meaningful. At present, then, an age intermediate between the Kutjamarpu and Hamilton faunas or possibly contemporary with the Hamilton fauna (early Pliocene, Kalimnan) and pre-Awe, pre-Palankarinna, is the best age estimate for the Alcoota fauna.

At Lake Palankarinna in the eastern Lake Eyre Basin (Lawson Quarry, UCMP V-5769), the Mampuwordu Sands (containing the Palankarinna fauna) have produced a partial synsacrum (UCMP 60613) of a dromornithid. Miller (1963) referred the specimen to *Genyornis*, but until additional synsacral remains are known, particularly from other genera within the Dromornithidae, the Palankarinna specimen should be identified only as Dromornithidae gen. et sp. indet. Age assignment of the Palankarinna fauna is based primarily on its contained *Zygomaturus*, which appears to be 'older than typical Pleistocene forms, and later than Awe, Beaumaris, or Alcoota zygomaturines' (Stirton et al., 1968, p. 16). At Lake Palankarinna the Mampuwordu Sands are overlain by a maximum of 40 feet of unfossiliferous Tirari Formation and the Kati-piri Sands containing a Mulkuni fauna.

An unnamed unit composed of 'drift pebbles and boulders' (Clarke, 1869, 1877) overlain by 30 feet of black 'trappean' soil produced the type femur of *Dromornis australis* (AM F10950; Owen, 1872). Unfortunately no other fossils accompanied the dromornithid that was recovered from a 180-ft. well in the Peak Downs, between Lord's Table Mountain and the head of Theresa Creek, near the track from Clermont to Broad Sound, central Queensland. Woods (1960) noted that a 'doubtful

weathered specimen' of *Euryzygoma dunense* (also found in the Chinchilla Sands of south-eastern Queensland) has been recorded from Logan Downs Station, near Clermont on the Peak Downs, and further stressed the great thickness of fluviatile deposits that occur all around Clermont. He thus intimated that such units might have been deposited contemporaneously with the Chinchilla Sands. The Chinchilla fauna, recovered from a fluviatile sand and conglomerate sequence (Chinchilla Sands) exposed along the Condamine River (Condamine and Warra townships), includes diprotodontids such as *Euryzygoma dunense* and *Palorchestes parvus*, more advanced than *P. painei* in the Alcoota fauna (Stirton et al., 1968), but lacks those forms characteristic of the Pleistocene deposits of the eastern Darling Downs such as *Diprotodon optatum*, *Nototherium mitchelli*, and *Palorchestes azael*. Stratigraphic superposition and faunal differences have been interpreted to indicate an age difference (Woods, 1960) for the Chinchilla Sands, which have been assigned a Plio-Pleistocene (Stirton et al., 1968) or a ?Pliocene (Woods, 1960) age. Plane (1972) further noted the occurrence of the macropodid *Protemnodon otibandus* in the Chinchilla fauna (Bartholomai, 1972, believed that the Chinchilla form might be a separate, but closely related, species) as well as in the Awe fauna (New Guinea) and in the Kalimnan (early Pliocene) Lake Tyers Fauna (in the Upper Shell Bed of the Jemmy's Point Formation, Victoria). Despite the possible contemporaneity of the *Dromornis* and *Euryzygoma* specimens, however, fluviatile sediments in the Peak Downs region may, as in the Darling Downs, represent deposition at several different periods. Until more faunal elements from any one locality are known, dating of sediments bearing the type of *Dromornis australis* must remain tentative, but the age probably lies within the Pliocene or Pleistocene. Nonetheless, it is interesting to note that at no other locality where more precise dating is possible is the genus *Dromornis* known in sediments younger than Pliocene.

From the Canadian Gold Lead lying to the west of Cooyal Creek, due west of Wyaldra, approximately 6 miles southeast of Gulgong, and 13 miles northeast of Mudgee (as deduced from Jones, 1940), County Phillip, New South Wales a partial synsacrum (BM(NH) 49160) and the internal condyle of a femur (BM(NH) 49160a) (Etheridge, 1889; Stirling and Zietz,

1900; Lydekker, 1891), both representing dromornithids, were found associated (Lydekker, 1891) in auriferous deposits 200 feet below ground surface. Owen (1879a, b) mentioned the synsacrum but not the femoral fragment, although he referred '*Dromornis*' remains from Goree (= Geurie), near Mudgee, New South Wales that might represent the latter specimen. Although marsupial remains have been reported from the Gulgong district (Jones, 1940), identifications have not been refined sufficiently to be very useful biostratigraphically. David (1950), Jones (1940), and Dun (1894-5) reported the occurrence of several vertebrates in the deep leads of the Gulgong district: *Meiolania platyceps*¹⁴, *Chelodina sulcifera*, *Megalania*, *Echidna* (*Proechidna*) *robusta*¹⁴, *Ornithorhynchus maximus*, *Diprotodon*, *Halmaturus*¹⁴, *Macropus*, and birds¹⁴. Bird remains only verify the presence of the Dromornithidae, one taxa (represented by a femoral fragment) is definitely not the Pleistocene *Genyornis*, but no more precise identifications are possible. Additional information on the age of some of the deep leads in the Gulgong district, in many places fluvial fillings of limestone caverns, has been provided by Dulhunty (1971), who dated basalts overlying some of the gold bearing sediments. Only the leads at Ford's Creek, Gulgong, and Two Mile Creek, all overlain by basalt (Dulhunty, 1971: samples R1216, R1341), were sampled and produced dates of 14.8 ± 1.2 and 13.8 ± 1.1 respectively (mid-Miocene; Berggren, 1969, 1971). Unfortunately the Canadian Lead is not capped by volcanic rocks and thus cannot be assigned a minimum age. Dulhunty (1971) concluded that all the auriferous gravels in the Gulgong Gold Fields were thus of late early Miocene or early medial Miocene, but it remains to be demonstrated that those leads lying east of the presently recognized eastern extent of volcanic rocks (including Canadian Lead) are contemporaneous with the more western leads.

Pliocene-Pleistocene

Only one species of dromornithid, *Genyornis newtoni*, has been recognized in sediments thought to be Pleistocene in age, and this species is known widely throughout eastern Australia. Although close relatives are known from pre-Pleistocene sediments, the genus *Genyornis* is presently restricted to the Pleistocene. A number of other skeletal fragments known in Pleistocene sediments can only be

assigned to the family Dromornithidae, no more precise identification being possible with such limited material.

Sediments from possibly two localities in Queensland have produced fragments of dromornithids, probably *Genyornis* (see systematics section). From sediments along the Diamantina River (no more precise locality known; data on a tag with specimens) two fragments of the hind limb and two phalanges of cf. *Genyornis* (SAM P17135, P17136, P17137, P17138) have been recovered. The genus *Diprotodon* has been collected along the Diamantina River in the Gregory South district indicating a Plio-Pleistocene age for the marsupial occurrence (Woods, 1960). The relationship of the latter locale, however, and that producing the dromornithid is undetermined at present. Since the dromornithid remains are in the collections at the South Australian Museum in Adelaide, it is also quite possible that they were collected along the Warburton River, the downstream continuation of the Diamantina and sometimes called the Diamantina in South Australia (R. H. Tedford, pers. comm., 1973).

The only other sediments in Queensland producing probable Pleistocene dromornithids occur at Thorbindah (= ?Thorlindah, Devery, 1968) along the Paroo River in the Warrego district, southwestern Queensland. Only the tibiotarsus (cast AM L529; actual specimen lost) recorded by Etheridge (1889) and Stirling and Zietz (1900) is a dromornithid; the fibula (MM F12072) is not avian. The bird remains were collected along with bone fragments of 'kangaroos' and *Diprotodon* (Stirling and Zietz, 1900, p. 44) in a well 20 feet deep at Thorbindah (see above) near Cainwarra (?Caiwarro, Devery 1968) station on Paroo River.

The femoral fragment described by DeVis (1884, 1891) as *Dinornis queenslandiae* supposedly from King's Creek in the Darling Downs region was later found by Scarlett (1969) to be that of *Pachyornis elephantopus*, most probably derived from a moa-hunter midden on South Island, New Zealand. It should be dismissed as a valid record of this ratite genus in Australia.

Two localities in New South Wales have produced remains probably of Pleistocene age: Cuddie Springs and Wellington Caves,

Immediately below a layer of hard, compact clay, 'somewhat resembling crumbling cement'

¹⁴ Fauna occurring in Canadian Lead, New South Wales.

is a conglomerate consisting of 'broken bones and pebbles' (Anderson and Fletcher, 1934, p. 156). Several hind limb fragments of *Genyornis newtoni* (AM F33402, F33405, F33406, F33408, F33409, MM F16777) were recovered at Cuddie Springs, near Brewarrina on 'Gelgoine Station' (Anderson and Fletcher, 1934). The productive conglomerate was underlain by approximately five feet of 'biscuit-coloured and white clay' sparsely fossiliferous (Ibid., p. 156), followed by a bluish clay barren of fossils. The blue clay merged into a 'sandy layer' (Ibid., p. 157). At the same stratigraphic level as *Genyornis*, *Diprotodon* cf. *optatum* was also found, suggesting a Pleistocene age. Other vertebrates reported (although stratigraphic position was not indicated) included *Megalanina*, *Dromaius*, and *Phascolonus*.

Cave breccia in 'breccia cave' (Mitchell, 1839), one of several bone producing caves in the Wellington Valley district, produced the first reported bone of a dromornithid (now lost; see Mitchell, 1839, pl. 51, figs. 12-13). The bird femur was collected near the entrance to 'breccia cave', whereas the remaining taxa from that cave were collected further inside and much deeper vertically in the cave (Ibid., pp. 362-363). Mitchell collected from a number of caverns in the Wellington Valley and sent this mixed fauna to Owen for identification. His collection, as well as later additions, have produced a diverse fauna that has been considered Quaternary by most workers (David, 1950): *Megalanina prisca*; *Zaglossus ramsayi*; Marsupalia—Dasyuridae (*Sarcophilus lanianus*, *Thylacinus spelaeus*), Thylacoleonidae (*Thylacoleo carnifex*, *T. robustus*), Vombatidae, Macropodidae (*Macropus titan*, *Procoptodon goliah*, *Protemnodon brehus*, *P. anak*, *P. mimas*, *Sthenurus andersoni*, *S. atlas*, *S. brehus*, *S. oreas*, *S. orientalis*, *S. pales*); Primates—*Homo*; Rodentia *Conilurus*, *Mastacomys*; Carnivora—*Canis familiaris dingo*. The fauna contains both extant and extinct forms, and due to the mixing of fossils from several caves and levels within caves, it is impossible to determine the relative ages of the various elements of the fauna without recollection (see Tedford, 1967). Tedford (1966) and others have pointed out quite rightly that fissure filling in the Wellington district probably occurred at various times during the Pleistocene. Based on present evidence, a Pliocene to recent age is possible for the Mitchell dromornithid femur. A more precise dating will be forth-

coming only when individual caves and their included fauna are analyzed.

One locality on the south coast of Western Australia may have produced a dromornithid egg. A large egg measuring 276 mm in maximum length 'was found in coastal dunes south of Scott River' (Butler, 1969) (34°20'S, 155°25'E) between that river and the 'Southern Ocean' on property owned by G. Dunnett. From the same general area remains of *Sarcophilus*, *Setonix*, *Macropus*, *Pseudocheirus*, *Isoodon*, *Dasyurus*, 'murid, fox, and rabbit' as well as 'kookaburra and frogmouth, emu egg shell', 'an Aboriginal implement (microlith) and some pieces of an iron nail', 'snake, lizard, bird, bovid, and human remains', as well as marine material including 'cetacean, fish, mollusc, crustacean, and echinoderm remains' (Ibid., p. 88). No extinct genera are yet known in the fauna, although in the recent fauna *Sarcophilus* is restricted to Tasmania. Thus a probable late Pleistocene age seems appropriate based on present evidence.

Mammoth Cave, 4 miles southwest of Witchcliffe, in southwestern Western Australia has produced the sacral vertebra (WAM 65/4/152) of a Dromornithidae gen. et sp. indet. that is the size of *Genyornis newtoni*. A diverse non-avian fauna has also been reported from the cave (Tedford, 1966, 1967): *Zyglossus hacketti*, *Tachyglossus aculeatus*, *Sminthopsis* sp., *Phascogale tapoatafa*, *Dasyurinus geoffroi*, *Sarcophilus harrisii*, *Thylacinus cynocephalus*, *Isoodon obesulus*, *Macrotis lagotis*, *Trichosurus vulpecula*, *Pseudocheirus occidentalis*, *Phascolarctos cinereus*, *Thylacoleo carnifex*, *Vombatus hacketti*, *V. parvus*, *Bettongia lesueuri*, *B. penicillata*, *Potorous gilberti*, *Sthenurus occidentalis*, *S. brownei*, *Macropus titan*, *Macropus fuliginosus*, *Protemnodon* cf. *brehus*, *Macropus irma*, *Setonix brachyurus*, *Zygomaturus trilobus*, *Palorchestes* sp., and *Rattus fuscipes*. Carbon-14 dating of charcoal 'from top of Glauert excavation, from immediately below to four feet below a dripstone floor' (Tedford, 1967, p. 150) resulted in dates of 37 000 years BP (Lundelius, 1960) and 31 500 years BP (Tedford, 1967). Tedford noted that Glauert 'doubted the contemporaneity of all elements in this assemblage' (Ibid., p. 150; Glauert, 1910, 1948).

All of the remaining dromornithid producing localities are in South Australia and include: Baldina Creek, Brothers Island, Lake Callabonna, Mt Gambier Range, Salt Creek (Normanville), Penola, two of J. W. Gregory's

Localities on Cooper Creek, as well as several University of California - South Australian Museum localities along the Warburton River and Cooper Creek in the eastern Lake Eyre Basin.

Red coarse sand and fine conglomerates (based on matrix adhering to specimens) at Baldina Creek, 'on the edge of the Eastern Plains' (Stirling and Zietz, 1900) near Burra have produced a partial femur (with both proximal and distal articular surfaces eroded away; SAM P17102) of cf. *Genyornis newtoni*. *Diprotodon* cf. *optatum* was associated with the avian remains suggesting a Pleistocene age.

From a highly indurated aeolianite of beach sands and invertebrate shells a femur fragment of *Genyornis newtoni* (SAM P17104) was recovered on Brothers Island in Coffin Bay, approximately 30 miles WNW of Port Lincoln, 5 miles west of Wangary. Similar deposits on Brothers Island have produced a specimen of *Sthenurus* cf. *browni* (R. Tedford, pers. comm., 1973), thus suggesting a Pleistocene age for such deposits.

The basal sands and overlying gypsiferous laminated clays (Tedford, 1971) at Lake Calabonna have produced a large sample of *Genyornis newtoni* (including the type of the species and other remains described in a number of papers by Stirling and Zietz, 1896, 1900, 1905, 1913; Stirling, 1896) associated with *Dromiceius*, *Diprotodon optatum*, *Phascolonus gigas*, *Sthenurus*, *Protemnodon*, and *Macropus* in addition to invertebrates and plant remains. This lower stratigraphic unit (overlain by a sequence of silts and sands) has been dated at greater than 40 000 years BP (Tedford, 1971) and greater than 39 000 (Isotopes No. 5479, R. H. Tedford, pers. comm., 1973) years BP. The Carbon-14 dates in conjunction with the faunal composition (in particular *Diprotodon optatum*) suggest a Pleistocene age.

Two localities in southeastern South Australia have produced Dromornithidae. The distal end of a tibiotarsus with the supratendinal bridge eroded away (BM (NH) 44011) of *Genyornis newtoni* was recovered from 'a cavern in the Mount Gambier Range' (Lydekker, 1891, p. 355) and described by Owen (1879a). The specimen is extremely water-worn according to Lydekker (1891), suggesting fluvial transport into the cavern. No more exact locality or stratigraphic data were available, and there is no report of any associated fauna. Thus the age is uncertain but most probably within the Pleistocene. A second

locality, 'a well on the edge of a swamp fourteen miles north-northwest of Penola' (Woods, 1866; Dennant and Kitson, 1903), produced two tibiotarsii and two tarsometatarsii probably of a dromornithid. Woods, who found the bones personally (Woods, 1866), stated that the avian remains and aboriginal flints were associated (in a 'kitchen midden') and both lay about fifty yards away from a native well. He further noted that 'the bones were marked by scrapings and cuttings of flint knives of the blacks' (Ibid., p. 387). Unfortunately the four bones have been lost, and there is no way to check the authenticity of Woods' observations. If he were correct, the Penola occurrence would be the first documented association of aboriginal man and dromornithid and would date the occurrence as Pleistocene. Also unfortunately, his description was so incomplete that determination of identification beyond Dromornithidae is impossible even though the taxon, *Dromaeus australis*, established for these remains by Woods, if it had been properly diagnosed, would hold priority over Owen's *Dromornis australis* or Stirling and Zietz's *Genyornis newtoni*. *Dromaeus australis* is, however, a nomen nudum.

A locality in the stream bed of Salt Creek near Normanville (information from museum tag accompanying specimens in the South Australian Museum) produced hind limb material (femur: SAM 17098; tibiotarsii: SAM 17099, 17100A-C) of a dromornithid, probably *Genyornis* based on size and the conformation of the midshaft of the bones. The avian material was associated with *Diprotodon*, *Macropus*, *Phascolonus gigas*, *Phascolomys*, *Bettongia*, and *Thylacoleo* (Stirling and Zietz, 1900) of Pleistocene age. No detailed stratigraphic or more precise geographic data is available.

Several localities in northeastern South Australia in the eastern Lake Eyre Basin have produced probable Pleistocene dromornithids, localities found and collected by the expeditions of J. W. Gregory in the early 20th century and the University of California-South Australian Museum in the 1950s-1970s. The Gregory localities include Lower Cooper Creek Locality 2 and Emu Camp, both on Cooper Creek. The University of California-South Australian Museum localities include the Cassidy Locality on the Warburton River and several localities along the lower part of Cooper Creek: Cooper Creek Site 5, Cooper Creek Site 8, Katipiri (Kuttiipirra) Waterhole or

Cooper Creek Site 9, and Markoni Locality or Cooper Creek Site 6.

Some of Gregory's localities are discussed and plotted on his map in *The Dead Heart of Australia* (1906), but he does not discuss the remaining fauna that might have been associated with the birds. Thus the age of sediments producing the dromornithids is uncertain, although the productive deposits quite likely are Pleistocene Katipiri Sands (containing a Mulkuni fauna) discussed by Stirton et al. (1961) that crop out at many places along Cooper Creek and produced the bulk of the vertebrate fossils collected by the University of California-South Australian Museum in that area. In fact, one of Gregory's localities, Emu Camp, is synonymous with the UC-SAM locality Malkuni Waterhole (UCMP V-5382) that has produced the 'type' Malkuni fauna. At Emu Camp Gregory recovered the distal fragment of a tarsometatarsus including trochleae III and IV (HM B1011) and at the Lower Cooper Creek Locality 2 the distal fragment of trochlea III of a tarsometatarsus (HM B774) and vertebrae fragments (HM B768, B769, B968), all assignable only to Dromornithidae, gen. et sp. indet.

At the Cassidy Locality (UCMP V-5539) vertebrate remains including bones of Dromornithidae cf. *Genyornis newtoni* (a tarsometatarsus (UCMP 119353) and a phalanx (UCMP 47957) fragment) were recovered from sand bars in the Warburton (Diamantina) River approximately 1½-2 miles north of Lake Miamiana and about 8 miles southwest of Cowarie Station in the easternmost channel of the river (Grid Coordin. 635-556, Innamincka Sheet, 1:506 880, Aust. Army H.Q. Cartogr. Co., 1942). No producing bone layer could be located, all remains being collected on the sand and gravel bar surfaces.

All of the vertebrate producing channels along Cooper's Creek prospected by the University of California/South Australian Museum expeditions, some of which have also yielded dromornithids, are probably of late Pleistocene age (Stirton et al., 1961; R. H. Tedford, pers. comm., 1973), the productive channels are part of the Katipiri Sands (containing the Malkuni fauna). The non-avian fauna includes dipnoans, teleosts, chelonians, crocodilians, lacertilians, rodents (*Rattus* and *Notomys*), and the marsupials *Sarcophilus*, several other dasyurids, *Trichosurus*, *Phascolonus*, several macropodids, *Bettongia lesueuri*, *Protemnodon*, *Macropus*, *Sthenurus*, *Procoptodon*, *Diprotodon*,

and possibly other diprotodonts, indicating a fauna with representatives of both living and extinct forms. Many of the localities along the Warburton to the north of Cooper Creek have produced faunas comparable to those from the Katipiri Sands along Cooper Creek and are thus in part of late Pleistocene age; a radiocarbon date of 23 000 to 25 000 years BP is available for one of these fossiliferous channels on the Warburton (Geochron. No. GX 1872, *Diprotodon* bone sample).

At Pirranna Soakage (= Tilla Tilla Waterhole, Cooper Creek Site 5, UCMP V-5381, 28°35'S, 138°12'E, Grid. Coordin. 638456, Kopperamanna Sheet, SH 54-1, Edn. 1, Ser. R502, I: 250 000, 1965) the ?Katipiri Sands produced the phalanx (UCMP 47918) of a dromornithid. Associated fauna included Teleostei, Vombatidae (*Ramsaya*), *Sthenurinae* (*Sthenurus*), Macropodinae (*Protemnodon*), and Diprotodontidae (*Diprotodon*). All fossils at this locality were collected from sandbars in the bed of the main channel of Cooper Creek (Univ. Calif. locality summary).

Cooper Creek Site 8 (UCMP Loc. V-5860) includes the sand and sandstone concretion strewn bars in the Lower Cooper Creek, one-half mile south of Katipiri (Kuttipirra) Waterhole (at approximately Grid. Coordin. 622-457, Grid Zone 5, Maree Sheet, 1:506 880, Aust. Army H.Q. Cartogr. Co., 1942). All the vertebrate remains including dromornithid (a vertebra, UCMP 56331) were surface pick-up on gravel and sand bars but probably were derived from the base of channel sands (Katipiri Sands) that overlie red arenaceous Tirari clays.

Katipiri (Kuttipirra) Waterhole (= Cooper Creek Site 9, UCMP V-5861), type locality of the Katipiri Sands, is composed of the bars and bluffs on the north bank of Cooper Creek below Katipiri (Kuttipirra) Hill adjacent to the Waterhole (Grid Coordin. 620-458, Aust. Army H.Q. Cartogr. Co., 1942). Vertebrates including dromornithids (vertebra fragment, UCMP 56336) occurred both in situ or were float derived from the base of a 17 foot thick channel sand (Katipiri Sands) cut into red and green mottled arenaceous Tirari clays and overlain disconformably by up to 17 feet of grey-brown argillaceous sandstone and up to 30 feet of dune sand.

At the Markoni (= Malkuni Locality (Cooper Creek Site 6, UCMP V-5382, Grid Coordin. 627-455, Maree Sheet, 1:506 880, Aust. Army H.Q. Cartogr. Co., 1942) fossil

vertebrates (including dromornithids; a vertebra, UCMP 56376) were recovered from sand bars in Cooper Creek below 40-ft. cliffs forming the north bank of the channel. Fossils were probably derived from the base of cross-bedded/turbulent bedded buff to white quartz sand (Katipiri Sands) with gypseous green clay lenses, pipey sandstone concretions, and ferruginous bands. This unit is disconformably overlain by up to 8 feet of massive red-orange dune sands, which are in turn overlain by up to 6 feet of active yellow-orange dune sand.

From the Katipiri Sands or possibly the Tirari Formation at Lake Kanunka (R. H. Tedford, pers. comm., 1973) A. H. Miller (in Stirton et al., 1961) reported four bone fragments that he assigned to the Dromornithidae, noting that they were smaller than *Genyornis newtoni* but that they probably belonged to that genus. Reexamination of this phalangeal material (UCMP 56849, 60563, 94679, 94680 from UCMP V-77015) indicates that it is instead *Dromaius* sp., and, thus, there is no record of Dromornithidae from the late Pliocene or early Pleistocene Kanunka fauna as previously reported.

A Brief Characterization of the Dromornithidae

or

'What You've Always Wanted to Know About
Dromornithids But Were Afraid to Ask'

The dromornithids comprise a group of medium-sized to truly gigantic ground birds that were endemic to Australia during the mid to late Cenozoic. In the classic sense of the word, they are 'ratites', definitely lacking a true keel on the sternum. No palatal region of the skull is preserved in this group, however, and allocation of the dromornithids to the palaeognathous birds is based entirely on postcranial similarities of that group to the emus and casuaries.

Birds in the Dromornithidae range in size from slightly smaller than the living ostrich to a bird possibly exceeding in weight any bird previously known, including *Aepyornis maximus* (see table 43). None of the dromornithids known equalled or exceeded the height reached by members of the Dinornithidae (moas) but certainly exceeded them in mass. Limb proportions within the Dromornithidae also varied somewhat from the massive limbed *Dromornis stirtoni*, to the moderately slender, moderately elongate limbed *Genyornis*, to the elongate, slender limbed, medium-sized *Ilbandornis? lawsoni*.

In none of the dromornithids is the complete vertebral count known. *Genyornis* has the most complete vertebral series known in any of these Australian ratites, but there are many vertebrae, particularly in the cervical region, that are missing.

The sternum, as mentioned above, is more elongate than broad in contrast to the short, broad element in aepyornithids and the squared-up sternum of apterygids. The attachment area for the costal ribs is elongate, comprising about 60% of the sternum's lateral margin, quite in contrast to most other ratites (Struthionidae, Rheidae, Dinornithidae, Emeidae) where less than 40% of the lateral margin is involved with rib articulation. There are no sternal notches present in contrast to all other ratite groups excluding the Casuariidae. Articulation with the scapulocoracoid is restricted and limited to the far lateral margins of the anterior border, certainly not overlapping along the midline of the sternum as in the Struthionidae and Casuariidae, but on the other hand not as restricted as in Emeidae, Dinornithidae, and Apterygidae. The scapula and coracoid are completely fused into a single element that contains a very small glenoid facet, and attachment for an equally reduced forelimb, much more reduced than that in the Struthionidae and Rheidae. The forelimb is comprised of a relatively short, stout humerus that lacks well-defined articular surfaces, more elongate radius-ulna that are often fused at several points along the shaft, and a triangular carpometacarpus, shorter than the humerus, so completely fused that most often no intermetacarpal space is visible. There was probably at least one phalanx, a very small element that articulated with the carpometacarpus. No articular facets are present on the carpometacarpus that would indicate occurrence of a first digit that is known in the struthionids and rheids.

The synsacrum of dromornithids is only of moderate width posterior to the articulation with the femur, not broad as in many ratite groups including the dinornithids, emeids, and aepyornithids. Articulation with the hind limb occurs about midway between anterior and posterior ends of the synsacrum in contrast to the struthionids where this articulation is shifted forward of the midpoint and in the apterygids where it is shifted posteriad of the midpoint. The pubes, ischia, and ilia are subequal in posterior extension; there is no pubic fusion as in the struthionids. In adults the pubes fuse with the ischium and it in turn with

the ilium to produce an elongate ilio-ischiatic fenestra, and a short ischio-pubic fenestra, a nearly unique arrangement within the ratites (aepyornithids apparently closely approach this condition).

The femur is stout and often the shortest element in the hind limb. The trochanter projects about the same distance proximad of the shaft or slightly further than the head, but not exceedingly further proximad as in the aepyornithids. The external condyle, on the other hand, extends somewhat further distally than does the internal condyle but nowhere so disproportionately as in Struthionidae or Rheidae and is not subequal as in the Apterygidae. No extensive muscle scars are present in the popliteal area unlike in the dinornithids-emeids and aepyornithids. The internal condyle is uniquely shaped in that its distal-most extension occurs anterior to the condylar midpoint, and the condyle approaches an elliptical shape with the major axis forming an acute angle with the posterior margin of the shaft. The condyle is not semicircular as in *Dromaius*, the dinornithids, emeids, aepyornithids, nor distally flattened as in the rheids or struthionids. The condyles are of subequal depth or nearly so, thus differing from the casuariids, dinornithids, emeids, rheids, and struthionids.

The tibiotarsus is by far the most elongate element in the hind limb, not being decidedly mediolaterally compressed near the proximal end as this element is in the struthionids, rheids, and aepyornithids. It is more compressed, however, than the same element in the casuariids, apterygids, dinornithids and emeids. The inner cnemial crest extends far proximad of the proximal articular surface unlike the more subdued crest in the struthionids,

rheids, and aepyornithids. The supratendinal bridge of the tibiotarsus is still present, thus differing from all other ratites except the dinornithids and emeids. However, unlike in this latter group, the tendinal canal is centrally located rather than being laterally displaced.

The tarsometatarsus is either subequal to or somewhat more elongate than the femur. On the proximal end the hypotarsal region is broad and triangular in outline when viewed proximally. The two hypotarsal canals are shallow and are positioned near the medial and lateral boundaries of the hypotarsus. This arrangement differs markedly from the rectangular hypotarsus dissected by a single deep hypotarsal canal in the dinornithids, emeids, and apterygids. It differs also from the narrow, laterally offset hypotarsus of the struthionids and rheids and the low, rectangular hypotarsus of the aepyornithids. A single, prominent ridge on the posterior surface of the shaft extends most of the length of the tarsometatarsus and differs markedly from the short, double ridges in the dinornithids, emeids, apterygids; the short, narrow ridge in the rheids, struthionids; and the lack of a ridge in the aepyornithids. There is no indication of an articulation for metatarsal I, and thus the first digit, unlike the arrangement in the dinornithids, emeids, and apterygids. Three trochleae are well developed unlike only two in the struthionids.

The pes has a phalangeal count of 3-4-4, not the 3-4-5 characteristic of the casuariids, rheids, apterygids, dinornithids, and some emeids. There is a tendency in the later forms, such as *Genyornis*, to develop blunted, hoof-like unguals rather than the claws with triangular or rounded cross-sections as in most other ratites.

DISCUSSIONS AND CONCLUSIONS

Ferment among systematists regarding their basic premises and procedures in determining relationships of animals has led to a thorough reexamination of this science in recent years. Mayr (1973, 1974) has recently summarized the three current methodologies in wide usage: (1) phenetic, (2) cladistic, and (3) 'evolutionary' (Mayr, 1973, p. 4) systematics. Briefly, phenetic systems ally taxa on the basis of overall similarity only, determined by the use of a number of unweighted character comparisons (Sokal and Sneath, 1963). Cladistic systems group animals according to the recency of common ancestry. In this system, characters are weighed, i.e. primitive (plesiomorphic) and specialized or derived (apomorphic) characters are recognized and only the latter used to determine phylogenetic relationships (Hennig, 1966). The 'evolutionary' systems advocated by Mayr (1973, 1974) among others utilize two sets of criteria in determining relationships: (1) recency of common ancestry ('phylogenetic branching', Mayr, 1973, p. 5) and (2) amount of evolutionary divergence between branching points. The 'evolutionary' system would in effect lump together two forms (A, B) which were genetically quite similar, but one of which (B) had acquired a specialization that it shares with a third form (C) (i.e. B and C share a derived character state) that in many other characters had far diverged from either A and B. This system is satisfying initially in that it lumps together taxa with the most similar genotypes, those with the greatest phenotypic resemblance. It does not, however, when used as the basis of a classification, allow a reconstruction of the phylogenetic history of the group under consideration directly from the classification since dual criteria are utilized, and it is difficult to determine which criterion commands precedence at any one time.

In the following study the cladistic approach has been implemented, but it too is still fraught with operational difficulties. Determination of primitive and derived conditions is a most serious problem in using either the cladistic or the 'evolutionary' approach. A number of criteria have been suggested by Hennig (1966), Kluge (1971), Schaeffer et al. (1972), and Maslin (1952) among others to aid in the determination of polarity of a given morphocline. These include:

1. Time

- a. 'A character state is primitive when it is identical or very similar to one occurring in temporally antecedent organisms presumed to be directly ancestral, or at least closely related, to the ancestors of the more modern group being studied', Kluge, 1971, p. 26.
- b. 'If in a monophyletic group a particular character condition occurs only in older fossils, and another only in younger fossils, then obviously the former is the plesiomorphous and the latter the apomorphous condition of a morphocline a, a', a'', Hennig, 1966, p. 95.

2. Ontogeny

- a. 'This assumes that the transformation of a character during ontogeny "recapitulates" the phylogenetic transformation of this character, so that the direction of the transformation from plesiomorphous to apomorphous condition during phylogeny can be determined from the sequence of ontogenetic stages', Hennig, 1966, p. 95-96.
- b. 'Neozoologists may determine the primitive state of a morphocline by: . . . (2) similarities in morphogenesis and organogenesis', Schaeffer et al., 1972.

3. General Occurrence, Commonality of Occurrence, Common Occurrence Within Group and Closest Relatives

- a. 'A character state is primitive when it is identical or very similar to one that is universally or frequently exhibited by contemporaneous groups of organisms presumed to be related to the group being studied. The more widely an identical or very similar character state occurs among related organisms, the more probable that it results from an identical or very similar genetic origin', Kluge, 1971, p. 26.
- b. 'A character state that is restricted to the group of organisms being studied is primitive when it is universally or frequently exhibited by the individuals in that group. The probability that a character state is primitive increases very rapidly with the increase in the number of individuals in the group that exhibits that state', Kluge, 1971, p. 26.
- c. 'Neozoologists may determine the primitive state of a morphocline by: (1)

common occurrence of a character within a particular group and its closest relatives; Schaeffer et al., 1972.

Other methods of determination of primitive versus derived states are discussed by Hennig (1966) and Kluge (1971), but these are all secondary, depending on correlation with an already determined morphocline. Thus the above criteria are those available for initial determination of primitive and derived character states.

In my study on the Dromornithidae, it became obvious that time was a useless parameter for determination of polarity. Sample size was simply too small, and samples were limited basically to two time periods, mid to late Miocene and late Pliocene to Pleistocene. I seriously question the use of the second criterion, ontogeny, except in cases of major morphologic changes such as the reduction in number of digits, etc. Assuming that ontogeny faithfully recapitulates phylogeny ignores embryonic adaptations to a pre-natal environment, presuming that all changes during gestation plot the genealogical history of any group. Operationally this criterion has its limits, since the ontogeny of a large number of the characters used in my dromornithid study, particularly at the generic and specific levels, is unknown for the ratites, or for that matter for most or all birds, in particular not known for the extinct Dromornithidae.

Thus, general occurrence or commonality of occurrence, as well as common occurrence between one group and its most closely related group, were the two criteria exclusively used in the following study.

Method of Approach for Determining Relationships of Genera within the Dromornithidae

As a starting point, a phenetic analysis was performed. This narrowed the search space but, of course, may also have allowed inclusion of organisms in the sample to be studied that were similar due to convergence rather than due to a close common ancestor. Probability of close relationship increases, however, with close similarity of greater and greater numbers of comparable characters utilized. In the case of the Dromornithidae, the search space was restricted to the ratites and tinamous, as these forms, particularly the ratites, formed a much more phenetically similar group including the Dromornithidae than any group of non-ratites-non-tinamous containing the dromornithids. Other large, non-flying ground birds (Diatry-

midæ, Phorusrhachidae, and Sagittariidae) were examined and found to be decidedly phenetically distinct from the ratites, much more closely allied with birds in the orders Gruiformes and Falconiformes. Additionally Bock (1963) has previously pointed out a number of derived characters in the palate, common to the ratites and tinamous but unique among birds, that favour a monophyletic origin of those two groups.

Next, a character analysis was carried out to determine common and rare occurrence of certain character states. The basic comparative unit in this study was the family, and at least one genus for each family was used as a representative for each of those morphologically uniform groups. If more than one character state for a particular character was observed in any family, this was also noted, but in practice was rarely encountered in those characters utilized in diagnosing the dromornithids from other families. By using a single morphotype designation for each family, varying degrees of speciation within the families compared were compensated for. By using the criteria that rarely occurring character states within a group of otherwise closely comparable taxa, most probably represent the specialized or derived extremes and common character states in the same group represent the primitive character state, an estimate of phylogenetic relationship was made using all characters whose polarity could be determined with this technique. The number of characters was limited by the number of elements represented for each of the fossil taxa (see Table 1). Only the femur and tarsometatarsus are known for all five genera of the Dromornithidae, and thus meaningful phylogenetic comparisons within the family were limited to these two elements (see tables 2, 4). From among the character states not shared by all members of the family, a number of other characters are expressed by nearly equal percentages of 2 or 3 character states within the ratites. Thus, it is difficult or impossible to decide polarity of those characters, and they were discarded from consideration. Those that remained, were considered and summarized in figure 43 and are plotted to indicate the phyletic hypothesis obtained in this analysis.

Relationships within the Dromornithidae

Figure 43 precisely summarizes the phyletic relationships postulated for the five genera presently known to constitute the family Dromornithidae. *Barawertornis*, the oldest known

dromornithid taxon, from medial Miocene sediments of northern Australia, is the most primitive of all known dromornithids, having 14 of the 21 characters studied in the primitive character state. Only 2 characters show character states that are judged highly derived based on the 'commonality of occurrence' criterion (characters 14, 15 of the femur). Several interpretations could explain the seemingly anomalous presence of the character states seen in characters 14 and 15 of the femur: (1) the character states of characters 14 and 15 in *Barawertornis* are actually primitive for the Dromornithidae; or (2) in the case of character 15, *Genyornis* has reacquired the 'primitive' character state; or (3) in the case of character 15, the common ancestor to both *Barawertornis* and the *Dromornis-Ilbandornis-Genyornis* lineage had the primitive character state, and it was derived separately in the two different lineages except in *Genyornis*, where the primitive character state was retained; or (4) in the case of character 14, the common ancestor of the *Barawertornis* lineage and the lineage composed of all other dromornithids had the primitive character state, this was then modified in *Barawertornis* after its divergence while the remaining dromornithids retained the primitive character state. Determining the reality of this particular situation seems futile. The most parsimonious explanation for the character state of character 14 in *Barawertornis* would seem to be either (1) or (4) and for 15 (1). But what relationship parsimony and reality have to one another remains unresolved in this case.

Under the present phyletic hypothesis, however, *Barawertornis* is specialized over the primitive morphotype for the Dromornithidae in having (1) trochlea II and IV of the tarsometatarsus subequal in distal extension (char. 9); and on the femur (2) the internal condyle is moderately broader than the external (char. 22); (3) the fibular condyle protrudes only moderately laterad (char. 15); (4) the popliteal area is deep (char. 14); and (5) the shaft is moderately anteroposteriorly compressed (char. 15).

The remaining dromornithids including *Dromornis*, *Ilbandornis*, *Genyornis*, and *Bullockornis* are derived with respect to *Barawertornis* in that on the femur (1) the neck is not decidedly constricted (char. 3); (2) the internal condyle has a decidedly elliptical shape (char. 18); and on the tarsometatarsus (3) trochlea II is moderately to highly reduced (char. 11).

Within the above lineage it is evident, again based on shared-derived characters as well as general phenetic similarity, that *Dromornis*, *Ilbandornis*, and *Genyornis* (late Miocene to Pleistocene in occurrence) are closely related and form a natural grouping separate from *Bullockornis*. Shared-derived characters for the former lineage include: femur—(1) the medial surface of the internal condyle is decidedly ridged (char. 19); (2) the fibular condyle extends as far or nearly as far posteriorly as the internal condyle (char. 26); tarsometatarsus—(3) trochlea III is moderately to decidedly broader than trochlea IV (char. 16). Although decidedly derived over the condition of *Barawertornis*, the *Dromornis-Ilbandornis-Genyornis* lineage, even if its most specialized member (*Genyornis*) is considered, does not possess so many derived characters within the Dromornithidae as does *Bullockornis* (12 out of 21, *Genyornis*; 14 out of 21, *Bullockornis*). The major trend in this group was the reduction of the median toe (digit II) and in this the group is convergent towards the Struthionidae, which have completely lost the internal toe.

Bullockornis, the only member of the Dromornithidae remaining to be discussed here, is the most highly derived member of the family, even though it occurs quite early in the recorded history of that group, medial to late Miocene. Unique-derived characters in this group include: femur—(1) deep shaft (char. 10); (2) the long axis of the external condyle is nearly in line with the shaft's long axis (char. 16); (3) the condyles are deep with respect to width of the distal end (char. 21); (4) the internal and external condyles are nearly subequal in depth (char. 23); tarsometatarsus—(5) the intertrochlear space between trochlea III and IV is broad (char. 2); (6) the subhypotarsal ridge is prominent (char. 5); (7) trochlea III is extremely deep (char. 15); and (9) the medial and lateral margins of trochlea III are markedly convergent posteriorly (char. 17).

Classification of the Genera within the Dromornithidae

In many ways classifications are a hindrance to the understanding of relationships of animals, because it is not always clear what criteria are being utilized to place an organism in a certain category. What seems most useful to me for expression of phylogenetic relationship is a dendrogram derived from a study of weighted, shared-derived characters. I would

prefer to stop categorizing at that point. Since Linnean classification is so widely used at present, however, I will propose a number of possible classifications for the Dromornithidae based on data available at this time.

A cladistic classification that allows ready retrieval of the phylogenetic dendrogram could be as follows:

- Family: Dromornithidae
 - Subfamily: Barawertornithinae
 - Barawertornis*
 - B. tedfordi*
 - Subfamily: Dromornithinae
 - Tribe: Dromornithini
 - Subtribe: Dromornithina
 - Dromornis*
 - D. australis*
 - D. stirtoni*
 - Subtribe: Genyornithina
 - Ilbandornis*
 - I. woodburnei*
 - I. lawsoni*
 - Genyornis*
 - G. newtoni*
 - Tribe: Bullockornithini
 - Bullockornis*
 - B. planei*
 - B. sp.*

An 'evolutionary' classification that would emphasize the genetic similarities, evidenced by phenotypic expression, and phenetic distance of subgroups within the Dromornithidae would be:

- Family: Dromornithidae
 - Subfamily: Barawertornithinae
 - Barawertornis*
 - B. tedfordi*
 - Subfamily: Dromornithinae
 - Dromornis*
 - D. australis*
 - D. stirtoni*
 - Ilbandornis*
 - I. woodburnei*
 - I. lawsoni*
 - Genyornis*
 - G. newtoni*
 - Subfamily: Bullockornithinae
 - Bullockornis*
 - B. planei*
 - B. sp.*

Relationships of the Dromornithidae to Other Ratite Groups

Other methods of approach were utilized in determining relationships of the Dromornithi-

dae to the remaining ratites in order to test their workability and theoretical bases, and due to lack of time to carry out a complete survey of character states within the Class Aves, which would have been required if the criterion of commonality of general occurrence had been invoked to determine primitiveness. In the first method employed an initial phenetic analysis was used to determine the most closely related sister group of the ratites, and then the primitive character state for the ratites was defined as that which occurred in both the sister group (the Tinamidae) and the ratites. Ideally, a wider survey of avian groups phenetically similar to the tinamous and ratites is needed in the future to aid in evaluation of possible parallel development of some derived character states in both the tinamous and ratites, rather than simply assuming that such character states represent a primitive condition for the ratites because they are held in common by ratites and tinamous. A second method employed involved surveying all of the ratites and defining as primitive the most commonly occurring character state for each character. Those characters that rarely occurred within the ratites were considered derived or specialized. Theoretically this method should work in determining the later phyletic splits where a derived character state or suite is held by 3 or fewer of the families of ratites. Derived characters occurring early in the history of the ratites, however, and thus possibly possessed by a large number of the members of this group would be misinterpreted by this method. A third method employed a phenetic analysis of all the ratite groups which tallied those characters of the 56 studied shared by various ratites regardless of their polarity, a numerical approach. In all cases only the sternum, synsacrum, and hind limb were considered because of lack of available information on other parts of the skeleton and because of the near or total loss of the forelimb in the Dinornithidae-Emeidae lineage. Data on the forelimb of the remaining ratite groups that do possess those elements are available in figure 44. In all ratite groups there is a tendency for loss or reduction as well as fusion of various forelimb elements. In this study the primary aim was to determine the avian group most closely related to the Dromornithidae, and relationships of the remaining ratite groups are mentioned only briefly.

Application of the method 1 approach resulted in an analysis of 56 characters that could be used to diagnose the Dromornithidae

from other ratite groups; these results are summarized in tables 46-47. Table 46 tabularizes the shared, derived characters used exclusively to delimit relationships, while table 47 summarizes shared, primitive characters. The Dromornithidae share decidedly more derived character states (19 of the 56 characters studied) with the Casuariidae (including both cassowaries and emus) than with any other ratite group, but both groups share few primitive character states (see table 47) with one another. Both the Casuariidae and Dromornithidae are highly derived within the ratites with 33 and 38 (respectively) characters out of the 56 total in a derived, rather than a primitive state (see table 45). Other ratites such as the Struthionidae and Rheidae have nearly the same number of derived character states (37, 38 respectively), but the Aepyornithidae, Apterygidae, Dinornithidae-Emeidae (30, 23, 22 respectively) have fewer characters in a derived state. Among the 19 derived character states shared between the Casuariidae and Dromornithidae (see figure 44 and tables 46-47 for a tally and explanation of character states shared by the Dromornithidae and the remaining ratites) are four derived character states unique to these two groups among the ratites: synsacrum (e), the ilium, ischium, and pubis all protrude about the same distance posteriorly; femur (n), the internal condyle is triangular or elliptical, closely approaching triangular with the apex forming the distalmost projection of the condyle; tibiotarsus (c), the inner cnemial crest extends far proximad of the proximal articular surface; and tarsometatarsus (c), the hypotarsus and intercotylar prominence extend about equal distance proximal to proximal articular surfaces. The remaining 15 derived character states that both the Casuariidae and Dromornithidae share are likewise shared with at least one other ratite group, often more: sternum (f), the costal margin can occupy more than 50% of the lateral margin; sternum (g), no sternal notches are present; sternum (j), the ventral surface of the sternum is moderately, not highly, curved, not flattened; synsacrum (a), the dorsal surface of the synsacrum posterior to the antitrochanter is of moderate width to narrow, not broad; synsacrum (d), the antitrochanter is positioned at about the fore-aft midpoint of the synsacrum; femur (b), the trochanter and the head extend about an equal distance proximad; femur (c), the long axis of the condyles are not closely parallel to the shaft's long axis; femur (d), the external condyle extends a

moderate distance, not far, beyond the internal condyle; femur (g), the fibular condyle is approximately one-half to three-fourths the length of the external condyle; femur (j), the proximointernal region of the shaft lacks a large muscle scar that is present in some ratite groups; tibiotarsus (d), a deep concavity incises the external margin of the proximal end between the outer cnemial crest and the external articular surface; tibiotarsus (g), the intercondylar eminence has no channel crossing it; tarsometatarsus (a_3), the hypotarsus is located near or on the midline and is not noticeably offset either medially or laterally; tarsometatarsus (f), the internal cotyla is deeper anteroposteriorly than the external cotyla; tarsometatarsus (h), only one hypotarsal ridge is present.

Thus, based on the method 1 analysis, the extinct Dromornithidae, apparently endemic to Australia, seem to be most closely related to the Casuariidae (cassowaries and emus) of Australia and New Guinea. A single, common ancestral stock could have given rise to each of the two groups and two separate colonizations or developments within Australia-New Guinea are not required to account for the presence of two ratite groups there. The Australian ratites are decidedly distinct from the New Zealand moas and kiwis, the most primitive of all the ratite groups (see figure 44, table 45). The Casuariidae, but not the Dromornithidae, in turn share a large number of derived characters with the Struthionidae and Rheidae, which are both quite closely related to one another (see table 46). Without further, more expanded analysis, however, it is difficult to evaluate how many of those character states shared in the Struthionidae-Rheidae lineage on the one hand and in the Casuariidae lineage on the other may be separate parallel developments or were actually derived in a common ancestral stock. It seems quite conceivable that the ancestral stock which produced the Casuariidae-Dromornithidae lineage could have produced the Struthionidae-Rheidae lineage. With the present knowledge of the above four groups, at least two possible interpretations of phylogenetic relationship are possible, one more generalized (Figure 45A) and inclusive of the second (Figure 45B). Based on method 1 analysis the interrelationships of the remaining three ratite groups are not certain, because the character sorts for family pairs within the ratites are all very similar (see table 46). The low number of derived character states in all three groups, particularly the Dinornithidae-

Emeidae and Apterygidae suggest their primitive nature within the ratite complex. The relationship of the Aepyornithidae to the Dromornithidae and other ratite groups is not clear based on this study.

Based on the tallies resulting from the method 2 approach certain relationships suggested by the method 1 approach are reinforced, and some are clarified, none are contradicted. Only those characters marked with a X in the right hand column on figure 44 were included in this analysis, because the polarity in all the other characters was not clearly ascertainable using the criterion of commonality or rarity of a given character state within the ratites. Dromornithids and Casuariids are clearly more closely related or at least as closely related to one another than to (as) any other ratite group (see table 48) in that they share 7 derived character states. The next closest related group to the Casuariidae in this analysis are the Aepyornithidae that share 3 derived character states. The Dromornithidae on the other hand share 6 derived characters with the Aepyornithidae and 7 derived character states with the Dinornithidae-Emeidae. Another relationship reinforced in this study is the close relationships of the Rheidae and Casuariidae. Additionally, method 2 analysis suggests that the New Zealand groups Din-

ornithidae-Emeidae and Apterygidae are quite closely related (see table 48), sharing more characters with one another than they do with any other group.

When method 3, a straightforward phenetic approach, was utilized again several of the relationships suggested by methods 1 and 2 were reinforced, but some were obscured or contradicted (see table 49). Dromornithidae still shared more characters with the Casuariidae (26) than any other group, but the Casuariidae shared more characters with the Rheidae and the Apterygidae (33, 33) than with any other ratite groups including the Dromornithidae. The Struthionidae and Rheidae are quite clearly related (sharing 39 characters) as are the Dinornithidae-Emeidae and Apterygidae (38). The Aepyornithidae share the most characters with the Dinornithidae.

Thus at present at least three phylogenetic dendrograms offer possible explanations for the relationships of the Dromornithidae and are depicted in figure 45. Figure 45A is the most generalized of all, more nearly reflecting the state of analysis in this paper. In order to resolve which phylogenetic hypothesis (45B or 45C) more closely approaches reality, the analysis must be expanded beyond the tinamous and ratites.

REFERENCES

- ALEXANDER, J. M., 1947—Sluicing at Endurance Tin Mine. *Chem. Eng. Min. Rev.*, 39(9), 344-357.
- AMADON, D., 1943—Bird weights and egg weights. *Auk*, 60, 221-234.
- AMADON, D., 1947—An estimated weight of the largest known bird. *Condor*, 49, 159-164.
- ANDERSON, M. A. & FLETCHER, H. O., 1934—The Cuddie Springs bone bed. *Aust. Mus. Mag.*, 5, 152-158.
- ANONYMOUS, 1962—Giant egg sets a problem for science. *The West. Aust.* (newspaper), 3 May, 1.
- ARCHEY, G., 1941—The moa. A study of the Dinornithiformes. *Bull. Auckland Inst. Mus.*, 1.
- BARTHOLOMAI, A., 1972—Aspects of the evolution of the Australian marsupials. *Proc. Roy. Soc. Queensland*, 83, v-xviii.
- BERGGREN, W. A., 1969—Cenozoic chronostratigraphy, planktonic foraminiferal zonation and the radiometric time scale. *Nature*, 244, 1072-1075.
- BERGGREN, W. A., 1971—Neogene stratigraphy, planktonic foraminiferal zonation and the radiometric time scale. *Hungar. Geol. Soc. Bull.*, 101, 162-169.
- BOCK, W. J., 1963—The cranial evidence for Ratite affinities. *Proc. XIII the Internat. Ornith. Congress*, 1, 39-54.
- BUTLER, W. H., 1969—Remains of *Sarcophilus* the 'Tasmanian' Devil (Marsupialia, Dasyuridae) from coastal dunes South of Scott River, Western Australia. *West. Aust. Nat.*, 11(4), 87-88.
- CLARKE, W. B., 1869—*Dinornis* an Australian genus. *Geol. Mag.*, 6, 383-384.
- CLARKE, W. B., 1877—On *Dromornis australis* (Owen), a new fossil bird of Australia. *Jour. Proc. Roy. Soc. New South Wales*, 11, 41-49.
- DAVID, T. W. E., 1950—THE GEOLOGY OF THE COMMONWEALTH OF AUSTRALIA, 1. *Edward Arnold and Co., London*, 747 pp.
- DENNANT, J., & KITSON, A. E., 1903—Catalogue of the described species of fossils (except Bryozoa and Foraminifera) in the Cainozoic fauna, Victoria, South Australia, and Tasmania. *Rec. Geol. Surv. Victoria*, 1, 87-147.
- DEVERY, P. J., 1968—THE READER'S DIGEST COMPLETE ATLAS OF AUSTRALIA. *Read. Digest Assoc. Pty Ltd., Sydney*, 183 pp.
- DEVIS, C. W., 1884—The moa (*Dinornis*) in Australia. *Proc. Roy. Soc. Queensland*, 1, 23-28.
- DEVIS, C. W., 1891—The moa in Australia. *New Zealand Jour. Sci.*, 1(3), 97-101.
- DULHUNTY, J. A., 1971—Potassium-argon dates and their significance in the Ilford-Mudgee-Gulgong region. *Jour. Proc. Roy. Soc. New South Wales*, 104, 39-44.
- DUN, W. S., 1894-95—Notes on the occurrence of monotreme remains in the Pliocene of New South Wales. *Rec. Geol. Surv. New South Wales*, 4, 118-126.
- EDWARDS, H., 1962a—Journey into the past. *Week-end News* (newspaper), 12 May, 1.
- EDWARDS, H., 1962b—Prehistoric egg. *People*, 19 Dec., 27-30.
- ETHERIDGE, R., 1889—On further evidence of a large extinct struthious bird (*Dromornis* Owen) from the post Tertiary deposits of Queensland. *Rec. Geol. Surv. New South Wales*, 126-136.
- EVERDEN, J. F., SAVAGE, D. E., CURTIS, G. H., & JAMES, G. T., 1964—Potassium-argon dates and the Cainozoic mammalian chronology of North America. *Amer. Jour. Sci.*, 262, 145-198.
- GILL, E. D., 1972—Eruption date of Tower Hill Volcano, Western Victoria, Australia. *Victoria Nat.*, 89(7), 188-192.
- GLAUERT, L., 1910—The Mammoth Cave. *Rec. West. Aust. Mus. and Art Gall.*, 1(1), 11-36.
- GLAUERT, L., 1914—The Mammoth Cave (con'd). *Rec. Western Australian Mus. Art Gall.*, 1(3), 244-251.
- GLAUERT, L., 1948—The cave fossils of the south-west. *West. Aust. Nat.*, 1(5), 101-104.
- GREGORY, J. W., 1906—THE DEAD HEART OF AUSTRALIA. London, xvi + 384 pp.
- HALL, F. J., MCGOWAN, R. G., & GULEKSEN, G. F., 1951—Aboriginal rock carvings: a locality near Pimba, S.A. *Rec. Sth Aust. Mus.*, 9, 375-380.
- HARRIS, W. K., 1968—Tasmanian Tertiary and Quaternary microfloras summary report. *Dept. Mines Sth Aust., Geol. Surv., Paleo. Sect., Rept. Bk. 67/43, G.S. 4017, Pal. Rept. 5/68*.
- HENNIG, W., 1966—PHYLOGENETIC SYSTEMATICS. *Univ. Illinois Press, Urbana* 263 pp.
- HYSLOP, R. C., 1967—AUGUSTA JEWEL CAVES AND OTHER POINTS OF INTEREST. *Lamb, Perth*, 16-17.
- JONES, L. J., 1940—The Gulgong goldfield. *Dept. Mines, Geol. Surv. New South Wales, Min. Res.*, 38, 1-134.
- KLUGE, A. G., 1971—Concept and principles of morphologic and functional studies. In: Waterman, A. J. (ed.), CHORDATE STRUCTURE AND FUNCTION. *Macmillan Co., New York*, 3-41.
- LAMBRECHT, K., 1931—*Protoplotus beauforti* n.g., n.sp., ein schlangenhalsvögel aus dem Tertiär von W. Sumatra. *Wet. Meded. Dienst. Mijnb. E. Indies*, 17, 15-24.

- LAMBRECHT, K., 1933—HANDBUCH DER PALAEOORNITHOLOGIE. *Borntraeger, Berlin*, 1024 pp.
- LUNDELIUS, E., Jr., 1960—Post-Pleistocene faunal succession in Western Australia and its climatic interpretation. *Rep. 21st Internat. Geol. Cong.*, IV, 142-153.
- LYDEKKER, R., 1891—CATALOGUE OF THE FOSSIL BIRDS IN THE BRITISH MUSEUM. *Taylor and Francis, London* 368 pp.
- LYDEKKER, R., 1892—Remarks on some recently described extinct birds of Queensland. *Ibis*, Ser. 6(4), 530-533.
- MASLIN, T. P., 1952—Morphological criteria of phyletic relationships. *Systematic Zoo*, 1(2), 49-70.
- MAYR, E., 1973 (ms.)—Die Kladistische Methode der Klassifikation: Ein Kritische Untersuchung.
- MAYR, E., 1974—Cladistic analysis or cladistic classification? *Zeit. zool. Syst. Evolut.-forsch.* 12(2), 94-128.
- MILLER, A. H., 1963—Fossil ratite birds of the late Tertiary of South Australia. *Rec. Sth Aust. Mus.*, 14(3), 413-420.
- MITCHELL, T. L., 1839—THREE EXPEDITIONS INTO THE INTERIOR OF EASTERN AUST., 2. *T. and W. Moore, London*, 415 pp.
- NEWTON, A., 1893—Palaeontological discovery in Australia. *Nature*, 47(1226), 606.
- OLIVER, W. R. B., 1949—The moas of New Zealand and Australia. *Bull. Dominion Mus.*, 15.
- OWEN, R., 1872—Untitled. *Proc. Zool. Soc. London*, 682-683.
- OWEN, R., 1874—On *Dinornis* Pars 19: containing a description of a femur indicative of a new genus of large wingless birds (*Dromornis australis*) from a post-Tertiary deposit in Queensland. *Trans. Zool. Soc. London*, 8, 381-384.
- OWEN, R., 1879a—MEMOIRS ON THE EXTINCT WINGLESS BIRDS OF NEW ZEALAND, with an appendix on those in England, Australia, Newfoundland, Mauritius and Rodriguez. *John van Voorst, London*, vol. 1, 512 pp., vol. 2, pls. 1-130.
- OWEN, R., 1879b—On *Dinornis*: containing a restoration of the skeleton of *Dinornis maximus* (Owen), with an appendix on additional evidence of the genus *Dromornis* in Australia. *Trans. Zool. Soc. London*, 10(3), 147-188.
- PAGE, R. W., & MCDUGALL, I., 1972—Ages of mineralisation of gold and porphyry copper deposits in the New Guinea highlands. *Econ. Geol.*, 67, 1034-1048.
- PLANE, M. D., 1972—A New Guinea fossil macropodid (Marsupalia) from the marine Pliocene of Victoria, Australia. *Mem. Nat. Mus. Vic.*, 33, 33-36.
- PLANE, M., & GATEHOUSE, C. G., 1968—A new vertebrate fauna from the Tertiary of northern Australia. *Aust. Journ. Sci.*, 30(7), 272-273.
- RICH, P. V., & GREEN, R. H., 1974—Bird footprints at South Mt Cameron, Tasmania. *Emu* 74, 245-248.
- SCARLETT, R., 1969—On the alleged Queensland moa, *Dinornis queenslandiae* DeVis. *Mem. Queensland Mus.*, 15(3), 207-212.
- SCHAEFFER, B. HECHT, M. K., & ELDREDGE, N., 1972—Phylogeny and palaeontology. In Dobzhansky, T., Hecht, M. K., and Steere, W. C. (eds), *EVOLUTIONARY BIOLOGY*, 6. *Appleton-Centry-Crofts, New York*, 31-46.
- SOKAL, R., & SNEATH, P., 1963—PRINCIPALS OF NUMERICAL TAXONOMY. *Freeman and Co., San Francisco*, 359 pp.
- SPRY, A., & BANKS, M. R., (eds), 1962—The geology of Tasmania. *Jour. Geol. Soc. Australia*, 9(2), 107-362 + ix.
- STIRLING, E. C., 1896—The newly discovered extinct gigantic bird of South Australia. *Ibis*, 7(11), 593.
- STIRLING, E. C., & ZEITZ, A. H. C., 1896—Preliminary notes on *Genyornis newtoni*; a new genus and species of fossil struthious bird found at Lake Callabonna, South Australia. *Trans. Proc., Roy. Soc. Sth Aust.*, 20, 171-190.
- STIRLING, E. C., & ZEITZ, A. H. C., 1900—Fossil remains of Lake Callabonna: 1. *Genyornis newtoni*. A new genus and species of fossil struthious bird. *Mem. Roy. Soc. Sth Aust.*, 1(2), 41-80.
- STIRLING, E. C., & ZEITZ, A. H. C., 1905—Fossil remains of Lake Callabonna, Pt. III. Description of the Vertebræ of *Genyornis newtoni*. *Mem. Roy. Soc. Sth Aust.*, 1(3), 81-110.
- STIRLING, E. C., & ZEITZ, A. H. C., 1913—Fossil remains of Lake Callabonna, Pt. IV. Description of some further remains of *Genyornis newtoni*. *Mem. Roy. Soc. Sth Aust.*, 1(4), 111-126.
- STIRTON, R. A., TEDFORD, R. H., & MILLER, A. H., 1961—Cenozoic stratigraphy and vertebrate palaeontology of the Tirari Desert, South Australia. *Rec. Sth Aust. Mus.*, 14, 19-61.
- STIRTON, R. A., TEDFORD, R. H., & WOODBURNE, M. O., 1967—A new Tertiary formation and fauna from the Tirari Desert, South Australia. *Rec. Sth Aust. Mus.*, 15(3), 427-462.
- STIRTON, R. A., TEDFORD, R. H., & WOODBURNE, M. O., 1968—Australian Tertiary deposits containing terrestrial mammals. *Univ. Calif. Publ. Geol. Sci.*, 77.
- TEDFORD, R. H., 1966—A review of the macropod genus *Sthenurus*. *Univ. Calif. Pub. Geol. Sci.*, 57.

- TEDFORD, R. H., 1967—The fossil Macropodidae from Lake Menindee, New South Wales. *Univ. Calif. Pub. Geol. Sci.*, 64.
- TEDFORD, R. H., 1968—Fossil mammal remains from the Tertiary Carl Creek Limestone, north-western Queensland. *Bull. Bur. Min. Res., Geol. and Geophys.*, 92, 217-237.
- TEDFORD, R. H., 1969—Principles and practices of mammalian geochronology in North America. *Proc. North Amer. Paleont. Convent.*, 666-703.
- TEDFORD, R. H., 1971—Quaternary vertebrates and environments, Lake Callabonna, South Australia. (Abst.) 43rd Cong. *Australian and New Zealand Association Adv. Sci., Sect. 3*, 7-8.
- TINDALE, N. B., 1951—Comments on supposed representations of giant bird tracks at Pimba. *Rec. Sth Aust. Mus.*, 9, 381-382.
- TURNBULL, W. D., & LUNDELIUS, E. L., 1970—The Hamilton Fauna. A late Pliocene mammalian fauna from the Grange Burn, Victoria, Australia. *Fieldiana; Geol.*, 19.
- TURNBULL, W. D., LUNDELIUS, E. L., & McDUGALL, I. A., 1965—A potassium/argon dated Pliocene marsupial fauna from Victoria, Australia. *Nature*, 206 (4986), 816.
- WETMORE, A., 1967—Re-creating Madagascar's giant extinct bird. *Nat Geog.* 132 (4), 488-493.
- WHITEHOUSE, F. W., 1940—Studies in the late geological history of Queensland. *Pap. Dep. Geol. Univ. Qld.*, 2(n.s. 1), 1-74.
- WOODBURNE, M., 1967—The Alcoota Fauna, central Australia. *Bull. Bur. Min. Res. Geol. and Geophys.*, 87, 1-187.
- WOODBURNE, M., 1969—A lower mandible of *Zygomaturus gilli* from the Sandringham Sands, Beaumaris, Victoria, Australia. *Mem. Nat. Mus. Victoria*, 29, 29-39.
- WOODS, J. E. T., 1866—Report of the geology and mineralogy of the southeastern district of the colony of South Australia.
- WOODS, J. E. T., 1882—Physical structure and geology of Australia. *Proc. Linn. Soc. New South Wales*, 7, 371-389.
- WOODS, J. T., 1960—Fossiliferous fluviatile and cave deposits. In: Hill, D. and Denmead, A. K., (eds), *The geology of Queensland. Jour. Geol. Soc. Aust.*, 7, 393-403.

TABLE 1. SPECIMENS AVAILABLE FOR EACH TAXON OF DROMORNITHIDAE

Element	Skull	Femur	Tibiotarsus	Tarsometatarsus	Sternum	Scapulacoracoid	Synsacrum	Humerus	Radius	Ulna	Carpometacarpus	Pes	Vertebrae
<i>Barawertonia tedfordi</i>	—	1i,1d	—	1d	—	—	—	—	—	—	—	—	1i
<i>Bullockornis planei</i>	—	2i	—	1	—	—	—	—	—	—	—	—	1
? <i>Bullockornis</i> sp.	—	—	—	1p	—	—	—	—	—	—	—	—	—
<i>Dromornis stirtoni</i>	—	3,2i	1	5i,1d	1	1	—	—	—	—	?1	Moderate sample	5i
<i>Dromornis australis</i>	—	1	—	—	—	—	—	—	—	—	—	—	—
<i>Ilbandornis woodburnei</i>	—	1	2d	1i,1d	—	—	—	—	—	—	—	Large sample	6i
? <i>Ilbandornis lawsoni</i>	—	—	1i,1d	1i,1p,5d	—	—	—	—	—	—	—	—	—
<i>Genyornis newtoni</i>	1	1,1c	2c,1,2d,1i	3,11d,1cd	1	3	1,5i	1,2i,2d	2,2p	1i	1,?1i	Large sample	Large sample

i—incomplete p—proximal end only; d—distal end only; s—actual specimens studied; more available in collections in Australia; c—cast.

TABLE 2. SUMMARY OF DIAGNOSTIC CHARACTERS ON THE FEMUR FOR GENERA WITHIN THE FAMILY DROMORNITHIDAE

Character	<i>Barawertornis</i>	<i>Bullockornis</i>	<i>Ilbandornis</i>	<i>Dromornis</i>	<i>Genyornis</i>
1	npa	None posterior; far anterior	None posterior; np anterior	Slight posterior; moderate anterior	None posterior moderate anterior
2	Internal half of posterior margin concave posteriorly	Straight	Straight	Concave posteriorly	Straight
3	Distinctly narrower than head	Distinctly narrower than head	Equal to depth of head	Distinctly narrower than head	Only slightly narrower than head
4	np	Abrupt angulation at internal base of trochanter	Smoothly curved from head	Smoothly curved from head	Smoothly curved from head
5	Elongate	Elongate	Moderate	Moderate	Elongate
6	Slender	Slender	Moderately broad	Moderately broad	Moderately broad
7	Moderately curved	Highly curved	Only slightly curved	Moderately curved	Highly curved
8	Proximad of midpoint	@ at midpoint	Distad of midpoint	Either at midpoint or proximad of midpoint	Either at midpoint or distad of midpoint
9	np	Extends far anterior	np	Extends slightly anterior	Extends slightly anterior
10	Shallow	Deep	Moderate	Moderate to shallow	Moderate
11	@ 75°	70°-75°	@ 75°	@ 55°-60°	65°-75°
12	np	Not present	Prominent, extending about 1/3 shaft length	Not present	Low broad discontinuous ridge extending ½ length of shaft
13	Prominent	Small tubercles, but no continuous ridge present	Not present	Not present; small tubercles sometimes present	Not present; small tubercles present
14	Deep	Moderate	Moderate	Moderate	Moderate
15	Moderate	Moderate	Moderate	Moderate	Protrudes far externally
16	25°	5°-10°	20°	20°-30°	20°-25°
17	Well developed	np	np	Present but only slightly indicated	Well developed
18	Semicircular, distalmost projection near midpoint	Semiovoid, distalmost projection anterior of midpoint	Semiovoid, distalmost extension anterior of midpoint	Semiovoid, distalmost extension anterior of midpoint	Semiovoid distalmost extension slightly anterior of midpoint
19	Smooth, not ridged	Smooth, not ridged	Short, low ridge near proximal end of internal condyle	Can be smooth or can have short ridge near proximoposterior end of internal condyle	Entire distal end of internal condyle raised medially, abruptly above shaft surface
20	Trapezoidal, rounded edges	Trapezoidal approaching triangular	Trapezoidal, rounded edges	Trapezoidal, rounded edges	Trapezoidal, rounded edges
21	Moderately compressed	Deep	Moderately compressed	Moderately compressed	Highly compressed, shallow
22	Wide, about 1/3 that of internal condyle	Narrow about ½ that of internal condyle	Wide, about 1/3 that of internal condyle	Wide, about 1/3 to 2/5 that of internal condyle	Very wide 2/5-½ that of internal condyle
23	External distinctly deeper	Nearly subequal, external slightly deeper	External distinctly deeper	External distinctly deeper	External distinctly deeper
24	Convergent anteriorly	Convergent anteriorly, posteriorly	Convergent anteriorly	Slightly convergent anteriorly	Parallel, or only slightly convergent anteriorly
25	Straight line	Slightly convex internally	Straight line	Markedly convex internally	Straight line to slightly convex internally
26	Fibular condyle anterior to internal condyle	Fibular condyle far anterior to internal condyle	About same position	About same position or fibular slightly anterior	About same position or fibular slightly anterior

a. Not preserved.

TABLE 3. SUMMARY OF DIAGNOSTIC CHARACTERS ON THE TIBIOTARSUS FOR GENERA WITHIN THE FAMILY DROMORNITHIDAE

Charac- ter	<i>Barawertornis</i>	<i>Bullockornis</i>	<i>Ilbandornis</i>	<i>Dromornis</i>	<i>Genyornis</i>
1	np	np	Broadly convex exter- nally, protrudes only slightly laterad	np	Highly convex, U- shaped, protrudes far laterad
2	np	np	Deep	np	Shallow
3	np	np	Narrow	np	Moderately broad
4	np	np	Condyles either decidedly or slightly broader than shaft near distal end	Condyles somewhat but not decidedly broader than shaft near distal end	Condyles broad with respect to shaft near distal end
5	np	np	Small obtuse angle	Moderate obtuse angle	Moderate acute angle
6	np	np	Slightly curved	np	Highly curved
7	np	np	Extends moderate dis- tance anteriad	Extends far anteriad	Extends far anteriad
8	np	np	Moderate to shallow	np	Deep

TABLE 4. SUMMARY OF DIAGNOSTIC CHARACTERS ON THE TARSOMETATARSUS FOR GENERA WITHIN THE FAMILY DROMORNITHIDAE

Charac- ter	<i>Barawertornis</i>	<i>Bullockornis</i>	<i>Ilbandornis</i>	<i>Dromornis</i>	<i>Genyornis</i>
1	np	Deep	Shallow	Probably shallow	Shallow
2	Narrow	Broad	Narrow	Narrow	Narrow
3	Moderate	Deep	Shallow	Shallow	Moderate
4	Moderate	Narrow	Moderate	Moderate	Moderate
5	Low	Prominent	Low	Low	Low
6	Narrow	Narrow	Moderate	Moderate	Moderate
7	Broad	Broad	Moderate	Moderate	Moderate
8	Parallel	Parallel	Proximally diver- gent over most of length	Proximally diver- gent over most of length	Proximally divergent over most of length
9	Subequal	II extends decidedly distad of IV	Subequal	Subequal	Subequal
10	Elongate	Elongate	Moderately elon- gate	Short	Short
10A	np	Lateral-posterior surfaces merged forming moderate acute angle with an- terior surface	Lateral-posterior surfaces merged forming small acute angle with anterior surface	Lateral-posterior surfaces merged forming small acute angle with anterior surface	Lateral-posterior surfaces distinct, lateral surface form- ing 90° angle with anterior surface
11	Not highly reduced	Not highly reduced	Moderately reduced	Not highly reduced	Highly reduced
12	Divergent pos- teriorly	Divergent pos- teriorly	Divergent pos- teriorly	Divergent pos- teriorly	Parallel
13	Shallow	Moderate	Moderate-deep	Moderate-deep	Moderate-deep
14	Posterior margin nearly twice that of anterior margin	Posterior margin nearly twice that of anterior margin	Nearly subequal	Nearly subequal	Nearly subequal
15	Moderate	Deep	Moderate	Moderate	Moderate
16	np	Slightly broader	Decidedly broader	Moderately broader	Moderately to decidedly broader
17	np	Moderately conver- gent posteriorly	Parallel or slightly convergent pos- teriorly	Moderately conver- gent posteriorly	Parallel or slightly convergent pos- teriorly

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES)

Character		Struthionidae (<i>Struthio</i>)	Rheidae (<i>Rhea</i>)	Casuariidae <i>Casuarius</i> <i>Dromaius</i>	
VERTEBRA. Atlas					
a.	Presence/absence of vertebral arterial canals (A) ¹	Absent	Absent	Lateral protuberances present	
b.	Comparison of breadth and depth of vertebrae (A)	Deep, moderate width	Deep, moderate width	Broad, shallow	
c.	Orientation of dorsal surface of neural arch (D)	Nearly horizontal	Nearly horizontal	Nearly horizontal	
STERNUM					
a.	Outline of sternum—lateral margins (P)	Concave laterally	Straight, convergent posteriorly	Concave laterally	
b.	Comparative length and breadth of sternum (P)	Longer than wide	Longer than wide	Longer than wide	
c.	Nature of sternocoracoidal processes (P)	Directed dorsally, short	Directed anterodorsally, elongate	Directed dorsally, short	
d.	Shape of anterior border of sternum (P)	Convex anteriorly with small lateral concavities	Concave anteriorly centrally, slightly convex anteriolaterally	Convex anteriorly	
f.	Length of costal margin with respect to that of lateral margin of sternum (P)	Costal margin 40% of lateral margin	Costal margin less than 30% of lateral margin	Costal margin about 50% of lateral margin	
g.	Presence/absence of sternal notches (P)	Four shallow notches	Absent	Absent	
h.	Shape of posterior sternal margin (P)	Concave posteriorly, double notched	Concave posteriorly, entire	Convex posteriorly, entire	
i.	Presence/absence of carina (V)	Absent	Absent	Absent	
j.	Nature of ventral surface of sternum (V)	Median flattened area on posterior half of sternum	Highly curved well defined low central ridge	Moderately curved	
k.	Depth, size, and location of coracoidal sulci (A)	Deep, nearly meeting in centre of anterior margin	Moderate depth, occupying lateral thirds of anterior margin	Moderate depth, meeting in centre of anterior margin	
SCAPULOCORACOID					
	Nature of scapula and coracoid	Fused	Fused	Fused	
a.	Shape of coracoid (A)	Ventromedially directed process fused with main body of coracoid in two places, surrounds large foramen		Large process extending mediad of glenoid facet	
b.	Orientation of glenoid facet (A)	Directed dorsolaterad	Directed dorsolaterad	Directed laterad	
c.	Presence/absence of groove mediad of glenoid facet (A)	Present, broad	Absent	Absent	Present
d.	Nature of anterior surface between glenoid facet and medial margin of scapulocoracoid (A)	Knob present	Knob present	Absent	
e.	Shape of scapular blade (L)	Concave externally	Concave externally	Concave externally	Slightly convex externally
HUMERUS					
a.	General proportions of humerus	Slender, elongate	Slender, elongate	Stout, short	Slender, short

1. A, anterior view; Pt, posterior view; V, ventral view; M, medial view; P, proximal view; Dt, distal view; D, dorsal view; An, anconal; Pm, palmar; L, lateral view.

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (Cont.)

Character	Struthionidae (<i>Struthio</i>)	Rheidae (<i>Rhea</i>)	Casuariidae	
			<i>Casuarius</i>	<i>Dromaius</i>
b. Nature of ligamental furrow (P)	Moderately indicated	Slightly indicated	Slightly indicated	Moderately indicated
c. Presence/absence of pneumatic fossa (An)	Absent	Absent	Deep	Present, moderate
d. Degree of internal projection of internal tuberosity (An)	Far internally	Far internally	Far internally	Moderate
e. Relative proximal protrusion of head and internal tuberosity (An)	Internal tuberosity projects further proximad than head	Internal tuberosity projects further proximad than head	Subequal in proximal protrusion	
f. Location of head on proximal end (An)	Shifted dorsally (of midpoint)	Shifted slightly dorsad of midpoint	Near midpoint	Shifted far dorsad of midpoint
g. Presence/absence of ligamental attachment at proximo-distal midpoint of ventral surface of shaft (V)	Absent	Absent		Absent
h. Depth and size of brachial depression (Pm)	Shallow and small or lacking	Shallow and small or lacking	Shallow and small or lacking	
i. Presence/absence of ridge trending from base of deltoid crest to dorsal margin (Pm)	Present	Ridge present, but doesn't pass all the way to dorsal margin		Absent
j. Development of ectepicondylar prominence (Pm)	Well developed	Moderately developed	Only slightly indicated	
k. Degree of definition of articular surfaces (Dt)	Well defined	Well defined		Well defined
l. Cross-sectional outline of shaft (Dt)	Triangular	Triangular		Circular
m. Shape of distal end (Dt)	Narrowest in area of ectepicondyle, uninflated	Narrowest in area of ectepicondyle, uninflated	Of nearly same width throughout	
n. Degree of development of olecranal fossa (Dt)	Slightly indicated	Absent		Absent
ULNA-RADIUS				
a. Nature of proximal articular surface (P)	Distinct cotyla developed	Distinct cotyla developed	Distinct cotyla developed	
b. Nature of olecranon (P)	Narrow, well developed	Narrow, well developed	Broad, well developed	
c. Depth of proximal end (P)	Deep	Deep	Shallow	
d. Degree of fusion of radius-ulna-carpometacarpus (An)	Unfused	Unfused	Unfused to somewhat fused	
e. Comparative widths of radius-ulna (An)	Ulna decidedly broader	Subequal	Ulna decidedly broader	Subequal
f. Comparative depths of proximal and distal ends of radius (An)	Broadest distally	Broadest proximally	Radius broadens distally to elliptical articulation	
g. Comparative lengths of radius-ulna and humerus (An)	Shorter than humerus	Shorter than humerus	Shorter than humerus	
CARPOMETACARPUS				
a. Degree of flattening of carpal trochlea (P)	Highly curved, convex proximally	Highly curved, convex proximally, groove moderately developed	Moderately curved, convex proximally	Slightly convex proximally

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (Cont.)

Character	Struthionidae (<i>Struthio</i>)	Rheidae (<i>Rhea</i>)	Casuariidae <i>Casuaris</i> <i>Dromaius</i>	
b. Presence/absence of phalangeal articulation on metacarpal I (M)	Present	Present	Absent	
c. Degree of fusion of metacarpals II and III (M)	Large intermetacarpal space present	Large intermetacarpal space present	Completely fused	
d. Distinctness of metacarpal I from remainder of carpometacarpus (M)	Distinct, though fused	Distinct, though fused	Distinct, though fused	Only slightly indicated, but fused
e. Comparative depths of distal and proximal ends of carpometacarpus (M)	Subequal in depth	Subequal in depth	Decidedly shallowed distally	Subequal in depth
f. Breadth of metacarpal II (M)	Compressed palmoanconally	Compressed palmoanconally	Compressed palmoanconally	
g. Number of metacarpals with phalangeal articulations (Dt)	3	3	1	1
SYNSACRUM				
a. Nature of dorsal surface of synsacrum posteriad of antitrochanter (D)	Narrow	Very narrow	Narrow	
b. Width of dorsal surface of synsacrum posteriad of antitrochanter (D)	Decreases in width posteriorly	Decreases in width posteriorly	Decreases slightly in width posteriorly, then broadens near posterior end	
c. Presence/absence of canals in anterior and of ilium (that exist dorsally) (D)	Absent	Absent	Absent	
d. Fore-aft location of antitrochanter (D)	Anteriad of midpoint	Anteriad of midpoint	At or only slightly anteriad of midpoint	
e. Relative posterior protrusion of ilium, ischium, pubis (D)	In order of posterior protrusion: pubis, ischium, ilium	Pubis and ischium extend far posteriad of ilium	About subequal, pubis may be slightly shorter	
f. Pubes fused/unfused along midline posteriorly (L)	Fused	Unfused	Unfused	
g. Pubes fused/unfused with ischium, ischium with ilium (L)	Pubes and ischium fused; ilium unfused	All fused	Fused (in most adults) two fenestrae of subequal length	
h. Ischia fused/unfused along midline (L)	Unfused	Fused or closely apposed	Unfused	
i. Caudal Vertebrae fused/unfused to ischia (L)	Unfused	Fused	Unfused	
j. Depth of ilium dorsad of acetabulum (L)	Shallow	Shallow	Deep	
k. Nature of pectinal process (L)	Elongate, slender	Low, narrow knob	Low, narrow knob	
l. Depth (dorsoventral) of pubic and ischial bars (L)	Over much of length nearly subequal	Ischial bar slightly deeper than pubic	Pubic bar decidedly shallower	
FEMUR				
a. Shape of posterior margin of proximal articular surface (P)	Moderately concave anteriorly	Moderately concave anteriorly	Highly concave anteriorly	
b. Comparative proximal extension of trochanter and head (A)	Head extends proximad of trochanter	Nearly subequal; trochanter may extend slightly proximad of head	Nearly subequal; trochanter may extend slightly proximad of head	

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (Cont.)

Character	Struthionidae (<i>Struthio</i>)	Rheidae (<i>Rhea</i>)	Casuariidae <i>Casuaris</i> <i>Dromaius</i>	
c. Orientation of long axes of condyles with respect to long axis of shaft (A)	Form 160-165° angle with long axis of shaft	Form 140-160° angle with long axis of shaft	Form 130-165° angle with long axis of shaft	
d. Comparative distal extension of internal and external condyles (A)	External condyle extends far distad of internal	External condyle extends far distad of internal	External condyle extends moderately distad of internal	
e. Comparative lengths of internal and external condyles (A)	External extremely elongate with respect to internal	External decidedly more elongate than internal	External slightly to decidedly more elongate than internal	
f. Shape of dorsal margin of external condyle (L)	U-shaped (highly concave proximally)	U-shaped (highly concave proximally)	U-shaped (highly concave proximally)	
g. Comparative lengths of fibular and external condyles (L)	Nearly, if not, subequal	Fibular about one half as long as external condyle	Fibular about one-half to three-fourths as long as external condyle	
h. Degree of posterior extension of external condyle beyond shaft (L)	Extends moderate distance to far posteriad of shaft	Extends moderate distance to far posteriad of shaft	Extends moderate distance to far posteriad of shaft	
i. Shape of internal margin of trochanter (Pt)	Slightly to moderately convex laterally	Straight	Straight	
j. Presence/absence of muscle scar near proximo-internal region of popliteal area (Pt)	Absent	Absent	Absent	
k. Shape and extent of popliteal area (Pt)	Restricted to small area at base of internal condyle, triangular	See Struthionidae; slightly larger than in Struthionidae	Elliptical, of moderate width	
l. Comparative breadths of fibular and external condyles (Pt)	External condyle broader than fibular	Subequal	Subequal or fibular broader than external	
m. Location of distal-most extension of internal condyle with respect to remainder of distal end of femur (M)	Anteriad of midpoint	Anteriad of midpoint	Near midpoint or slightly posteriad	
n. Shape of internal condyle	Flattened distally	Flattened distally	Triangular, apex along distal margin at approximately antero-posterior midpoint	Semicircular
o. Shape of shaft near distal end (M)	Flattened	Moderately concave internally	Flattened to moderately concave internally	
p. Location of posterior-most extension of internal condyle (M)	Somewhat distad of proximal end		Somewhat distad of proximal end	
q. Comparative depths of internal and external condyles (Dt)	External deeper	External deeper	External deeper	
r. Comparative breadth and depth of distal end (Dt)	Nearly subequal	Slightly broader than deep	Nearly subequal	
s. Shape of internal margin of internal condyle (Dt)	Nearly straight	Straight	Straight to slightly concave internally	
TIBIOTARSUS				
a. Degree of mediolateral compression of cnemial crests (P)	Highly compressed	Highly compressed	Little compressed	

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (*Cont.*)

Character	Struthionidae (<i>Struthio</i>)	Rheidae (<i>Rhea</i>)	Casuariidae <i>Casuarius</i> <i>Dromaius</i>	
b. Comparative depths of inner cnemial crest and remaining proximal articular surface (P) (inter-articular area included in crest measure)	Cnemial crest deeper	Cnemial crest deeper	Cnemial crest deeper	
c. Degree of proximal extension of inner cnemial crest (P)	Only slightly proximad of articular surface	Only slightly proximad of articular surface	Far proximad of articular surface	
d. Degree of lateral protrusion of external articular surface; shape of margin between outer cnemial crest and external articular surface (P)	Slight to moderate; concave near anterior border convex near posterior border	Slight to moderate; concave near anterior border, convex near posterior border	Far laterad; deeply concave	
e. Angle formed between inner cnemial crest and medial margin of internal articular surface (P)	@ 120-130°	@ 120-130°	@ 180°	
f. Angle formed by projection of internal margin of inner cnemial crest and another line passing through anteriormost extensions of condyles (P)	@ 90°	Slightly greater (or less) than 90°	@ 90°	
g. Degree of channelling of intercondylar eminence (P)	Present, of moderate depth	Present, shallow	Absent	
h. Presence/absence of intercondylar eminence (P)	Present, both subequal	Present, doesn't extend as far external as articular surface	Absent	
i. Breadth of internal and external articular surfaces (P)	Broad	Mediolaterally compressed	Mediolaterally compressed	
j. Location of inner cnemial crest with respect to midline of shaft (A)	Slightly medial to midline	Near midline	Mediad of midline	
k. Presence/absence of supratendinal bridge (A)	Absent	Absent	Absent	
l. Location of tendinal canal on shaft with respect to midline (A)	Absent	Displaced far mediad	Displaced far mediad	
m. Presence/absence of ridge extending laterad from distal border of supratendinal bridge or area laterad of tendinal canal (A)	Absent	Present	Present	
n. Shape of proximal margin of condyles (A)	Slightly concave proximally	Slightly concave proximally	Slightly concave proximally	
o. Degree of posterior extension of posterior surface of shaft in vicinity of fibular crest (L)	Slight extension	Moderate extension	Moderate to slight extension	
p. Outline of anterior and distal margins of external condyle (L)	Elliptical	Elliptical	Semicircular	
q. Position along external condyle of anteriormost projection (L)	Decidedly proximad of midpoint	Decidedly proximad of midpoint	At or slightly proximad of midpoint	

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (*Cont.*)

Character	Struthionidae (<i>Struthio</i>)	Rheidae (<i>Rhea</i>)	Casuariidae <i>Casuaris</i>	Dromaius
r. Degree of posterior extension of external condyle (L)	Far	Far	Moderate distance	
s. Presence/absence of deep excavation near anterior end of external condyle (L)	Present, deep	Present, deep	Present, moderate	
t. Presence/absence of knob extending far laterad near antero-posterior midpoint of external condyle (L)	Absent	Absent	Low knob present	
u. Depth and length of internal condyle (M)	Deep; proximo-distally compressed	Deep; proximodistally compressed	Of moderate depth; somewhat compressed proximodistally	
v. Shape of proximal margin of internal condyle (M)	Straight	Slightly convex proximally	Prominent process projects decidedly anteriad	
w. Comparative depths of internal and external condyles (Dt)	Subequal	Subequal	Nearly subequal	
x. Shape of condylar fossa (Dt)	Broad, intermediate between Aepyornithidae and Dromornithidae	Broad, intermediate between Struthionidae and Dromornithidae	Broadly U-shaped; of moderate depth	
y. Shape of anterior margin of internal condyle (Dt)	See Diagnoses for detail			
TARSOMETATARSUS				
a. Shape of hypotarsus; presence/absence of Calcaneal (= hypotarsal) canals (P)	Narrow, offset towards lateral margin	Narrow, offset towards lateral margin	Narrow, centrally located, triangular	
b. Conformation of internal border of proximal end (P)	Low, not ridged	Low, not ridged	Low, not ridged	
c. Comparative proximal extension of hypotarsus and intercotylar prominence (P)	Subequal	Subequal	Hypotarsus extends much further proximad	
d. Presence/absence of marked depression between intercotylar area and hypotarsus (P)	Absent	Present	Slightly indicated	
e. Presence/absence of ridge projecting externally from lateral margin of cotylar surface (P)	Present, broad	Absent	Present	
f. Comparative depths of internal and external cotyla (P)	@ Subequal	@ Subequal	Internal slightly deeper than external	
g. Depth of metatarsal canal (A)	Narrow, shallow	Narrow, shallow	Narrow, deep, extends entire length of shaft	
h. Number and length of subhypotarsal ridges (Pt)	Single, short, narrow	Single, short, narrow	Single, elongate	
i. Degree of grooving of posterior shaft surface (Pt)	Slightly grooved	Deeply grooved	Deeply grooved	
j. Presence/absence of metatarsal I articulation (Pt)	Absent	Absent	Absent	
k. Presence/absence of distal foramen (Pt)	Present	Present	Present	
l. Number of trochleae present (Pt)	2	3	3	

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (*Cont.*)

Character	Struthionidae (<i>Struthio</i>)	Rheidae (<i>Rhea</i>)	Casuariidae <i>Casuarus</i> <i>Dromaius</i>	
m. Degree of grooving of distal margin, trochlea IV (Pt)	Only slightly grooved	Grooved	Grooved	
n. Comparative distal extensions of trochleae IV and II (Pt)	II absent	IV moderately distad of II	IV moderately to slightly distad of II	
o. Degree of distal extension of trochlea III beyond II and IV (Pt)	III moderately distad of IV	III decidedly distad of II and IV	III moderately distad of II and IV	
p. Depth of trochleae (Dt)	Moderate	Moderate	Moderate	
q. Relationship of medial and lateral margins of trochlea III (parallel, divergent)	Parallel-sided	Parallel-sided	Parallel-sided	
PES				
a. Phalangeal count for digits II, III, IV	0-4-5	3-4-5	3-4-5	
c. Comparative lengths of proximal phalanges of digits	III longer than IV; II absent	II longest; IV shortest	III longest, IV shortest	
d. Shape of proximal margins of many phalanges (2, II; 3, III; 2, 3, IV) (D)	V-shaped	V-shaped	V-shaped	
h. Degree of excavation of proximal articular surface; degree of development of dorsoventrally oriented median ridge (2, II; 2, III; 2, IV)	Absent	Deeply biconcave	Deeply biconcave	
y. Shape of terminal phalanges (claw shaped, spade shaped—dorsally)	Claw-like	Claw-like	Claw-like	
Character	Aepyornithidae (<i>Aepyornis</i>)	Dinornithidae (<i>Dinornis</i>)	Emeidae (<i>Pachyornis</i>)	
VERTEBRA. Atlas				
a. Presence/absence of vertebrarterial canals (A) ¹	Lateral protuberances present	Present	Present	
b. Comparison of breadth and depth of vertebrae (A)	—	Broad, shallow	—	
c. Orientation of dorsal surface of neural arch (D)	Nearly horizontal	Nearly horizontal	Nearly horizontal	
STERNUM				
a. Outline of sternum—lateral margins (P)	Divergent posteriorly, two striking excavations in lateral margin, one on either side	Concave laterally	Concave laterally	
b. Comparative length and breadth of sternum (P)	Wider than long	Longer than wide	Longer than wide	
c. Nature of sternocoracoidal processes (P)	Directed anteriorly, short	Directed, laterodorsally, elongate	Directed laterodorsally, elongate	
d. Shape of anterior border of sternum (P)	Concave anteriorly	Straight	Straight	

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (Cont.)

Character	Aepyornithidae (<i>Aepyornis</i>)	Dinorithidae (<i>Dinornis</i>)	Emeidae (<i>Pachyornis</i>)
f. Length of costal margin with respect to that of lateral margin of sternum (P)	—	Costal margin 20% of lateral margin	Costal margin 20% of lateral margin
g. Presence /absence of sternal notches (P)	Two shallow notches	Two notches of moderate depth	Two notches of moderate depth
h. Shape of posterior sternal margin (P)	Slightly concave posteriorly, entire	Single notched	Single notched
i. Presence/absence of carina (V)	Absent	Absent	Absent
j. Nature of ventral surface of sternum (V)	Flattened	Flattened	Flattened
k. Depth, size, and location of coracoidal sulci (A)	?Moderate depth, restricted to lateral quarters of anterior border	Shallow, restricted to lateral one-sixth of anterior margin	
SCAPULOCORACOID			
Nature of scapula and coracoid	Fused	Fused	Fused
a. Shape of coracoid (A)	See struthionidae	About same width overall, with medial process with foramen near mediolateral midpoint on level with glenoid facet	
b. Orientation of glenoid facet (A)	Directed laterad or laterodorsally	Reduced or absent	—
c. Presence/absence of groove mediad of glenoid facet (A)	?Present	?Absent	—
d. Nature of anterior surface between glenoid facet and medial margin of scapulo-coracoid (A)	?Knob may be present	—	—
e. Shape of scapular blade (L)	Concave externally	Concave externally	—
HUMERUS			
a. General proportions of humerus	Stout, short	Absent	—
b. Nature of ligamental furrow (P)	Slightly indicated	Absent	—
c. Presence/absence of pneumatic fossa (An)	Absent	Absent	—
d. Degree of internal projection of internal tuberosity (An)	Moderate	Absent	—
e. Relative proximal protrusion of head and internal tuberosity (An)	Subequal in proximal protrusion	Absent	—
f. Location of head on proximal end (An)	Head shifted ventrally	Absent	—
g. Presence/absence of ligamental attachment at proximo-distal midpoint of ventral surface of shaft (V)	—	Absent	—
h. Depth and size of brachial depression (Pm)	Shallow and small or lacking	Absent	—
i. Presence/absence of ridge trending from base of deltoid crest to dorsal margin (Pm)	Present	Absent	—

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (Cont.)

Character:	Aepyornithidae (<i>Aepyornis</i>)	Dinornithidae (<i>Dinornis</i>)	Emeidae (<i>Pachyornis</i>)
j. Development of ectepi-condylar prominence (Pm)	Moderately rounded	Absent	—
k. Degree of definition of articular surfaces (Dt)	Apparently moderately well defined	Absent	—
l. Cross-sectional outline of shaft (Dt)	—	Absent	—
m. Shape of distal end (Dt)	—	Absent	—
n. Degree of development of olecranal fossa (Dt)	Probably absent	Absent	—
ULNA-RADIUS			
a. Nature of proximal articular surface (P)	—	Absent	—
b. Nature of olecranon (P)	—	Absent	—
c. Depth of proximal end (P)	—	Absent	—
d. Degree of fusion of radius-ulna-carpometacarpus (An)	Complete fusion of all elements + carpal phalanx	Absent	—
e. Comparative widths of radius-ulna (An)	—	Absent	—
f. Comparative depths of proximal and distal ends of radius (An)	—	Absent	—
g. Comparative lengths of radius-ulna and humerus (An)	Shorter than humerus	Absent	—
CARPOMETACARPUS			
a. Degree of flattening of carpal trochlea (P)	—	Absent	—
b. Presence/absence of phalangeal articulation on metacarpal I (M)	—	Absent	—
c. Degree of fusion of metacarpals II and III (M)	—	Absent	—
d. Distinctness of metacarpal I from remainder of carpometacarpus (M)	Fused indistinct	Absent	—
e. Comparative depths of distal and proximal ends of carpometacarpus (M)	Shallowest distad	Absent	—
f. Breadth of metacarpal II (M)	—	Absent	—
g. Number of metacarpals with phalangeal articulations (Dt)	?	Absent	—
SYNSACRUM			
a. Nature of dorsal surface of synsacrum posteriad of antitrochanter (D)	Broad	Broad	Broad
b. Width of dorsal surface of synsacrum posteriad of antitrochanter (D)	Decreases only slightly in width posteriorly	Decreases in width posteriorly	Decreases in width posteriorly
c. Presence/absence of canals in anterior end of ilium (that exist dorsally) (D)	—	Absent	Absent

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (Cont.)

Character	Aepyornithidae (<i>Aepyornis</i>)	Dinornithidae (<i>Dinornis</i>)	Emeidae (<i>Pachyornis</i>)
d. Fore-aft location of anti-trochanter (D)	At or only slightly anterior of midpoint	At, posterior of, or anterior of midpoint	
e. Relative posterior protrusion of ilium, ischium, pubis (D)	Ischium protrudes furthest, ilium-pubis approximately subequal	See Struthionidae	
f. Pubes fused/unfused along midline posteriorly (L)	Unfused	Unfused	Unfused
g. Pubes fused/unfused with ischium, ischium with ilium (L)	Unfused	Unfused	Unfused
h. Ischia fused/unfused along midline (L)	Unfused	Unfused	Unfused
i. Caudal Vertebrae fused/unfused to ischia (L)	Unfused	Unfused	Unfused
j. Depth of ilium dorsad of acetabulum (L)	Deep	Shallow to moderate	
k. Nature of pectinal process (L)	—	Low, broad knob or absent	
l. Depth (dorsoventral) of pubic and ischial bars (L)	Ischial bar decidedly deeper	Ischial bar decidedly deeper, particularly over posterior half of bar	
FEMUR			
a. Shape of posterior margin of proximal articular surface (P)	Highly concave anteriorly	Moderately concave posteriorly between head and trochanter, trochanter slightly convex posteriorly	As in Dinornithidae except trochanter can be more highly convex
b. Comparative proximal extension of trochanter and head (A)	Trochanter extends far proximad of head	Trochanter extends moderately proximad of head	As in Dinornithidae
c. Orientation of long axes of condyles with respect to long axis of shaft (A)	Closely parallel to long axis of shaft	Form 150° to nearly 180° angle with long axis of shaft	Form 150-160° angle with long axis of shaft
d. Comparative distal extension of internal and external condyles (A)	External condyle extends far distad of internal	External condyle extends moderately to far distad of internal	
e. Comparative lengths of internal and external condyles (A)	Nearly subequal; external may be slightly more elongate	External slightly to moderately longer than internal	
f. Shape of dorsal margin of external condyle (L)	Nearly, if not, straight	Slightly concave dorsally or straight	
g. Comparative lengths of fibular and external condyles (L)	Nearly, if not, subequal	Nearly, if not, subequal	Nearly, if not, subequal
h. Degree of posterior extension of external condyle beyond shaft (L)	Extends only short to moderate distance posterior of shaft	Extends only short to moderate distance posterior of shaft	Extends only short to moderate distance posterior of shaft
i. Shape of internal margin of trochanter (Pt)	See Dinornithidae, Emeidae	Straight over much of length moderately convex latero-proximally near proximal end	
j. Presence/absence of muscle scar near proximo-internal region of popliteal area (Pt)	Well developed	Well developed	Well developed
k. Shape and extent of popliteal area (Pt)	See Struthionidae, but more proximo-distally elongate	Elliptical, broad	
l. Comparative breadths of fibular and external condyles (Pt)	Nearly subequal	Fibular condyle broader than external	Fibular condyle broader than external

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (Cont.)

Character:	Aepyornithidae (<i>Aepyornis</i>)	Dinornithidae (<i>Dinornis</i>)	Emeidae (<i>Pachyornis</i>)
m. Location of distal-most extension of internal condyle with respect to remainder of distal end of femur (M)	Anteriad of midpoint	Near midpoint	Near midpoint
n. Shape of internal condyle	Semicircular	Semicircular	Semicircular
o. Shape of shaft near distal end (M)	Flattened	Flattened	Flattened
p. Location of posterior-most extension of internal condyle (M)	Near proximal end	Near proximal end	Near proximal end
q. Comparative depths of internal and external condyles (Dt)	External only slightly deeper; nearly subequal	External moderately deeper	External moderately deeper
r. Comparative breadth and depth of distal end (Dt)	Broader than deep	Broader than deep	Broader than deep
s. Shape of internal margin of internal condyle (Dt)	Highly convex	Highly convex	Highly convex
TIBIOTRASUS			
a. Degree of mediolateral compression of cnemial crests (P)	Highly compressed	Little compressed	Little compressed
b. Comparative depths of inner cnemial crest and remaining proximal articular surface (P) interarticular area included in crest measure)	Cnemial crest shallower	Cnemial crest shallower	Cnemial crest shallower
c. Degree of proximal extension of inner cnemial crest (P)	Only slightly proximad of articular surface	Moderately beyond articular surface	Moderately beyond articular surface
d. Degree of lateral protrusion of external articular surface; shape of margin between outer cnemial crest and external articular surface (P)	Far laterad; deeply concave	Slight to moderate; shallow concavity	Slight to moderate; shallow concavity
e. Angle formed between inner cnemial crest and medial margin of internal articular surface (P)	>150°	@ 180°	@ 180°
f. Angle formed by projection of internal margin of inner cnemial crest and another line passing through anteriormost extensions of condyles (P)	@ 90°	@ 90°	@ 90°
g. Degree of channeling of intercondylar eminence (P)	Absent	Present	Present
h. Presence/absence of intercondylar eminence (P)	Present, doesn't extend as far as external articular surface	Present, both subequal	Present, both subequal
i. Breadth of internal and external articular surfaces (P)	Mediolaterally compressed	Mediolaterally compressed	Mediolaterally compressed
j. Location of inner cnemial crest with respect to midline of shaft (A)	Displaced for laterad	Far mediad of midline	Far mediad of midline

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (*Cont.*)

Character	Aepyornithidae (<i>Aepyornis</i>)	Dinornithidae (<i>Dinornis</i>)	Emeidae (<i>Pachyornis</i>)
k. Presence/absence of supratendinal bridge (A)	Absent	Present	Present
l. Location of tendinal canal on shaft with respect to midline (A)	Displaced far mediad	Displaced far mediad	Displaced far mediad
m. Presence/absence of ridge extending laterad from distal border of supratendinal bridge or area laterad of tendinal canal (A)	?Absent	Present	Present
n. Shape of proximal margin of condyles (A)	Straight over much of width	Concave proximally	Concave proximally
o. Degree of posterior extension of posterior surface of shaft in vicinity of fibular crest (L)	Slight extension	Slight extension	Slight extension
p. Outline of anterior and distal margins of external condyle (L)	Ovaloid in outline; large radius of curvature	Semicircular	Semicircular
q. Position along external condyle of anteriormost projection (L)	Approximately at midpoint	At or slightly proximad of midpoint	Somewhat proximad of midpoint
r. Degree of posterior extension of external condyle (L)	Extremely short distance	Moderate distance	Moderate distance
s. Presence/absence of deep excavation near anterior end of external condyle (L)	Present, deep	Present, moderate	Present, moderate
t. Presence/absence of knob extending far laterad near anteroposterior midpoint of external condyle (L)	Present	Absent	Absent
u. Depth and length of internal condyle (M)	Deep; proximodistally compressed	Of moderate depth and length	Of moderate depth and length
v. Shape of proximal margin of internal condyle (M)	U-shaped, highly concave proximally	Prominent process projects decidedly anteriad	Prominent process projects decidedly anteriad
w. Comparative depths of internal and external condyles (Dt)	Internal deeper than external	Internal deeper than external	Internal deeper than external
x. Shape of condylar fossa (Dt)	Only slightly indicated	U-shaped; of moderate depth	U-shaped; of moderate depth
y. Shape of anterior margin of internal condyle (Dt)		See Diagnoses for detail	

TARSOMETATARSUS

a. Shape of hypotarsus; presence/absence of Calcaneal (= hypotarsal) canals (P)	Broad, triangular, centrally located, at least one shallow calcaneal canal	One deep calcaneal canal bisecting rectangular hypotarsus	One deep calcaneal canal bisecting rectangular hypotarsus
b. Conformation of internal border of proximal end (P)	Low, not ridged	Low ridge present	Low ridge present
c. Comparative proximal extension of hypotarsus and intercotylar prominence (P)	Lacks intercotylar prominence	Intercotylar prominence extends furthest proximad	Intercotylar prominence extends furthest proximad

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (*Cont.*)

Character	Aepyornithidae (<i>Aepyornis</i>)	Dinornithidae (<i>Dinornis</i>)	Emeidae (<i>Pachyornis</i>)
d. Presence/absence of marked depression between intercotylar area and hypotarsus (P)	Absent	Absent	Absent
e. Presence/absence of ridge projecting externally from lateral margin of cotylar surface (P)	Present	Present	Present
f. Comparative depths of internal and external cotyla (P)	External cotyla much deeper than internal	Internal decidedly deeper; margins angular	Internal decidedly deeper; margins angular
g. Depth of metatarsal canal (A)	Broad, shallow	Moderate width, shallow	Shallow or absent
h. Number and length of subhypotarsal ridges (Pt)	Single, extends about one-half shaft length, broad	Two, short	Two, short
i. Degree of grooving of posterior shaft surface (Pt)	Ungrooved	Ungrooved	Ungrooved
j. Presence/absence of metatarsal I articulation (Pt)	Absent	Present or absent	Present or absent
k. Presence/absence of distal foramen (Pt)	Present	Absent	Absent
l. Number of trochleae present (Pt)	3	3	3
m. Degree of grooving of distal margin, trochlea IV (Pt)	Grooved	Grooved	Grooved
n. Comparative distal extensions of trochleae IV and II (Pt)	Nearly subequal to IV being slightly more elongate than II	II decidedly distad of IV	II decidedly distad of IV
o. Degree of distal extension of trochlea III beyond II and IV (Pt)	III moderately distad of II and IV	III moderately distad of II and IV	III moderately distad of II and IV
p. Depth of trochleae (Dt)	Moderate	Moderate	Deep
q. Relationship of medial and lateral margins of trochlea III (parallel, divergent)	Nearly parallel-sided	Slightly convergent posteriorly	Parallel-sided
PES			
a. Phalangeal count for digits II, III, IV	3-4-5	3-4-5	3-4-5 or 3-4-4
c. Comparative lengths of proximal phalanges of digits	III and IV subequal; II shortest	III longest, II shortest	III longest, IV shortest
d. Shape of proximal margins of many phalanges (2, II; 3, III; 2, 3, IV) (D)	Broadly V-shaped	V-shaped	V-shaped
h. Degree of excavation of proximal articular surface; degree of development of dorsoventrally oriented median ridge (2, II; 2, III; 2, IV)	Deeply biconcave	Deeply biconcave	Deeply biconcave
y. Shape of terminal phalanges (claw shaped, spade shaped—dorsally)	Claw-like	Claw-like	Claw-like

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (Cont.)

Character:	Apterygidae (<i>Apteryx</i>)	Tinamidae (<i>Nothura</i> or <i>Nothoprocta</i>)	Dromornithidae (several genera)
VERTEBRA. Atlas			
a. Presence/absence of vertebrarterial canals (A) ¹	Absent	Absent	Absent
b. Comparison of breadth and depth of vertebrae (A)	Broad, shallow	Moderate depth and width	Deep and narrow
c. Orientation of dorsal surface of neural arch (D)	Nearly horizontal	Nearly horizontal	Tilted anteroventrally
STERNUM			
a. Outline of sternum—lateral margins (P)	Slightly concave laterally	Convex laterally	Straight and nearly, if not, parallel
b. Comparative length and breadth of sternum (P)	About as long as wide	Longer than wide	Longer than wide
c. Nature of sternocoracoidal processes (P)	Directed laterodorsally, elongate	Directed anterodorsally, elongate	Directed anteriorly, moderately elongate
d. Shape of anterior border of sternum (P)	Concave anteriorly	Biconcave anteriorly	Concave anteriorly centrally, straight on either side
f. Length of costal margin with respect to that of lateral margin of sternum (P)	Costal margin about 50% of lateral margin	Costal margin 10% of lateral margin	Costal margin 60% of lateral margin
g. Presence/absence of sternal notches (P)	Two notches of moderate depth	Two deep notches	Absent
h. Shape of posterior sternal margin (P)	Concave posteriorly, entire	Extremely narrow, convex posteriorly, single notched	Broadly convex posteriorly, entire
i. Presence/absence of carina (V)	Absent	Present	Absent
j. Nature of ventral surface of sternum (V)	Flattened	Narrowly V-shaped, deep	Moderately convex ventrally, smoothly rounded
k. Depth, size, and location of coracoidal sulci (A)	Shallow, restricted to lateral one-sixth of anterior margin	Deep, cover anterior margin, meet in midline	Shallow, restricted to lateral quarters of sternal margin
SCAPULOCORACOID			
Nature of scapula and coracoid	Fused	Unfused	Fused
a. Shape of coracoid (A)	About same width overall, with medial process with foramen near mediolateral midpoint on level with glenoid facet	Broadest ventrally, narrowest just ventrad of glenoid facet	Broadest ventrally, lacking any medial process internal to glenoid facet
b. Orientation of glenoid facet (A)	Absent	Directed laterad	Directed laterad
c. Presence/absence of groove mediad of glenoid facet (A)	Absent	Absent	Moderate depth narrow
d. Nature of anterior surface between glenoid facet and medial margin of scapulocoracoid (A)	Ridge present	Absent	Smooth, lacking knob
e. Shape of scapular blade (L)	Concave externally	Concave externally	Concave medially
HUMERUS			
a. General proportions of humerus	Slender, of moderate length	Slender to moderate, of moderate length	Short and deep

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (*Cont.*)

Character	Apterygidae (<i>Apteryx</i>)	Tinamidae (<i>Nothura</i> or <i>Nothoprocta</i>)	Dromornithidae (several genera)
b. Nature of ligamental furrow (P)	Slightly indicated	Well defined	Absent
c. Presence/absence of pneumatic fossa (An)	Absent	Present, small	Shallow
d. Degree of internal projection of internal tuberosity (An)	Slight projection	Moderate projection	Not projecting far internally
e. Relative proximal protrusion of head and internal tuberosity (An)	Internal tuberosity projects further proximad than head	Head projects far proximad of internal tuberosity	Head projects as far or further proximad than internal tuberosity
f. Location of head on proximal end (An)	Near middle of proximal end	Near middle of proximal end	Head located in middle of proximal end
g. Presence/absence of ligamental attachment at proximo-distal midpoint of ventral surface of shaft (V)	Present	Absent	Large ligamental scar near proximodistal midpoint of shaft
h. Depth and size of brachial depression (Pm)	Shallow and small or lacking	Shallow and small or lacking	Of moderate depth and size
i. Presence/absence of ridge trending from base of deltoid crest to dorsal margin (Pm)	Present, slightly indicated	Absent	Absent
j. Development of ectepicondylar prominence (Pm)	Only slightly indicated	Well developed	Well developed
k. Degree of definition of articular surfaces (Df)	Moderately well defined	Well defined	Not well defined
l. Cross-sectional outline of shaft (Df)	Triangular proximally, approaching ellipse distally	Elliptical	Elliptical
m. Shape of distal end (Df)	Inflated	Deepest externally, narrowest internally	About same depth over entire width, uninflated
n. Degree of development of olecranal fossa (Df)	Absent	Not well defined	Well developed
ULNA-RADIUS			
a. Nature of proximal articular surface (P)	Absent	Distinct cotyla developed	Lacks distinct cotyla
b. Nature of olecranon (P)	Broad, slightly indicated	Narrow, well developed	Not distinct
c. Depth of proximal end (P)	Shallow	Deep	Deep
d. Degree of fusion of radius-ulna-carpometacarpus (An)	Unfused	Unfused	All fused, but parts of radius-ulna remain distinct
e. Comparative widths of radius-ulna (An)	Nearly subequal	Ulna decidedly broader	Nearly the same width
f. Comparative depths of proximal and distal ends of radius (An)	Radius apparently slightly broader distally	Radius broadens distally to elliptical articulation	Radius tapers distally to rounded articulation
g. Comparative lengths of radius-ulna and humerus (An)	Shorter than humerus	Subequal	Longer than or subequal to length of humerus
CARPOMETACARPUS			
a. Degree of flattening of carpal trochlea (P)	Flattened	Highly curved, convex proximally, groove well developed	Almost planar lacking central groove

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (Cont.)

Character	Apterygidae (<i>Apteryx</i>)	Tinamidae (<i>Nothura</i> or <i>Nothoprocta</i>)	Dromornithidae (several genera)
b. Presence/absence of phalangeal articulation on metacarpal I (M)	Absent	Present	Absent
c. Degree of fusion of metacarpals II and III (M)	Completely fused	Large intermetacarpal space present	Nearly complete or complete
d. Distinctness of metacarpal I from remainder of carpometacarpus (M)	Fused, indistinct	Distinct, though fused	Distinct, but fused
e. Comparative depths of distal and proximal ends of carpometacarpus (M)	Subequal in depth	Slightly shallower distally	Proximal end decidedly deeper
f. Breadth of metacarpal II (M)	Compressed palmoanconally	Deep palmoanconally	Deep palmoanconally
g. Number of metacarpals with phalangeal articulations (Dt)	1	3	1
SYNSACRUM			
a. Nature of dorsal surface of synsacrum posterior of antitrochanter (D)	Very narrow	Broad	Of moderate width
b. Width of dorsal surface of synsacrum posterior of antitrochanter (D)	Decreases in width posteriorly	Decreases in width posteriorly	Remains about same width to posterior end
c. Presence/absence of canals in anterior end of ilium (that exit dorsally) (D)	Absent	Present	Absent
d. Fore-aft location of antitrochanter (D)	Decidedly posterior of midpoint	Decidedly posterior of midpoint	Approximately at antero-posterior midpoint
e. Relative posterior protrusion of ilium, ischium, pubis (D)	Pubis and ischium subequal, both more elongate than ilium	Pubis and ischium extend far posterior of ilium	Pubis and ischium not extending far posterior of ilium
f. Pubes fused/unfused along midline posteriorly (L)	Unfused	Unfused	Unfused
g. Pubes fused/unfused with ischium, ischium with ilium (L)	Unfused	Unfused	Fused; ischiopubic fenestra decidedly more elongate than ilioischiatric
h. Ischia fused/unfused along midline (L)	Unfused	Unfused	Unfused
i. Caudal Vertebrae fused/unfused to ischia (L)	Unfused	Unfused	Unfused
j. Depth of ilium dorsad of acetabulum (L)	Moderate	Extremely shallow	Shallow
k. Nature of pectinal process (L)	Moderate width, elongate	Broad, elongate	Absent
l. Depth (dorsoventral) of pubic and ischial bars (L)	Pubic bar decidedly shallower	Pubic bar decidedly shallower	Subequal
FEMUR			
a. Shape of posterior margin of proximal articular surface (P)	Nearly straight except for slight convexity between head and trochanter	Highly concave anteriorly	Nearly straight or only slightly indented
b. Comparative proximal extension of trochanter and head (A)	About subequal	Trochanter extends moderately proximad of head	Trochanter extends about same distance proximad as head or moderately proximad of head

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (Cont.)

Character	Apterygidae (<i>Apteryx</i>)	Tinamidae (<i>Nothura</i> or <i>Nothoprocta</i>)	Dromornithidae (several genera)
c. Orientation of long axes of condyles with respect to long axes of shaft (A)	Form very large obtuse angle with long axis of shaft nearly parallel to long axis	Closely parallel to long axis of shaft	Do not closely parallel long axis of shaft
d. Comparative distal extension of internal and external condyles (A)	Subequal in distal extension	Subequal in distal extension	External condyle extends moderately distad of internal
e. Comparative lengths of internal and external condyles (A)	Nearly subequal; internal slightly more elongate than external	Nearly subequal; external only slightly more elongate	External moderately more elongate than internal
f. Shape of dorsal margin of external condyle (L)	Moderately concave dorsally	Straight	Nearly straight or only slightly concave proximally
g. Comparative lengths of fibular and external condyles (L)	Fibular about 2/3 length of external condyle	Nearly, if not, subequal	Fibular condyle $\frac{1}{2}$ - $\frac{2}{3}$ depth of external
h. Degree of posterior extension of external condyle beyond shaft (L)	Extends far posteriad of shaft	Extends moderate distance to far posteriad of shaft	Extends far posterior of shaft
i. Shape of internal margin of trochanter (Pt)	Slightly convex laterally	Convex externally, recurving over proximal articular surface	Nearly, if not, straight
j. Presence/absence of muscle scar near proximo-internal region of popliteal area (Pt)	Slightly indicated or absent	Present	Absent
k. Shape and extent of popliteal area (Pt)	Triangular, broad, elongate	Extremely shallow, triangular	Elliptical, broad
l. Comparative breadths of fibular and external condyles (Pt)	Fibular condyle broader than external	Nearly subequal	Fibular condyle narrower than external
m. Location of distal-most extension of internal condyle with respect to remainder of distal end of femur (M)	Near midpoint	Near midpoint, to slightly anteriad of midpoint	Anteriad of anteroposterior midpoint
n. Shape of internal condyle	Semicircular	Semicircular	Approaching elliptical shape
o. Shape of shaft near distal end (M)	Slightly concave internally	Slightly concave internally	Highly concave internally
p. Location of posterior-most extension of internal condyle (M)	Near proximal end	Near proximal end	Near proximal end
q. Comparative depths of internal and external condyles (Dt)	Subequal	External slightly deeper	Nearly subequal
r. Comparative breadth and depth of distal end (Dt)	Broader than deep	Broader than deep	Broader than deep
s. Shape of internal margin of internal condyle (Dt)	Straight to slightly concave internally	Straight	Straight to slightly convex internally
TIBIOTARSUS			
a. Degree of mediolateral compression of cnemial crests (P)	Little compressed	Little compressed	Moderately compressed
b. Comparative depths of inner cnemial crest and remaining proximal articular surface (P) (inter-articular area included in crest measure)	Cnemial crest slightly shallower	Subequal	Subequal

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (Cont.)

Character	Apterygidae (<i>Apteryx</i>)	Tinamidae (<i>Nothura</i> or <i>Nothoprocta</i>)	Dromornithidae (several genera)
c. Degree of proximal extension of inner cnemial crest (P)	Moderately beyond articular surface	Moderately beyond articular surface	Far proximad of articular surface
d. Degree of lateral protrusion of external articular surface; shape of margin between outer cnemial crest and external articular surface (P)	Slight to moderate; shallow concavity	Slight to moderate; shallow concavity	Far laterad; margin deeply concave externally
e. Angle formed between inner cnemial crest and medial margin of internal articular surface (P)	@ 180°	@ 180°	@ 130°
f. Angle formed by projection of internal margin of inner cnemial crest and another line passing through anteriormost extensions of condyles (P)	Moderate obtuse (or acute)	@ 90°	@ 90°
g. Degree of channeling of intercondylar eminence (P)	Present	Present	Absent
h. Presence/absence of intercondylar eminence (P)	Absent	Present, both subequal	Present, extends further proximad than external articular surface
i. Breadth of internal and external articular surfaces (P)	Moderate	Broad	Broad
j. Location of inner cnemial crest with respect to midline of shaft (A)	Far mediad of midline	Proximally at midline; distally trends to lateral shaft margin	On midline near proximal end
k. Presence/absence of supratendinal bridge (A)	Absent	Present	Present
l. Location of tendinal canal on shaft with respect to midline (A)	Displaced far mediad	Displaced far mediad	Centrally located
m. Presence/absence of ridge extending laterad from distal border of supratendinal bridge or area laterad of tendinal canal (A)	Present	Present	Absent
n. Shape of proximal margin of condyles (A)	Concave proximally	Concave proximally	Concave proximally
o. Degree of posterior extension of posterior surface of shaft in vicinity of fibular crest (L)	Moderate extension	Moderate extension	Slight extension
p. Outline of anterior and distal margins of external condyle (L)	Semicircular	Semicircular	Highly curved, forming semicircular outline, small radius of curvature
q. Position along external condyle of anteriormost projection (L)	At or slightly proximad of midpoint	Approximately at midpoint	Near or slightly distad of proximodistal midpoint of condyle
r. Degree of posterior extension of external condyle (L)	Moderate distance	Moderate distance	Short distance

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (*Cont.*)

Character	Apterygidae (<i>Apteryx</i>)	Tinamidae (<i>Nothura</i> or <i>Nothoprocta</i>)	Dromornithidae (several genera)
s. Presence/absence of deep excavation near anterior end of external condyle (L)	Present, moderate	Absent	Absent
t. Presence/absence of knob extending far laterad near anteroposterior midpoint of external condyle (L)	Absent	Absent	Absent
u. Depth and length of internal condyle (M)	Of moderate depth to deep; somewhat proximodistally compressed	Of moderate depth and length	Of moderate depth and length
v. Shape of proximal margin of internal condyle (M)	Moderately concave proximally	Straight to slightly convex proximally	Straight or only slightly concave proximad
w. Comparative depths of internal and external condyles (Dt)	Nearly subequal	Nearly subequal	Internal deeper than external
x. Shape of condylar fossa (Dt)	U-shaped; deep and narrow	U-shaped; deep end narrow	Broadly U-shaped; or moderate depth
y. Shape of anterior margin of internal condyle (Dt)	See Diagnoses for detail		
TARSOMETATARSUS			
a. Shape of hypotarsus; presence/absence of Calcaneal (= hypotarsal) canals (P)	One deep canal bisecting rectangular hypotarsus	Rectangular hypotarsus, laterally offset, 3 canals	Broad, triangular; two shallow canals, one on either side of hypotarsus
b. Conformation of internal border of proximal end (P)	Low, unridged	Narrow ridge, extends far proximad	Narrow ridge, extends far proximad
c. Comparative proximal extension of hypotarsus and intercotylar prominence (P)	Subequal	Intercotylar prominence extends furthest proximad	Hypotarsus projects slightly to decidedly further proximad than intercotylar prominence
d. Presence/absence of marked depression between intercotylar area and hypotarsus (P)	Present	Present	Present
e. Presence/absence of ridge projecting externally from lateral margin of cotylar surface (P)	Present, near posterior margin of cotylar surface	Present, broad	Present, anteriad of anteroposterior midpoint
f. Comparative depths of internal and external cotyla (P)	Internal decidedly deeper; margins angular	Approximately subequal	Internal moderately deeper than external; margins rounded
g. Depth of metatarsal canal (A)	Narrow, shallow	Moderate width, deep over proximal half	Moderately deep; restricted to proximal half of shaft
h. Number and length of subhypotarsal ridges (Pt)	Two, short	Three, broadly divergent	Single, elongate, broadest near proximal end
i. Degree of grooving of posterior shaft surface (Pt)	Ungrooved	Slightly grooved	Ungrooved
j. Presence/absence of metatarsal I articulation (Pt)	Present	Present	Absent
k. Presence/absence of distal foramen (Pt)	Present	Present	Present

TABLE 5. SUMMARY OF DIAGNOSTIC CHARACTERS OF THE POST-CRANIAL SKELETON OF BIRDS WITH PALAEOGNATH PALATES (TINAMOUS AND RATITES) (*Cont.*)

Character	Apterygidae (<i>Apteryx</i>)	Tinamidae (<i>Nothura</i> or <i>Nothoprocta</i>)	Dromornithidae (several genera)
l. Number of trochleae present (Pt)	3	3	3
m. Degree of grooving of distal margin, trochlea IV (Pt)	Grooved	Grooved	Ungrooved
n. Comparative distal extensions of trochleae IV and II (Pt)	IV moderately to slightly distad of II	IV decidedly distad of II	IV extends slightly distad of II
o. Degree of distal extension of trochlea III beyond II and IV (Pt)	III decidedly distad of II and IV	III decidedly distad of II and IV	III extends only slightly distad of II and IV
p. Depth of trochleae (Dt)	Moderate	Moderate	Deep
q. Relationship of medial and lateral margins of trochlea III (parallel, divergent)	Parallel-sided	Convergent anteriorly	Narrow; margins decidedly convergent posteriorly
PES			
a. Phalangeal count for digits II, III, IV	3-4-5	3-4-5	3-4-4
c. Comparative lengths of proximal phalanges of digits	II and III nearly subequal; IV shortest	III longest, IV shortest; sometimes III and II subequal	II longest, IV shortest
d. Shape of proximal margins of many phalanges (2, II; 3, III; 2, 3, IV) (D)	V-shaped	V-shaped	Straight
h. Degree of excavation of proximal articular surface; degree of development of dorsoventrally oriented median ridge (2, II; 2, III; 2, IV)	Deeply biconcave	Deeply biconcave	Flattened, slightly concave proximally
y. Shape of terminal phalanges (claw shaped, spade shaped—dorsally)	Claw-like	Claw-like	Hoof-like, spade shaped, broad, shallow

TABLE 6. MEASUREMENTS (IN MILLIMETRES) OF THE STERNA OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA

	<i>Dromornis stirtoni</i>	<i>Genyornis newtoni</i>
	UCMP 11349	No number ¹
1. Length along pre-post axial midline	>275	@306
2. Maximum breadth across sternocoracoidal processes	>225	@254
3. Length from anterior-most extension of sternocoracoidal processes to posterior extension of coastal margin	@185	—
1. Measurements given in Stirling and Zietz, p. 72.		

TABLE 7. MEASUREMENTS (IN MILLIMETRES) OF THE SCAPULOCORACOIDS OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA

	<i>Dromornis stirtoni</i>	<i>Genyornis newtoni</i>		
	UCMP 113050	SIAM 51	SAM P13872a, b ¹	
			Fig. 1	Fig. 2
1. Length of glenoid cavity	25.2	24.3	22	21
2. Depth of glenoid cavity at dorsoventral midpoint	14.0	11.0	13	13
3. Minimum width of coracoid	18.4	26.0	—	—
4. Width across glenoid cavity to medial border of scapulocoracoid	@27.8	28.8	—	—
5. Maximum depth of scapulocoracoid in glenoid area	15.9	16.0	—	—
6. Minimum width of scapula	@10.8	—	—	—
7. Maximum width, sternal end coracoid	@63.3	64.3	—	—
8. Total length of scapulocoracoid	>239.3	—	—	—
	left	right	?left	?left
1. Stirling and Zietz, 1900, p. 76, Pl. XXIV, fig 1 (also see figs. 2, 3).				

TABLE 8. MEASUREMENTS (IN MILLIMETRES) OF THE SYNSACRA OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA

	BM (NH) 49160	UCMP 119211	UCMP 60613	UCMP 109180 (=RAS 5361)	SAM P17041 right	SAM P17041 left	SAM P17048	SAM P17049
1. Diameter of acetabulum	@62.1 (left)	@60.6 (max.) 53.9 (min.) (left)	>60.0 (right)	—	62.9	65.0	—	77.0 (right)
2. Maximum length of acetabular area (including antitrochanter)	—	—	—	—	—	—	—	121.9 (right)
3. Depth of synsacrum above acetabulum	53.3 (left)	—	—	—	—	—	—	133.9 (right)
4. Length of synsacrum from anterior end of ischio-pubic fenestra to posterior-most extension of pubes	—	—	—	—	—	—	—	296.1 (right)
5. Width of synsacrum across anterior end of pubis	—	—	—	—	126.2	>91.5	99.1	
6. Width of synsacrum across posterior extension of antitrochanter	—	—	—	—	—	—	—	172.9 (right)
7. Width of synsacrum at narrowest point anterior to acetabular region	83.3	—	—	—	—	—	—	—
8. Maximum depth of anterior ischio-pubic fenestra	—	—	15.5 (right)	18.6 (right)	—	—	—	—
9. Length from anterior part of acetabulum to center of anteriormost vertebra	—	—	—	—	@203.1	@202.8	—	191.6
10. Depth of synsacrum midway between acetabulum and anteriormost vertebra	—	—	—	—	—	—	—	25.4
11. Length of ilio-ischiatic fenestra	—	—	—	—	—	—	—	156.2
12. Length of anterior ischio-pubic fenestra	—	—	54.0 (right)	>58.6 (right)	—	55.5	46.2	
13. Length of posterior ischio-pubic fenestra	—	—	—	—	—	—	256.0	
14. Width of anteriormost vertebra included in synsacrum	—	—	—	—	—	—	>61.7	
Centrum only	—	—	—	—	—	—	43.8	
					(a)	(b)	(c)	

(a) Stirling and Zietz, 1913, Pl. XXXIX, Fig. 1

(b) Stirling and Zietz, 1913, Pl. XXXIX, Fig. 3

(c) Stirling and Zietz, 1913, Pl. XXXVIII, Fig. 1

TABLE 9. MEASUREMENTS (IN MILLIMETRES) OF THE HUMERI OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA

	<i>Genyornis newtoni</i>					
	SAM P13871	SAM P17065	SAM P17066	SAM P17068	SIAM 51A	SIAM 61
1. Depth of proximal end from external to internal tuberosity	25.2	—	—	—	—	25.0
2. Width of proximal end across internal tuberosity	15.9	—	—	—	—	8.7
3. Length of deltoid crest	@18.1	crest not well defined	—	—	@16.1	—
4. Depth of distal end	19.6	23.8	22.2	19.4	—	—
5. Width of external condyle	@10.9	12.1	10.3	12.6	—	—
6. Width of internal condyle	11.6	13.8	—	13.2	—	—
7. Minimum Depth	13.2	16.6	—	—	11.8	—
8. Minimum Width	8.5	10.6	—	—	9.0	—
9. Total length of humerus, internal tuberosity to internal condyle	89.2	—	—	—	—	—
	right	right	right	left	right	right

TABLE 10. MEASUREMENTS (IN MILLIMETRES) OF THE ULNAE OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA

	<i>Genyornis newtoni</i>			
	SAM P13873	SIAM 51	SIAM 58	SIAM 58
1. Maximum width of proximal end across olecranon to palmar surface	14.8	14.9	—	14.5
2. Maximum depth of proximal end across cotyla	11.8	11.9	—	11.4
3. Width of shaft at level of bicipital attachment	8.8	11.4	10.2	9.4
4. Depth of shaft at level of bicipital attachment	7.9	@9.9	8.8	9.6
5. Total length of ulna	—	@90.6	>106.8	>91.3
	left	left	right	left

TABLE 11. MEASUREMENTS (IN MILLIMETRES) OF THE RADII OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA

	<i>Genyornis newtoni</i>						
	SAM P13873	SAM P17069	SAM P17070	SAM P17071	SIAM 51	SIAM 58	SIAM 58
1. Palmoanconal width of proximal end	12.9	12.8	12.7	>13.7	14.1	11.4	11.8
2. Dorsoventral depth of proximal end	9.0	10.2	10.1	@11.1	10.8	10.8	9.8
3. Width of shaft at bicipital tubercle	8.7	9.4	—	10.2	10.9	9.2	8.7
4. Depth of shaft at bicipital tubercle	7.5	7.2	—	8.8	8.5	—	@7.4
5. Width of distal end	@5.4	4.8	—	—	4.8	—	4.6
6. Depth of distal end	@5.9	7.2	—	—	5.9	—	—
7. Total length of shaft	93.1	97.8	—	—	100.9	@95.1	86.7
	left	left	?right	?right	left	right	left

TABLE 12. MEASUREMENTS (IN MILLIMETRES) OF THE CARPOMETACARPI OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA

	<i>cf. Dromornis stirtoni</i>	<i>Genyornis newtoni</i>			
	UCMP 70996	SAM P13875	SAM P17072	SIAM 51	SIAM 58
1. Maximum depth (dorsoventral) of proximal end	23.9	16.2	—	18.1	@16.4
2. Maximum width (palmo-anconal) of proximal end	10.5	8.6	—	10.2	8.9
3. Length of metacarpal I	19.9	—	—	11.4	—
4. Length of metacarpal II	@59.7	42.0	>39.1	50.2	42.4
5. Length of metacarpal III	58.5	40.4	>34.4	43.3	>41.3
6. Maximum length of carpometacarpus (from ventral border of proximal end to distal tip of metacarpal II)	@63.6	43.8	—	—	@42.8
	right	left	left	left	right

TABLE 13. MEASUREMENTS (IN MILLIMETRES) OF THE ATLAS VERTEBRAE OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA

	<i>Dromornis stirtoni</i>	<i>Ibandornis</i> sp.					<i>Genyornis newtoni</i>		
	UCMP 111306 (=MOW 63-177)	UCMP 108609 (=MOW 63-186a)	UCMP 108610 (=MOW 63-186b)	UCMP 113048	UCMP 119207	UCMP 70861	SAM P13928	SAM P13929	SAM P17134
1. Length of centrum, ventral border	17.0	>9.6	—	11.6	17.8	11.4	19.3	>16.6	14.9
2. Maximum width of centrum	31.5	@18.3	16.3	23.1	20.8	22.9	>25.3	>21.7	>24.8
3. Depth of centrum (anterior)	32.4	20.4	—	18.4	15.2	@18.7	19.4	19.6	18.7
4. Depth of atlas from midpoint of anterior neural arch border to antero-ventral margin of centrum	49.0	—	—	—	—	—	—	—	—
5. Minimum length of lateral walls of neural arch right	12.6	—	—	—	—	—	—	6.7	—
left	@12.6	—	—	—	—	—	—	—	—
6. Maximum width across neural arch (across post zygapophysis)	>48.9	—	—	—	—	—	—	—	—

TABLE 14. MEASUREMENTS (IN MILLIMETRES) OF THE AXIS VERTEBRA OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA

<i>Genyornis newtoni</i>	
SIAM 51	
1. Length of centrum, dorsal border	>55.3
2. Width of neural canal (anteriorly)	10.4
3. Anterior width across prezygapophyses	@25.2
4. Length of lateral wall of neural arch, ventral base	
right	34.4
left	33.6
5. Depth from dorsal-most extension of neural arch to dorsal border (midpoint) of posterior articular surface of centrum	47.4
6. Width from midpoint (mediolateral) of neural arch to external border of postzygapophysis	@33.5

TABLE 15. MEASUREMENTS (IN MILLIMETRES) OF THE ANTERIOR CERVICAL VERTEBRA OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA

cf. <i>Genyornis newtoni</i>	
SAM P17320	
1. Maximum length of centrum along right lateral side	72.8
2. Length of lateral wall of neural arch, ventral base, right side	48.6
3. Length of pleurapophysis (right side)	41.0
4. Width across pleurapophyses at their posterior extensions	>51.4
5. Depth from anterior end of pleurapophysis to dorsal-most extension of diapophysis (right side)	66.4
6. Ventral width of centrum, posterior articular surface	24.1
7. Width of vertebrarterial canal (right)	16.4

TABLE 16. MEASUREMENTS (IN MILLIMETRES) OF THE MIDDLE CERVICAL VERTEBRAE OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA

<i>Genyornis newtoni</i>											
	SAM P13935 A	SAM P13935 B	SAM P17078	SAM P17079	SAM P17080	SAM P17081	SAM P17084	SAM P17086	SAM P17087	SAM P17089	SIAM 51
1. Maximum length of centrum											
dorsal border	62.6	63.0	@61.4	61.7	—	57.8	—	—	60.0	—	66.8
ventral border	66.4	66.2	@62.2	65.0	62.8	@60.1	—	—	63.5	—	70.4
2. Width of centrum (posteroventral)	32.6	>35.0	>30.3	35.8	>31.5	>23.0	33.6	35.2	32.6	—	34.4
3. Maximum depth of articular surface on centrum											
anterior (r/l)	21.8/23.4	—/—	—/—	—/23.9	—/—	—/—	—/—	—/—	—/—	—/—	—/—
posterior (r/l)	25.1/—	—/26.9	24.6/—	26.4/23.8	23.1/—	—/22.2	>22.2/22.8	—/28.7	24.6/26.4	—/—	24.8/24.5
midpoint (a/p)	10.0/	13.6/19.7	—/—	12.6/18.4	—/18.0	12.5/15.5	—/12.3	—/23.3	14.0/19.0	—/—	—/14.5
4. Length from anterior end of prezygapophyses to posterior end of postzygapophyses											
right	—	—	—	—	—	—	—	—	78.3	—	—
left	76.2	>78.0	—	—	—	—	—	—	@77.7	@87.5	—
5. Minimum length of lateral wall of neural arch, ventral base											
right	46.1	46.1	46.6	45.9	41.1	—	—	—	40.7	—	—
left	45.8	46.0	@46.9	46.5	—	40.1	—	—	40.2	—	—
6. Maximum width across post-zygapophyses	@44.7	54.4	48.7	—	47.9	—	—	—	>52.7	—	45.8
7. Minimum width of centrum, ventral surface	—	29.1	21.2	28.4	21.4	—	23.2	20.8	—	—	23.8

TABLE 17. MEASUREMENTS (IN MILLIMETRES) OF THE POSTERIOR CERVICAL VERTEBRAE OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA

	<i>Dromornithidae</i>		<i>Genyornis newtoni</i>			
	UCMP 56376	HM B769	SAM P13935 C	SAM P13935 D	SAM P13935 E	SAM P17091
1. Maximum length of centrum dorsal border	@47.1	60.0	61.0	64.4	57.5	@68.2
ventral border	—	63.6	68.1	@63.6	63.9	68.2
2. Width of centrum (posteroventral)	28.7	>34.3	37.8	38.7	37.7	39.6
3. Maximum depth of articular surface on centrum						
anterior (r/l)	@30.8/—	25.6/—	—/—	—/—	—/27.4	30.1/—
posterior (r/l)	32.5/—	—/—	28.1/29.1	31.3/29.6	31.4/31.6	31.0/32.0
midpoint (a/p)	19.0/@26.7	17.1/22.3	14.6/20.6	15.2/24.4	27.6/25.4	17.1/26.8
4. Length from anterior end of prezygapophyses to posterior end of postzygapophyses						
right	—	—	—	83.2	—	—
left	—	—	—	—	—	91.7
5. Minimum length of lateral wall of neural arch, ventral base						
right	38.5	43.3	48.5	49.2	49.9	48.0
left	39.1	42.9	48.4	—	49.8	—
6. Maximum width across postzygapophyses	—	—	55.8	61.2	@64.2	60.9
7. Minimum width of centrum, ventral surface	22.9	25.6	27.6	26.4	@30.3	26.4

TABLE 18. MEASUREMENTS (IN MILLIMETRES) OF THE CERVICO-DORSAL VERTEBRAE OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA

	<i>Dromornis stirtoni</i>				<i>Genyornis newtoni</i>		
	UCMP 119206	UCMP 66973	UCMP 70108	UCMP 70657	SAM P13935 F	SAM P13935 G	
1. Maximum length of centrum							
dorsal border	65.4	—	67.7	66.6	59.7	52.5	
ventral border	—	—	—	75.8	@57.0	52.2	
2. Width of centrum (posteroventral)	42.3	>43.6	—	—	>36.8	34.6	
3. Maximum depth of articular surface of centrum							
anterior (r/l)	44.6/49.7	40.2/39.8	—/—	@47.9/—	30.7/33.0	—/—	
posterior (r/l)	48.8/—	—/—	—/—	—/47.2	34.0/33.0	33.6/30.4	
midpoint (a/p)	28.4/—	26.9/—	—/—	22.4/36.3	20.6/@27.7	22.1/29.0	
4. Length from anterior end of prezygapophyses to posterior end of postzygapophyses							
right	—	—	>82.4	98.6	—	—	
left	—	—	—	—	—	—	
5. Minimum length of lateral wall of neural arch, ventral base							
right	56.2	47.6	58.1	—	46.7	42.5	
left	@55.4	—	—	63.4	46.6	39.7	
	UCMP 109178 (=MOW 63-79)						
6. Maximum width across postzygapophyses	—	—	—	92.5	—	63.8	
<i>Genyornis newtoni</i>							
	SAM P13935 H	SAM P13935 I	SAM P17082	SAM P17083	SAM P17085	SAM P17088	SAM P17090
1. Maximum length of centrum							
dorsal border	51.5	@54.9	53.7	56.1	57.2	58.1	>50.1
ventral border	46.7	47.4	47.4	—	—	—	—
2. Width of centrum (posteroventral)	33.9	@37.9	35.3	—	—	—	—
3. Maximum depth of articular surface of centrum							
anterior (r/l)	24.1/25.1	—/30.9	29.0/27.1	—/26.6	—/30.7	—/—	—/24.8
posterior (r/l)	—/32.0	33.5/32.5	35.4/28.9	30.8/—	—/—	—/—	—/—
midpoint (a/p)	24.5/@27.9	—/27.7	—/—	21.7/—	24.0/—	24.0/—	—/—
4. Length from anterior end of prezygapophyses to posterior end of postzygapophyses							
right	—	89.0	—	—	—	>80.2	—
left	—	—	—	—	—	—	—
5. Minimum length of lateral wall of neural arch, ventral base							
right	—	—	—	—	—	42.2	40.1
left	—	—	—	41.2	—	—	40.4
6. Maximum width across postzygapophyses	—	55.8	—	>51.6	—	>50.8	—

TABLE 19. MEASUREMENTS (IN MILLIMETRES) OF THE DORSAL VERTEBRAE OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA

	<i>Barawertornis tedfordi</i>	<i>Bullockornis planei</i>	<i>Dromornithidae cf. Ilbandornis sp.</i>
	CPC 7348	CPC 13846	CPC 13847
			UCMP 111305 (=MOW 63-151)
1. Maximum length of centrum			
dorsal border	>55.1	—	62.9
ventral border	—	—	59.6
2. Width of centrum (posteroventral)	>18.4	—	@42.4
3. Maximum depth of articular			
surface of centrum			
anterior (r/l)	—/—	—/—	44.9/40.5
posterior (r/l)	@21.4/—	—/—	47.8/—
midpoint (a/p)	—/—	—/—	22.8/—
4. Length from anterior end of			
prezygapophyses to posterior end			
of postzygapophyses			
right	—	—	94.0
left	—	>74.5	94.8
5. Minimum length of lateral wall			
of neural arch, ventral base			
right	—	—	47.9
left	—	—	51.2
6. Maximum width across			
postzygapophyses	>29.6	—	72.7
7. Maximum width across			
diapophyses	—	—	145.2

1. Requires further preparation for accurate measurement

	<i>Genyornis newtoni</i>					
	SAM P13935 J	SAM P13935 L	SAM P17092	SAM P17093	SAM P17094	SAM P17095
1. Maximum length of centrum						
dorsal border	54.8	56.6	—	59.8	58.7	52.9
ventral border	50.3	55.0	—	57.8	—	—
2. Width of centrum						
(posteroventral)	37.7	27.8	—	42.4	28.8	—
3. Maximum depth of articular						
surface of centrum						
anterior (r/l)	—/30.4	—/—	—/37.2	26.9/30.2	—/—	—/—
posterior (r/l)	32.7/—	39.3/—	—/—	—/—	—/—	—/—
midpoint (a/p)	—/—	—/33.6	34.1/—	29.8/30.1	—/29.4	—/—
4. Length from anterior end of						
prezygapophyses to posterior						
end of postzygapophyses						
right	—	—	—	—	—	—
left	—	—	74.3	—	—	—
5. Minimum length of lateral wall						
of neural arch, ventral base						
right	—	—	—	—	—	—
left	—	—	45.0	—	—	36.4
6. Maximum width across						
postzygapophyses	—	—	>69.8	—	—	—
7. Maximum width across						
diapophyses	—	—	—	—	—	—

TABLE 19. MEASUREMENTS (IN MILLIMETRES) OF THE MIDDLE CERVICAL VERTEBRAE OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA (Cont.)

	<i>Genyornis newtoni</i>				<i>Dromornithidae</i> cf. <i>Genyornis</i>	
	SAM P17096	SAM P17097	SIAM 51	SIAM 58	SIAM 61	UCMP 56336
1. Maximum length of centrum						
dorsal border	—	53.6	—	47.6	@38.4	52.3
ventral border	@58.7	51.3	53.9	45.9	37.4	>47.3
2. Width of centrum (posteroventral)	—	—	@33.0	—	24.8	29.8
3. Maximum depth of articular surface of centrum						
anterior (r/l)	—/—	—/—	—/—	—/—	19.0/18.6	—/—
posterior (r/l)	—/—	—/—	—/—	—/—	23.4/23.0	—/—
midpoint (a/p)	—/30.5	31.2/32.2	—/35.4	24.4/30.2	19.3/19.4	23.2/—
4. Length from anterior end of prezygapophyses to posterior end of postzygapophyses						
right	—	—	—	—	48.1	—
left	—	—	—	—	47.9	—
5. Minimum length of lateral wall of neural arch, ventral base						
right	—	—	—	—	30.8	37.0
left	—	—	—	—	31.0	38.3
6. Maximum width across postzygapophyses	—	—	—	—	27.6	—
7. Maximum width across diapophyses	—	—	—	—	65.8	—

TABLE 20. MEASUREMENTS (IN MILLIMETRES OF THE CAUDAL VERTEBRAE OF DROMORNITHIDAE FROM THE CENOZOIC OF AUSTRALIA

	<i>Dromornis stirtoni</i>
	UCMP 113047
1. Maximum length of centrum	
dorsal border	17.8
ventral border	16.9
2. Maximum width of centrum	
anterior	29.9
posterior	23.2
3. Depth of centrum at midpoint (laterolateral)	
anterior	17.8
posterior	18.6
4. Maximum depth of vertebra along midline	37.2
5. Maximum width across diapophyses	39.8

TABLE 21. MEASUREMENTS (IN MILLIMETRES) OF THE PHALANGES OF DIGIT II OF TERTIARY (PRE-PLEISTOCENE) DROMORNITHIDAE FROM AUSTRALIA

	<i>Dromornis stirtoni</i>	<i>Ilbandornis</i> sp.				
	UCMP 66234	UCMP 108612 (=RAS 5429A)	UCMP 66233	UCMP 70102	UCMP 70804	UCMP 71019
Phalanx 1, Digit II						
1. Total length ^a	99.9	54.3	59.0	64.3	>63.9	49.8
2. Maximum width, proximal end	34.4	12.1	14.7	—	>19.8	—
3. Maximum width, distal end	34.3	12.2	11.5	17.1	—	9.4
4. Maximum depth, proximal end	50.0	21.7	22.1	—	>22.7	@18.8
5. Depth, internal condyle	@28.5	14.1	13.8	15.4	—	11.4
6. Depth, external condyle	24.9	14.4	>13.1	>15.4	—	—
<i>Ilbandornis</i> sp.						
	UCMP 66618a	UCMP 66618b	UCMP 66628	UCMP 70679		
?Phalanx 2, Digit II						
1. Total length	—	—	11.1	11.7		
2. Maximum width, proximal end	—	—	15.0	12.2		
3. Maximum width, distal end	—	—	14.7	15.4		
4. Maximum depth, proximal end	—	—	10.1	10.1		
5. Maximum depth, distal end	—	—	7.8	8.3		
<i>Ilbandornis</i> sp.						
	UCMP 66618	UCMP 119212	UCMP 66628	UCMP 70679		
Phalanx 3, Digit II						
1. Total length	19.6	20.0	—	—		
2. Maximum width, proximal end	14.4	14.5	—	—		
3. Maximum depth, proximal end	8.2	7.9	—	—		

a. Measurement taken on dorsal surface

TABLE 22. MEASUREMENTS (IN MILLIMETRES) OF THE PHALANX 1 OF DIGIT III OF TERTIARY (PRE-PLEISTOCENE) DROMORNITHIDAE FROM AUSTRALIA

	<i>Dromornis stirtoni</i>							
	UCMP 119210	UCMP 70084	UCMP 70085	UCMP 70086	UCMP 70087	UCMP 70995		
1. Total length ^a	—	100.1	98.0	102.1	@91.8	102.2		
2. Maximum width, proximal end	—	@62.1	@58.1	>59.9	—	56.2		
3. Maximum width, distal end	>47.8	51.4	—	—	—	48.2		
4. Maximum depth, proximal end	—	56.3	46.6	54.0	51.9	>47.5		
5. Depth, internal condyle	>?26.0	>29.3	—	—	>30.2	32.6		
6. Depth, external condyle	—	32.7	@25.3	—	27.7	>27.4		
	<i>Ilbandornis</i> sp.							
	UCMP 108607 (=RAS 5421)	UCMP 66203a	UCMP 67039	UCMP 70097	UCMP 70098	UCMP 70655	UCMP 71016	UCMP 71017
1. Total length ^a	>71.7	>69.3	—	73.8	64.1	—	54.7	>65.5
2. Maximum width, proximal end	>34.4	>38.1	—	39.3	@34.8	—	37.6	>34.3
3. Maximum width, distal end	—	>31.2	@29.8	@33.2	31.2	28.1	32.6	—
4. Maximum depth, proximal end	>28.8	—	—	@35.4	@33.4	—	31.7	—
5. Depth, internal condyle	—	@21.3	@20.3	@23.2	>19.8	>18.9	21.0	—
6. Depth, external condyle	22.4	—	>17.6	19.8	@19.5	17.5	18.9	—
	<i>Ilbandornis</i> sp.						<i>Dromornithidae</i>	
	UCMP 71018	UCMP 71021	UCMP 71024	UCMP 71025	UCMP 71026	UCMP 71027	UCMP 88188	
1. Total length ^a	—	>69.7	67.9	>68.7	>65.8	@65.2	56.6	
2. Maximum width, proximal end	32.3	—	33.7	>36.6	—	34.8	25.1	
3. Maximum width, distal end	—	—	27.8	>28.1	—	@32.4	20.9	
4. Maximum depth, proximal end	30.5	>30.6	30.1	>33.1	—	33.1	24.6	
5. Depth, internal condyle	—	—	18.3	—	>18.2	21.8	@15.4	
6. Depth, external condyle	—	@17.4	16.9	19.4	—	—	13.7	
a. Measurement taken on dorsal surface								

TABLE 23. MEASUREMENTS (IN MILLIMETRES) OF PHALANX 2 DIGIT III OF TERTIARY
(PRE-PLEISTOCENE) DROMORNITHIDAE FROM AUSTRALIA

	<i>Ilbandornis</i> sp.														
	UCMP 66125	UCMP 66203b	UCMP 67017	UCMP 109179	UCMP 67080	UCMP 67089	UCMP 67090	UCMP 70590	UCMP 70591	UCMP 70592	UCMP 70594	UCMP 70595	UCMP 70646	UCMP 108611	
1. Total length	36.9	>41.4	38.6	>37.6	38.4	>39.6	40.0	38.7	37.8	41.2	>39.1	40.5	—	41.7	
2. Maximum width, proximal end	29.8	@28.8	26.1	>23.6	28.2	>24.6	30.7	27.8	27.8	>32.8	—	31.1	>30.4	>28.8	
3. Maximum width, distal end	25.7	>24.4	25.0	>23.6	26.2	—	>26.2	25.1	23.9	>30.4	—	27.0	—	—	
4. Maximum depth, proximal end	20.4	@20.0	18.6	18.4	19.1	19.6	20.4	17.9	17.4	22.6	>18.4	20.6	20.4	>21.2	
5. Depth, internal condyle	13.6	—	13.6	?	12.8	—	—	13.4	13.9	>16.2	—	14.9	—	—	
6. Depth, external condyle	>11.8	—	12.4	?	12.0	—	—	11.4	12.1	>13.5	—	14.6	—	—	

TABLE 24. MEASUREMENTS (IN MILLIMETRES) OF PHALANGES 3 AND 4 OF DIGIT III OF TERTIARY (PRE-PLEISTOCENE) DROMORNITHIDAE FROM AUSTRALIA

	<i>Dromornis stirtoni</i>	<i>Ilbandornis</i> sp.					
	UCMP 67094	UCMP 70599	UCMP 70601	UCMP 70602	UCMP 70627	UCMP 67038	UCMP 70630
Phalanx 3, Digit III							
1. Total length	>31.9	18.6	21.4	19.8	19.4	—	—
2. Maximum width, proximal end	>37.9	25.4	23.2	26.0	26.1	—	—
3. Maximum width, distal end	>35.5	21.3	23.7	24.8	24.5	—	—
4. Maximum depth, proximal end	@27.1	11.2	13.9	24.7	16.9	—	—
5. Maximum depth, distal end	14.5	9.4	12.0	11.3	>11.6	—	—
Phalanx 4, Digit III							
1. Total length	—	—	—	—	—	28.6	27.4
2. Maximum width, proximal end	—	—	—	—	—	23.8	22.7
3. Maximum depth, distal end	—	—	—	—	—	13.2	11.9

TABLE 25. MEASUREMENTS (IN MILLIMETRES) OF PHALANX 1 OF DIGIT IV OF TERTIARY (PRE-PLEISTOCENE) DROMORNITHIDAE FROM AUSTRALIA

	<i>Dromornis stirtoni</i>						<i>Ilbandornis</i> sp.								<i>Dromornithidae</i>	
	UCMP 70088	UCMP 70090	UCMP 70654	UCMP 111304	UCMP 66203c	UCMP 67042	UCMP 70099	UCMP 70100	UCMP 70101	UCMP 70103	UCMP 70104	UCMP 70105	UCMP 71020	UCMP 71023	UCMP 88186	
1. Total length ^a	>90.9	89.5	72.8	86.4	54.1	52.0	@54.8	—	—	@60.1	49.6	56.1	57.6	—	>70.6	
2. Maximum width, proximal end	>53.3	52.6	41.5	50.9	>27.6	21.9	>23.8	>22.8	—	>20.9	21.2	27.2	20.7	—	—	
3. Maximum width, distal end	—	42.2	—	44.7	>19.7	19.9	—	—	>15.9	—	>16.8	23.0	18.5	>20.9	—	
4. Maximum depth, proximal end	@41.7	44.8	39.4	41.4	22.7	22.4	23.9	23.5	—	22.7	>19.8	28.2	23.1	—	>28.2	
5. Depth, internal condyle	—	—	—	27.4	—	13.1	>15.9	—	?	12.7	>11.7	16.7	13.3	—	—	
6. Depth, external condyle	—	—	24.4	22.5	—	16.1	>15.3	—	?	—	>14.0	15.6	15.2	—	—	

a. Measurement taken on dorsal surface of phalanx

TABLE 26. MEASUREMENTS (IN MILLIMETRES) OF PHALANX 2 DIGIT IV OF TERTIARY (PRE-PLEISTOCENE) DROMORNITHIDAE FROM AUSTRALIA

	<i>Dromornis stirtoni</i>			<i>Ilbandornis</i> sp.									<i>Dromornithidae</i>	
	UCMP 67031	UCMP 67072	UCMP 70593	UCMP 108613 (=RAS 5429B)	UCMP 108615 (=RAS 5429D)	UCMP 67010	UCMP 67037	UCMP 67093	UCMP 70596	UCMP 70597	UCMP 70600	UCMP 108614 (=RAS 5429C)		
1. Total length	>31.6	31.8	26.6	24.5	25.0	—	>24.5	25.9	—	25.4	23.2	23.8		
2. Maximum width, proximal end	>31.8	33.5	27.2	21.4	21.8	20.8	21.8	19.6	20.9	20.2	20.1	>23.3		
3. Maximum width, distal end	>31.4	31.2	26.5	15.6	19.0	—	19.3	—	—	18.4	17.9	22.9		
4. Maximum depth, proximal end	@20.5	20.3	17.0	14.4	14.4	14.1	—	13.1	14.6	14.1	14.2	14.2		
5. Depth, internal condyle	—	14.3	11.3	8.1	—	—	—	—	—	—	9.9	>12.6		
6. Depth, external condyle	—	15.7	12.1	—	—	—	—	—	—	—	10.1	>11.5		

TABLE 27. MEASUREMENTS (IN MILLIMETRES) OF THE DISTAL PHALANGES OF DIGIT III OR IV OF TERTIARY (PRE-PLEISTOCENE) DROMORNITHIDAE FROM AUSTRALIA

	<i>Dromornis stirtoni</i>	<i>Dromornithidae</i>
	UCMP 70626	UCMP 114732
Terminal Phalanx Digit?		
1. Total length	36.8	—
2. Maximum width, proximal end	21.6	—
3. Maximum depth, proximal end	16.5	—
Phalanx 2 or 3, Digit III or Phalanx 2, Digit IV		
1. Total length	—	38.3
2. Maximum width, proximal end	—	33.6
3. Maximum width, distal end	—	29.1
4. Maximum depth, proximal end	—	21.8
5. Maximum depth, distal end	—	10.9

TABLE 28. MEASUREMENTS (IN MILLIMETRES) OF THE PHALANGES OF PLEISTOCENE DROMORNITHIDAE FROM AUSTRALIA

	<i>Genyornis newtoni</i>																	<i>Dromornithidae</i> gen. et. sp. indet.						
	AMNH			SAM											SIAM			UCMP		SAM				
	2646	2647	2648	P13868	P13869	P13870	P13870	P17044	P17045	P17057	47	51	51	51	58	85	47957	P17137	P17138	47918				
				A			B	C	K			A		B	C									
Phalanx 1, Digit II																								
1. Total length ^a	—	81.8	—	84.9	—	—	—	—	84.4	84.5	—	—	90.6	@88.2	—	83.2	83.6	—	—	—	—			
2. Maximum width, proximal end	—	17.4	—	—	—	—	—	—	20.3	17.9	—	—	19.3	—	—	17.2	19.4	—	—	—	—			
3. Maximum width, distal end	—	17.3	—	19.8	—	—	—	—	19.0	18.6	—	18.3	18.9	—	—	—	—	—	—	—	—			
4. Maximum depth, proximal end	—	—	—	—	—	—	—	—	33.8	@31.4	—	—	32.2	—	—	28.9	32.4	—	—	—	—			
5. Depth, internal condyle	—	16.0	—	17.7	—	—	—	—	18.9	17.9	—	16.8	18.9	—	—	—	16.4	—	—	—	—			
6. Depth, external condyle	—	@16.4	—	20.2	—	—	—	—	19.4	19.2	—	>18.1	19.1	—	—	—	—	—	—	—	—			
Phalanx 2, Digit II																								
1. Total length	—	18.9	—	21.3	—	—	—	—	19.2	18.1	—	17.4	17.9	20.9	—	—	20.0	—	—	—	—			
2. Maximum width, proximal end	—	17.2	—	19.0	—	—	—	—	18.5	20.0	—	19.6	20.6	16.8	—	—	18.0	—	—	—	—			
3. Maximum width, distal end	—	17.4	—	18.7	—	—	—	—	18.4	18.6	—	21.2	19.3	17.4	—	—	20.4	—	—	—	—			
4. Maximum depth, proximal end	—	12.6	—	14.4	—	—	—	—	13.6	14.2	—	13.6	13.3	13.2	—	—	13.1	—	—	—	—			
5. Maximum depth, distal end	—	9.7	—	10.6	—	—	—	—	—	11.4	—	11.6	10.1	9.5	—	—	9.7	—	—	—	—			
Phalanx 3, Digit II																								
1. Total length	—	>20.0	—	—	—	—	—	—	>14.8	@ 17.9	—	18.7	16.6	17.6	—	—	15.1	—	—	—	—			
2. Maximum width, proximal end	—	15.3	—	—	—	—	—	—	11.2	17.4	—	16.8	14.3	12.0	—	Arthritic	12.7	—	—	—	—			
3. Maximum depth, proximal end	—	8.8	—	—	—	—	—	—	7.1	11.4	—	10.8	9.4	9.1	—	—	7.5	—	—	—	—			
Phalanx 1, Wigit III																								
1. Total length	74.6	—	—	—	76.2	—	—	—	78.7	79.1	—	72.1	77.2	76.1	76.6	76.7	78.8	—	—	68.7	—			
2. Maximum width, proximal end	39.2	—	—	—	44.4	—	—	—	44.6	45.2	—	45.5	43.7	@39.9	44.7	41.6	42.7	—	—	35.3	—			
3. Maximum width, distal end	38.1	—	—	—	41.4	—	—	—	41.9	42.8	—	38.3	38.9	36.4	—	37.2	40.3	40.4	—	—	—			
4. Maximum depth, proximal end	40.7	—	—	—	43.0	—	—	—	44.8	45.0	—	—	42.4	42.4	41.5	38.7	43.9	—	—	>29.2	—			

TABLE 28—Cont.

	<i>Genyornis newtoni</i>																	<i>Dromornithidae</i> gen. et sp. indet			
	AMNH		2648	P13868	P13869	P13870	SAM			P17045	P17057	47	51	SIAM		58	85	USMP	SAM		
	2646	2647					P13870	P17044	P17045					51	51				P17137	P17138	47918
							A	B	C		K		A	B	C						
5. Depth, internal condyle	25.7	—	—	—	28.4	—	—	—	29.9	29.4	—	25.4	24.0	26.2	26.4	23.1	29.3	>27.6	—	@18.6	—
6. Depth, external condyle	—	—	—	—	22.8	—	—	—	24.2	24.5	—	20.6	28.3	21.8	—	19.7	>23.7	>22.4	—	—	—
Phalanx 2, Digit III																					
1. Total length	41.3	—	—	—	—	—	—	—	45.0	46.4	47.0	39.7	45.5	44.6	—	42.0	46.9	—	38.6	—	37.3
2. Maximum width, proximal end	36.7	—	—	—	—	—	—	—	41.9	42.1	39.3	37.8	36.2	34.6	—	35.7	38.8	—	29.3	—	27.8
3. Maximum width, distal end	32.5	—	—	—	35.0	—	—	—	34.3	36.2	33.8	31.4	31.6	30.4	—	30.1	—	—	26.7	—	25.8
4. Maximum depth proximal end	25.0	—	—	—	—	—	—	—	26.6	27.3	@32.1	24.1	25.5	25.2	—	23.1	27.4	—	@22.6	—	20.8
5. Depth, internal condyle	14.9	—	—	—	17.4	—	—	—	>17.1	17.6	16.9	14.6	17.2	15.3	—	12.6	17.1	—	—	—	—
6. Depth, external condyle	14.5	—	—	—	16.7	—	—	—	15.8	17.4	15.8	15.0	15.2	14.3	—	—	@15.8	—	—	—	—
Phalanx 3, Digit III																					
1. Total length	19.5	—	—	—	—	—	—	—	20.8	22.6	—	18.1	19.3	19.6	—	15.3	22.5	—	—	—	—
2. Maximum width, proximal end	29.8	—	—	—	—	—	—	—	34.4	34.2	—	29.1	26.9	19.4	—	26.2	31.4	—	—	—	—
3. Maximum width, distal end	—	—	—	—	—	—	—	—	34.3	32.9	—	28.5	30.6	29.3	—	27.4	31.9	—	—	—	—
4. Maximum depth, proximal end	—	—	—	—	—	—	—	—	18.6	29.1	—	16.1	16.9	15.8	—	15.3	@18.2	—	—	—	—
5. Maximum depth distal end	12.6	—	—	—	—	—	—	—	15.1	14.3	—	13.3	12.9	12.9	—	11.6	13.9	—	—	—	—
Phalanx 4, Digit III																					
1. Total length	25.0	—	—	—	—	—	—	—	26.9	26.5	—	25.6	28.6	24.2	—	24.4	26.1	—	—	—	—
2. Maximum width, proximal end	—	—	—	—	—	—	—	—	31.0	30.7	—	27.4	23.6	25.6	—	22.8	28.6	—	—	—	—
3. Maximum depth, proximal end	—	—	—	—	—	—	—	—	13.9	14.0	—	13.2	15.1	13.8	—	13.1	13.8	—	—	—	—
Phalanx 1, Digit IV																					
1. Total length	—	—	66.5	—	—	69.3	—	—	70.9	72.1	—	66.3	72.8	69.8	—	67.7	70.2	—	—	—	—
2. Maximum width, proximal end	—	—	31.1	—	—	—	—	—	36.7	36.8	—	32.9	34.6	31.6	—	31.9	34.0	—	—	—	—
3. Maximum width, distal end	—	—	26.7	—	—	@29.2	—	—	28.8	29.3	—	28.0	29.3	25.9	—	>25.9	29.8	—	—	—	—

TABLE 28—Cont.

	Genyornis newtoni																Dromornithidae gen. et sp. indet				
	2646	AMNH 2647	2648	P13868	P13869	P13870	SAM							SIAM				USMP 47957		SAM P17138	47918
						P13870	P13870	P17044	P17045	P17057	47	51	51	51	58	85					
4. Maximum depth, proximal end	—	—	33.4	—	—	—	—	37.7	—	—	34.2	36.6	34.8	—	31.9	35.2	—	—	—	—	
5. Depth, internal condyle	—	—	—	—	—	21.4	—	21.5	20.8	—	19.4	23.9	19.8	—	>17.6	21.6	—	—	—	—	
6. Depth, external condyle	—	—	19.8	—	—	19.8	—	20.3	—	—	18.4	>22.4	19.3	—	>16.4	—	—	—	—	—	
Phalanx 2, Digit IV																					
1. Total length	—	—	30.6	—	—	—	—	30.3 @32.4	28.5	—	25.4	29.8 @27.4	—	26.1	31.2		—	—	—	—	
2. Maximum width, proximal end	—	—	29.0	—	—	—	—	29.4	27.0	26.7	—	28.1	28.3	25.4	—	25.4	28.6	—	—	—	
3. Maximum width, distal end	—	—	25.1	—	—	—	—	@28.5	—	23.9	—	24.6	25.1	12.6	—	22.9	24.8	—	—	—	
4. Maximum depth, proximal end	—	—	29.4	—	—	—	—	18.7	18.1	17.8	—	17.4	19.6	—	—	17.5	21.7	—	—	—	
5. Depth, internal condyle	—	—	11.4	—	—	—	—	14.1	12.3	—	11.9	14.2	13.2	—	10.4	14.9	—	—	—	—	
6. Depth, external condyle	—	—	14.3	—	—	—	—	14.1	—	10.0	—	10.3	10.4	11.0	—	9.8	12.4	—	—	—	
Phalanx 3, Digit IV																					
1. Total length	—	—	11.7	—	—	—	—	>21.1	12.4	12.4	—	9.1	12.4	12.2	—	9.8	15.2	—	—	—	
2. Maximum width, proximal end	—	—	20.5	—	—	—	—	32.6	22.1	23.7	—	11.0	23.4	21.8	—	18.9	25.6	—	—	—	
3. Maximum width, distal end	—	—	24.7	—	—	—	—	30.9	21.9	21.9	—	20.6	23.4	21.2	—	18.6	26.0	—	—	—	
4. Maximum depth, proximal end	—	—	11.4	—	—	—	—	17.8	11.9	12.9	—	10.9	11.9	11.4	—	11.0	13.8	—	—	—	
5. Maximum depth, distal end	—	—	9.5	—	—	—	—	14.6	9.6	9.1	—	9.0	10.1	9.2	—	8.5	11.6	—	—	—	
Phalanx 4, Digit IV																					
1. Total length	—	—	—	—	>27.4	—	19.6	—	19.6	21.0	—	>21.9	19.8	—	—	18.1	19.4	—	—	—	
2. Maximum width, proximal end	—	—	—	—	24.9	—	21.4	—	>13.0	14.8	—	16.2	15.7	—	—	13.9	18.1	—	—	—	
3. Maximum depth, proximal end	—	—	—	—	>13.3	—	10.1	—	8.9	7.8	—	8.6	9.1	—	—	8.2	7.8	—	—	—	

@ = Measurement taken on dorsal surface.

@ = Measurement taken on dorsal surface.

TABLE 29. MEASUREMENTS (IN MILLIMETRES) OF TERMINAL PHALANGES OF UNKNOWN CLASS

	UCMP 109178 (=MOW 63-79)	UCMP 70091	UCMP 70092	UCMP 70643
1. Total length	>69.5	@71.2	>42.1	>65.5
2. Maximum width, proximal end	35.1	36.7	23.2	33.1
3. Maximum depth, proximal end	25.0	22.8	17.9	24.0
4. Maximum depth, proximal articular surface	19.1	18.1	13.9	21.2

TABLE 30. STATISTICAL TREATMENT OF FEMORAL MEASUREMENTS OF *DROMAIUS MINOR*

	n	M	SD	SE	CV	R (in mm)	
Proximal end							
1. Maximum width	47	42.8	6.4	0.9	14.8	28.0–	52.9
2. Depth of head	55	18.1	2.4	0.3	13.1	12.0–	20.8
3. Maximum depth, proximal end	18	39.8	4.5	1.1	11.3	>25.6–	45.3
Distal end							
4. Maximum width across condyles	42	48.7	6.3	1.0	12.9	@26.6–	55.5
5. Maximum width, internal condyle, posterior surface	13	18.7	2.3	0.6	12.1	15.4–	22.3
6. Maximum depth, internal condyle	30	33.8	5.2	1.0	15.4	>19.3–	39.0
7. Maximum length, internal condyle, internal margin	11	28.6	1.8	0.5	6.2	26.6–	31.9
8. Maximum width, external condyle, posterior surface	12	13.8	1.8	0.5	13.0	9.3–	16.0
9. Maximum depth, external condyle	63	46.5	4.6	0.6	9.8	@27.6–	53.9
10. Maximum depth, fibular condyle							
11. Minimum shaft width	93	20.2	2.8	0.3	13.7	11.3–	25.5
12. Minimum shaft depth	93	18.0	2.5	0.3	14.1	10.4–	22.4
13. Total length of femur	59	161.8	16.4	2.1	10.1	@106.5–>	188.4

TABLE 31. MEASUREMENTS (IN MILLIMETRES) OF THE FEMORA OF DROMORNITHIDAE FROM THE TERTIARY (PRE-PLEISTOCENE) OF AUSTRALIA

	<i>Barawertornis tedfordi</i>		<i>Bullockornis planei</i>		<i>Ilbandornis woodburnei</i>	<i>Dromornis stirtoni</i>				<i>Dromornis australis</i>	
	CPC 7341 (type)	7347	CPC 13845	13844 (type)	13850 (type)	70648	UCMP 70112	70114	70115	CPC 13851 (type)	AM F10950 (type)
Proximal end											
1. Maximum width	—	—	140.3	—	106.9	140.9	@197.5	169.2	—	>193.4	131.2
2. Depth of head	31.0	—	61.6	—	@41.3	—	94.1	>70.0	—	>96.3	52.8
3. Maximum depth, proximal end	—	—	—	141.1	55.1	—	174.5	—	—	>129.5	—
Distal end											
4. Maximum width across condyles	87.6	—	160.0	>152.2	112.1	170.6	205.2	202.8	—	214.2	@120.1
5. Maximum width, internal condyle, posterior surface	48.7	—	83.7	76.2	64.2	>88.9	115.5	122.2	—	122.9	—
6. Maximum depth internal condyle	—	>59.6	—	122.2	80.6	100.0	—	—	—	—	—
7. Maximum length, internal internal condyle,	@44.1	—	@86.3	@80.3	@52.5	—	@105.9	—	—	@71.1	—
8. Maximum width, external condyle, posterior surface	19.4	—	—	22.9	@21.8	34.4	—	29.0	@37.5	@46.1	—
9. Maximum depth, external condyle	68.6	—	137.0	@125.8	>76.2	—	143.0	126.2	>118.4	153.6	—
10. Maximum depth, fibular condyle	57.0	46.3	—	90.0	72.5	@86.9	—	100.4	—	119.7	—
11. Distal width rotular groove	@51.2	—	—	@73.3	@59.2	94.2	—	—	—	—	—
12. Minimum shaft width	—	—	—	64.4	@54.9	74.6	92.3	77.3	—	@88.5	61.2
13. Minimum shaft depth	29.7	—	@67.4	60.6	@46.8	53.1	82.1	@56.7	—	@81.9	42.8
14. Total length of femur (trochanter to distal end external condyle)	226.2	—	349	>359 (slightly)	281.3	390	470.0	443	—	425	>280.8
15. Total length of femur (head to distal end internal condyle)	216.0	—	303.7	—	260.3	—	—	365.6	—	@343.7	—

TABLE 32. MEASUREMENTS OF FEMORA OF *GENYORNIS NEWTONI*, INCLUDING STATISTICAL TREATMENT; MEASUREMENTS (IN MILLIMETRES)

	P13864	P13878	P17001	P17002	P17003	P17004	SAM		P17006	P17007
							P17005			
Proximal end										
1. Maximum width	—	179.8	159.9	—	@177.0	>193.4	@168.6	—	—	—
2. Depth of head	70.9	70.3	59.7	63.6	64.3	@62.3	62.0	—	—	—
3. Maximum depth, proximal end	—	120.0	100.8	119	—	—	—	—	—	—
Distal end										
4. Maximum width across condyles	176.7	172.6	163.3	@172.7	>168.3	164.4	—	—	—	161.9
5. Maximum width, internal condyle, posterior surface	83.7	77.4	76.0	71.6	75.4	73.1	—	—	—	75.8
6. Maximum depth, internal condyle	—	—	99.0	>95.8	—	—	—	—	—	84.2
7. Maximum length, internal condyle, internal margin	67.0	75.7	65.1	>74.7	62.0	@63.6	—	—	—	73.3
8. Maximum width, external condyle, posterior surface	41.0	39.8	34.1	—	—	34.9	—	—	43.1	37.3
9. Maximum depth, external condyle	124.9	119.9	109.4	—	—	—	—	—	—	95.3
10. Distal width, rotular groove	113.0	110.6	96.0	@101.2	—	—	—	—	—	106.0
11. Minimum shaft width	78.2	90.1	68.3	74.5	—	75.3	79.4	@74.5	—	—
12. Minimum shaft depth	61.9	55.7	51.3	57.9	—	55.0	—	@48.0	—	—
13. Total length of femur	>333	>338	328	300	>330	>320	—	—	—	—

	P17008	P17009	P17010	P17011	P17043	n	Statistics					R (in mm)
							M	SD	SE	CV		
Proximal end												
1. Maximum width	—	—	—	—	—	4	171.5	9.1	4.6	5.3	159.9–179.8	
2. Depth of head	59.0	62.6	—	—	—	9	64.0	4.2	1.4	6.5	59.0– 70.9	
3. Maximum depth, proximal end	—	—	—	—	—	2	110.4	13.6	9.6	12.3	100.8–120.0	
Distal end												
4. Maximum width across condyles	—	—	159.7	@155.8	—	8	165.9	7.3	2.6	4.4	155.8–176.7	
5. Maximum width, internal condyle, posterior surface	—	79.4	—	75.9	—	9	76.5	3.5	1.2	4.6	71.6– 83.7	
6. Maximum depth, internal condyle	—	—	@89.7	99.6	—	4	93.1	7.5	3.7	8.0	84.2– 99.6	
7. Maximum length, internal condyle, internal margin	—	—	@75.7	75.7	—	8	69.8	5.9	2.1	8.5	62.0– 75.7	
8. Maximum width, external condyle, posterior surface	—	—	32.1	—	32.7	8	36.9	4.1	1.4	11.1	32.1– 43.1	
9. Maximum depth, external condyle	—	—	@107.9	—	115.8	6	112.2	10.4	4.3	9.3	95.3–124.9	
10. Distal width, rotular groove	—	—	@91.5	—	—	6	103.1	8.4	3.4	8.1	91.5–113.0	
11. Minimum shaft width	—	@69.3	64.9	—	—	9	74.9	7.4	2.5	9.9	64.9– 90.1	
12. Minimum shaft depth	—	@63.6	57.2	—	—	8	56.3	5.1	1.8	9.1	48.0– 63.6	
13. Total length of femur	—	—	—	—	—	1	—	—	—	—	328 –>338	

TABLE 33. STATISTICAL TREATMENT OF TIBIOTARSAL MEASUREMENTS OF *DROMAIUS MINOR*

	n	M	SD	SE	CV	R (in mm)	
Proximal end							
1. Width							
Anterior border	6	45.5	2.2	0.9	4.7	43.4–	49.2
Posterior border	47	36.9	3.7	0.5	10.0	28.2–	45.8
2. Depth (across inner cnemial crest)	12	66.6	4.4	1.3	6.6	60.8–	>77.1
3. Length of fibular crest	17	73.0	7.9	1.9	10.8	61.8–	87.8
4. Width of shaft at proximal end of crest	76	25.1	3.4	0.4	13.6	18.9–	33.5
Distal end							
5. Width across condyles	51	34.0	2.4	0.3	7.2	29.5–	41.7
6. Depth, internal condyles	50	30.4	2.2	0.3	7.4	26.2–	36.1
7. Depth, external condyle	47	30.0	2.4	0.4	8.0	26.3–	38.1
8. Width of distal end across internal ligamental process	26	35.0	3.0	0.6	8.5	30.4–	43.6
9. Minimum length of supratendinal bridge							
Internal	—	—	—	—	—	—	—
External	—	—	—	—	—	—	—
10. Minimum width of shaft	62	18.3	1.6	0.2	8.8	14.0–	23.2
11. Minimum depth of shaft	89	12.4	1.0	0.1	8.0	9.3–	14.9
12. Total length of tibiotarsus	13	302.7	27.6	7.6	9.1	275.0–	354.8

TABLE 34. MEASUREMENTS (IN MILLIMETRES) OF THE TIBIOTARSI OF DROMORNITHIDAE FROM THE TERTIARY (PRE-PLEISTOCENE) OF AUSTRALIA

	<i>I. cf. lawsoni</i>	<i>Ilbandornis</i>	<i>Ilbandornis</i> sp.		<i>Dromornis stirtoni</i>
	UCMP 70118	UCMP 108606	UCMP 108603 (=RAS 5403f)	UCMP 70649	UCMP 71415
Proximal end					
1. Width					
Anterior border	—	—	—	—	—
Posterior border	—	—	—	—	—
2. Depth (across inner cnemial crest)	>94.3	—	—	—	—
3. Length of fibular crest					
4. Width of shaft at proximal end of fibular crest	—	—	—	—	—
Distal end					
5. Width across condyles	>65.6	>66.7	@76.7	>76.5	>139.2
6. Depth, internal condyle	—	—	—	>62.0	>117.1
7. Depth, external condyle	@48.6	@52.2	>50.5	—	>70.0
8. Width of distal end across internal ligamental process	—	—	—	—	>142.8
9. Minimum length of supratendinal bridge					
Internal	—	—	—	20.5	—
External	—	—	—	@19.5	@23.9
10. Minimum width of shaft	@33.7	—	—	—	—
11. Minimum depth of shaft	@24.8	—	—	—	—
12. Total length of tibiotarsus	>520	—	—	—	—
	left	left	right	right	left

TABLE 35. MEASUREMENTS (IN MILLIMETRES) OF THE TRIBIOTARSI OF *GENYORNIS NEWTONI* AND OTHER PLEISTOCENE DROMORNITHIDAE INCLUDING STATISTICAL TREATMENT

Lake Callabonna, S.A. SAM																			
	P13866 (right)	P13927 (right)	P17026 (left)	P17027 (right)	P17028 (left)	P17029 (right)	P17030 (left)	P17031 (left)	P17032 (right)	P17033 (left)	AMNH 2499 (right)	Cuddie Springs N.S.W. AM 33402 (right)	Dromornithidae, gen. et sp. indet. Salt Ck., S.A. SAM P17099	n	Statistics of <i>Genyornis newtoni</i>				
															M	SD	SE	CV	Range
Measurements																			
Proximal end																			
1. Width Posterior border	—	147.1	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	147.1
2. Depth (across inner cnemial crest)	—	203.8	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	203.8
3. Length of fibular crest	—	181.6	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	181.6
4. Width of shaft at proximal end of fibular crest	—	88.1	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	88.1
Distal end																			
5. Width across condyles	87.9	94.0	86.8	88.0	85.0	79.9	89.3	76.7	74.0	87.5	>82.9	88.5	—	11	85.2	5.9	1.8	7.0	74.0–94.0
6. Depth, internal condyle	92.5	92.7	87.9	88.9	88.1	82.9	93.6	82.4	82.5	89.5	84.1	—	—	11	87.7	4.2	1.3	4.8	82.4–92.7
7. Depth, external condyle	72.0	74.5	67.6	69.8	69.1	65.9	71.1	@65.0	63.9	70.7	—	—	—	10	69.0	3.3	1.1	4.9	63.9–74.5
8. Width of distal end across intenal ligamental prominence	89.7	91.6	88.2	87.8	84.8	78.8	91.9	78.9	—	86.4	@84.1	87.2	—	11	86.3	4.4	1.3	5.1	78.8–84.1
9. Minimum length of supratendinal bridge																			
Internal	14.9	—	—	11.6	—	—	—	@17.9	—	—	—	18.1	—	4	15.6	3.1	1.5	19.6	11.6–18.1
External	12.8	—	—	17.1	—	—	—	17.4	—	—	—	19.8	—	4	16.8	3.0	1.5	17.4	12.8–19.8
10. Minimum width of shaft	53.2	55.3	52.1	48.0	46.2	—	51.2	47.0	—	50.1	47.5	—	46.8	9	50.1	3.1	1.0	6.2	46.2–55.3
11. Minimum depth of shaft	@38.1	38.6	36.5	39.4	@33.7	—	38.2	33.5	—	39.1	35.9	—	35.0	9	37.0	2.2	0.7	6.0	33.5–39.4
12. Total length of tibiotarsus	—	6021	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	602

1. From Stirling and Zietz, 1900. Figure d. specimen in that description.

TABLE 36. STATISTICAL TREATMENT OF TARSO METATARSAL MEASUREMENTS (IN MILLIMETRES) OF *DROMAIUS MINOR*

	n	M	SD	SE	CV	R
Proximal end						
1. Width	68	36.9	2.7	0.3	7.3	30.6– 46.0
2. Depth of internal cotyla	62	21.1	2.1	0.3	10.1	16.0– 27.4
3. Depth of external cotyla	28	18.2	2.0	0.4	10.8	14.8– 22.9
4. Depth across intercotylar area to posterior extension of hypotarsus	42	27.7	2.2	0.3	7.9	22.4– 31.2
Distal end						
5. Width	61	40.6	2.9	0.4	7.1	34.4– 47.4
6. Width of trochlea II	63	8.1	1.0	0.1	12.1	6.0– 11.4
7. Width of trochlea III	50	17.3	1.5	0.2	8.8	13.7– 19.9
8. Width of trochlea IV	52	11.3	1.5	0.2	13.5	8.4– 15.6
9. Depth of trochlea II						
Internal	62	12.0	1.3	0.2	10.5	8.4– 14.0
External	14	15.5	4.3	1.1	27.7	9.2– 22.0
10. Depth of trochlea III						
Internal	60	18.4	2.5	0.3	13.6	12.2– 22.8
External	6	17.1	3.5	1.4	20.5	12.0– 20.6
11. Depth of trochlea IV						
Internal	51	14.1	1.2	0.2	8.3	11.1– 16.1
12. Minimum shaft width	52	13.2	1.1	0.2	8.7	11.0– 16.1
13. Minimum shaft depth	79	9.4	0.7	0.1	7.9	7.6– 11.5
14. Total length of tarsometatarsus	50	235.3	18.6	2.6	7.9	207.8–285.4

TABLE 37. MEASUREMENTS (IN MILLIMETRES) OF THE TARSONOMETATARSUS OF

	<i>Barawer-</i> <i>tornis</i>	<i>Bullockornis</i>		<i>Ilbandornis</i>				
	<i>ted-</i> <i>fordi</i> CPC 7346 (left)	<i>B.</i> <i>sp</i> CPC 13849 (right)	<i>B.</i> <i>planei</i> CPC 13849 (right)	<i>I. wood-</i> <i>burnei</i> UCMP 67465 (right)	<i>I.</i> <i>lawsoni</i> CPC 13852 Type (right)	<i>I. cf.</i> <i>lawsoni</i> UCMP 108600 (=RAS 5403a) (right)	<i>I. cf.</i> <i>lawsoni</i> UCMP 108604 (=RAS 5403b) (right)	108602 (=RAS 5403d) ?
Proximal end								
1. Width	—	75.6	116.0	>91.8	—	—	@67.0	—
2. Depth of internal cotyla	—	50.4	71.6	54.0	—	—	—	—
3. Depth of external cotyla	—	36.4	55.4	41.9	—	—	39.4	—
4. Depth across intercotylar area to posterior extension of hypotarsus	—	65.9	>102.4	70.7	—	—	@56.0	—
Distal end								
5. Width	>61.4	—	120.3	—	>71.4	—	—	—
6. Width of trochlea II (anterior)	—	—	32.5	—	—	—	—	—
7. Width of trochlea III (anterior)	—	—	50.9	@37.9	>36.2	>36.8	—	36.8
8. Maximum width of trochlea IV (anterior)	21.8	—	26.2	—	@26.2	21.6	—	—
9. Depth of trochlea II								
Internal	—	—	36.9	—	—	—	—	—
External	—	—	53.6	—	24.4	—	—	—
10. Depth of trochlea III								
Internal	—	—	>73.4	—	>43.0	—	—	—
External	33.8	—	73.8	@45.2	@42.4	37.2	—	—
11. Depth of trochlea IV								
Internal	—	—	45.1	—	>36.4	31.0	—	—
12. Minimum shaft width	—	—	@45.0	37.5	30.5	—	—	—
13. Minimum shaft depth	—	—	@40.6	—	—	—	—	—
14. Total length of tarsometatarsus	—	—	—	@370.0	>447.0	—	—	—

DROMORNITHIDAE FROM THE TERTIARY (PRE-PLEISTOCENE) OF AUSTRALIA

<i>Ibandornis</i> sp.						<i>Dromornis stirtoni</i>					
108601 (=RAS 5403e) (left)	108605 (=RAS 5410) juvenile (left)	UCMP 70094 (right)	70095 (left)	70096 (left)	70653 (right)	108608 (=RAS 5420) ?	70117 (left)	UCMP 70106 (left)	70647 (right)	70652 (right)	70656 (left)
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	98.6	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	55.4	>71.7	@72.0	71.5	—	—	—	150.2	>124.5	@150.0	—
—	10.4	—	15.5	@14.8	16.1	—	—	33.8	>34.2	—	@40.5
33.5	28.2	@31.6	>34.8	>33.7	>36.5	@64.4	>72.8	65.2	>55.4	60.8	>62.0
—	16.1	24.9	>23.3	—	>27.2	—	34.7	>40.8	42.4	39.4	>47.8
—	16.7	—	—	—	—	—	—	48.3	—	—	—
—	16.3	—	@20.2	23.6	29.2	—	—	53.8	48.1	66.5	52.1
37.4	27.4	>37.6	@37.8	@36.5	@42.2	63.0	>79.9	@84.8	67.4	72.3	—
37.6	29.0	>35.9	41.9	@37.2	@43.8	63.0	87.3	>82.3	—	73.6	—
—	16.8	31.1	30.2	>32.4	—	—	66.4	—	>48.3	56.7	—
—	—	—	—	—	—	—	62.1	77.1	68.5	@66.4	61.1
—	—	20.4	—	—	—	—	62.4	32.0	56.8	@37.0	—
—	—	—	—	—	—	—	—	464.2	—	—	—

TABLE 38. MEASUREMENTS (C

Taxon Locality	LAKE CALLABONNA, S.A. (<i>Genyornis newtoni</i>)							
Specimen Numbers	AM F4486 (left)	P17013 (left)	P17014 (left)	P17015 (right)	P17016 (left)	P17017 (left)	P17018 (left)	P17019 (left)
Proximal end								
1. Width	@97.9	@102	@100	111.3	103.0	@96.4	>95	@104
2. Depth of internal cotyla	57.0	—	@50.8	56.9	47.9	51.9	—	—
3. Depth of external cotyla	—	43.2	45.0	49.8	42.2	44.8	38.7	45
4. Depth across intercotylar area to posterior extension of hypotarsus	81.8	79.5	77.8	84.3	77.1	80.3	@71.9	84
Distal end								
5. Width	90.6	99.0	90.5	106.6	92.3	94.6	88.8	@99
6. Width of trochlea II								
Anterior surface	15.7	@14.3	13.6	15.2	16.3	13.9	14.7	14
Posterior surface	—	@12.0	14.0	16.2	15.5	13.6	13.7	16
7. Width of trochlea III								
Anterior surface	38.8	42.6	43.8	45.5	44.8	43.4	40.2	45
Posterior surface	—	36.2	34.3	36.1	35.4	32.5	33.9	38
8. Width of trochlea IV								
Anterior surface	24.6	33.0	28.9	36.7	32.9	31.6	29.3	28
Posterior surface	—	22.3	23.8	26.8	—	—	21.6	26
9. Depth of trochlea II								
External	27.4	26.2	27.3	33.3	28.5	30.8	30.3	31
10. Depth of trochlea III								
Internal	52.9	54.4	—	58.1	52.9	52.2	53.8	55
External	51.2	51.7	51.3	56.6	51.7	51.2	—	56
11. Depth of trochlea IV								
Internal	44.2	45.5	43.7	47.8	44.6	43.8	43.3	46
12. Minimum shaft width	38.9	41.2	42.2	41.3	41.2	38.2	38.2	39
13. Minimum shaft depth	27.3	27.2	30.8	31.8	30.0	28.9	26.2	29
14. Total length of tarsometatarsus	—	356	347	355	346	330	>320	350

MILLIMETRES) OF *GENYORNIS NEWTONI* AND OTHER PLIO-PLEISTOCENE DROMORNITHIDAE FROM AUSTRALIA

Dromornithidae gen. et. sp. indet.																									
LAKE CALLABONNA, S.A. (<i>Genyornis newtoni</i>)								LANCE- FIELD VIC.	LAKE CALLABONNA, S.A.				CUDDIE SPRINGS N.S.W. (<i>Genyornis newtoni</i>)				WAR- BUR- TON RIVER, SA	COO- PERS CREEK, SA	WAR- BUR- TON RIVER, SA	Statistics for <i>G. newtoni</i>					
right)	(right)	SAM (right)	P17023 (left)	P17024 (right)	P17025 (left)	P17036 (right)	P13865 (right)	NMV 41827 (left)	AMNH 2654 (right)	SIAM 58 (right)	SIAM 85 (left)	AM 33406 (left)	AM 33408 (left)	AM 33409 (right)	AM F16777 (right)	UCMP 119353 (right)	HM G1011 (left)	SAM P17135 (left)	n	M	SD	SE	CV	R (in mm)	
108.2	98.5	100.7	107.2	>101.1	103.9	—	>96.3	—	—	—	—	>102.9	—	—	—	—	—	—	13	102.8	4.3	1.2	4.2	96.4–111.3	
—	—	60.6	54.8	54.5	60.5	—	55.8	—	53.6	—	—	55.6	—	—	—	—	—	—	12	55.0	3.7	1.1	6.7	47.9– 60.0	
—	41.9	49.5	47.3	48.1	48.5	—	45.3	—	—	—	—	@46.2	—	—	—	—	—	—	14	45.4	3.2	0.8	7.0	38.7– 49.8	
83.4	73.4	—	@85	75.9	—	—	84.5	—	77.3	—	—	79.6	—	—	—	—	—	—	15	79.7	4.2	1.1	5.2	71.9– 85.0	
103.1	—	98.0	102.1	93.8	93.1	—	101.4	—	93.2	90.3	97.5	94.5	—	—	—	—	—	—	18	96.1	5.1	1.2	5.3	88.8–106.6	
17.2	—	—	16.4	—	16.5	@16.3	17.6	—	15.5	14.9	—	—	—	—	—	—	—	—	15	15.5	1.2	0.3	7.6	13.6– 17.2	
14.6	—	15.1	16.8	—	15.3	15.3	—	—	14.7	13.7	—	15.0	—	15.2	—	—	—	—	16	14.8	1.2	0.3	8.1	12.0– 16.8	
46.8	40.2	44.5	47.2	40.7	43.7	—	41.8	—	—	40.8	—	—	—	—	—	40.6	>38.8	—	17	43.0	2.5	0.6	5.9	40.2– 47.2	
37.0	32.7	—	35.7	—	—	35.8	32.0	—	32.6	32.5	—	34.8	—	@31.2	—	29.2	>27.6	—	17	34.1	2.3	0.6	6.9	29.2– 38.2	
32.8	30.1	—	33.9	} 29.3	32.5	—	33.3	—	—	28.0	30.0	—	>28.0	—	—	—	—	—	16	30.9	3.0	0.8	9.7	28.0– 36.7	
—	21.6	33.5	27.0		26.7	24.9	25.8	—	23.6	21.8	—	23.6	—	—	—	—	—	—	14	25.0	3.2	0.8	12.7	21.6– 33.5	
130.8	—	@29.9	32.1	29.3	29.0	31.8	—	—	—	27.6	30.9	30.6	—	—	—	—	>27.6	—	17	29.8	1.9	0.5	6.5	26.2– 33.3	
57.4	—	51.6	59.1	53.1	53.2	—	57.7	—	—	—	—	—	—	—	56.4	47.7	47.4	46.8	14	54.2	3.1	0.8	5.6	47.7– 59.1	
58.8	51.6	50.1	—	52.4	50.4	—	59.6	—	51.5	49.9	—	—	—	—	>51.9	47.5	48.4	—	16	52.5	3.3	0.8	6.2	47.5– 58.8	
48.2	44.3	45.4	49.0	43.6	42.3	45.3	50.1	—	—	40.0	46.2	—	@42.4	—	—	—	—	—	19	45.1	2.5	0.6	5.5	40.0– 49.0	
41.1	37.6	42.7	42.5	39.4	40.1	—	42.9	40.2	—	37.8	40.1	39.6	—	—	—	—	—	—	18	40.3	1.7	0.4	4.3	37.6– 42.9	
28.8	26.4	29.2	32.1	26.7	28.9	—	31.7	30.5	30.0	28.2	30.6	29.0	—	—	—	—	—	—	19	29.1	1.8	0.4	6.2	26.2– 32.1	
160	323	365	358	—	—	—	379	—	364	—	—	358	—	—	—	—	—	—	13	353	14.7	4.1	4.1	323 –379	

TABLE 39. MEASUREMENTS OF MID-TERTIARY AVIAN FOOTPRINTS FROM THE ENDURANCE PIT, NE TASMANIA (IN MM AND DEGREES WHERE INDICATED)

Specimen Number	Cast/Original	A	B	C	D	E	F	G	H	I
1972/39/1	O	220	150	188	240	70	65	55	62°	56°
1972/39/2	O	220	165	170	245	—	—	55	55°	48°
1972/39/3	O	230	150	175	230	45	58	75	65°	56°
1972/39/4	C	147	125	125	194	60	60	55	69°	80°
1972/39/5	C	222	165	175	223	60	50	60	56°	60°
1972/39/6	C	245	185	200	270	55	75	70	59°	51°
1972/39/7	C	240	180	180	246	50	50	65	48°	47°
1972/39/8	C	240	170	185	250	44	52	55	59°	54°
Range		147–245	125–185	125–200	194–270	45–70	50–75	55–75	48°–69°	47°–80°
Mean		221	161	174	236	55	59	61	59	57
S.D.		31.3	19.2	23.8	23.9	8.8	9.2	7.9	6.4	10.4
S.E.		11.1	6.8	9.0	9.0	3.3	3.5	2.8	2.3	3.7
C.V.		14.2	11.9	13.7	10.1	15.9	15.6	12.9	10.9	18.5
n		8	8	7	7	7	7	8	8	8

A=Length of middle toe (III)
B=Length of shortest side toe (cf. II)
C=Length of longest side toe (cf. IV)
D=Maximum width across toes
E=Width of base of shortest side toe
F=Width of base of longest side toe
G=Width of base of mid-toe
H=Angle between small side toe (II) and mid-toe (III)
I=Angle between longest side toe (IV) and mid-toe (III)

TABLE 40. STATISTICAL SUMMARY OF FOOTPRINT MEASUREMENTS OF THE LIVING EMU (*DROMAIUS NOVAEHOLLANDIAE*) (IN MM AND DEGREES WHERE INDICATED)

Measurements	A	B	C	D	E	F	G	H	I
Statistics									
Range	190–280	120–150	115–165	160–210	28–80	30–50	25–45	30°–60°	30°–60°
Mean	215	135	145	187	41	39	35	47°	50°
S.D.	18.9	7.6	10.3	14.4	10.9	7.1	5.7	7.0	7.7
S.E.	3.1	1.7	2.2	2.4	2.6	1.7	1.2	1.5	1.7
C.V.	8.8	5.6	7.1	7.7	26.4	18.0	16.2	15.0	15.3
n	38	21	22	35	18	18	21	22	21

TABLE 41. MEASUREMENTS OF STRIDE LENGTH OF THE LIVING EMU, *DROMAIUS NOVAEHOLLANDIAE* (MEASURED HEEL TO HEEL, IN MILLIMETRES)

Print No. in trackway	Gait	Running		Walking	
		Accelerating Ind. 1	Decelerating Ind. 2	Ind. 1	Ind. 2
1–2		1200	1250	580	770
2–3		1360	1220	520	720
3–4		1450	1300	540	640
4–5		—	1190	580	—
5–6		—	1170	—	—
6–7		—	1110	—	—
7–8		—	940	—	—
Print No. in trackway		Length/Width of Prints			
1		225/200	230/195	—	230/195
2		215/205	250/170	—	280/195
3		220/195	210/—	230/190	230/195
4		—	220/210	—	220/190
5		—	225/175	—	—
6		—	225/210	—	—
7		—	236/165	—	—
8		—	225/192	—	—

TABLE 42. LOCALITIES PRODUCING DROMORNITHIDAE IN AUSTRALIA

LOCALITY	STATE	NATURE OF REMAINS	ROCK UNIT	FAUNA	REFERENCES
<i>MID-TERTIARY</i>					
Endurance Tin Mine	Tas.	Footprints	Unnamed white pipe clay	Unnamed	This paper
<i>MIOCENE</i>					
Snake Dam Locality	So. Aust.	Eggshell; Dromornithidae	Unnamed	Unnamed	This paper
Riversleigh	No. Terr.	Vertebra, tibiotarsi tarsometatarsi; <i>Barawertornis tedfordi</i>	Carl Creek Limestone	Riversleigh	This paper; Tedford, 1968; Stirton et al., 1968
Leaf Locality (UCMP V6213)	So. Aust.	Phalanges, synsacral frags; Dromornithidae	Wipajiri Fm.	Kutjamarpu	This paper Stirton et al., 1967, 1968
Bullock Creek	No. Terr.	Femora, tarsometatarsi, vertebrae frags; <i>Bullockornis planei</i> , <i>B. sp.</i>	Camfield Beds	Bullock Creek	This paper; Plane and Gatehouse, 1968; Stirton et al., 1968
<i>MIOCENE-PLIOCENE</i>					
Paine Quarry, Newsome Quarry, Rochow Loc., Alcoota (UCMP V-6345-7, V-6349)	No. Terr.	Many skeletal elements, two quadrates; <i>Dromornis stirtoni</i> , <i>Ilbandornis woodburnei</i> , ? <i>I. lawsoni</i>	Waite Fm.	Alcoota	This paper; Woodburne, 1967; Stirton et al., 1968
<i>PLIOCENE</i>					
Lawson-Daly Quarry (UCMP V-5769)	So. Aust.	Synsacral frag.; <i>Dromornithidae</i>	Mampuwordu Sands	Palanka-rinna	Miller, 1963a
Peak Downs	Qld.	Femur; <i>Dromornis australis</i>	Unnamed gravels	Unnamed	Clarke, 1869, 1877; Owen, 1872, 1879a
Canadian Gold Lead, Gulgong	N.S.W.	Synsacrum; femur (not <i>Genyornis</i>) frags.; Dromornithidae	Unnamed	Unnamed	This paper; Owen, 1891; Etheridge, 1889
Goree (=Geurie)	N.S.W.	Femur, fragment; cf. Dromornithidae	Unnamed	Unnamed	Owen, 1879; perhaps same as that mentioned by Lydekker, 1891, from Gulgong (see above).
<i>PLIOCENE-PLEISTOCENE</i>					
Diamantina River	Qld. or So. Aust.	Tibiotarsus, tarsometatarsus, phalanges; cf. <i>Genyornis</i>	Unnamed	Unnamed	This paper
Thorbindah, Paroo River	Qld.	Tibiotarsus; Dromornithidae	Unnamed	Unnamed	This paper; Stirling and Zietz, 1900
Cuddie Springs	N.S.W.	Tibiotarsi, tarsometatarsi; <i>Genyornis newtoni</i>	Unnamed bone-pebble 'agglomerate'	Unnamed	This paper; Anderson and Fletcher, 1934

TABLE 42. LOCALITIES PRODUCING DROMORNITHIDAE IN AUSTRALIA (Cont.)

LOCALITY	STATE	NATURE OF REMAINS	ROCK UNIT	FAUNA	REFERENCES
Wellington Caves ('breccia cave')	N.S.W.	Femur; Dromornithidae	Unnamed cave breccia	Unnamed	Mitchell, 1839; Owen, 1874
Scott River	W. Aust.	Egg; cf. Dromornithidae	Unnamed coastal dunes	Unnamed	This paper; Butler, 1969
Mammoth Cave	W. Aust.	Vertebra; Dromornithidae	Unnamed	Unnamed	This paper
Baldina Creek, nr. Burra	So. Aust.	Femur; <i>Genyornis</i>	Unnamed coarse red sands and conglomerate	Unnamed	Stirling and Zietz, 1900
Brothers Island, Coffin Bay	So. Aust.	Femur; <i>Genyornis newtoni</i>	Unnamed aeolianite	Unnamed	This paper
Lake Callabonna	So. Aust.	Much post-cranial; some cranial material; <i>Genyornis newtoni</i>	Unnamed lower stratigraphic unit	Unnamed	Stirling and Zietz 1893, 1896, 1900, 1905, 1913; Stirling, 1896; Newton, 1893
Mt. Gambier Range	So. Aust.	Tibiotarsus; <i>Genyornis newtoni</i>	Unnamed	Unnamed	Owen, 1879; Lydekker, 1891
Penola	So. Aust.	Tibiotarsi, tarsometatarsi; cf. Dromornithidae	Unnamed	Unnamed	Woods, 1866, 1882
Salt Creek Normanville	So. Aust.	Femur, tibiotarsi; cf. <i>Genyornis</i>	Unnamed	Unnamed	Stirling and Zietz, 1900
Gregory Localities					
Lower Cooper Creek Locality 2	So. Aust.	Tarsometatarsus; Dromornithidae	Katipiri Sands	Malkuni	This paper
Emu Camp (=Malkuni Waterhole, UCMP V-5382)	So. Aust.	Tarsometatarsus, vertebrae; Dromornithidae	Katipiri Sands	Malkuni	This paper
University of California-South Australian Museum Localities					
Cassidy Locality (UCMP V-5539)	So. Aust.	Tarsometatarsus, phalanx; <i>Genyornis newtoni</i>	Katipiri Sands or Unnamed channels	Malkuni or Unnamed	This paper
Cooper Creek Site 5 (UCMP V-5831)	So. Aust.	Phalanx; Dromornithidae	Katipiri Sands	Malkuni	This paper; Stirton et al., 1961

TABLE 42. LOCALITIES PRODUCING DROMORNITHIDAE IN AUSTRALIA (Cont.)

LOCALITY	STATE	NATURE OF REMAINS	ROCK UNIT	FAUNA	REFERENCES
Cooper Creek Site 8 (UCMP V-5860)	So. Aust.	Vertebra; Dromornithidae	Katipiri Sands	Malkuni	This paper; Stirton et al., 1961
Katipiri (Kutti Pirra) Waterhole (UCMP V-5861)	So. Aust.	Vertebra; Dromornithidae	Katipiri Sands	Malkuni	This paper; Stirton et al., 1961
Markoni Locality (UCMP V-5382)		Vertebra; Dromornithidae	Katipiri Sands	Malkuni	This paper; Stirton et al., 1961

TABLE 43. COMPARISON OF MAXIMUM SIZES ATTAINED IN THE HIND LIMB OF
DINORNITHIDAE, AEPYORNITHIDAE, DROMORNITHIDAE (IN MILLIMETRES)

	Aepyornithidae <i>Aepyornis maximus</i> ¹	Dinornithidae <i>Dinornis maximus</i> ²	Dromornithidae <i>Dromornis stirtoni</i>	Dromornithidae <i>Genyornis newtoni</i>
Femur				
1. Total length	(550) ⁴	470	470.0	>338
2. Proximal width	?	174	@197.5	179.8
3. Distal width	(222) ⁴	194	214.2	176.7
Tibiotarsus				
4. Length	810	990	>776	(prob. 820 or greater) 602
5. Proximal width	255	215	—	147
6. Distal width	170	135	@140	94
Tarsometatarsus				
7. Length	480	546	464.2	379
8. Proximal width	185	140	—	111
9. Distal width	170	184	150.2	107
Egg				
10. Maximum length	351 ³	?253	—	?@276
1. From Wiman, 1935 3. From Lambrecht, 1933 2. From Archey, 1941 4. From C. Walker, pers. comm., 1975				

TABLE 44

Character	Struthionidae (<i>Struthio</i>)	Rheidae (<i>Rhea</i>)	Aepyornithidae (<i>Aepyornis</i>)	Casuariidae (<i>Casuaris</i>)	(<i>Dromaius</i>)	Dinornithidae (<i>Dinornis</i>)	Emeidae (<i>Pachyornis</i>)	Apterygidae (<i>Apteryx</i>)	Tinamidae (<i>Nothura</i> or <i>Nothoprocta</i>)	Dromornithidae <i>Barawertornis</i>	<i>Bullockornis</i>	<i>Dromornis</i>	<i>Ilbandornis</i>	<i>Genyornis</i>
FEMUR														
1	B	B	B	D	D	C	C	B	C	—	A	B	A	A
9	B	C	C	C	C	B-C	B-C	A	A	—	C	A	—	A
10	B	A	C	A	A	B	B	A	A	C	A	B-C	B	B
11	B	A	B	A,C	A	B	B	A-B	A	C	C	D	C	C-D
14	C	D	C	B	B	B	B	C	A	C	B	B	B	B
15	C	C	B	C	C	C	C	B	A-B	B	B	B	B	C
16	C	C	C	C	C	C	C	B	A-B	C	B	C	C	C
18	C	C	A	B	A	A	A	A	A	A	C	C	C	C
19	A	A	A	A	A	A	A	A	A	A	A	B	B	B
21	C	C	B	C	C	A	A	A	A	A	C	A	A	B
22	D	C	C	C	C	C	C	B	C	B	A	B	B	C
23	B	B	B	C	C	A	A	A	A	C	A	C	C	C
24	B	A-B	A	A	B	A-B	A-B	A-B	A	B	B	B	A-B	A
26	A	A	B	A	A-B	A-B	A-B	A	A	A	A	B	B	B
TARSOMETATARSUS														
1	A	A	A	A	A	A	A	B	B	—	C	?A	A	A
2	A	B	C	C	C	B	B	B	B	A	C	A	A	A
3	B	B	A	B	B	A	A	A	A	B	B-C	A	A	B-C
5	B	A-B	A	B	B	A	A	A	A	A	C	A	A	A
6	A	B	B	B	C	C	A-B	B	B	C	C	B	B	B
9	A	C	D	C	C	B	B	C	B	D	E	D	D	D
11	D	C	A	B-C	A	A	A-B	A	A	B	B	B	B	C
12	—	C	A-B	B	A	A-B	A-B	A	B	B	B	B	B	A
15	A-B	A	A-B	A	A	A	B	A-B	A	A	B	A	A	A
16	C	A-B	A-B	A-B	C	A-B	A	A	B	—	A	B	C	B-C
17	A	A	C	B	B	B	B-C	B	A	—	B-C	B	A-B	A-B

KEY TO TABLE 44

FEMUR

1. Degree of posterior expansion of trochanter
 - A. None
 - B. Slight
 - C. Moderate
 - D. Marked
9. Degree of anterior extension of trochanter
 - A. Slight
 - B. Moderate
 - C. Far
10. Degree of anteroposterior compression of shaft
 - A. None
 - B. Slight
 - C. Marked
11. Size of angle formed between anteroposterior axis of fibular condyle and long axis of shaft
 - A. Approximately 90°
 - B. Small obtuse
 - C. Large acute
 - D. Moderate acute
14. Depth of popliteal area
 - A. Shallow
 - B. Moderate
 - C. Deep
 - D. Extremely deep
15. Degree of external protrusion of fibular condyle
 - A. Slight
 - B. Moderate
 - C. Marked
16. Angle formed by proximodistal axis of external condyle and long axis of shaft
 - A. 180°
 - B. Very large obtuse
 - C. Large obtuse
18. Shape of internal condyle
 - A. Semicircular
 - B. Triangular
 - C. Semielliptical
19. Nature of medial surface of internal condyle
 - A. Smooth, unridged
 - B. Ridged
21. Depth of condyles with respect to distal width
 - A. Moderate shallow
 - B. Shallow
 - C. Deep
22. Comparative widths of external and internal condyles
 - A. Internal 4 times as wide
 - B. Internal 3 times as wide
 - C. Internal 2 times as wide
 - D. Internal 1½ times as wide
23. Comparative depths of internal and external condyles
 - A. Subequal or nearly so
 - B. External slightly deeper than internal
 - C. External decidedly deeper
24. Degree of anterior and/or posterior convergence of long axis of condyles
 - A. Parallel
 - B. Converge anteriorly
26. Position of posterior margin of fibular condyle with respect to other condyles
 - A. Both internal/external condyles project further posterad than fibular condyle
 - B. Fibular extends as far posteriad or nearly as far as internal condyle

TARSOMETATARSUS

1. Depth of proximal end
 - A. Shallow
 - B. Moderate
 - C. Deep
2. Width of intertrochlear space between trochlea III and IV
 - A. Narrow
 - B. Moderate
 - C. Broad
3. Depth of shaft
 - A. Shallow
 - B. Moderate
 - C. Deep
5. Prominence of subhypotarsal ridge
 - A. Low
 - B. Moderate
 - C. Prominent
6. Width of shaft with respect to width of distal end
 - A. Distal end not decidedly broader
 - B. Moderately broader distal end
 - C. Decidedly broader distal end
9. Comparative distal extension of trochleae II and IV
 - A. No trochlea II present
 - B. Trochlea II extends much further
 - C. Trochlea IV extends moderately further
 - D. Trochleae II and IV nearly subequal
 - E. Trochlea II extends slightly distad of IV
11. Degree of reduction of trochlea II with respect to IV
 - A. Trochleae of subequal width
 - B. Trochlea IV moderately broader
 - C. Trochlea II decidedly narrower
 - D. Trochlea II lacking entirely
12. Relation of medial and lateral margins of trochlea II
 - A. Parallel
 - B. Slightly divergent posteriorly
15. Depth of trochlea III
 - A. Moderate
 - B. Deep
16. Comparative widths of trochleae III and IV
 - A. Trochlea III slightly wider than trochlea IV
 - B. Trochlea III approximately 1½ times wider than trochlea IV
 - C. Trochlea III 2 times wider than trochlea IV
17. Degree of posterior convergence of lateral and medial margins of trochlea III
 - A. Parallel
 - B. Slightly convergent posteriorly
 - C. Decidedly convergent posteriorly

TABLE 45. NUMBER OF DERIVED CHARACTER STATES (FORE-LIMB EXCLUDED) PRESENT IN EACH GROUP OF RATITES FOR 56 CHARACTERS STUDIED. See figure 44 for character state plots from which table 45 is tallied. Derived character states determined by lack of common occurrence of that character in both the Tinamidae and the ratites.

Struthionidae	37
Rheidae	33
Casuariidae	33
Dromornithidae	38
Aepyornithidae	30
Apterygidae	23
Dinornithidae-Emeidae	22

TABLE 46. TALLY OF DERIVED CHARACTER-STATES (DETERMINED BY LACK OF OCCURRENCE IN THE TINAMIDAE) OF THE STERNUM, SYNSACRUM AND HIND LIMB SHARED BY SEVERAL RATITE GROUPS

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

TABLE 47. TALLY OF PRIMITIVE CHARACTERS (DETERMINED BY COMMON OCCURRENCE IN BOTH THE RATITES AND TINAMIDAE) OF THE STERNUM, SYNSACRUM, AND HIND LIMB SHARED BY SEVERAL RATITE GROUPS

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

TABLE 48. TALLY OF DERIVED CHARACTERS (DETERMINED BY COMMONALITY OF OCCURRENCE WITHIN THE RATITES) OF THE STERNUM, SYNSACRUM AND HIND LIMB SHARED BY SEVERAL RATITE GROUPS

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

TABLE 49. TALLY OF CHARACTERS (UNWEIGHTED) OUT OF 56 STUDIED THAT ARE SHARED BY SEVERAL RATITE GROUPS (SUMS OF TOTALS IN TABLES 46-47) INDICATING PHENETIC SIMILARITY

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

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ILLUSTRATIONS

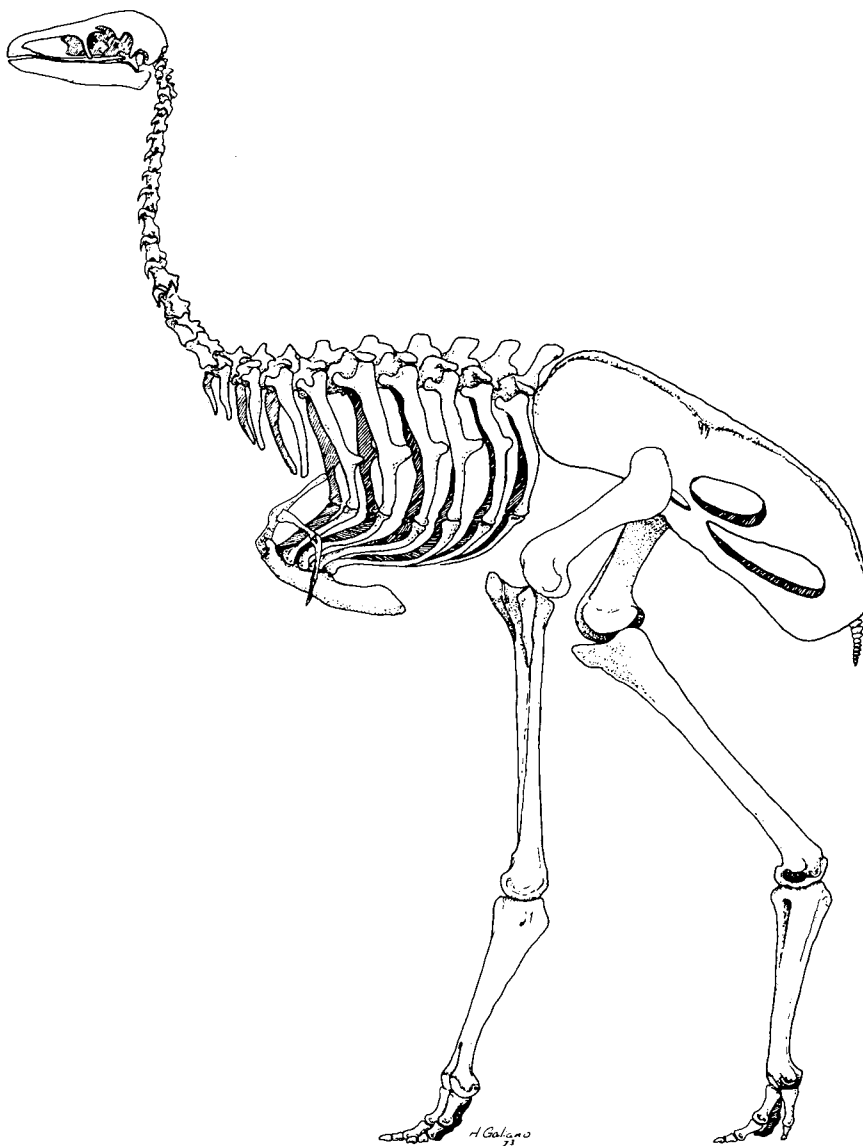


Fig. 1. *Genyornis newtoni*, reconstruction, about 2 metres high. Vertebral column, particularly cervicals, and skull highly speculative.

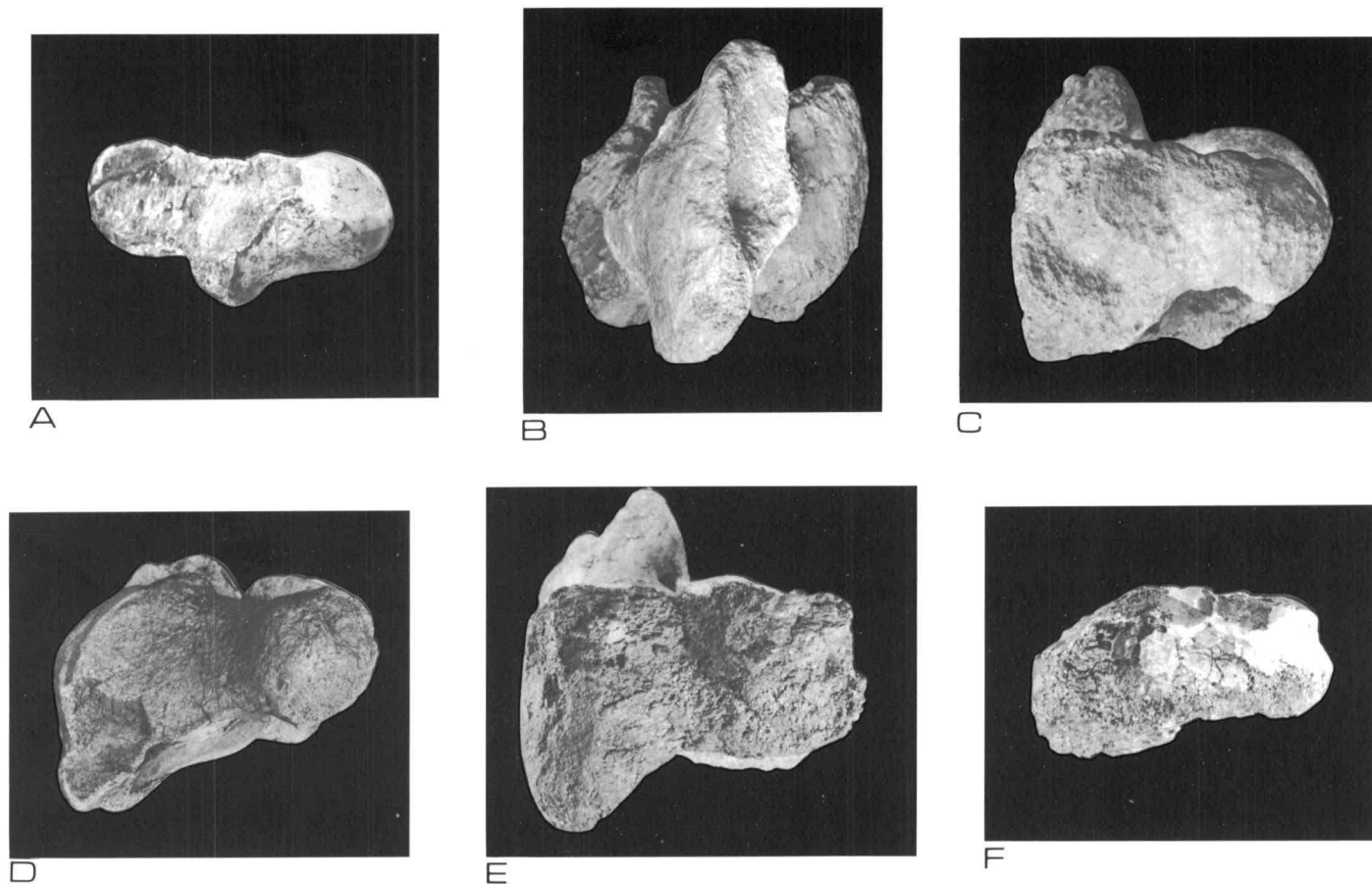
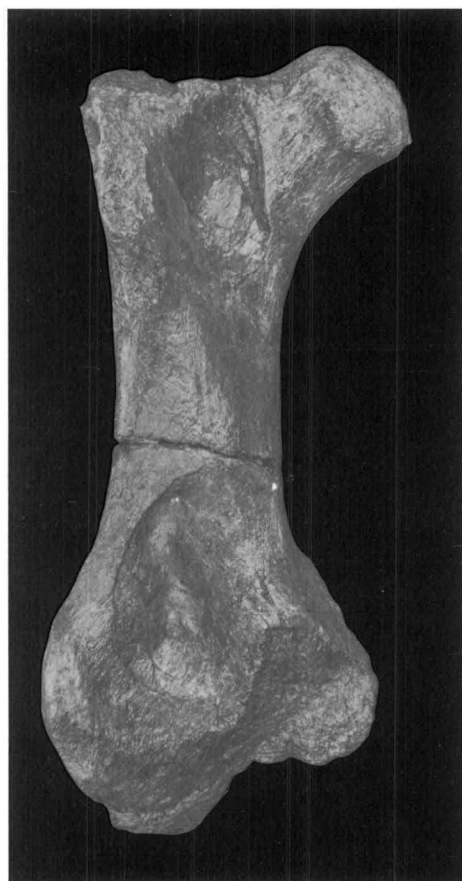
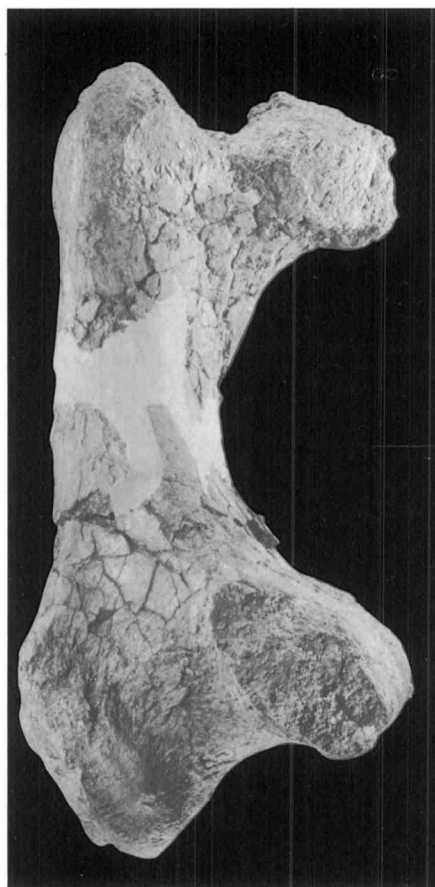


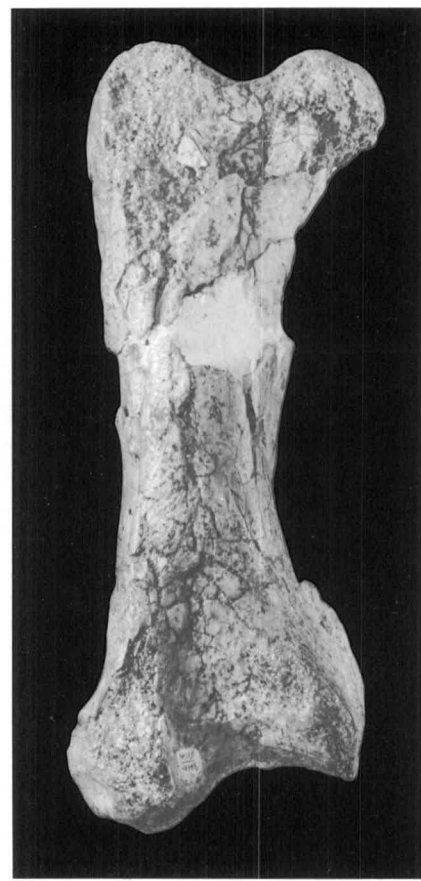
Fig. 2. Femora of Dromornithidae (proximal view) from Australian Cenozoic sediments: (A) CPC 7341 (type), *Barawertornis tedfordi*, Riversleigh Homestead, Queensland, Miocene; (B) CPC 13844 (type) and (C) CPC 13845, *Bullockornis planei*, Bullock Creek, Northern Territory, Miocene-Pliocene; (D) AM F10950 (type), *Dromornis australis*, Peak Downs, Queensland, Pliocene; (E) CPC 13851 (type), *Dromornis stirtoni*, and (F) CPC 13850 (type), *Ilbandornis woodburnei*, Alcoota Homestead, Northern Territory, Miocene-Pliocene.



A



B

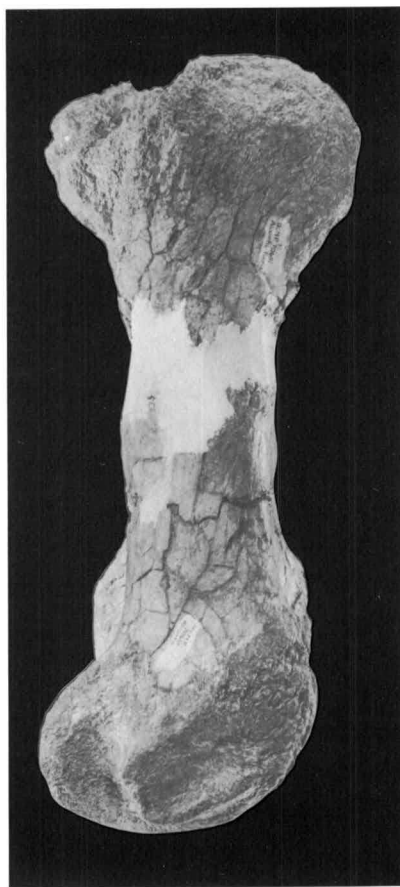


C

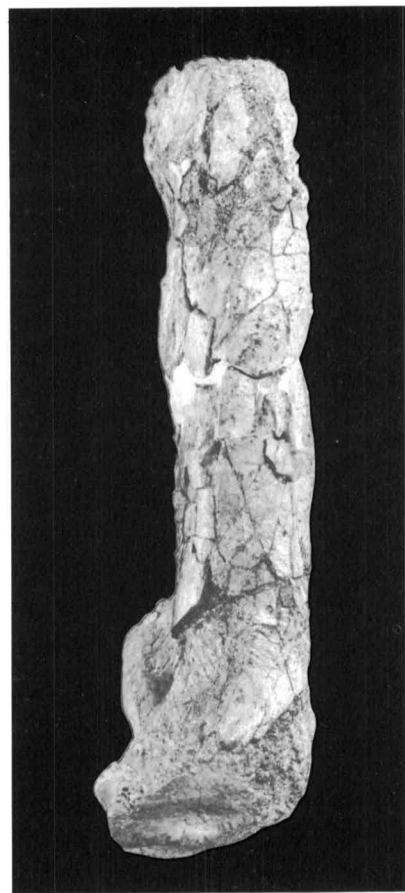
Fig. 3. Femora of Dromornithidae (anterior view) from Australian, Cenozoic sediments: (A) AM F10950 (type), *Dromornis australis*, (B) CPC 13851 (type), *Dromornis stirtoni*, and (C) CPC 13850 (type), *Ilbandornis woodburnei*. Printed at a standard size (see tables of measurement for scale).



A



B



C

Fig. 4. Femora of Dromornithidae (lateral view) from Australian Cenozoic sediments. See caption, figure 3.

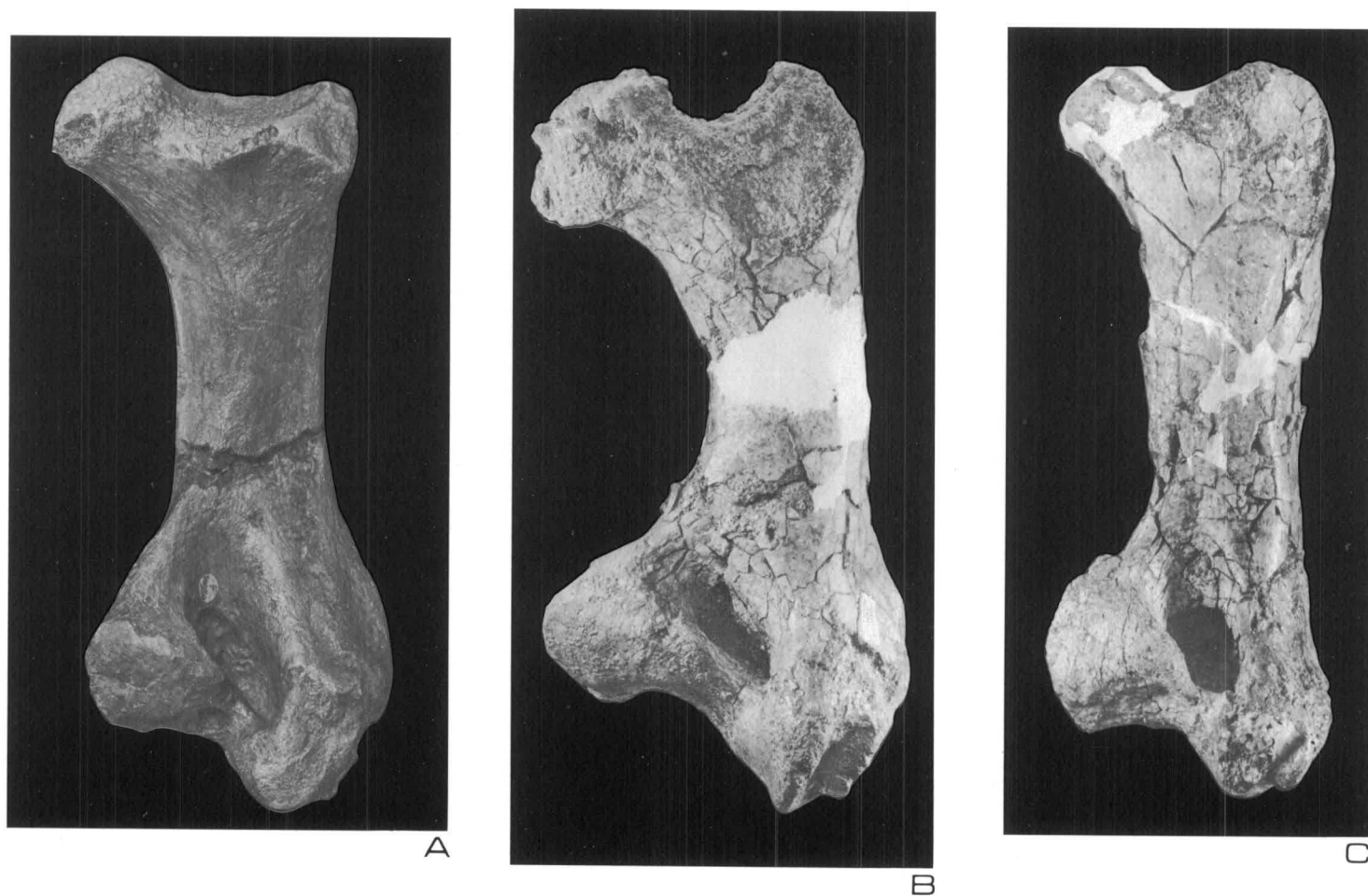
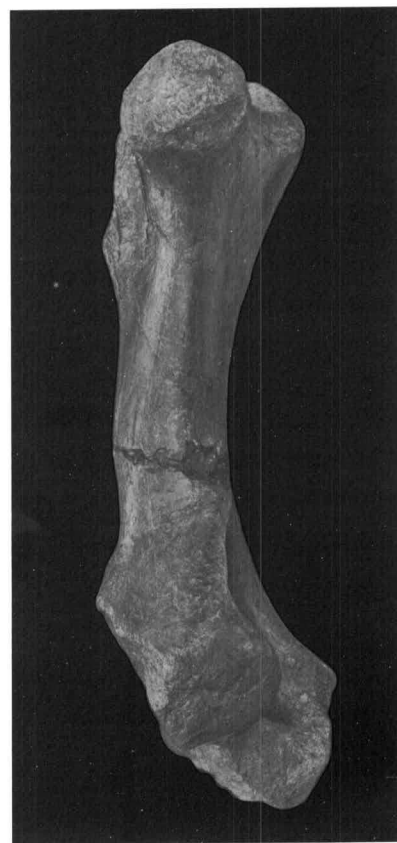
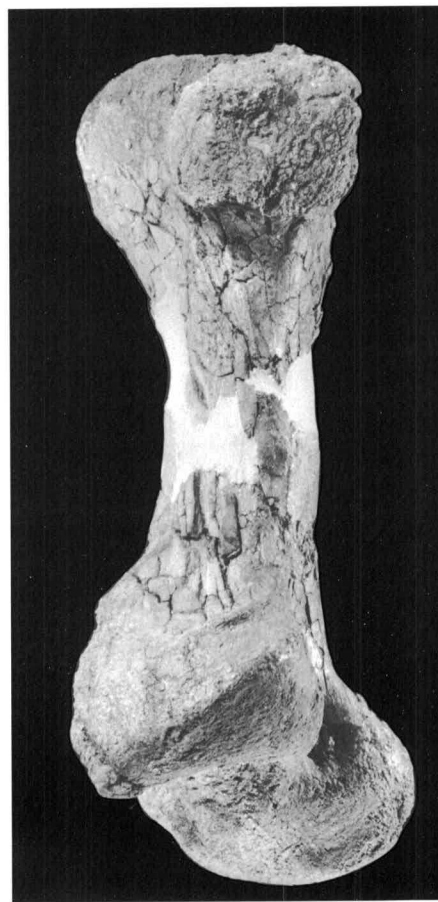


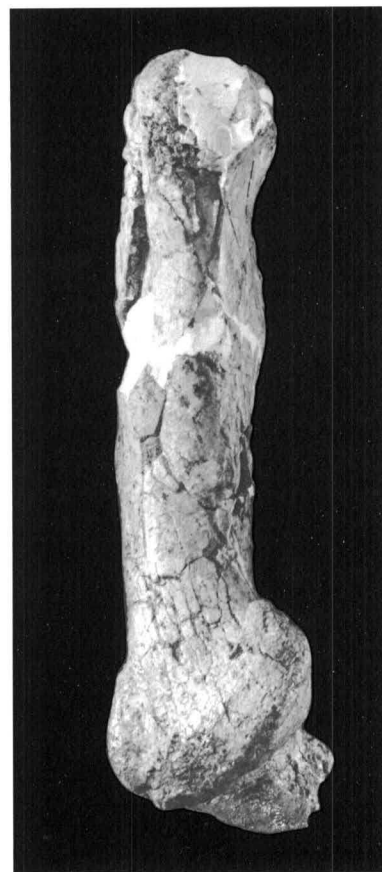
Fig. 5. Femora of Dromornithidae (posterior view) from Australian Cenozoic sediments. See caption, figure 3.



A



B



C

Fig. 6. Femora of Dromornithidae (medial view) from Australian Cenozoic sediments. See caption, figure 3.



Fig. 7. Restoration of *Genyornis newtoni*, restricted to the Pleistocene of Australia.

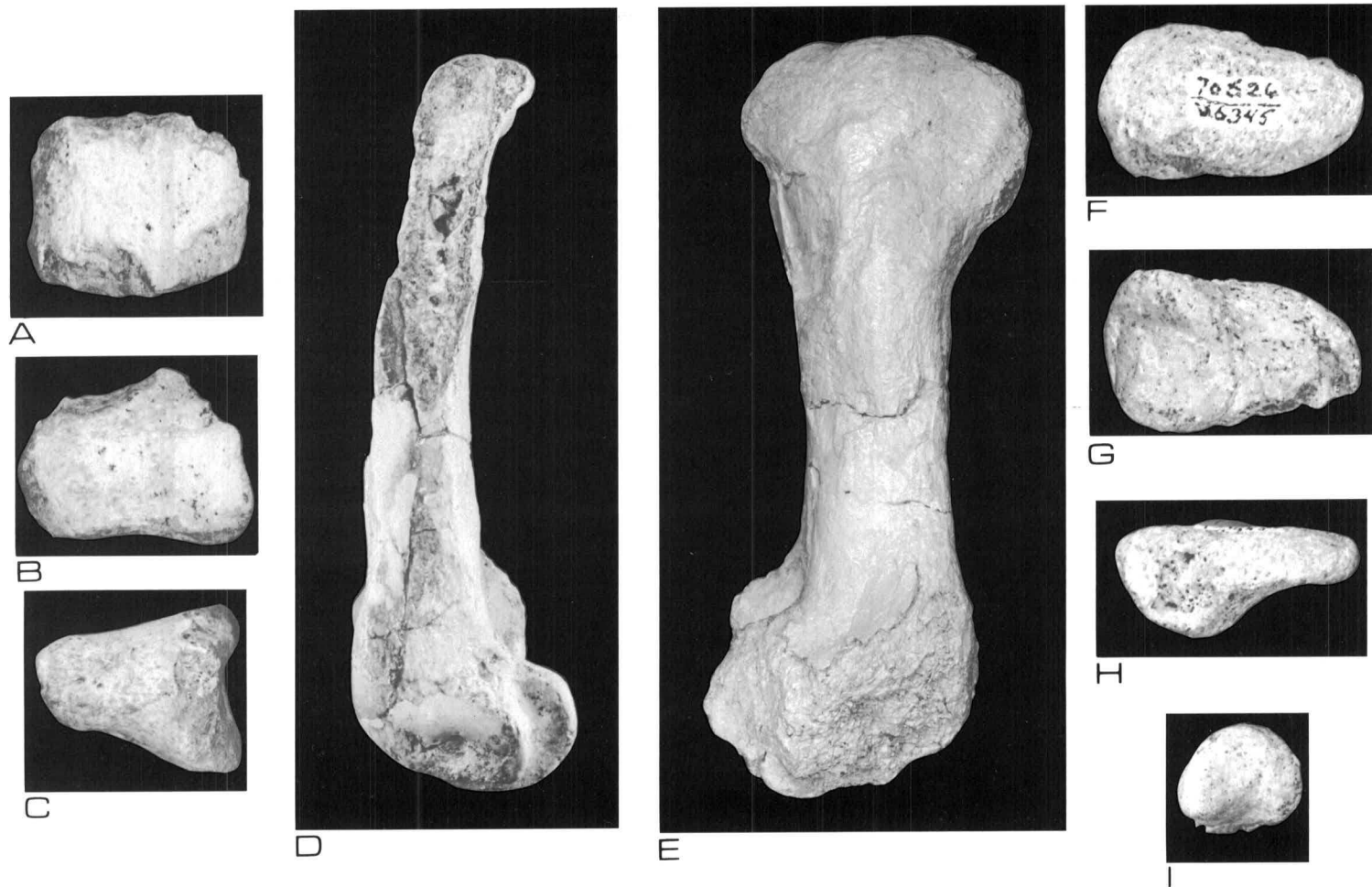


Fig. 8. *Dromornis stirtoni*, UCMP 67094, cf. phalanx 3, digit III: (A) dorsal, (B) proximal, and (C) side; UCMP 70626, terminal phalanx: (F) dorsal, (G) ventral, (H) side, and (I) proximal, Alcoota Homestead, Northern Territory, x 1. Lateral views of *Barawertornis tedfordi*, (D) CPC 7341 (type), Riversleigh Homestead, Queensland, and *Bullockornis planei*, (E) CPC 13844 (type), Bullock Creek, Northern Territory, printed at a standard size (see tables of measurement for scale).



Fig. 9. Femora of Dromornithidae (posterior view) from Australian Cenozoic sediments: (A) CPC 7341 (type), *Barawertornis tedfordi*; (B) CPC 13844 (type) and (C) CPC 13845, *Bullockornis planei*. See caption, figure 2.

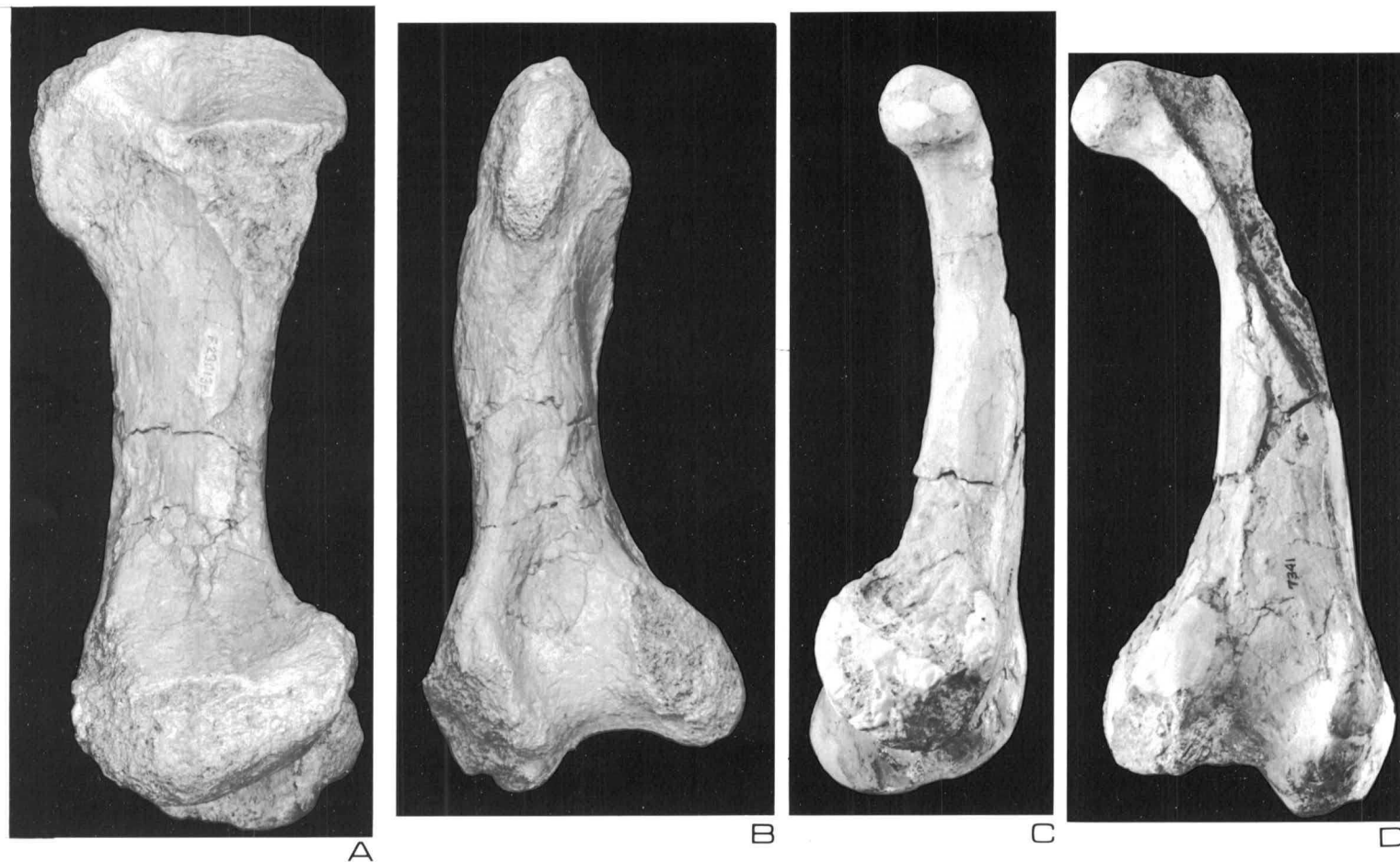


Fig. 10. Femora of Dromornithidae from Australian Cenozoic deposits: *Bullockornis planei*, CPC 13844 (type), (A) medial, (B) anterior views; *Barawertornis tedfordi*, CPC 7341 (type), (C) medial, (D) anterior views, see caption, figure 2.

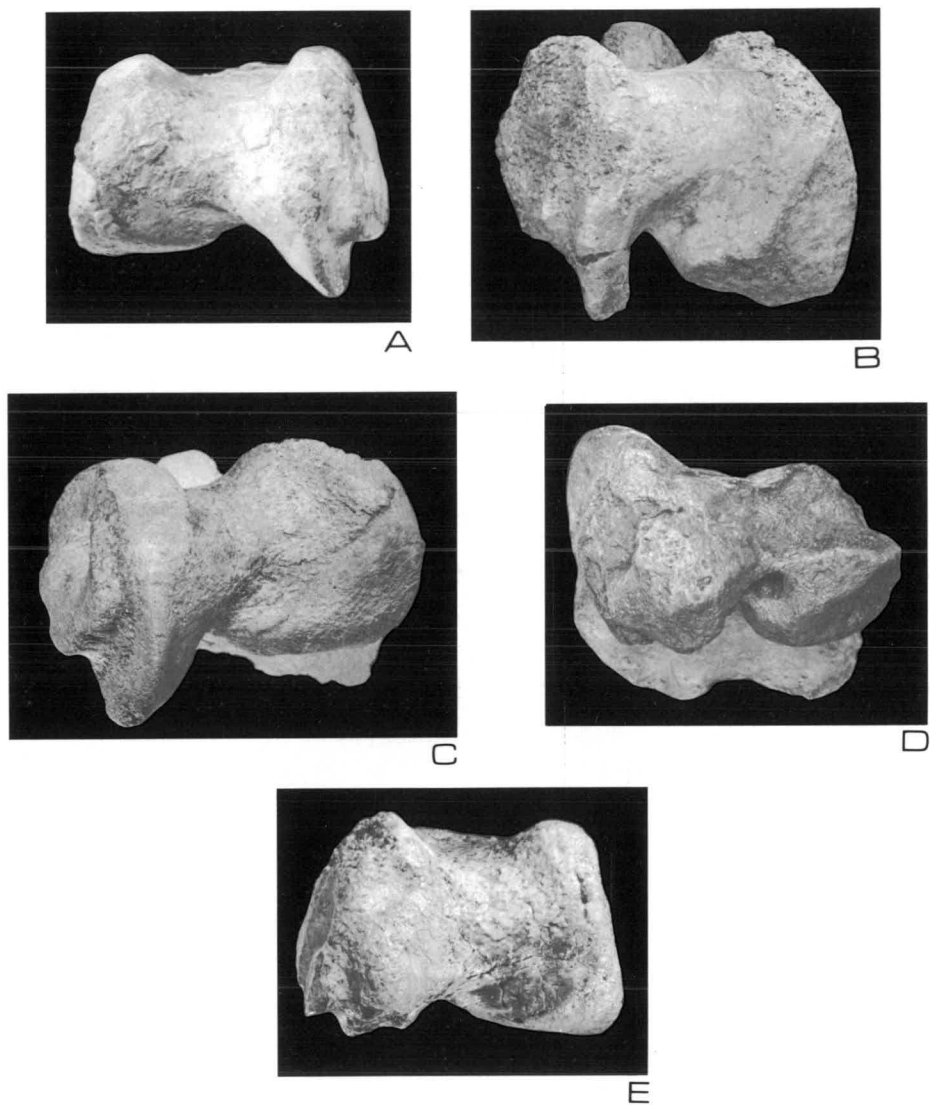


Fig. 11. Femora of Dromornithidae (distal end) from Australian Cenozoic sediments: (A) CPC 7341 (type), *Barawertornis tedfordi*, (B) CPC 13844 (type) and (C) CPC 13845, *Bullockornis planei*, (D) AM F10950 (type), *Dromornis australis*; (E) CPC 13851 (type), *Dromornis stirtoni*. See caption, figure 2.

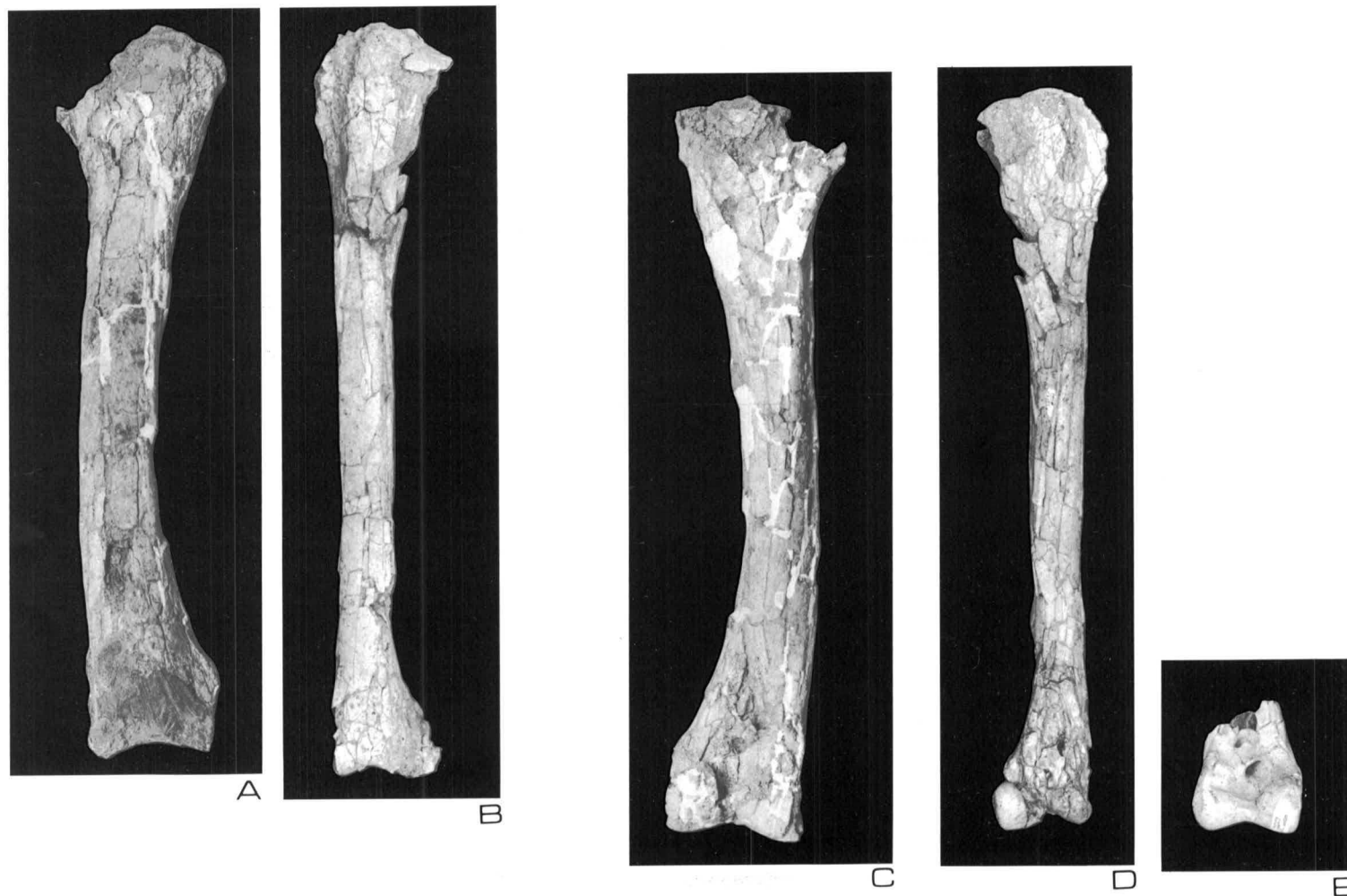


Fig. 12. *Dromornis stirtoni*, UCMP 71415, left tibiotarsus: (A) posterior and (C) anterior views; *?Ilbandornis lawsoni*, UCMP 70118, left tibiotarsus: (B) posterior and (D) anterior views; *Ilbandornis* sp., UCMP, 70649, right tibiotarsus: (E) anterior view; views printed at a standard size (see tables of measurement for scale); Alcoota Homestead, Northern Territory, Miocene-Pliocene.

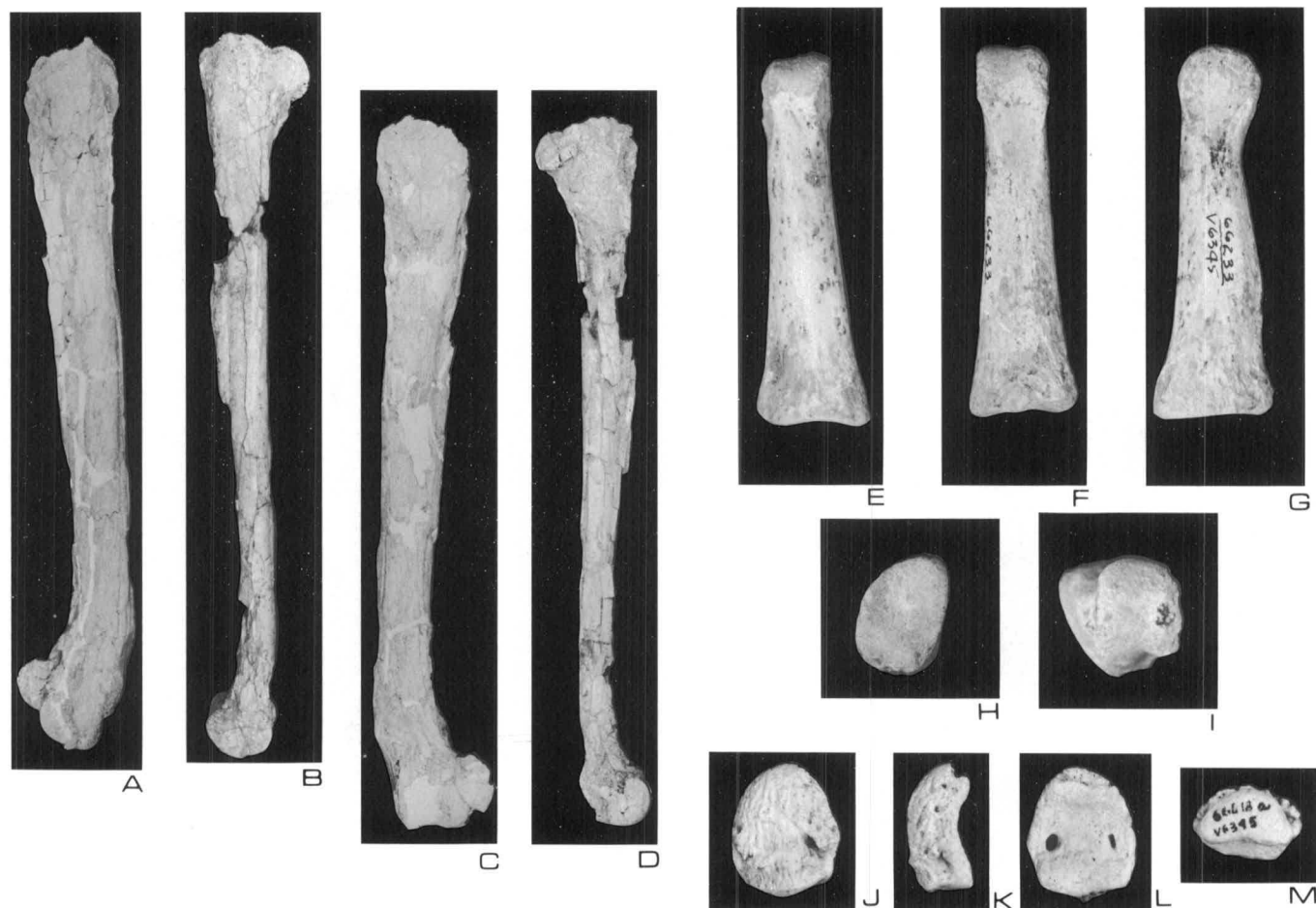


Fig. 13. *Dromornis stirtoni*, UCMP, left tibiotarsus: (A) lateral and (C) medial views; ?*Ilbandornis lawsoni*, UCMP 70118, left tibiotarsus: (B) lateral and (D) medial views printed at a standard size (see tables of measurement for scale); *Ilbandornis* sp., UCMP 66233, right phalanx 1, digit II: (E) dorsal, (F) ventral, (G) lateral, (H) proximal, and (I) distal views, x 1; UCMP 66618, cf. right phalanx 3, digit II: (J) dorsal, (K) lateral, (L) ventral, and (M) proximal views, x 1; Alcoota Homestead, Northern Territory, Miocene-Pliocene.

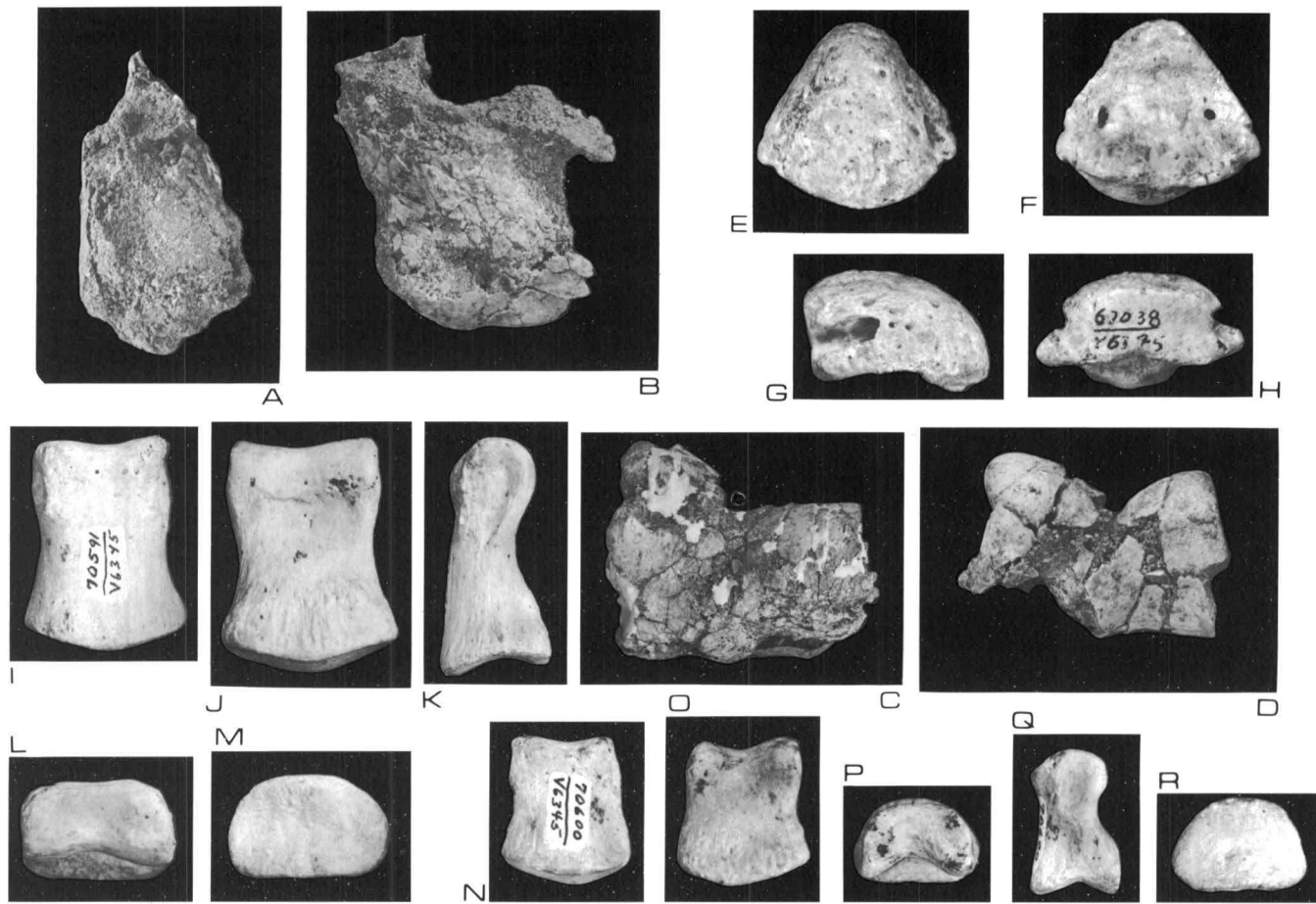


Fig. 14. *Dromornis stirtoni*, UCMP 71415, left tibiotarsus: (A) proximal and (C) distal; *?Ilbandornis lawsoni*, UCMP 70118, left tibiotarsus: (B) proximal and (D) distal views printed at a standard size (see tables of measurement for scale); *Ilbandornis* sp., UCMP 67038, phalanx 4, digit III: (E) dorsal, (F) ventral, (G) side, and (H) proximal views, x 1; UCMP 70591, right phalanx 2, digit III: (I) dorsal, (J) ventral, (K) lateral, (L) distal, and (M) proximal views, x 1; UCMP 70600, ? right phalanx 2, digit IV: (N) dorsal, (O) ventral, (P) distal, (Q) ? lateral, and (R) proximal views, x 1; Alcoota Homestead, Northern Territory, Miocene-Pliocene.



Fig. 15. Tarsometatarsi of Dromornithidae (proximal view) from Australian Cenozoic sediments: (A) CPC 13848, *Bullockornis planei* and (B) CPC 13849 *Bullockornis* sp., Bullock Creek, Northern Territory, Miocene-Pliocene; (C) UCMP 67465, *Ibandornis woodburnei*, Alcoota Homestead, Northern Territory, Miocene-Pliocene, printed at a standard size consistent with that for remaining illustrations of Dromornithidae tarsometatarsi (see tables of measurement for absolute scale); UCMP 88186b, Dromornithidae, phalanx 2 or 3, digit III or phalanx 2, digit IV (D) proximal, (E) distal, (F) dorsal, and (G) side views, Leaf Locality, South Australia, Pliocene, x 1. *Dromornis stirtoni*, UCMP 66234, left phalanx 1, digit II: (H) proximal, (I) dorsal, (J) medial, (K) ventral, (L) distal views, x $\frac{1}{2}$; *Ibandornis* sp., UCMP 70601, phalanx 3, digit III: (M) side, (N) proximal, (O) dorsal, (P) ventral, and (Q) distal views, @ x 1, Alcoota Homestead, Northern Territory, Miocene-Pliocene.



Fig. 16. Tarsometatarsii of Dromornithidae (anterior view) from Australian Cenozoic sediments: (A) CPC 7346, *Barawertornis tedfordi*, Riversleigh Homestead, Queensland, Miocene; (B) CPC 13848, *Bullockornis planei*, Bullock Creek, Northern Territory, Miocene; (C) UCMP 70106, *Dromornis stirtoni*, Alcoota Homestead, Northern Territory, Miocene-Pliocene; Overleaf: (D) UCMP 67465, *Ilbandornis woodburnei*, Alcoota Homestead, Northern Territory, Miocene-Pliocene; (E-F) UCMP 70650, *Ilbandornis lawsoni*, Alcoota Homestead, Northern Territory, Miocene-Pliocene, printed at a standard size based on proximal end of tarsometatarsus (see tables of measurement for scale).

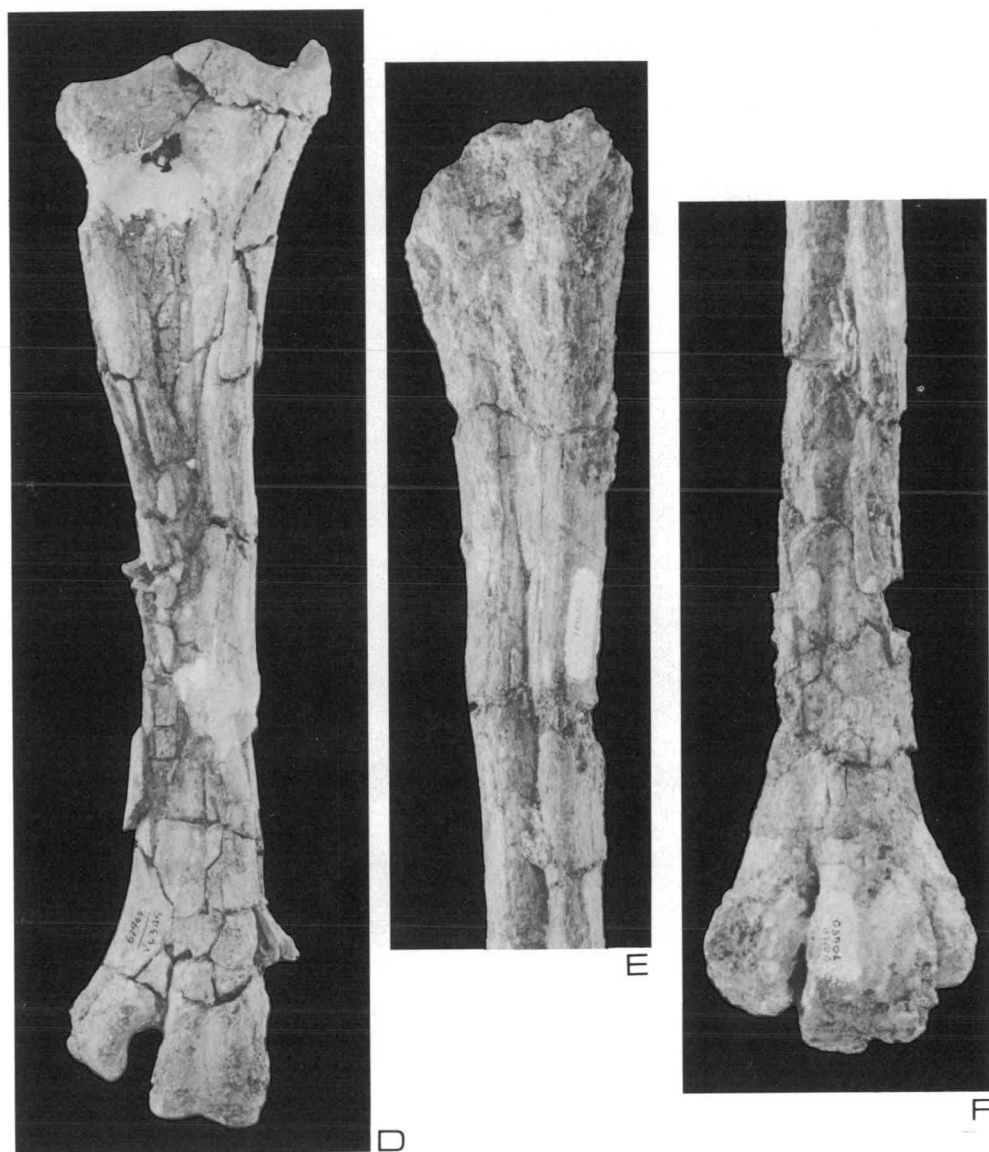


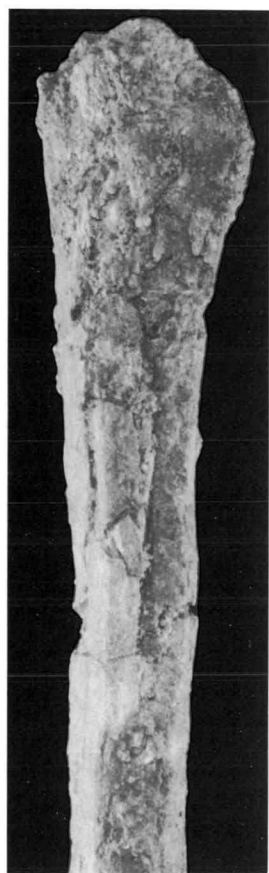
Fig. 16. (cont.)—See caption on previous page.



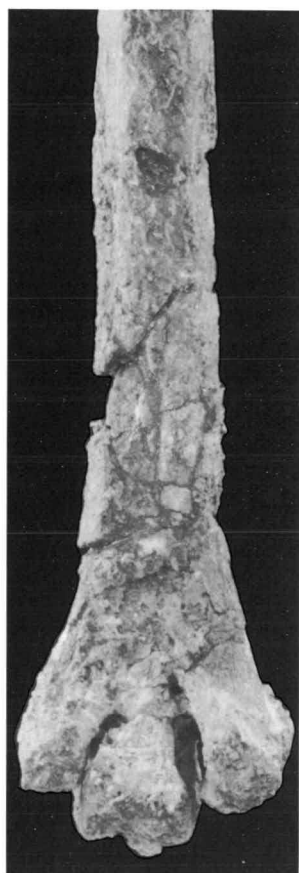
Fig. 17. Tarsometatarsi of Dromornithidae (lateral view) from Australian Cenozoic deposits: (A) CPC 7346, *Barawertornis tedfordi*; (B) UCMP 70652, *Dromornis stirtoni*, Alcoota Homestead, Northern Territory, Miocene-Pliocene; (C-D) CPC 13852, *Ilbandornis lawsoni*, Alcoota Homestead, Northern Territory, Miocene-Pliocene; (E) CPC 13849, *Bullockornis planei*; (F) UCMP 67465, *Ilbandornis woodburnei*, see caption, figure 16.



Fig. 18. Tarsometatarsi of Dromornithidae (posterior view) from Australian Cenozoic deposits: (A) CPC 7346, *Barawertornis tedfordi*; (B) CPC 13849, *Bullockornis* sp.; (C) CPC 13848, *Bullockornis planei*; (D) UCMP 70106, *Dromornis stirtoni*; (E-F) CPC 13852 (type), *Ilbandornis lawsoni*; (G) UCMP 67465, *Ilbandornis woodburnei*; and (H) UCMP 108605, *Ilbandornis* sp., juvenile, Alcoota Homestead, Northern Territory, Miocene-Pliocene, see caption, figures 15-16.



E



F



G



H

Fig. 18. (cont.).

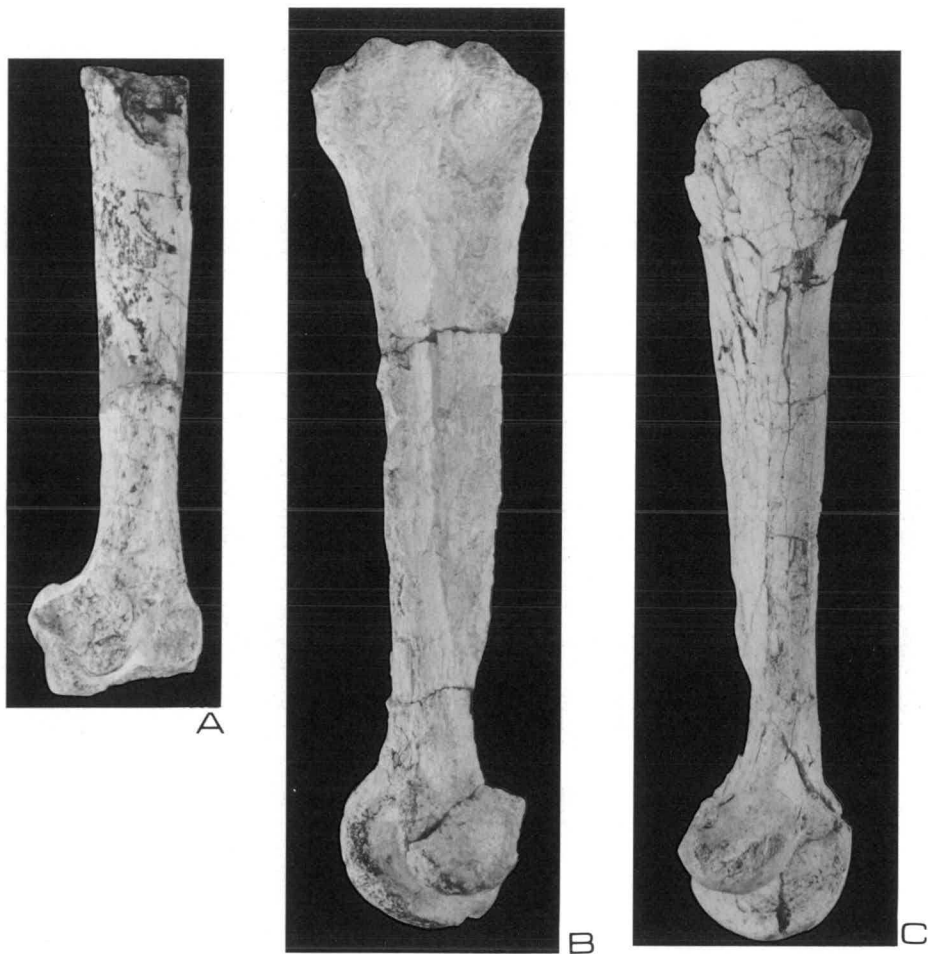
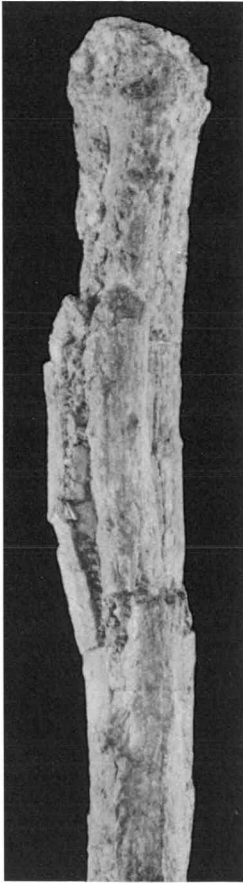


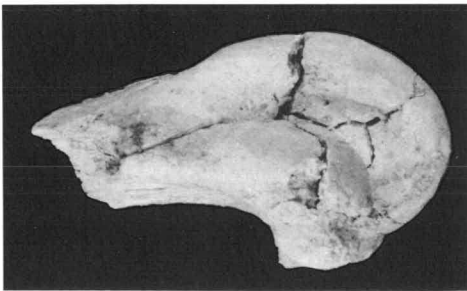
Fig. 19. Tarsometatarsi of Dromornithidae (medial view) from Australian Cenozoic deposits: (A) CPC 7346, *Barawertornis tedfordi*; (B) CPC 13848, *Bullockornis planei*; (C) UCMP 70106, *Dromornis stirtoni*; (D-E) CPC 13852 (type), *Ilbandornis lawsoni*; (F) UCMP 70095, *Ilbandornis* sp., Alcoota Homestead, Northern Territory, Miocene-Pliocene, enlarged scale; and (G) UCMP 67465, *Ilbandornis woodburnei*, see caption, figures 15-16.



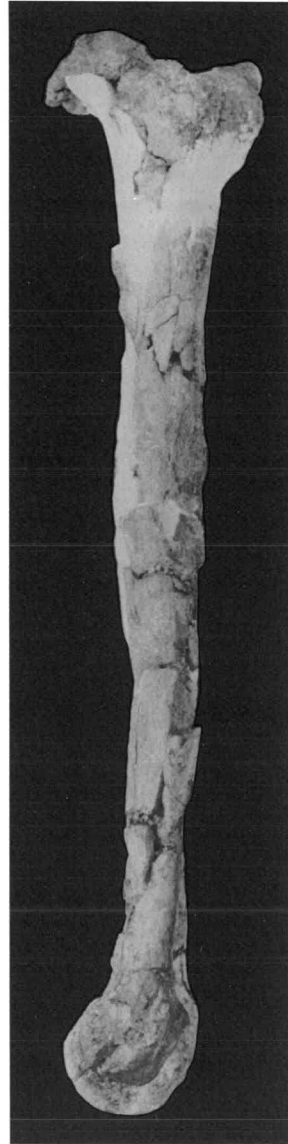
D



E



F



G

Fig. 19. (cont.).

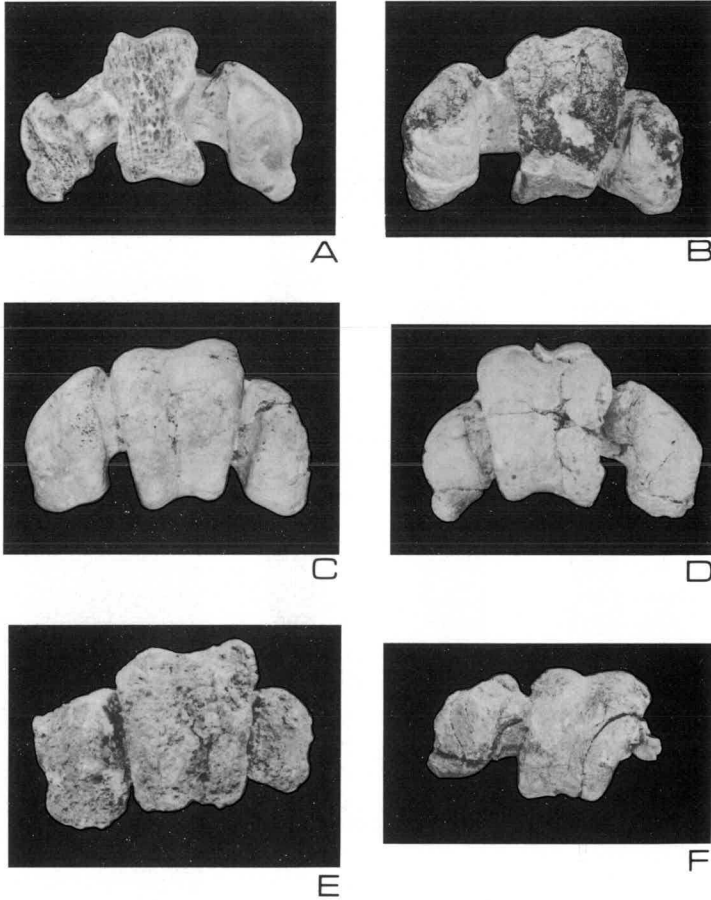


Fig. 20. Tarsometatarsi of Dromornithidae (distal view) from Australian Cenozoic deposits: (A) CPC 7346, *Barawertornis tedfordi*; (B) CPC 13848, *Bullockornis planei*; (C) UCMP 70652 and (D) UCMP 70106, *Dromornis stirtoni*; (E) CPC 13852 (type), *Ilbandornis lawsoni* and (F) UCMP 67465, *Ilbandornis woodburnei*, see caption, figures 15-16.



Figure 21. Map depicting localities in Australia which have produced remains of *Dromornithidae*: Diamantina River (1), Cassidy Locality and Lake Miamiana (2), Warburton River Localities (3), Cooper's Creek Localities (4), Lake Callabonna (5), Thorbindah (6), Cuddie Springs (7), Riversleigh (8), Bullock Creek (9), Canadian Lead (Gulgong) (10), South Mt Cameron (Endurance Tin Mine) (11), Wellington Caves (12), Leaf Locality (Lake Ngapakaldi) (13), Snake Dam Locality (Muloorina Station) (14), Baldina Creek (15), Normanville (Salt Creek) (16), Alcoota Homestead (17), Big Cave (Naracoorte) (18), Penola (19), Mt Gambier (20), Peak Downs (21), Lawson Quarry (Lake Palankarinna) (22), Scott River (23), Mammoth Cave (24), Brother's Island (Pt Lincoln) (25), and Lancefield (26). Symbols include: ■ Miocene, ▲ Pliocene, and △ Pleistocene.

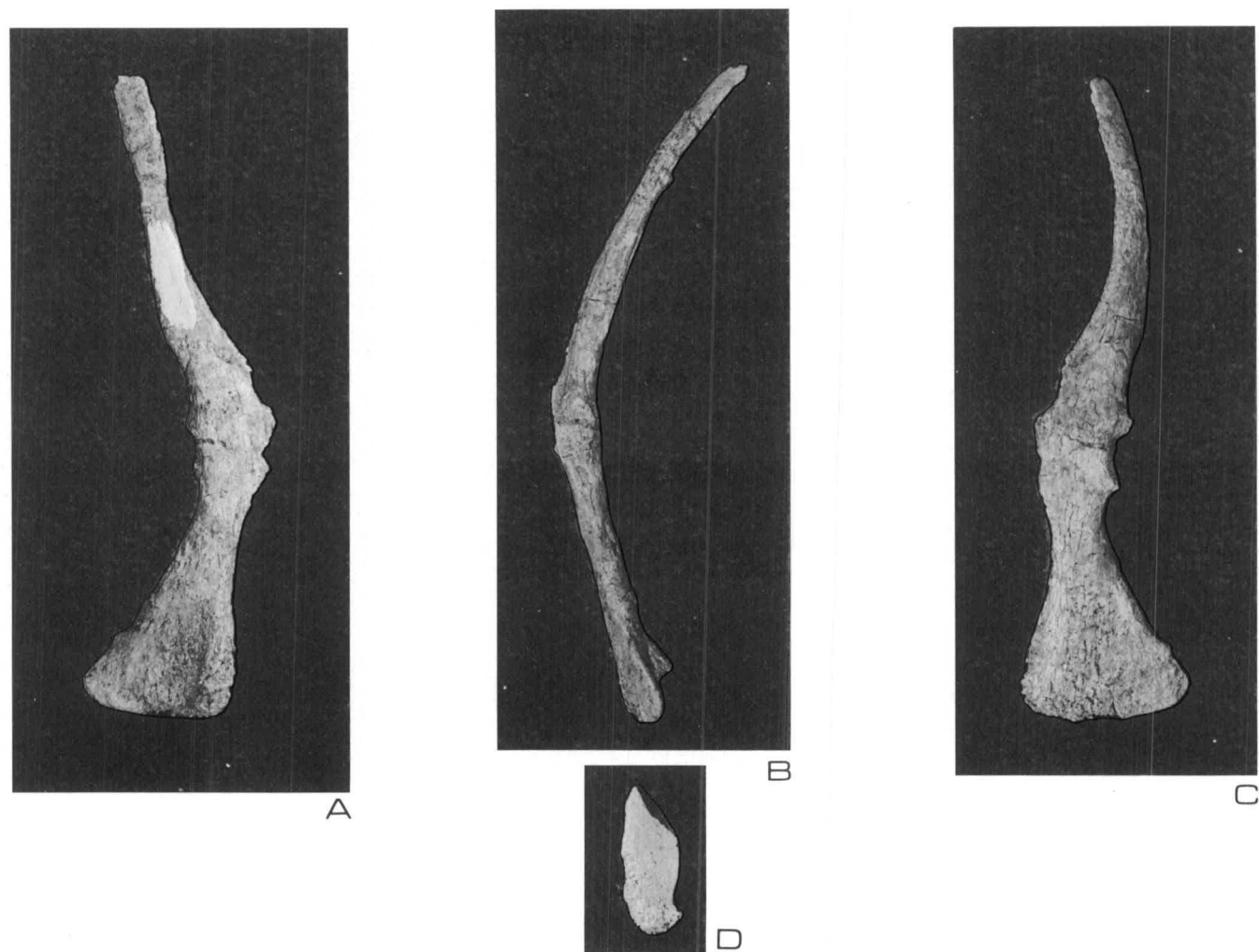


Fig. 22. *Dromornis stirtoni*, UCMP 113050, left scapulocoracoid: (A) posterior, (B) lateral, (C) anterior, and (D) ventral views, Alcoota Homestead, Northern Territory, Miocene-Pliocene, $\times \frac{1}{2}$.

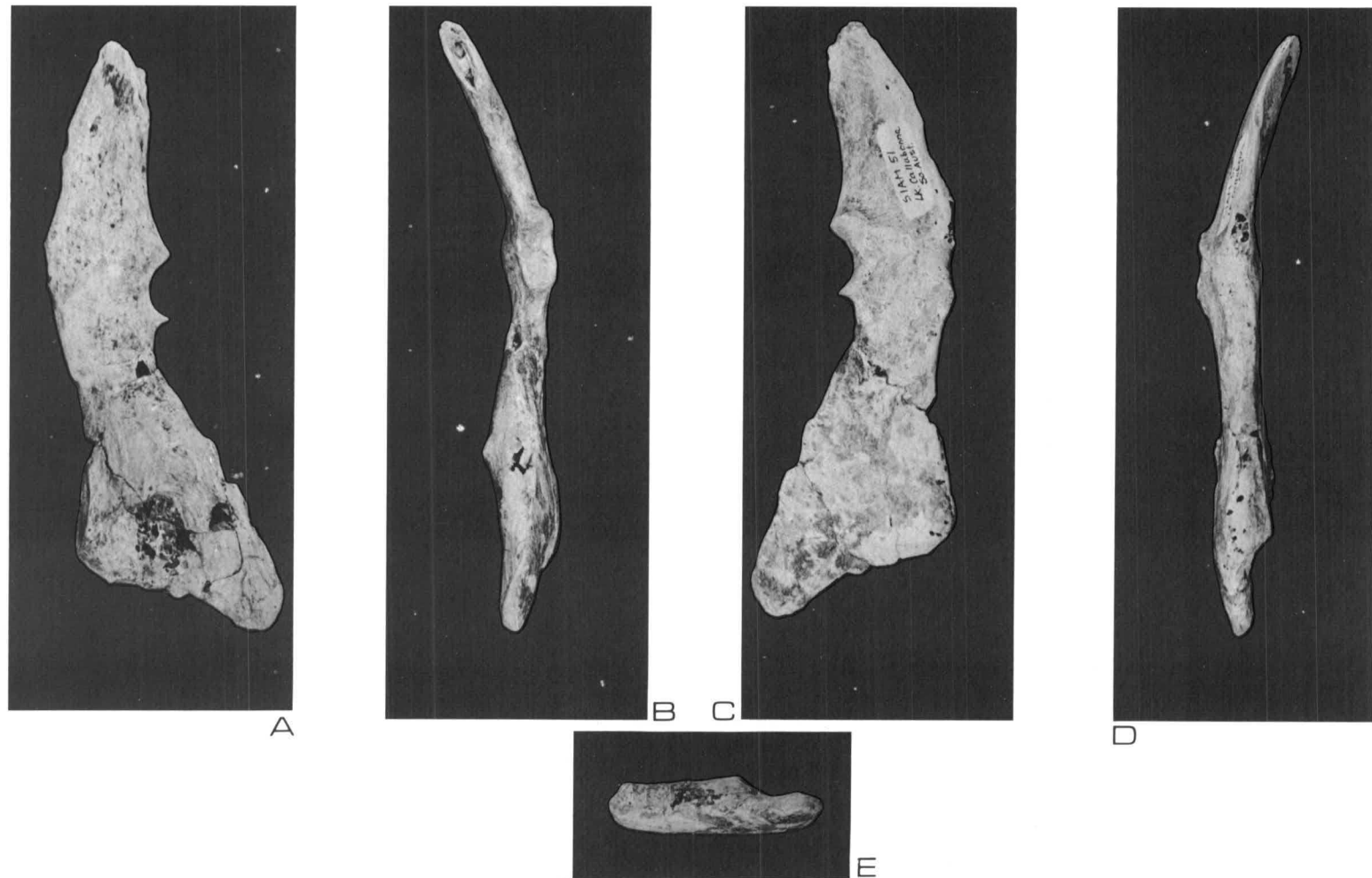


Fig. 23. *Genyornis newtoni*, SIAM 51, right scapulocoracoid: (A) posterior, (B) lateral, (C) anterior, (D) medial, and (E) ventral, Lake Callabonna, South Australia, Pleistocene, $\times \frac{1}{2}$.

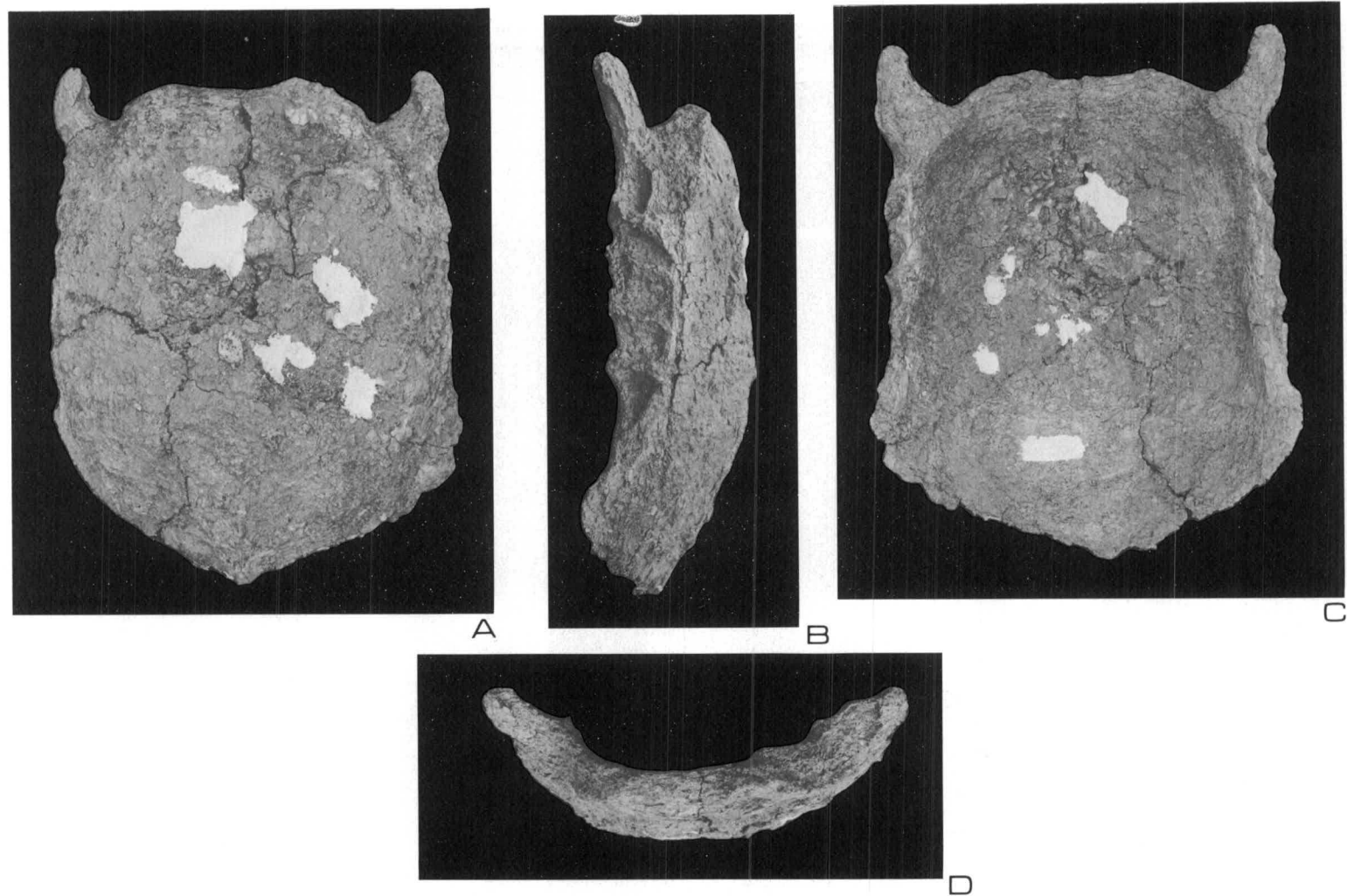
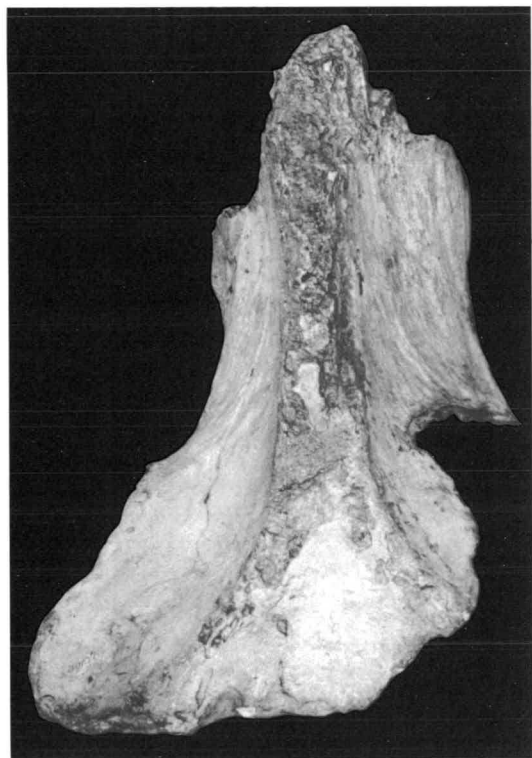


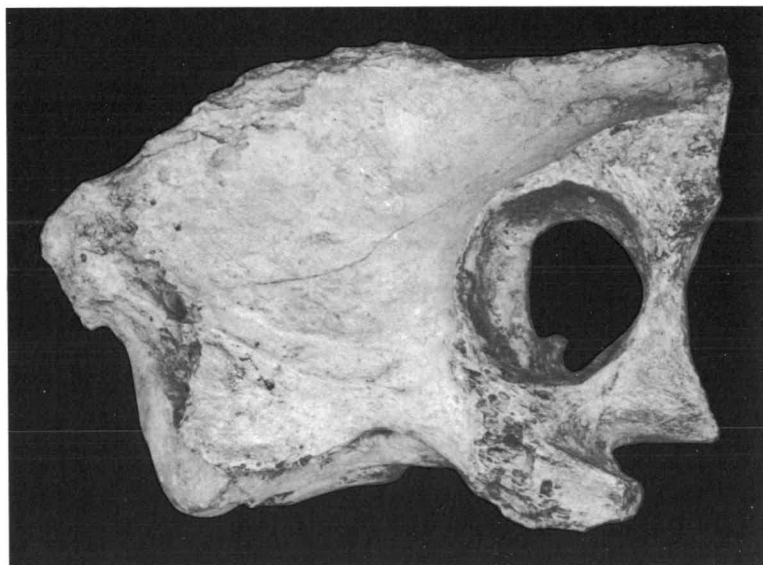
Fig. 24. *Dromornis stirtoni*, UCMP 113049 sternum: (A) ventral, (B) lateral, (C) dorsal, and (D) anterior views, Alcoota Homestead, Northern Territory, Miocene-Pliocene, x 4.



A



B



C

Fig. 25. Dromornithidae, BM(NH) 49160, synsacrum fragment (A) dorsal, (B) ventral, and (C) medial, Canadian Gold Lead, Mudgee, New South Wales, Pliocene-Pleistocene, slightly smaller than $\frac{1}{2}$ x.

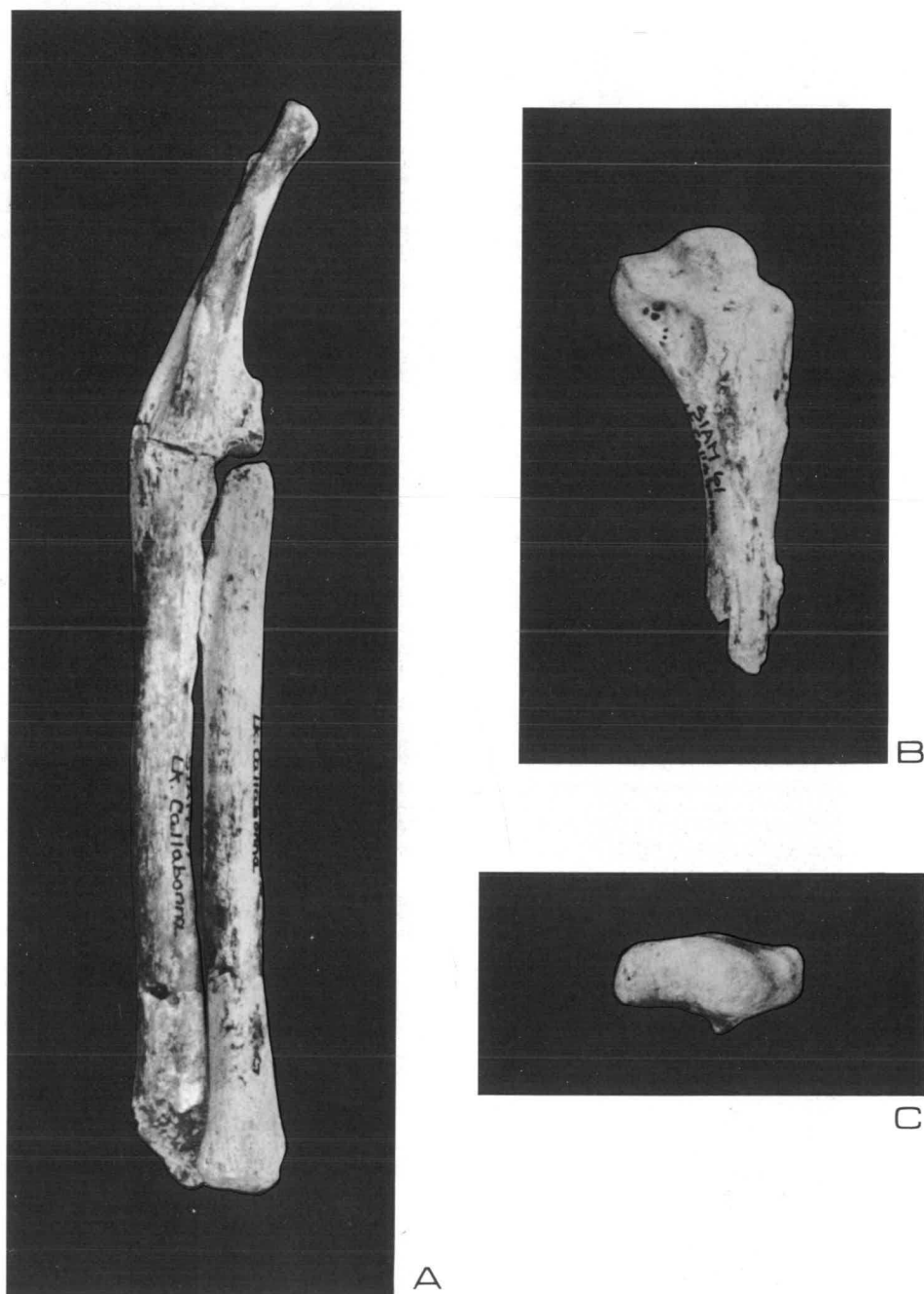
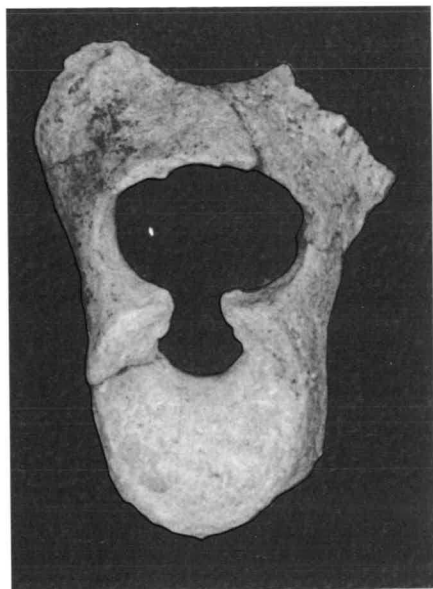


Fig. 26. *Genyornis newtoni*, (A) SIAM 51, left radius, ulna, carpometacarpus, approx. x 1; (B) SIAM 61, right humerus, proximal half only, anconal view and (C) proximal view, Lake Callabonna, South Australia, Pleistocene, x 1.



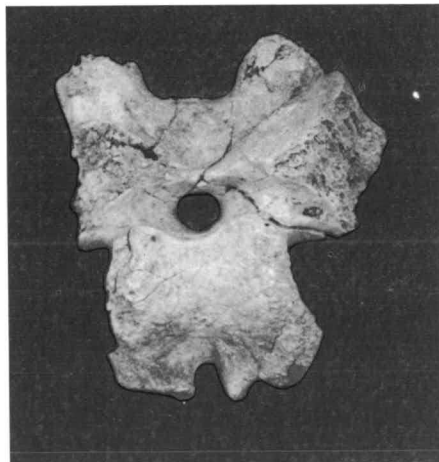
A



B



C



D

Fig. 27. *Dromornis stirtoni*, UCMP 111306, atlas vertebra, (A) anterior, (B) posterior, and (C) lateral views, x 1; UCMP 119206, cervico-dorsal or cervical vertebra, (D) anterior view, Alcoota Homestead, Northern Territory, Miocene-Pliocene, x $\frac{1}{2}$.

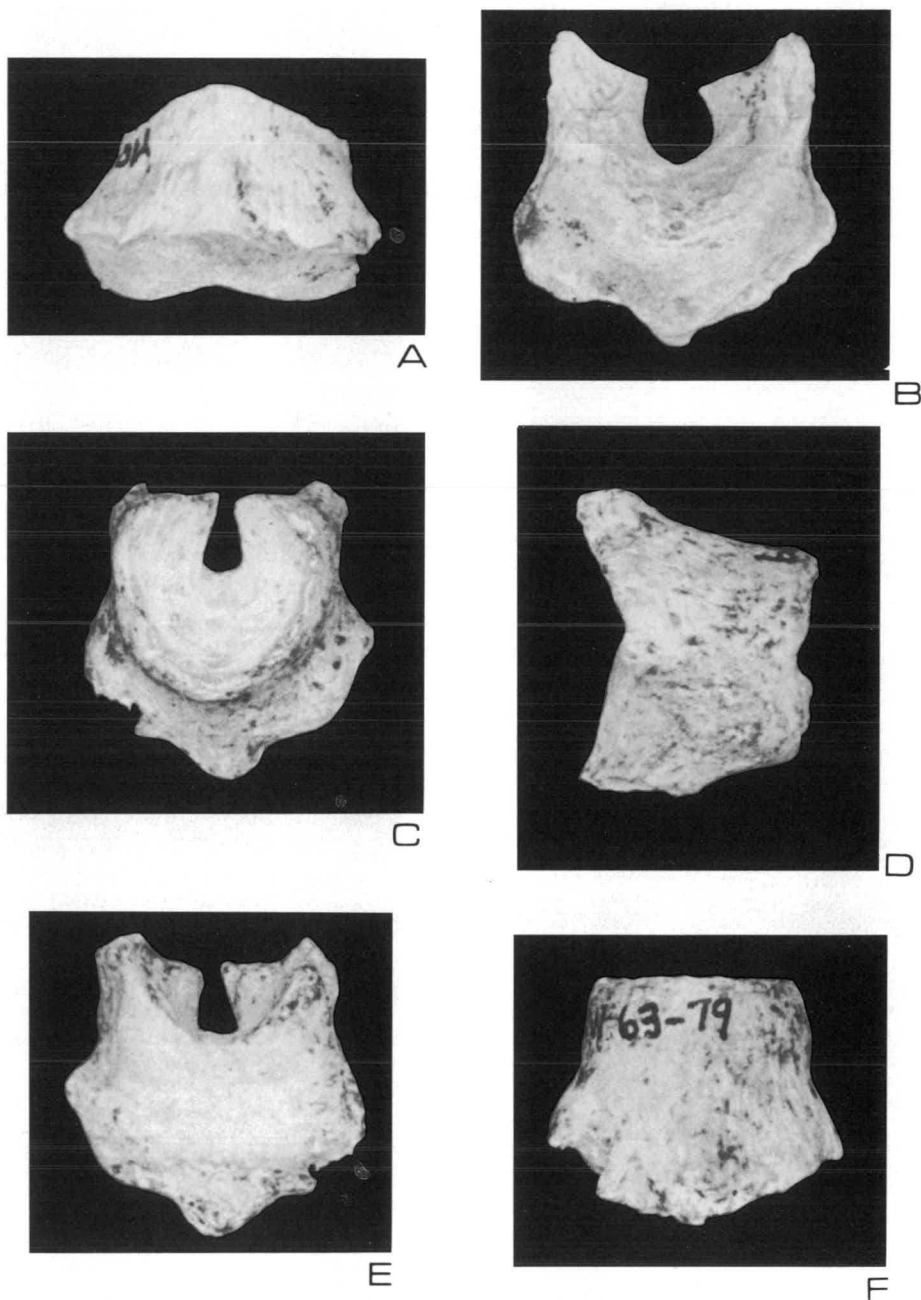


Fig. 28. *Ibandornis* sp., UCMP 113048, atlas vertebra: (A) ventral and (B) posterior views; UCMP 119207, (C) anterior, (D) lateral, (E) posterior and (F) ventral views, Alcoota Homestead, Northern Territory, Miocene-Pleistocene, x 2.

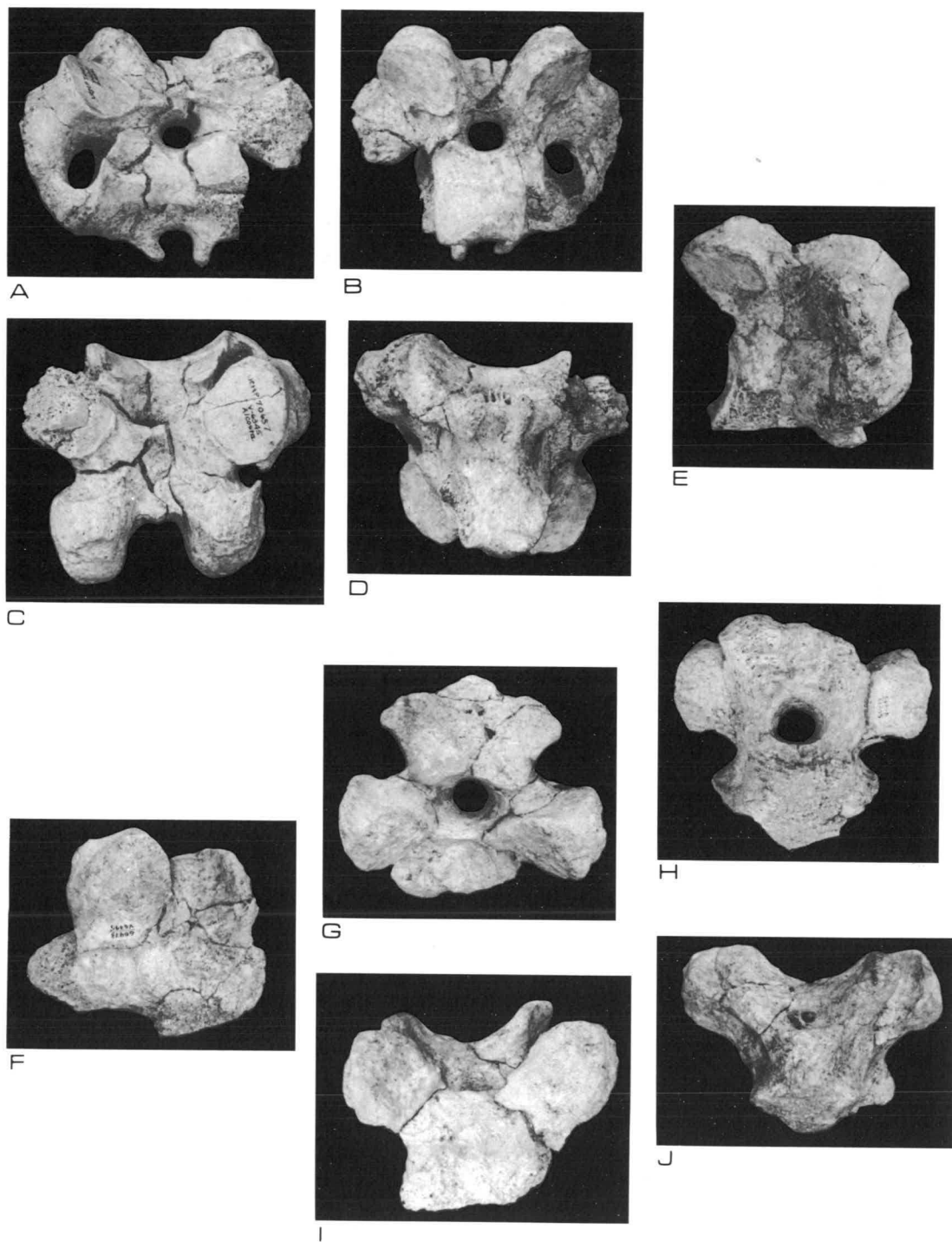


Fig. 29. *Dromornis stirtoni*, UCMP 70657, cervical or cervicodorsal vertebra: (A) anterior, (B) posterior, (C) dorsal, (D) ventral, and (E) lateral; UCMP 66973, cervico-dorsal vertebra, (F) lateral, (G) anterior, (H) posterior, (I) dorsal, and (J) ventral views, Alcoota Homestead, Northern Territory, Miocene-Pliocene, x $\frac{1}{2}$.

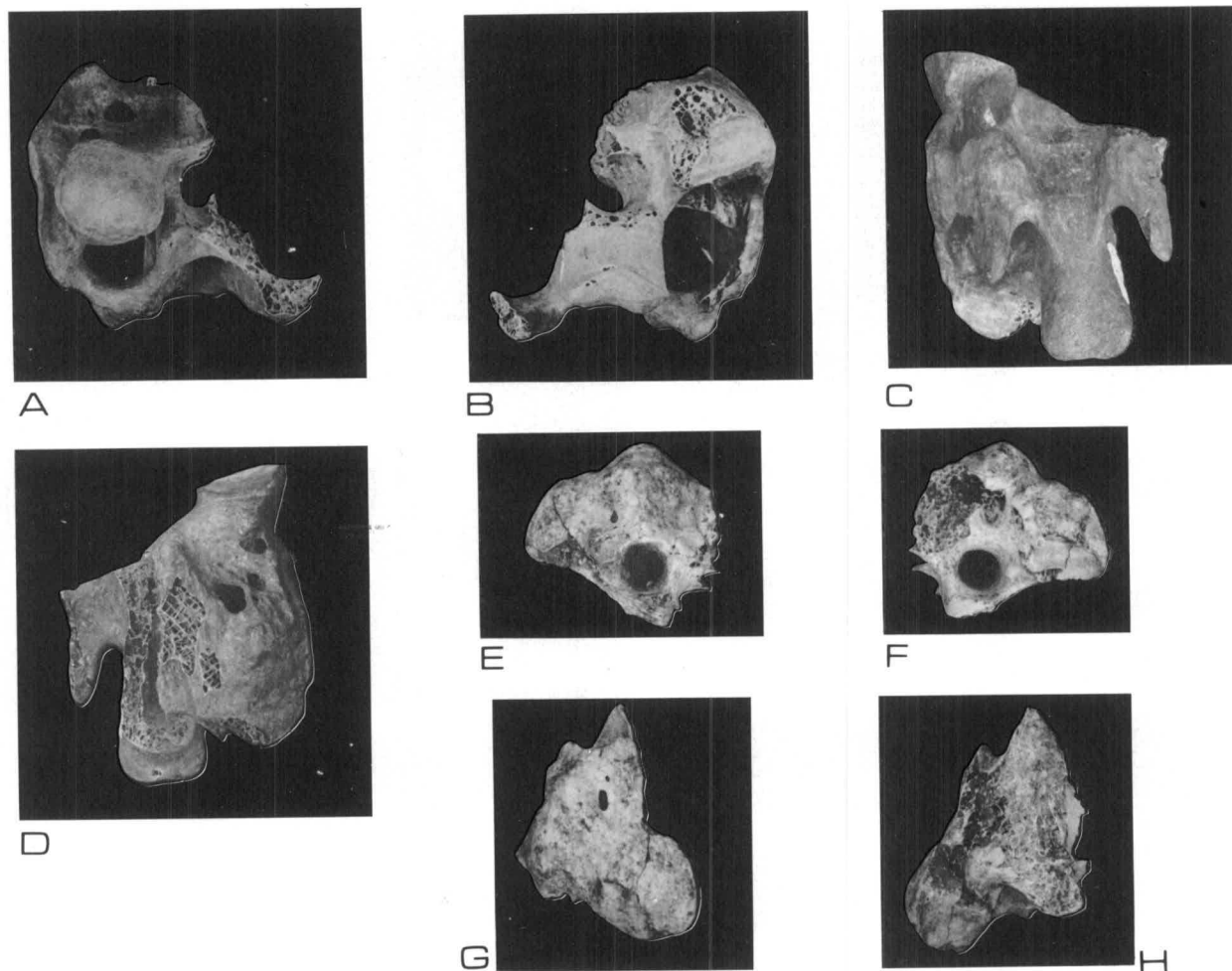
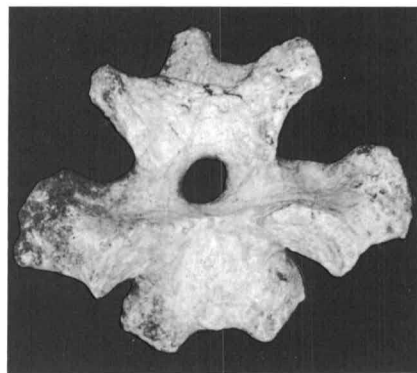
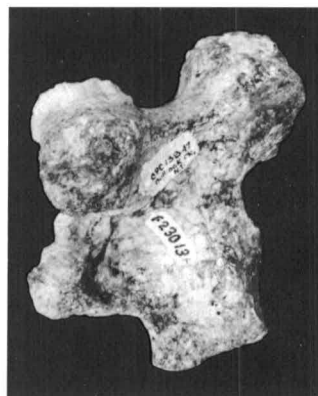


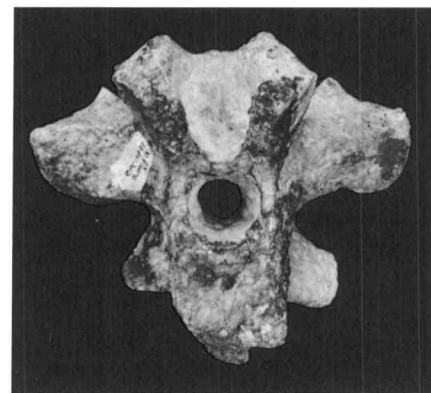
Fig. 30. cf. *Genyornis newtoni*, SAM P17320, anterior cervical vertebra, Naracoorte, Big Cave, South Australia, Pleistocene: (A) anterior, (B) posterior, (C) ventral, and (D) dorsal views; SIAM 51, axis vertebra, Lake Callabonna, South Australia, Pleistocene: (E) anterior, (F) posterior, (G) dorsal, and (H) ventral views, $\times \frac{1}{2}$.



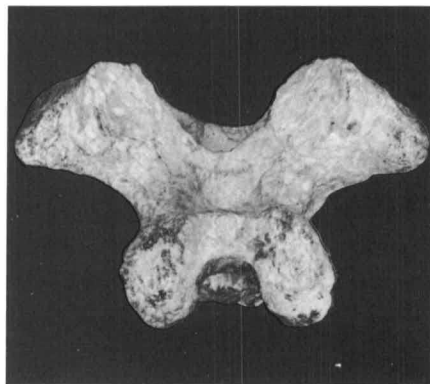
A



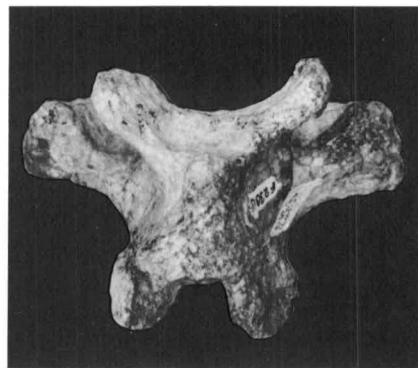
B



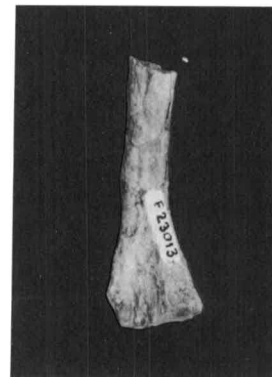
C



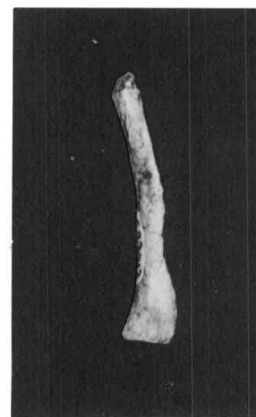
D



E

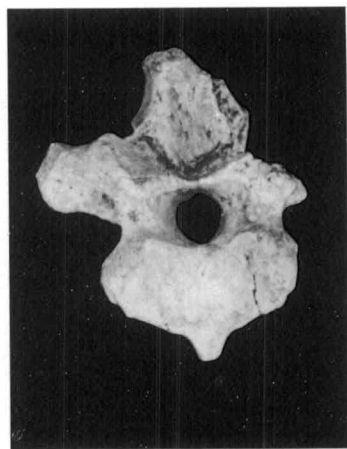


F

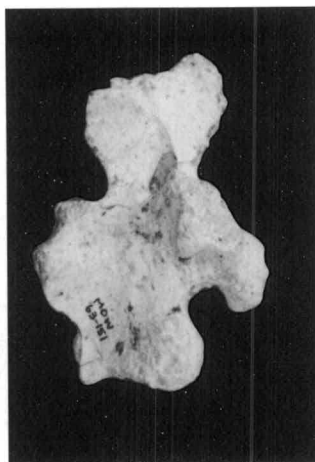


G

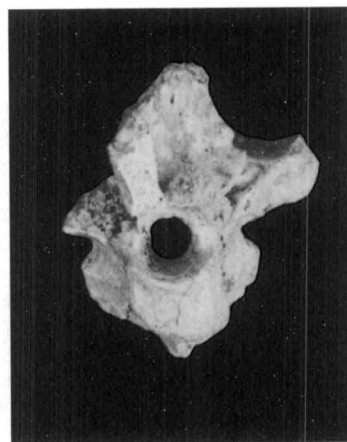
Fig. 31. *Bullockkornis planei*, cervico-dorsal or dorsal vertebra: (A) anterior, (B) lateral, (C) posterior, (D) dorsal, and (E) ventral views; costal rib: (F) posterior and (G) side views, Bullock Creek, Northern Territory, Miocene, x 1.



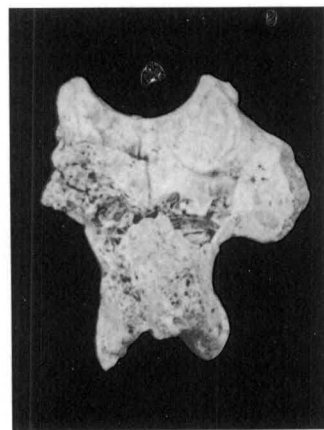
A



B



C

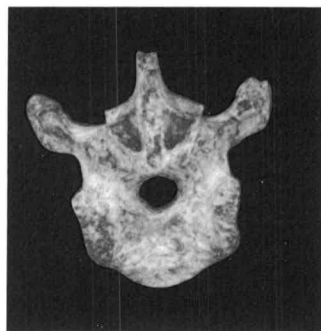


D

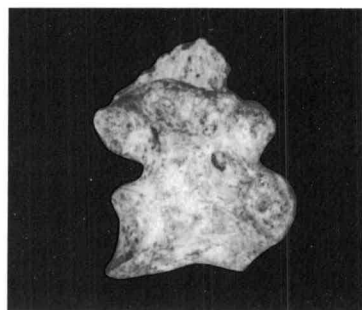


E

Fig. 32. *Ilbandornis* sp. UCMP 111305, dorsal vertebra: (A) anterior, (B) lateral, (C) posterior, (D) dorsal, and (E) ventral, Alcoota Homestead, Northern Territory, Miocene-Pliocene, $\times \frac{1}{2}$.



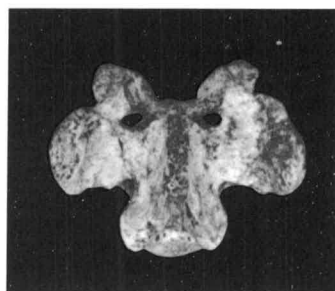
A



B



C



D



E

Fig. 33. *Genyornis newtoni*, SIAM 61, dorsal vertebra: (A) anterior, (B) lateral, (C) posterior, (D) dorsal, and (E) ventral views, Lake Callabonna, South Australia, Pleistocene, $\times \frac{1}{2}$.

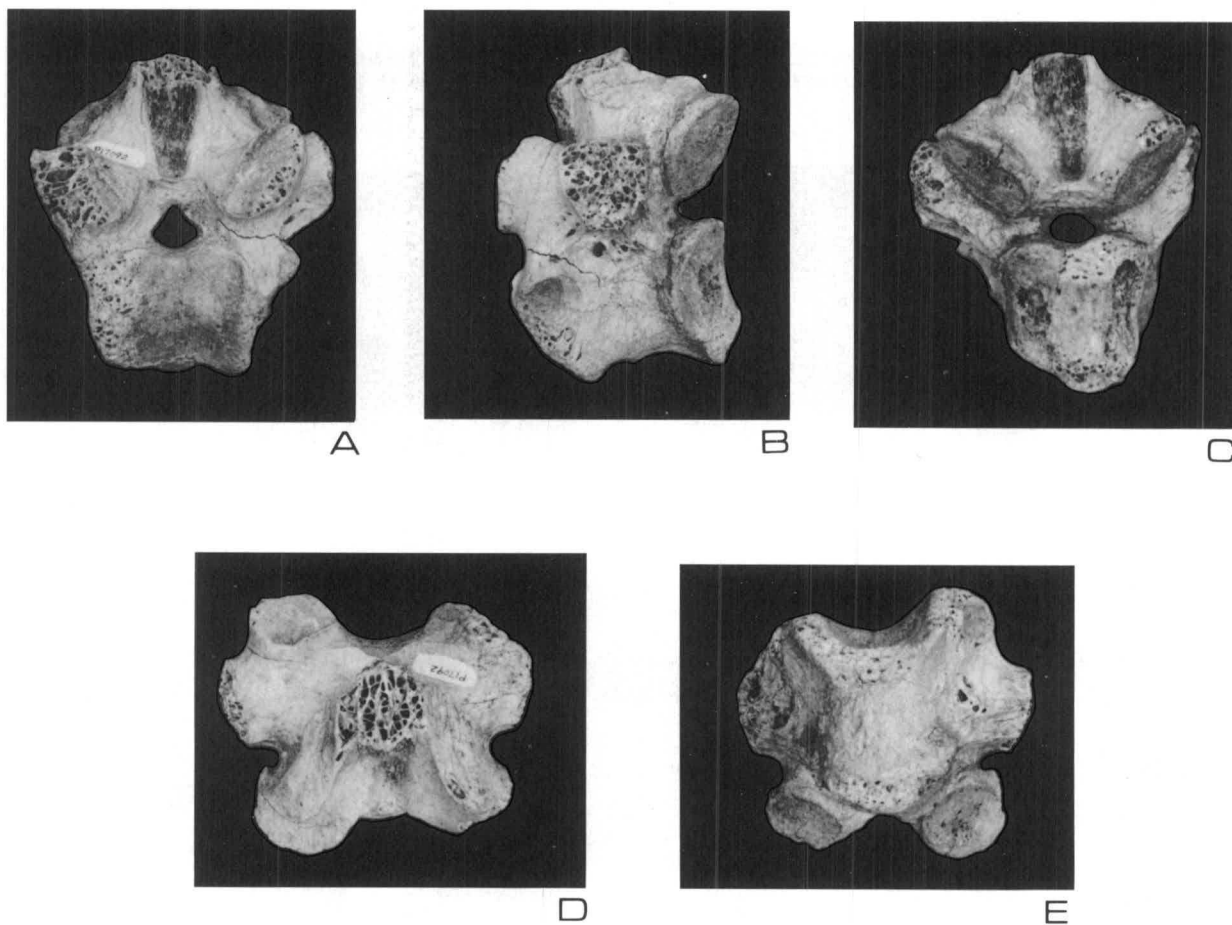


Fig. 34. *Genyornis newtoni*, SAM P17092, posterior dorsal vertebra: (A) anterior, (B) lateral, (C) posterior, (D) dorsal, and (E) ventral views, Lake Callabonna, South Australia, Pleistocene, x $\frac{1}{2}$.

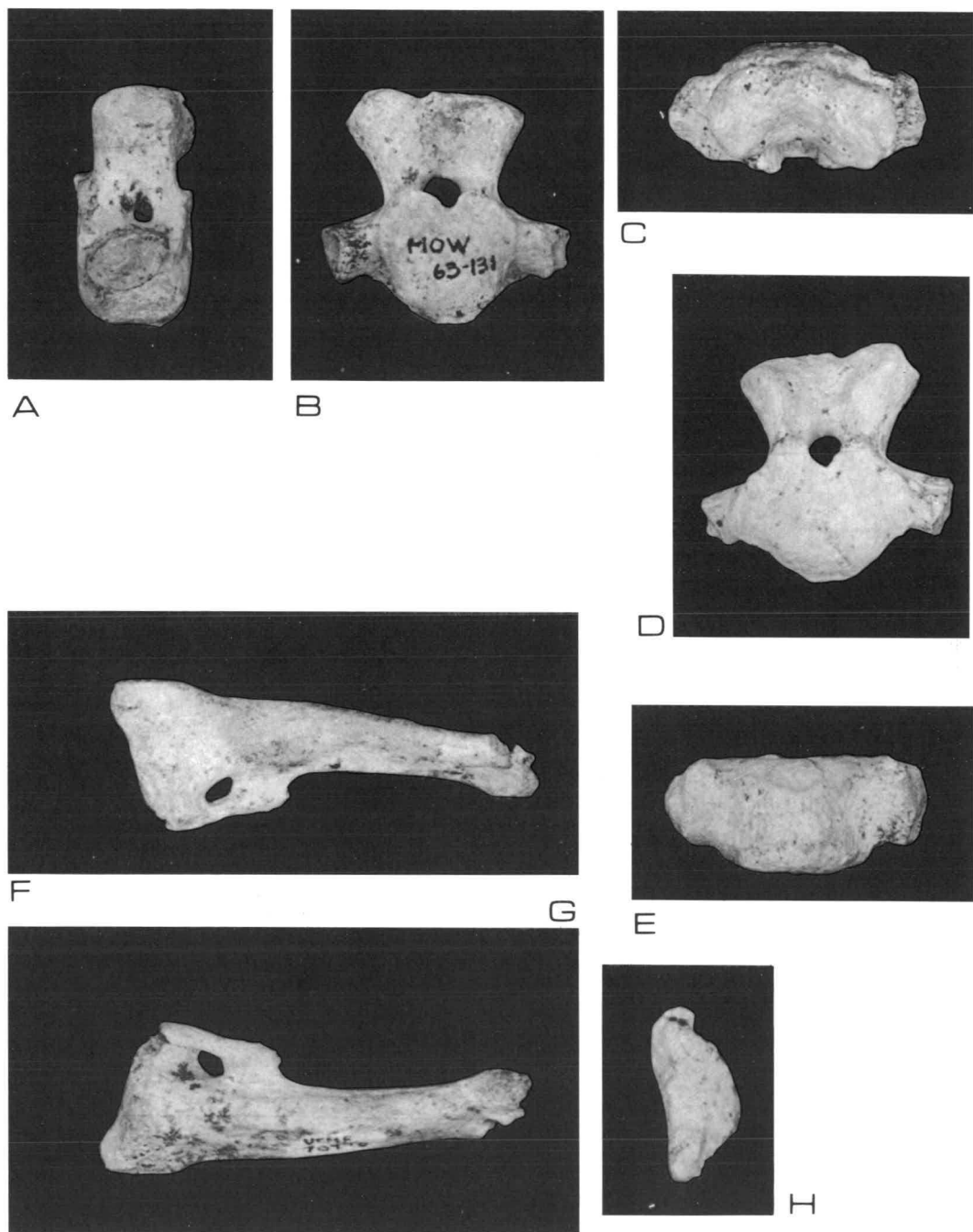


Fig. 35. *Dromornis stirtoni*, UCMP 113047, caudal vertebra: (A) lateral, (B) posterior, (C) dorsal, (D) anterior, and (E) ventral views; UCMP 70996, right carpometacarpus: (F) medial, (G) lateral, and (H) proximal views, Alcoota Homestead, Northern Territory, Miocene-Pliocene, about x 1.

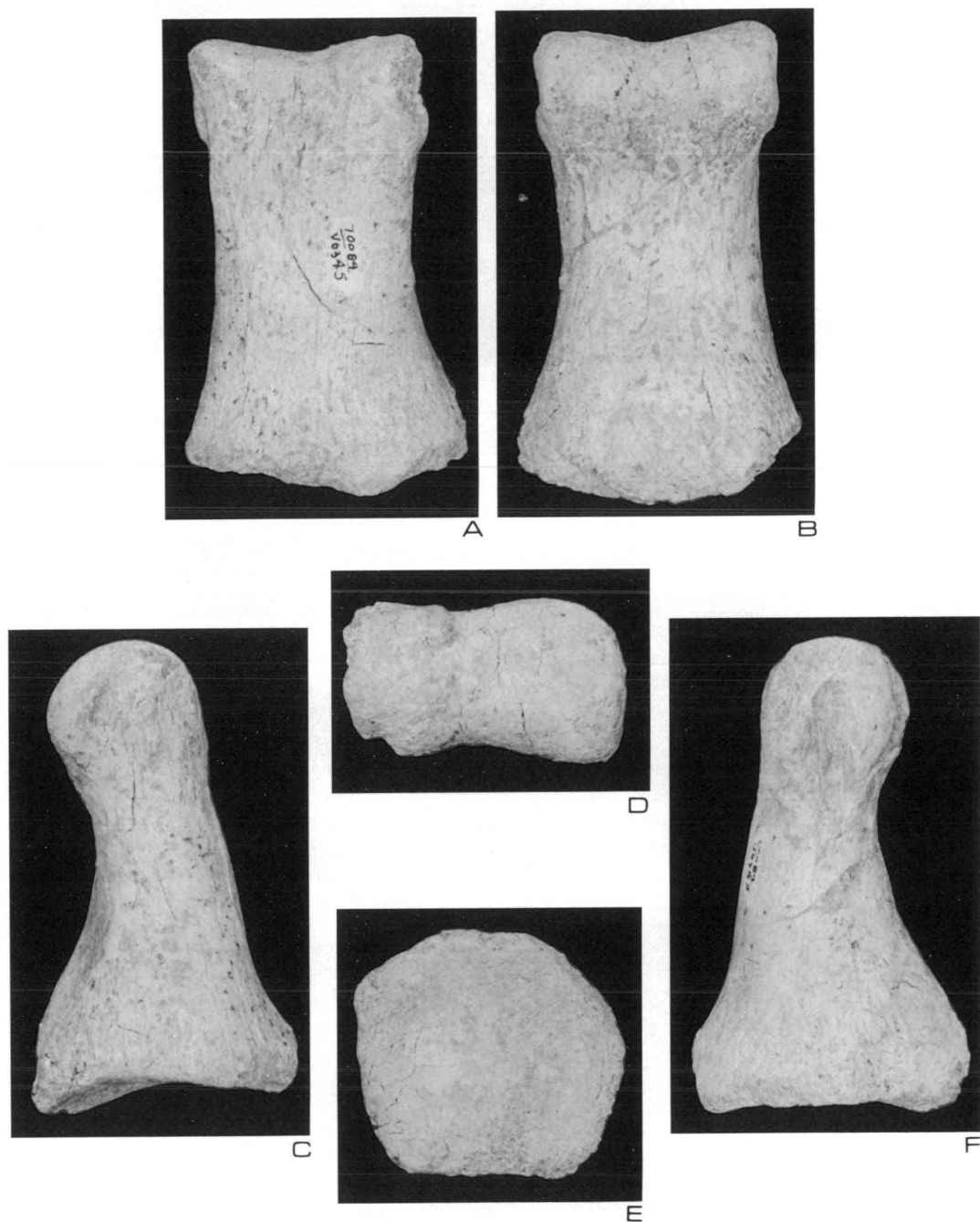
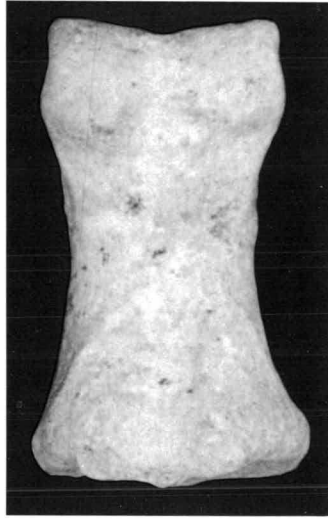


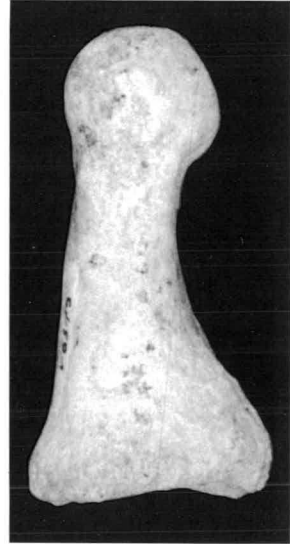
Fig. 36. *Dromornis stirtoni*, UCMP 70084, right phalanx 1, digit III: (A) dorsal, (B) ventral, (C) medial, (D) distal, (E) proximal, and (F) lateral views, Alcoota Homestead, Northern Territory, Miocene-Pliocene, x 3.



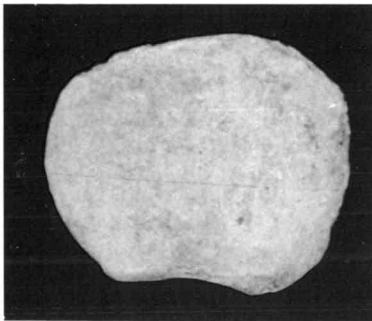
A



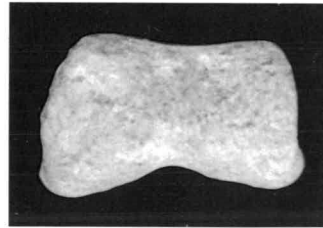
B



C



D



E

Fig. 37. *Ilbandornis* sp., UCMP 71016, left phalanx 1, digit III: (A) dorsal, (B) ventral, (C) medial, (D) proximal, and (E) distal, Alcoota Homestead, Northern Territory, Miocene-Pliocene, x 1.

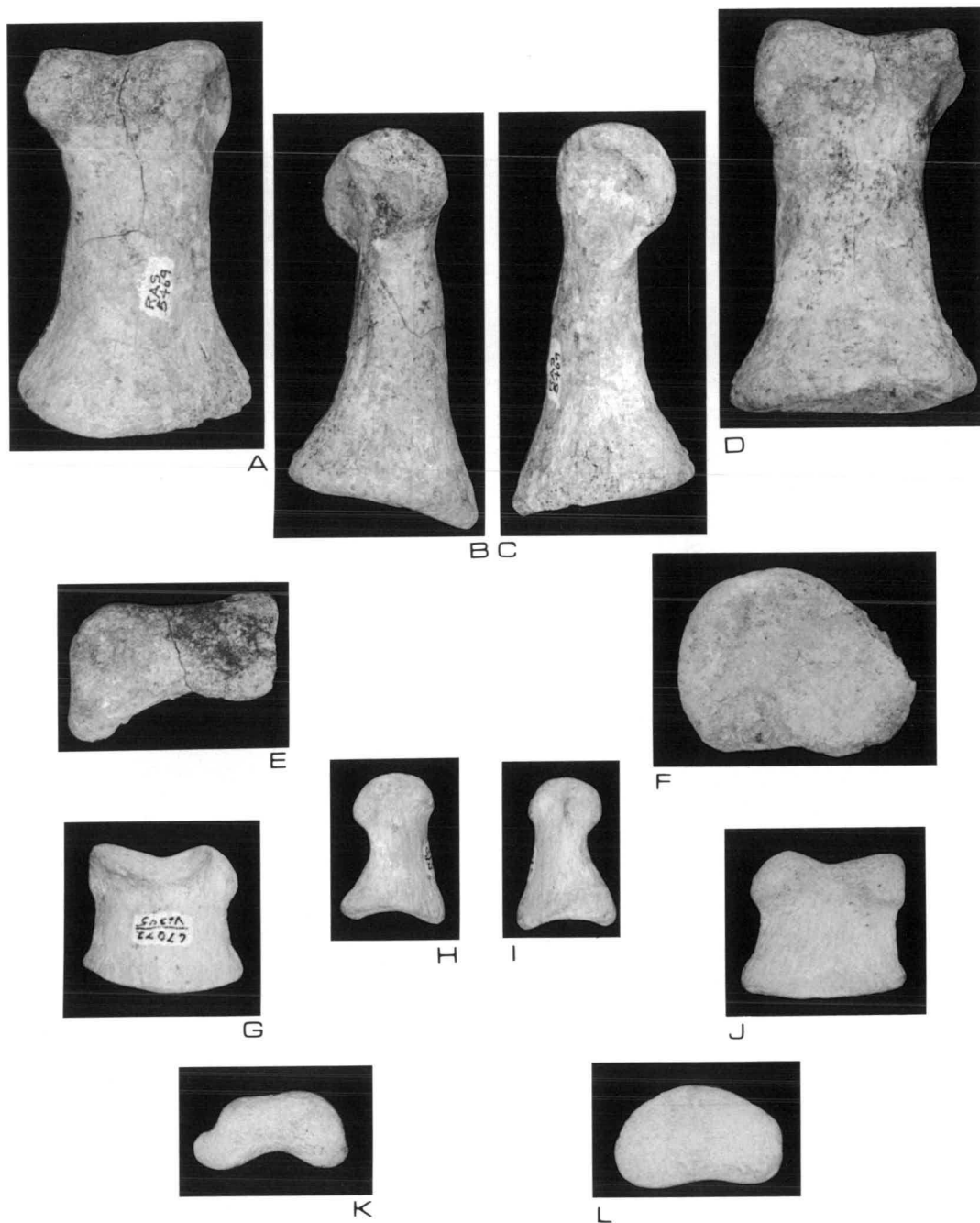


Fig. 38. *Dromornis stirtoni*, UCMP 111304, right phalanx 1, digit IV: (A) dorsal, (B) medial, (C) lateral, (D) ventral, (E) distal, and (F) proximal views; and UCMP 67072, left phalanx 2, digit IV: (G) dorsal, (H) lateral, (I) medial, (J) ventral, (K) distal, and (L) proximal views, Alcoota Homestead, Northern Territory, Miocene-Pliocene, x 3.

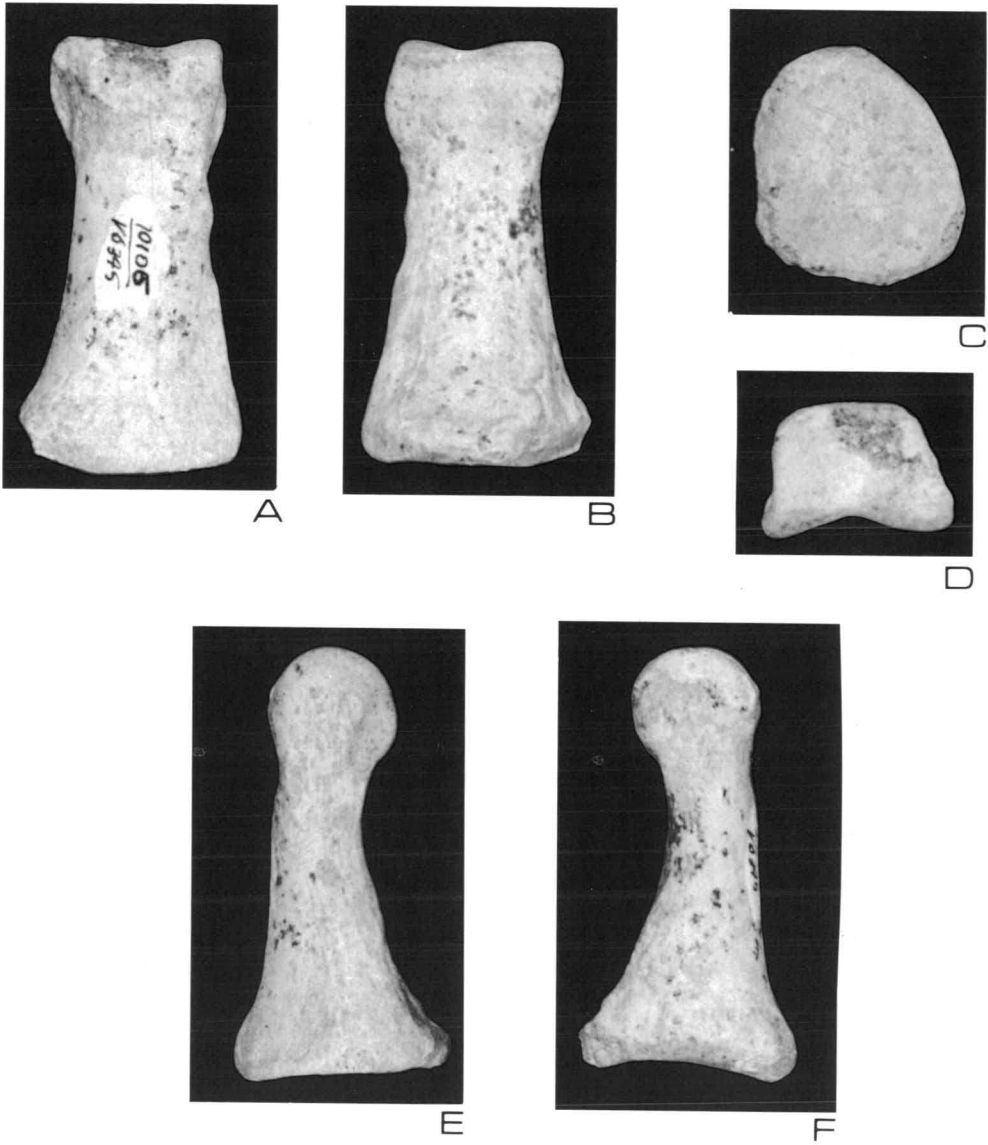
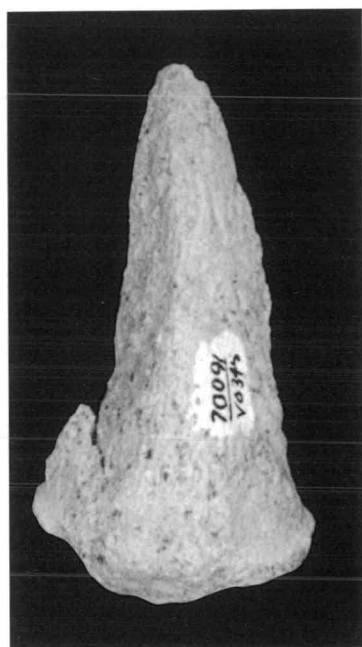
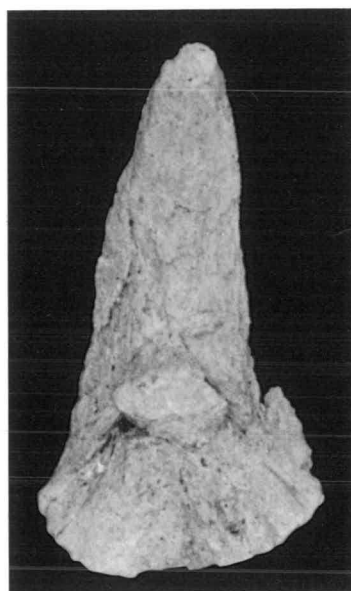


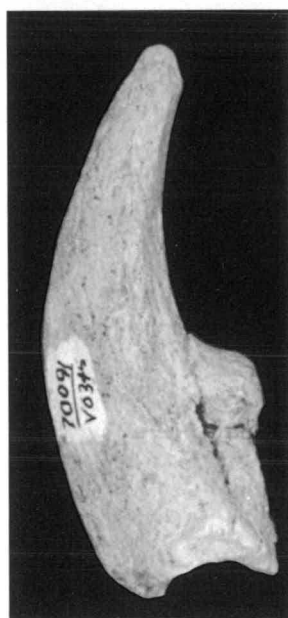
Fig. 39. *Ibandornis* sp., UCMP 70105, right phalanx 1, digit IV: (A) dorsal, (B) ventral, (C) proximal, (D) distal, (E) lateral, and (F) medial, Alcoota Homestead, Northern Territory, Miocene-Pliocene, x 1.



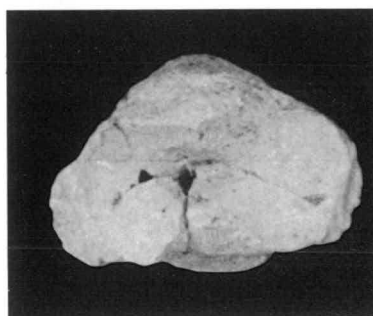
A



B



C

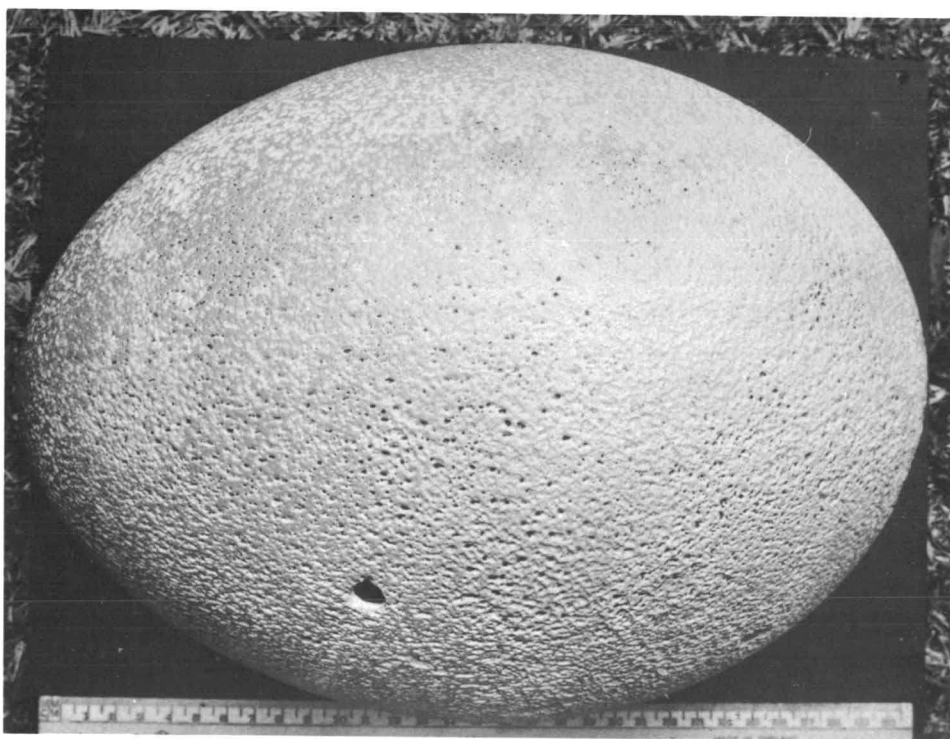


D

Fig. 40. Class indeterminate, UCMP 70091, terminal phalanx: (A) dorsal, (B) ventral, (C) medial or lateral, and (D) proximal views; Alcoota Homestead, Northern Territory, Miocene-Pliocene, x 1.



A



B

Fig. 41. (a) Trackway of ?dromornithids from the old Endurance Tin Mine pit at South Mount Cameron, five miles north of Pioneer, northeastern Tasmania; mid-Tertiary. Scale in lower left part of photograph 115 mm. (B) Egg of a ?dromornithid found in coastal dunes between the Scott River and the Southern Ocean, Southwestern Western Australia, Pleistocene. Scale along bottom of photograph is about 280 mm (12 inches). See Rich and Green, 1974.

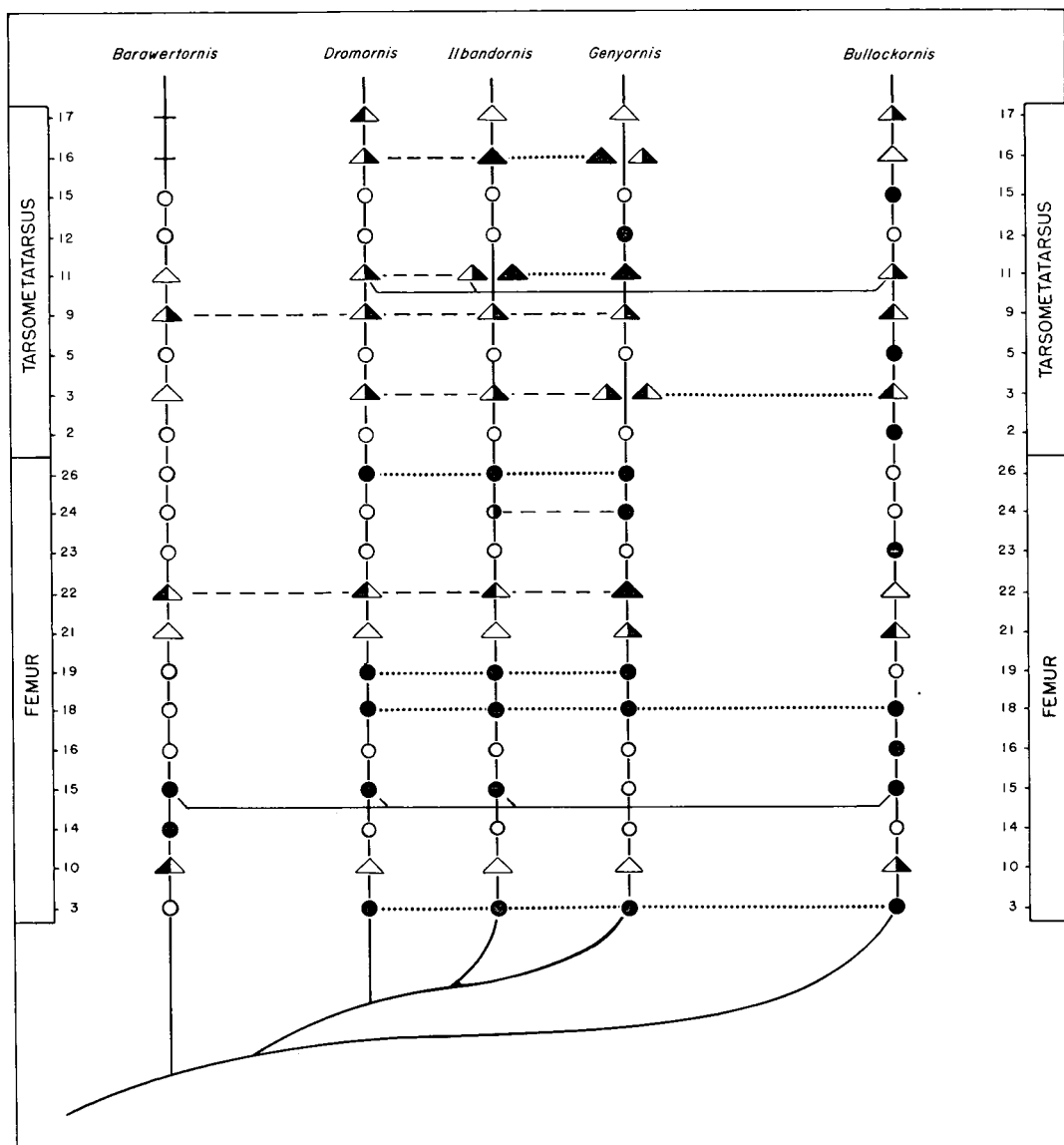
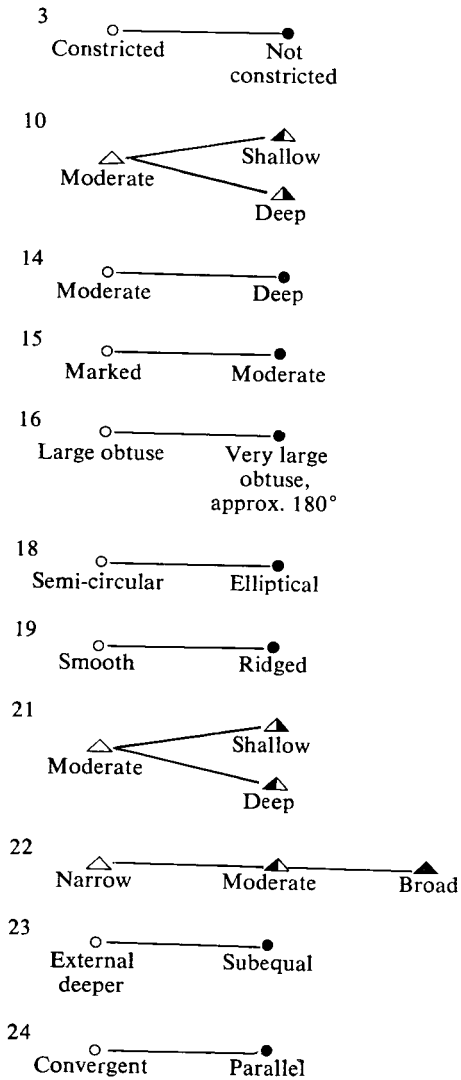


Fig. 43. Phylogenetic hypothesis of interrelationships of Cenozoic Dromornithidae. Character numbers refer to those utilized in the diagnoses for genera of Dromornithidae. See key for explanation of symbols. Fully black symbols indicate most highly derived character states, white most primitive. Lines connecting symbols indicate possession of shared, derived character states.

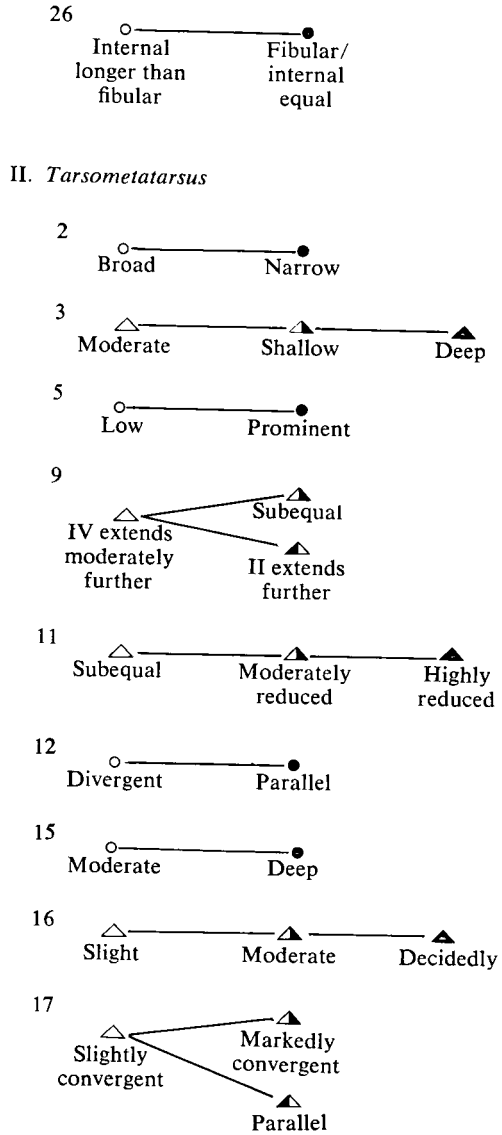
KEY TO FIGURE 43
Character State Symbols

Character
Number

I. *Femur*



Character
Number



KEY TO FIGURE 44

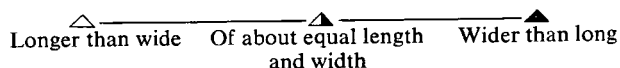
Character

Character State Symbols

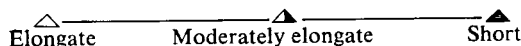
Letter

I. Sternum

b. Length vs. breadth



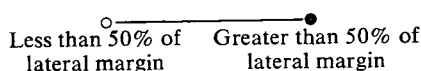
c. Sterno-coracoidal processes



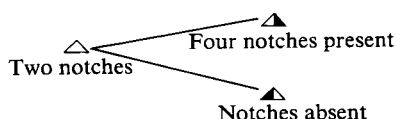
d. Anterior border of sternum



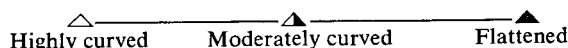
f. Length, costal margin



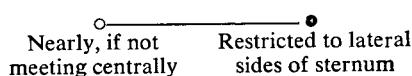
g. Sternal notches



j. Ventral surface of sternum



k. Coracoidal sulci

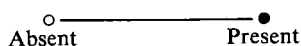


II. Scapulocoracoid

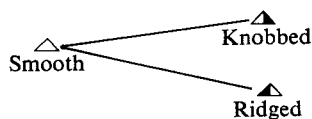
b. Orientation of glenoid facet



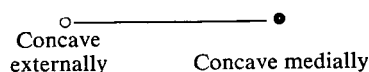
c. Groove medial of glenoid facet



d. Nature of anterior surface between glenoid and medial margin

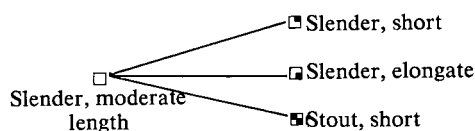


e. Shape of scapular blade



III. Humerus

a. Humeral proportions



b. Ligamental furrow

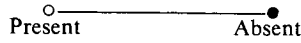


KEY TO FIGURE 44 (*continued*)

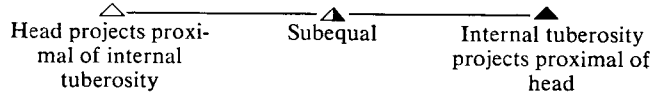
Character
Letter

Character State Symbols

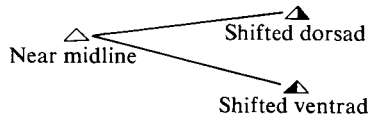
c. Pneumatic foramen



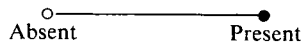
e. Relative proximal protrusion of internal tuberosity and head



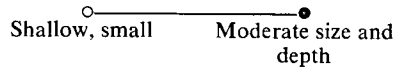
f. Location of head on proximal end



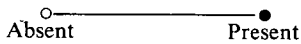
g. Ligamental scar near midpoint of shaft on ventral surface



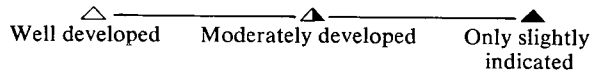
h. Brachial depression



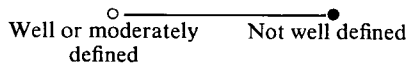
i. Ridge at base of deltoid crest



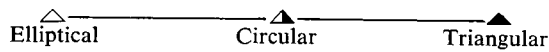
j. Ectepicondylar prominence



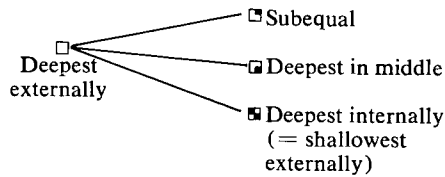
k. Definition of articular surfaces



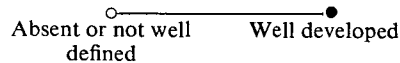
l. Cross-section



m. Width of distal end

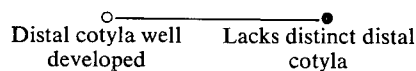


n. Olecranal fossa

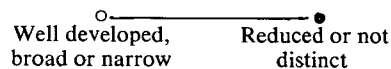


IV. *Ulna-radius*

a. Nature of proximal end



b. Nature of olecranon



KEY TO FIGURE 44 (continued)

Character

Character State Symbols

Letter

- c. Depth of proximal end

○ ————— ●
Deep Shallow

- d. Fusion of radius and ulna

○ ————— ●
Unfused Fused

- e. Widths of ulna and radius

○ ————— ●
Ulna decidedly broader Subequal

- g. Comparative lengths of radius-ulna and humerus

△ ————— △
Subequal Radius-ulna longer than humerus
Radius-ulna shorter than humerus

V. *Carpometacarpus*

- a. Flattening of carpal trochlea

△ ————— △ ————— △
Highly curved Moderately curved Flattened

- b. Phalangeal articulation on metacarpal I

○ ————— ●
Present Absent

- c. Degree of fusion of metacarpals II and III

○ ————— ●
Large intermetacarpal space Nearly complete fusion

- f. Breadth of metacarpal II

○ ————— ●
Broad Compressed

- g. Metacarpals with phalangeal articulation

○ ————— ●
3 1

VI. *Synsacrum*

- a. Width of dorsal surface of synsacrum posteriad of antitrochanter

○ ————— ●
Decreases in width posteriad Remains about same or decreases only slightly

- b. Comparative widths of dorsal surface of synsacrum posteriad of antitrochanter

○ ————— ●
Decreases in width posteriad Remains about same or decreases only slightly

- d. Antero-posterior location of antitrochanter

△ ————— △ ————— △
Posteriad of midpoint At midpoint Anteriad of midpoint

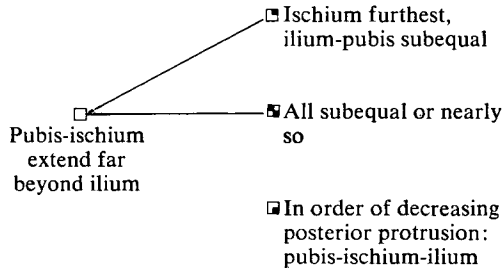
KEY TO FIGURE 44 (continued)

Character

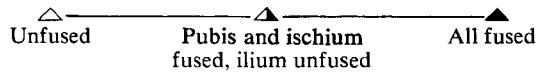
Character State Symbols

Letter

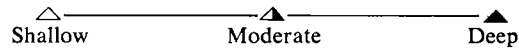
- e. Relative posterior protrusion of ilium, ischium, pubis



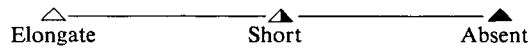
- f. Pubis fused or unfused with ischium, ischium fused or unfused with ilium



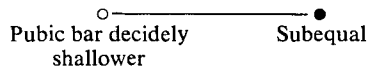
- j. Depth of ilium dorsad of acetabulum



- k. Length of pectinal process

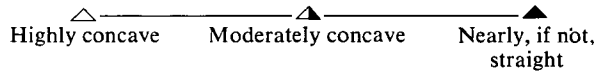


- l. Depth of pubic and ischial bars

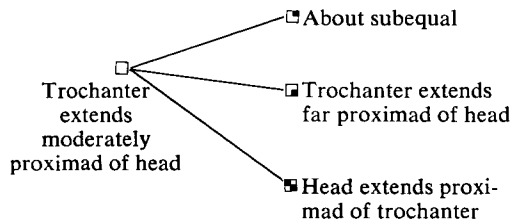


VII. Femur

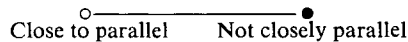
- a. Shape of posterior margin of proximal articular surface



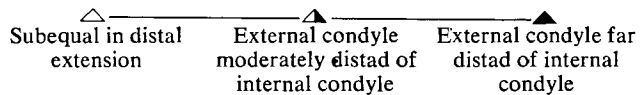
- b. Comparative proximal extension of trochanter and head



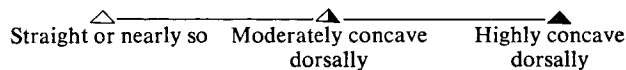
- c. Orientation of long axes of condyles with respect to long axis of shaft



- d. Comparative distal extension of internal and external condyles



- f. Shape of dorsal margin of external condyle



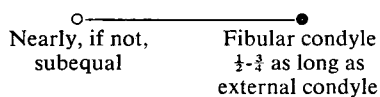
KEY TO FIGURE 44 (continued)

Character

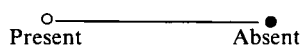
Character State Symbols

Letter

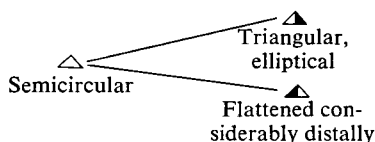
- g. Comparative length of fibular and external condyles



- j. Presence/absence of muscle scar near proximo-internal region

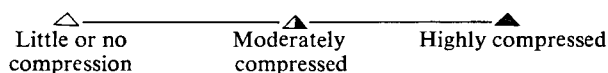


- n. Shape of internal condyle

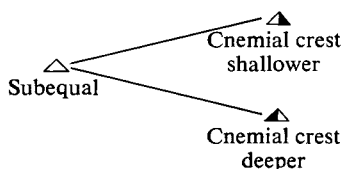


VIII. *Tibiotarsus*

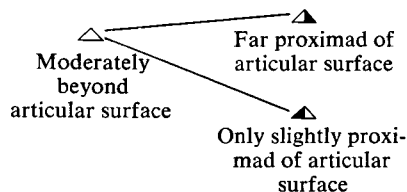
- a. Degree of medio-lateral compression of cnemial crests



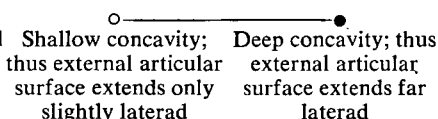
- b. Comparative depth of inner cnemial crest and remaining proximal articular surface



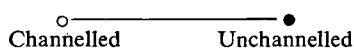
- c. Degree of proximal extension of inner cnemial crest



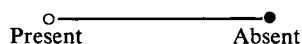
- d. Shape of external margin of proximal end between outer cnemial crest and external articular surface



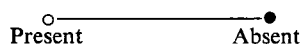
- g. Degree of channelling of intercondylar eminence



- h. Presence or absence of intercondylar eminence



- k. Supratendinal bridge



KEY TO FIGURE 44 (continued)

Character

Character State Symbols

Letter

- l. Location of ten-
dinal canal with
respect to midline
of shaft
- Displaced far mediad Centrally located
- m. Presence or
absence of marked
ridge extending
laterad from ten-
dinal canal
- Present Absent
- p. Outline of anterior
and distal margins
of external condyle
- Semicircular Elliptical
- q. Position along
external condyle
of anteriormost
projection
- At or near midpoint Decidedly proximad
of midpoint
- r. Degree of pos-
terior extension of
external condyle
- Moderate Short
Far
- s. Presence or
absence of deep
excavation near
anterior end
external condyle
- Absent Present
- u. Depth and length
of internal condyle
- Moderate in depth and length Deep, proximodistally
compressed
- w. Comparative
depths of internal
and external
condyles
- Nearly, if not, sub-
equal Internal condyle
deeper than external
condyle

IX. *Tarsometatarsus*

- a₁. Shape of hypo-
tarsus
- Broad rectangular Broad to narrow
triangular Narrow ridge
- a₂. Presence or
absence of cal-
caneal canals
- 3 2 1
- a₃. Location of hypo-
tarsus with respect
to midline
- Laterally offset Located near or on
midline
- b. Conformation of
internal border of
proximal end
- Ridged Low, unridged

^aA = intercotylar prominence absent.

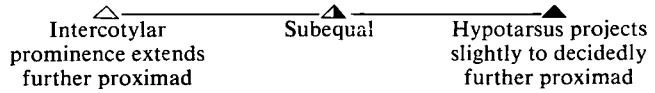
KEY TO FIGURE 44 (continued)

Character

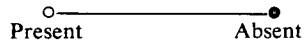
Character State Symbols

Letter

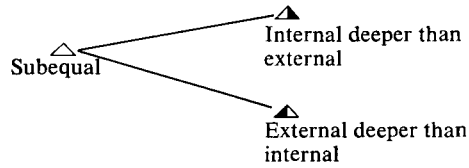
- c. Comparative proximal extension of hypotarsus and intercotylar prominence^a



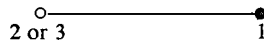
- d. Presence or absence of depression between intercotylar area and hypotarsus



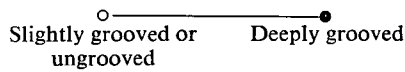
- f. Comparative depths of internal and external cotyla



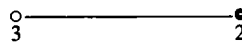
- h. Number of subhypotarsal ridges



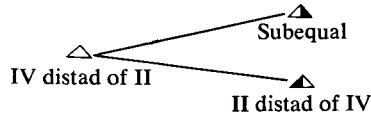
- i. Degree of grooving of posterior shaft surface



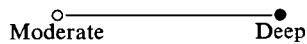
- l. Number of trochlea



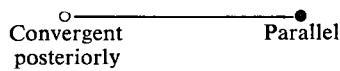
- n. Comparative distal extensions of trochleae IV and II^a



- p. Depth of trochleae

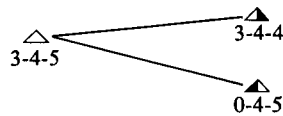


- q. Relationship of medial and lateral margins of trochlea III

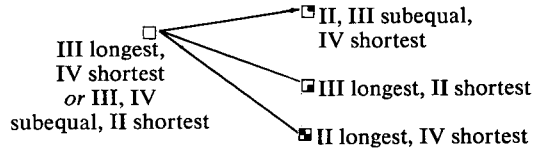


X. *Pes*

- a. Phalangeal counts for digits II-III-IV


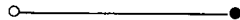



- c. Comparative lengths of proximal phalanges of digits^a



^aA = trochleae II absent.

KEY TO FIGURE 44 (*continued*)

Character	Character State Symbols
Letter	
d. Shape of proximal margins of many phalanges	 V-shaped Straight
h. Degree of proximal articular surface excavation	 Deeply biconcave Flattened, shallow
y. Shape of terminal phalanges	 Claw shaped Hoof-like

^aA = phalanx II absent.

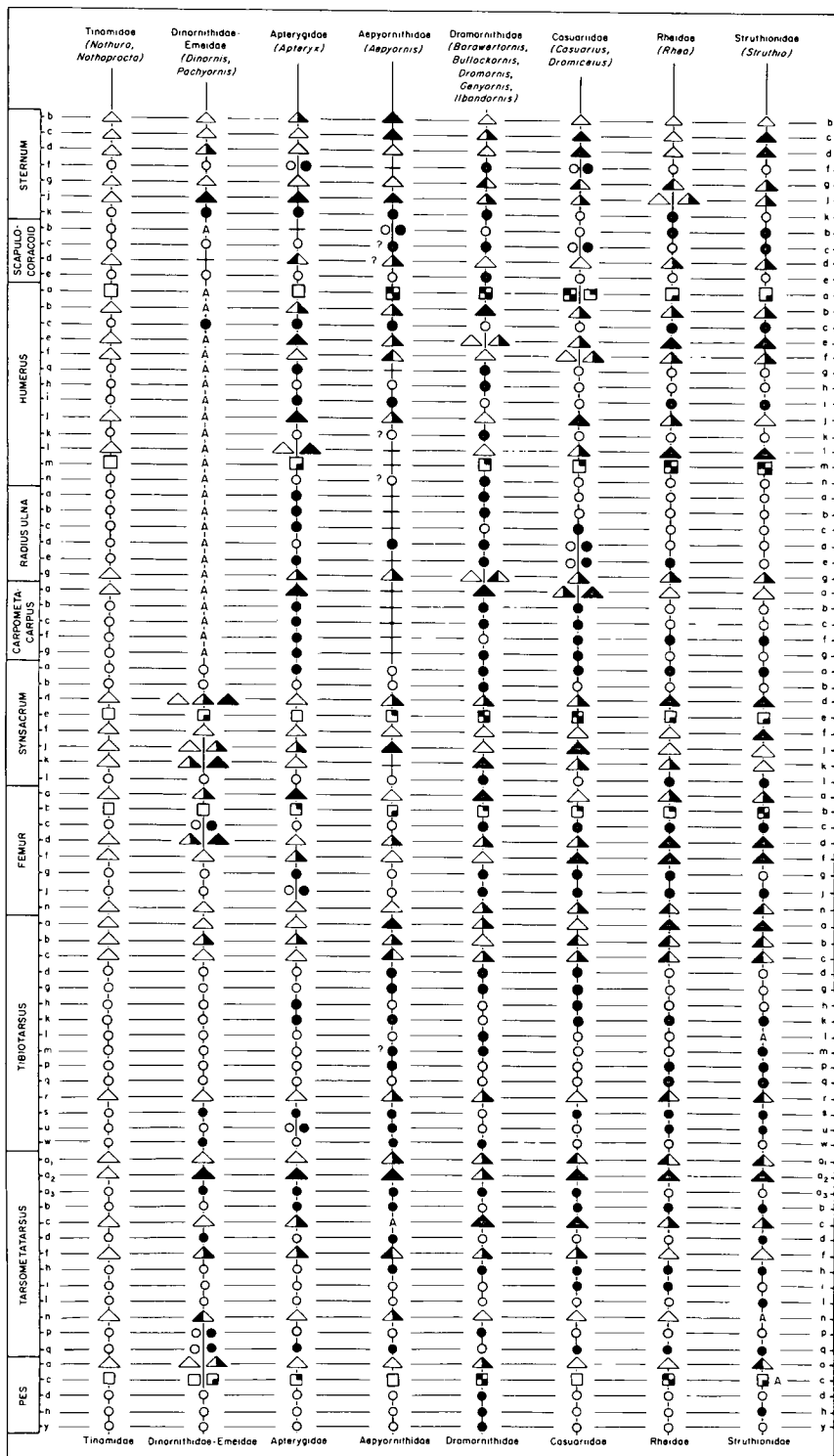
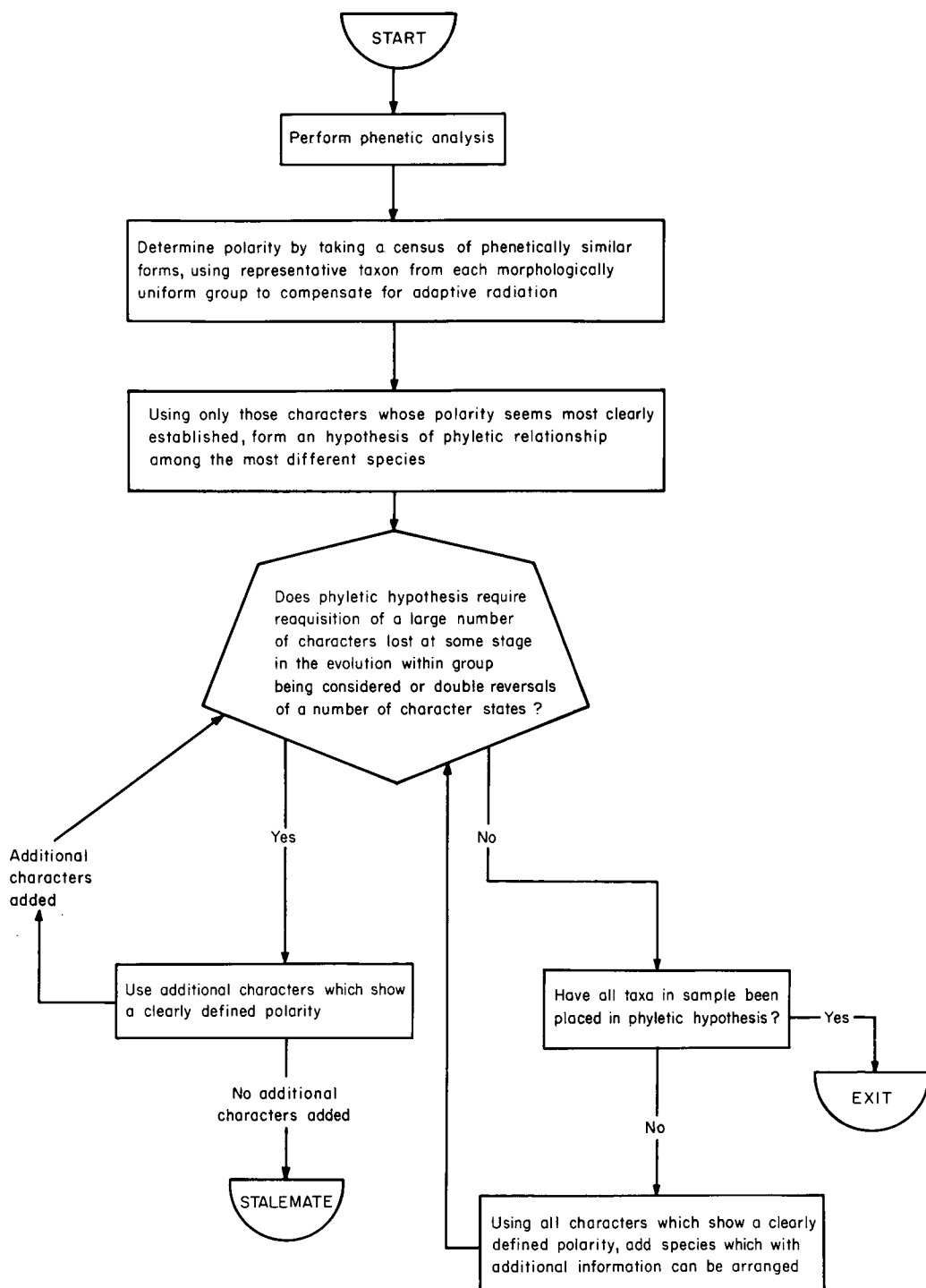
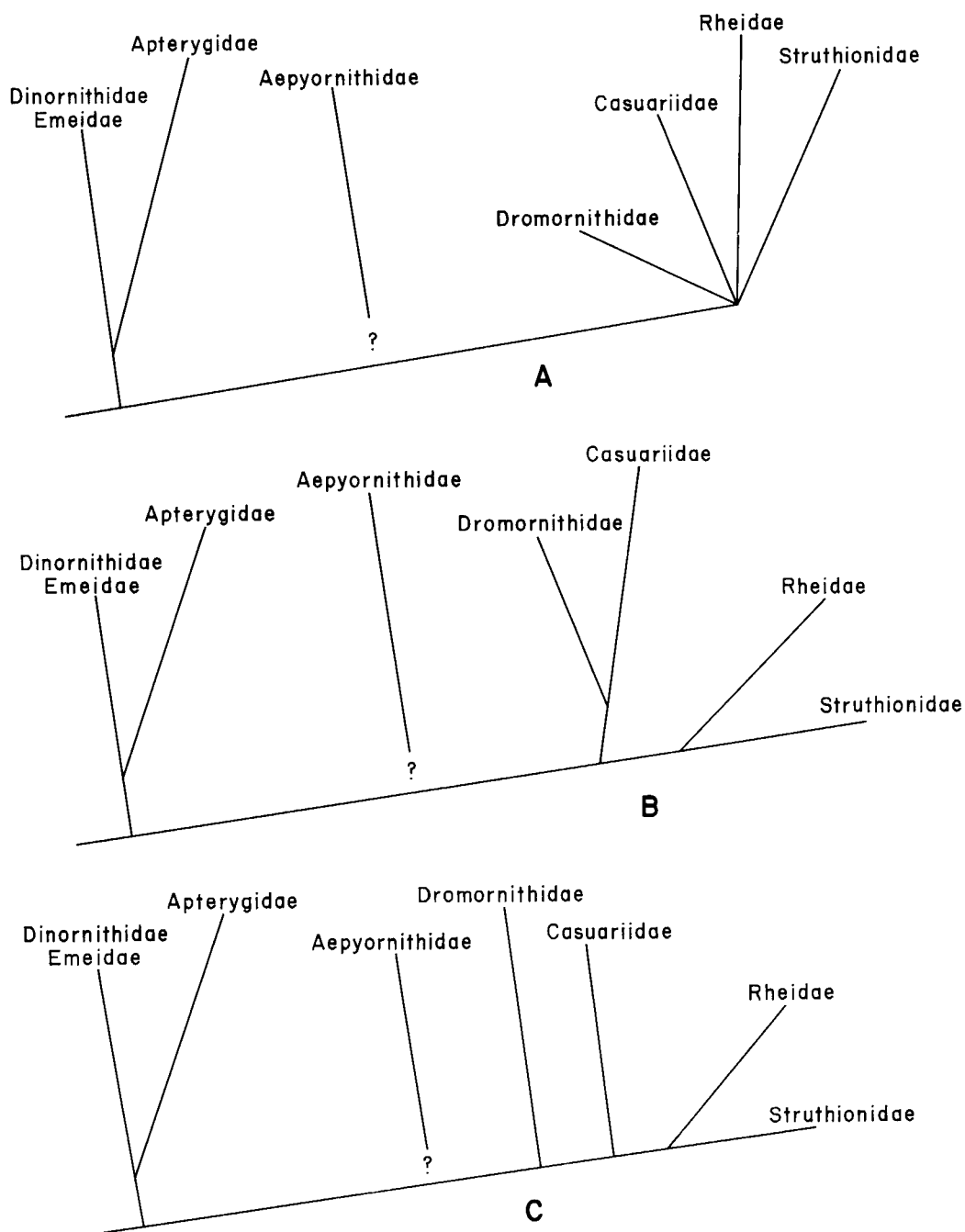


Fig. 44. Phylogenetic hypothesis of relationship of the Dromornithidae to other birds with emphasis on other ratites. Character states of those characters used in the construction of the cladogram are plotted following the key.



M (P) 768

Fig. 45. Flow chart depicting method utilized in determining phylogenetic relationships of genera within the Dromornithidae as well as that group to other avian families.



M (P) 769

Fig. 46. Phylogenetic hypotheses expressing possible inter-relationships of the ratites.

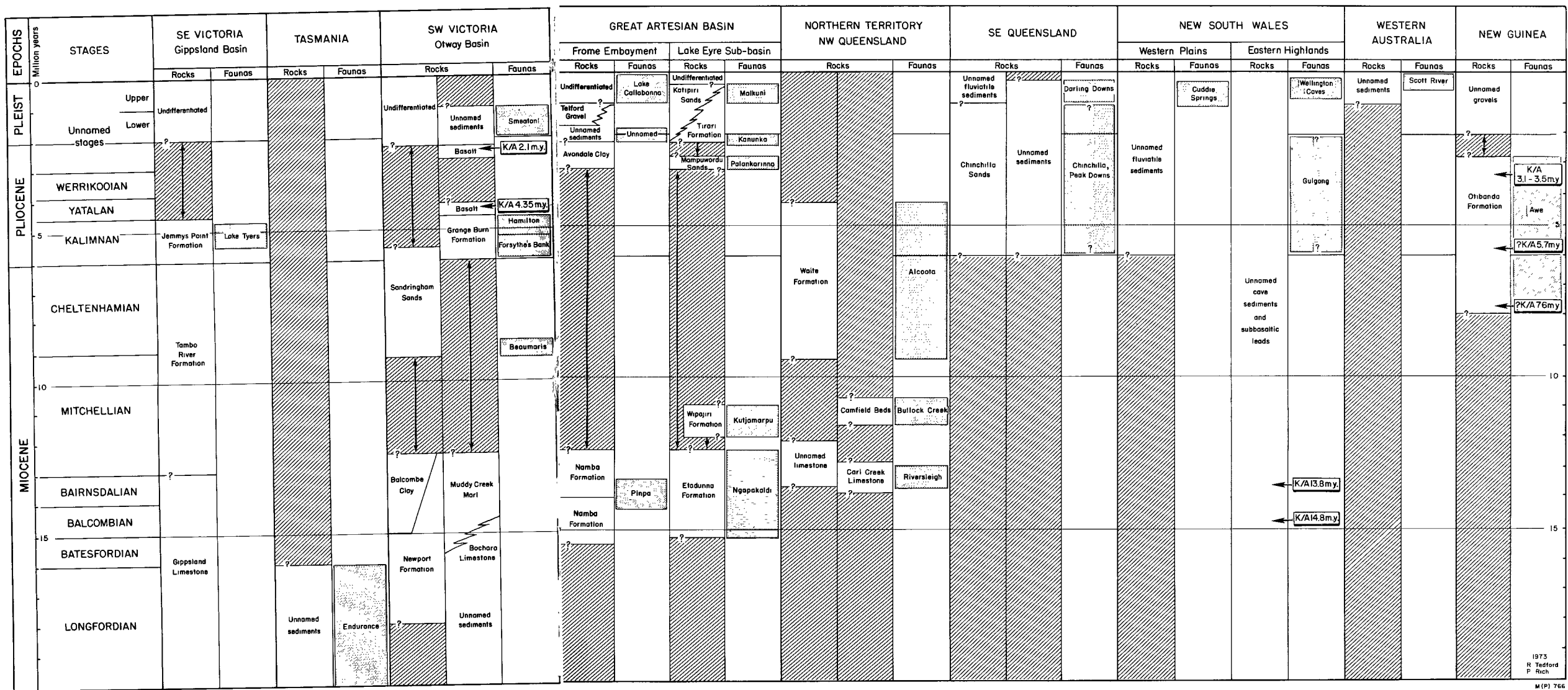


Fig. 42. Correlation table of sediments containing Dromornithidae in Australia. See text on stratigraphic and geographic distribution of this group for further explanation.

