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Records of the Australian Museum (2010) Vol. 62: 45–60. ISSN 0067-1975
doi:10.3853/j.0067-1975.62.2010.1539

New Material of *Barawertornis tedfordi*, a Dromornithid Bird from the Oligo-Miocene of Australia, and its Phylogenetic Implications

JACQUELINE M.T. NGUYEN,*[1] WALTER E. BOLES[1,2] AND SUZANNE J. HAND[1]

[1] School of Biological, Earth and Environmental Sciences,
University of New South Wales NSW 2052, Australia
jacqueline.nguyen@student.unsw.edu.au · s.hand@unsw.edu.au

[2] Research and Collections Branch, Australian Museum,
6 College Street, Sydney NSW 2010, Australia
walter.boles@austmus.gov.au

ABSTRACT. New fossil material of *Barawertornis tedfordi* (Aves: Dromornithidae) is described from Oligo-Miocene deposits in the Riversleigh World Heritage Area, northwestern Queensland, Australia. Phylogenetic analysis incorporating data from this new material casts some doubt on the generally accepted sister group relationship between *B. tedfordi* and all other dromornithids. However, the phylogenetic analysis is congruent with current hypotheses regarding intergeneric relationships among the other dromornithid taxa. A formal revision of dromornithid nomenclature that reflects these relationships is presented here. *Barawertornis tedfordi* may have closely resembled the unrelated Southern Cassowary *Casuarius casuarius* (Aves: Casuariidae), in that it was a rainforest-dwelling, flightless bird of similar size. *Barawertornis tedfordi* also appears to have had similar cursorial abilities to *C. casuarius*, based on its hind limb proportions.

NGUYEN, JACQUELINE M. T., WALTER E. BOLES & SUZANNE J. HAND, 2010. New material of *Barawertornis tedfordi*, a dromornithid bird from the Oligo-Miocene of Australia, and its phylogenetic implications. In *Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution*, ed. W.E. Boles and T.H. Worthy. *Records of the Australian Museum* 62(1): 45–60.

The Dromornithidae is an extinct family of large, flightless, terrestrial birds unique to Australia. It has one of the longest fossil records of any Australian group. These birds are known from the Late Oligocene to the Late Pleistocene, although an Early Eocene foot impression may be referable to Dromornithidae (Rich, 1979; Field & Boles, 1998; Miller *et al.*, 1999; Vickers-Rich & Molnar, 1996; Boles, 2006). Dromornithids were traditionally thought to be ratites because they are superficially similar: large bodied, flightless birds with long necks, reduced wings, fused scapulocoracoids and acarinate sterna (Owen, 1872, 1874; Stirling & Zietz, 1896, 1900, 1905; Stirling, 1913; Rich, 1979, 1980; Jennings, 1990). This relationship was disputed by Olson (1985), based on observations of the mandible, quadrate and pelvis, and subsequently Vickers-Rich (1991) upon examination of newly prepared skulls from Bullock Creek, Northern Territory. Most recently, Murray & Megirian's (1998) phylogenetic analysis and re-evaluation of the skeleton concluded that dromornithids are part of the waterfowl radiation (Anseriformes).

Dromornithids are among the best represented fossil birds in Australia (Rich & van Tets, 1982; Murray & Vickers-Rich,

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* author for correspondence

2004). However, the five known genera and eight described species of dromornithid differ greatly in the extent of their representation by fossil material. Some species, such as *Genyornis newtoni* Stirling & Zietz, 1896 and *Dromornis stirtoni* Rich, 1979, are represented by cranial material and associated skeletons. Other species, such as *Barawertornis tedfordi* Rich, 1979, are known only from fragmentary and anatomically limited remains.

Barawertornis tedfordi is one of the earliest known dromornithids. It was first discovered in 1963 in Oligo-Miocene deposits in the Riversleigh World Heritage Area, northwestern Queensland, Australia (Tedford, 1968). Description of the genus and only known species by Rich (1979) was based on three hind limb fragments and a single dorsal vertebra from Riversleigh. Fragmentary tibiotarsi of *B. tedfordi* were briefly described by Murray & Vickers-Rich (2004), but little else that adds to our understanding of this species has been published.

In this paper, new hind limb material of *B. tedfordi* from Riversleigh is described. The anatomical information from this material is used to test the hypothesis that *B. tedfordi* is the sister group of all other dromornithids (Rich, 1979, 1980; Murray & Vickers-Rich, 2004). Previous conclusions about the intrafamilial relationships within Dromornithidae (Rich, 1979, 1980; Murray & Vickers-Rich, 2004) are also reassessed. Hypotheses regarding the overall biology of *B. tedfordi* are also presented, based on estimates of its body mass and its locomotory mode (as inferred from hind limb proportions).

Material methods

Comparisons of *Barawertornis tedfordi* were made with the following dromornithid taxa: *"?Bullockornis"* sp. Rich, 1979 (after Murray & Vickers-Rich, 2004); *Bullockornis planei* Rich, 1979; *Dromornis australis* Owen, 1872; *Dromornis stirtoni* Rich, 1979; *Genyornis newtoni* Stirling & Zietz, 1896; *"Ilbandornis?" lawsoni* Rich, 1979 (after Murray & Vickers-Rich, 2004); *Ilbandornis woodburnei* Rich, 1979. For clarity, the taxa *"?Bullockornis"* sp. and *"Ilbandornis?" lawsoni* are herein referred to as *Bullockornis* sp. and *Ilbandornis lawsoni*.

Measurements of specimens were made with digital calipers and rounded to the nearest 0.1 mm. A measuring tape was used for larger measurements. Measurements of specimens besides those of *B. tedfordi* were taken from the literature, if not indicated otherwise. Osteological terminology follows Baumel & Witmer (1993) and Ballmann (1969) with the following exceptions: the term "incisura tibialis lateralis" (="incisura tibialis" in Baumel & Witmer, 1993) is preferred to "ectocnemial channel" (Murray & Vickers-Rich, 2004), and "incisura tibialis medialis" is preferred to "entocnemial notch" (Murray & Vickers-Rich, 2004). "Eminentia cnemialis" would be the appropriate Latinized form for "cnemial eminence" (Murray & Vickers-Rich, 2004), as is "eminentia intercondylaris" for "intercondylar eminence" (Rich, 1979). Systematics follows Murray & Megirian (1998) and Murray & Vickers-Rich (2004).

Phylogenetic analysis. Additional character state scores for *B. tedfordi* were incorporated into Murray & Vickers-Rich's (2004) data matrix for species of dromornithids (see Appendix). These scores were determined from material described here and from vertebrae described by Boles (2000). The matrix of 40 characters and eight taxa was analysed with PAUP* 4.0b10 (Swofford, 2003).

It is uncertain which parsimony method Murray & Vickers-Rich (2004) used in their phylogenetic analyses, but examination of their character descriptions indicates that some multi-state characters represent plausible morphoclines and so can be ordered. We, therefore, conducted two phylogenetic analyses. In the first analysis, all characters were treated as unordered. In the second analysis, nine of the 40 characters were treated as ordered (see Appendix).

Dromornis australis was excluded from Murray & Vickers-Rich's (2004) full character matrix because it is known from only a right femur. To test the phylogenetic relationships of *D. australis* with other dromornithids, they analysed a data matrix of femoral characters only. We also analysed the femoral matrix, modified based on the new material of *B. tedfordi* described here, in order to evaluate the relative position of *D. australis* within Dromornithidae.

All tree searches used the branch and bound algorithm, which is guaranteed to find the most parsimonious trees. Tree length (L), consistency index excluding uninformative characters (CI), and retention index (RI) were calculated. To assess the robustness of clades, bootstrap support (Felsenstein, 1985) using 2000 replicates and Bremer support (Bremer, 1994) values were calculated. Following Murray & Vickers-Rich (2004), we used the Magpie Goose *Anseranas semipalmata* (Latham, 1798) as our outgroup because it is thought to be the most plesiomorphic living member of the Anseriformes.

Table 1. Measurements (mm) of femora referred to *Barawertornis tedfordi*.

QM F specimen	30352	39901	40231	40232	45056
length (caput femoris to condylus medialis)	—	—	>200.6	—	—
proximal width	—	ca. 82.1	ca. 89.0	ca. 89.1	>73.3
proximal depth	—	>41.4	—	—	—
depth of caput femoris	—	>27.4	ca. 32.7	35.2	—
minimum shaft width	—	—	—	—	ca. 35.5
minimum shaft depth	—	—	—	—	ca. 29.2
minimum shaft circumference	—	—	—	—	ca. 103.6
distal width	>76.3	—	—	—	—
depth of condylus medialis	>42.2	—	—	—	—
width of condylus lateralis	>20.4	—	—	—	—
depth of condylus lateralis	>56.3	—	—	—	—

Table 2. Measurements (mm) of tibiotarsi referred to *Barawertornis tedfordi*.

QM F specimen	30377	30801	30802	30828	45416	45417	52257	52260
length	—	—	—	—	>390.6	—	—	—
proximal width (caudal border)	—	—	ca. 66.5	>57.4	—	—	>55.9	—
proximal depth	—	—	—	>80.7	>72.5	>49.6	—	—
length of crista fibularis	—	—	—	—	—	—	>88.0	—
minimum shaft width	—	—	—	—	30.5	—	—	—
minimum shaft depth	—	—	—	—	24.7	—	—	—
distal width	>50.2	>47.4	—	—	ca. 50.9	—	—	>49.5
distal width across epicondylus medialis	—	>52.1	—	—	ca. 52.7	—	—	>53.1
depth of condylus medialis	>48.4	—	—	—	56.2	—	—	>48.3
depth of condylus lateralis	ca. 43.7	>41.7	—	—	48.2	—	—	>39.0
minimum length of pons supratendineus								
medial	15.5	—	—	—	10.5	—	—	13.4
lateral	14.2	—	—	—	13.8	—	—	13.3

Estimates of body mass and locomotion. The body mass of *B. tedfordi* was estimated using regression equations determined by Anderson *et al.* (1985) and Campbell & Marcus (1992) for birds (Table 1). Anderson *et al.*'s (1985) equation is based on the allometric relationship between body mass (M, in g) and mid-shaft circumference of the femur (MC_F, in mm):

$$M = 1.08 \times MC_F^{2.28 \pm 0.1} \qquad (1)$$

Campbell & Marcus's (1992) equations use least shaft circumferences of the femur (LC_F) and tibiotarsus (LC_T), which do not always coincide with the mid-shaft circumference:

$$\log_{10} M = 2.411 \times \log_{10} LC_F - 0.065 \qquad (2)$$

$$\log_{10} M = 2.424 \times \log_{10} LC_T + 0.076 \qquad (3)$$

Mid-shaft and least shaft circumferences of CPC7341 (holotype femur), QMF45056 (femur missing distal end) and QMF45416 (tibiotarsus missing proximal end) were measured using string and calipers. The body masses of other dromornithids and ratites were also estimated for comparison.

To gain insight into its locomotory mode, the hind limb bone ratio (lengths of femur: tibiotarsus: tarsometatarsus) of *B. tedfordi* was calculated and compared with those of other dromornithids and ratites.

Institutional abbreviations. CPC, Commonwealth Palaeontological Collections, Bureau of Mineral Resources, Canberra, Australia (now Geoscience Australia); QM F, Queensland Museum paleontological collections, Australia.

Geological setting

The specimens described here were recovered from Tertiary limestone deposits that crop out discontinuously within the Riversleigh World Heritage Area, in Lawn Hill National Park, northwestern Queensland, Australia. These deposits are interpreted to be part of Riversleigh Faunal Zones A and B (formerly "Systems" A and B; Arena, 2004; Travouillon *et al.*, 2006) and, as such, Late Oligocene-Early Miocene in age (Archer *et al.*, 1997; Arena, 2004; Travouillon *et al.*, 2006). Faunal Zone A sites are distinctive in that they include a higher proportion of aquatic fauna and large-bodied animals than do other sites at Riversleigh. The presence of large freshwater crocodiles, turtles, fish and frogs suggests that there were substantial pools of water supporting these animals. Pools of water were also present in Faunal Zone B sites, but were probably shallow or temporary because the few remains of smaller aquatic vertebrates recovered from these sites represent relatively small individuals (Archer *et al.*, 1989). Riversleigh's Oligo-Miocene paleoenvironments appear to have ranged from relatively open forests in the Late Oligocene to closed, species-rich gallery rainforest in the Early and Middle Miocene (Archer *et al.*, 1997; Travouillon *et al.*, 2009). The latter forests were probably similar to those of mid-montane New Guinea and perhaps not unlike the dense rainforests of northern Australia, New Guinea and adjacent islands in which the Southern Cassowary *Casuarius casuarius* (Linnaeus, 1758) lives today (Crome, 1975; Davies, 2002). For further information about locality and associated faunas, see Archer *et al.* (1997) and Travouillon *et al.* (2009).

Systematic paleontology

Order Anseriformes Wagler, 1831

Suborder Anhimae Wetmore & Miller, 1926

Family Dromornithidae Fürbringer, 1888

Barawertornis Rich, 1979

Type species. *Barawertornis tedfordi* Rich, 1979.

Diagnosis. As for the type species.

Age and distribution. Late Oligocene-Middle Miocene; Riversleigh World Heritage Area, northwestern Queensland, Australia. Murray & Vickers-Rich (2004) noted that a synsacral fragment and phalanges referable to *B. tedfordi* were found in the Early Miocene Leaf Locality at Lake Ngapakaldi, Tirari Desert, South Australia, but these materials have not yet been described.

Barawertornis tedfordi Rich, 1979

Figs 1–4

Holotype. CPC7341, a left femur missing the trochanter femoris and lateral part of the upper shaft.

Referred material. The following specimens were all collected from the Riversleigh World Heritage Area, Lawn Hill National Park, northwestern Queensland, Australia.

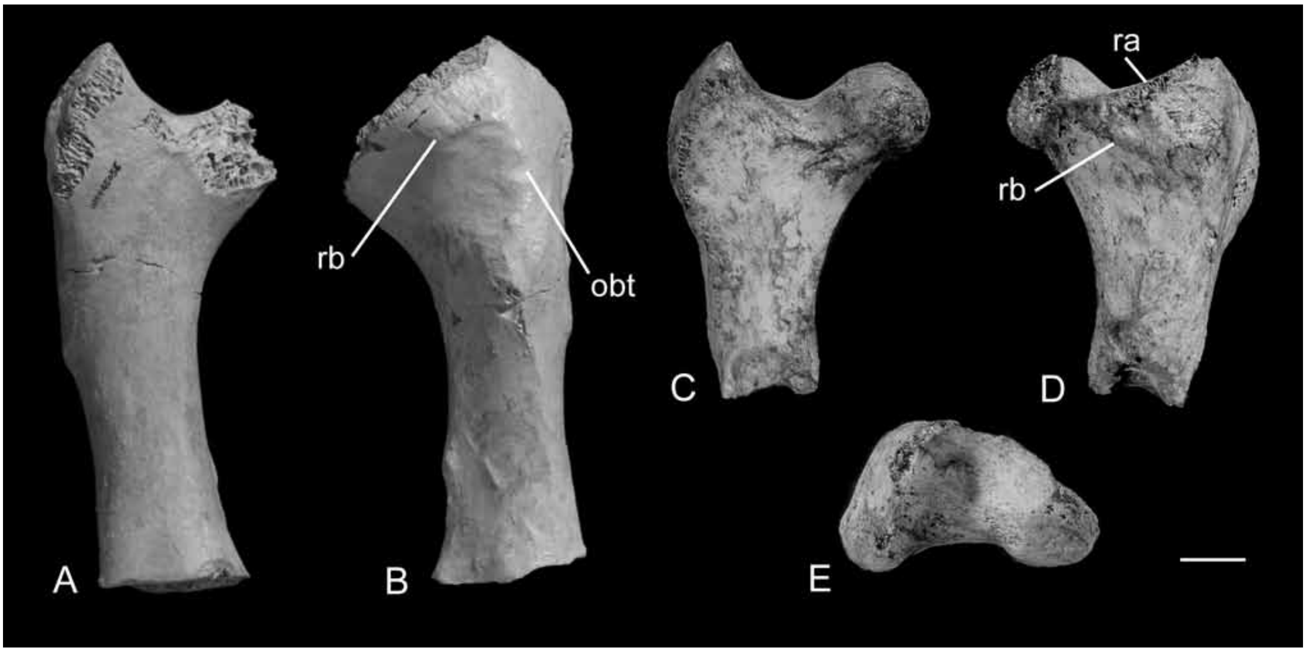

Figure 1. Specimens of *Barawertornis tedfordi*. (*A–B*) QM F45056, right femur missing distal third; (*A*) cranial view; (*B*) caudal view; (*C–E*) QM F39901, proximal end of right femur; (*C*) cranial view; (*D*) caudal view; (*E*) proximal view. Abbreviations: *ra* ridge A; *rb* ridge B; *obt* impressiones obturatoriae. Scale = 20 mm.

Localities are given in parentheses. *Femora*. QM F30352 (Wayne's Wok Site), distal end of left femur; QM F39901 (Upper Site), proximal end of right femur; QM F40231 (D Site), partial right femur; QM F40232 (Sticky Beak Site), proximal end of left femur; QM F45056 (Hiatus Site), right femur missing distal third; QM F45420 (Hiatus Site), shaft of right femur. *Tibiotarsi*. QM F30377 (White Hunter Site), distal end of right tibiotarsus; QM F30801 (White Hunter Site), distal end of left tibiotarsus; QM F30802 (White Hunter Site), proximal end of right tibiotarsus; QM F30828 (White Hunter Site), proximal end of left tibiotarsus; QM F45416 (Hiatus Site), left tibiotarsus missing proximal end; QM F45417 (Hiatus Site), proximal end of left tibiotarsus; QM F52257 (Lee Sye's Outlook Site), proximal half of right tibiotarsus; QM F52260 (Price Is Right Site), distal end of right tibiotarsus. *Tarsometatarsi*. QM F 24126 (Neville's Garden Site), distal end of right tarsometatarsus (trochleae metatarsi III and IV partially preserved); QM F30413 (Dirk's Towers Site), distal end of left tarsometatarsus (trochleae metatarsi II and III partially preserved); QM F45419 (Hiatus Site), heavily damaged right tarsometatarsus, broken into proximal and distal ends; QM F40223 (D Site), distal end of right tarsometatarsus; QM F40239 (Wayne's Wok Site), distal end of left tarsometatarsus (trochlea metatarsi IV partially preserved).

The following specimens of vertebrae, described by Boles (2000), were used for character scoring in phylogenetic analyses: QM F24377 (Neville's Garden Site), atlas-axis vertebral complex; QM F24378 (Neville's Garden Site), cervical vertebra.

Measurements. See Tables 1–3.

Type locality. D Site ("BMR Locality 103D" in Rich, 1979), Riversleigh World Heritage Area, Lawn Hill National Park, northwestern Queensland, Australia. Based on biostratigraphic and biocorrelative analyses, D Site forms part of Riversleigh's "Faunal Zone A", and as such is interpreted to be Late Oligocene in age (Archer *et al*., 1997; Arena, 2004; Travouillon *et al*., 2006).

Table 3. Measurements (mm) of tarsometatarsi referred to *Barawertornis tedfordi*.

QM F specimen	24126	30413	45419	52258	52259
length	—	—	>269.4	—	—
proximal width	—	—	62.4	—	—
dorsoplantar depth of cotyla medialis	—	—	23.7	—	—
dorsoplantar depth of cotyla lateralis	—	—	22.9	—	—
depth across area intercotylaris to hypotarsus	—	—	46.8	—	—
distal width	—	—	61.6	53.1	—
width of trochlea metatarsi II	—	>11.4	13.0	11.7	—
depth of trochlea metatarsi II					
medial	—	>17.3	17.9	20.1	—
lateral	—	>19.0	18.4	19.5	—
width of trochlea metatarsi III	26.1	>23.6	ca. 24.3	ca. 23.9	>23.8
depth of trochlea metatarsi III					
medial	—	—	32.0	>27.6	>34.4
lateral	31.8	—	30.3	ca. 32.5	>29.6
width of trochlea metatarsi IV	ca. 12.2	—	19.2	17.4	ca. 20.0
medial depth of trochlea metatarsi IV	>20.3	—	25.3	>22.3	ca. 27.1

Figure 2. Specimens of *Barawertornis tedfordi*. (*A*) QM F45417, proximal end of left tibiotarsus, cranial view; (*B*) QM F30828, proximal end of left tibiotarsus, proximal view; (*C*) QM F30802, proximal end of right tibiotarsus, proximal view; (*D–H*) QM F45416, left tibiotarsus; (*D*) cranial view; (*E*) caudal view; (*F*) lateral view; (*G*) medial view; (*H*) distal view. Scale = 20 mm.

Figure 3. Tarsometatarsus of *Barawertornis tedfordi*. (*A–D*) QM F45419, right tarsometatarsus broken into proximal and distal ends; (*A*) dorsal view; (*B*) plantar view; (*C*) proximal view; (*D*) distal view. Scale = 20 mm.

Description

Femur. Description of the femur is based on new specimens, with reference to the holotype specimen CPC7341. The proximal and distal ends of the femur are not well preserved together in any the new specimens. As such, a comprehensive comparison of the proximal end with the distal end cannot be made. In cranial view the trochanter femoris is moderately high, narrow and falcate. It extends slightly laterad of the shaft. The proximal extent of the trochanter femoris and caput femoris are roughly equal. The caput femoris is relatively small in depth compared to *Genyornis* and *Dromornis*, with a slightly narrow, elongate collum femoris. The facies articularis antitrochanterica is highly concave both craniocaudally and mediolaterally in a broad U-shape. The fossa trochanteris is shallow. Viewed laterally, the trochanter femoris is largely oval-shaped. Its cranial margin is semicircular and extends slightly craniad of the shaft. The caudal margin of the trochanter femoris is almost straight and does not extend beyond the shaft surface.

In caudal view, a sharp ridge (A) is formed by the caudal border of the facies articularis antitrochanterica merging with the proximal crest of the trochanter femoris (Fig. 1D). Distal to ridge (A) is a second ridge (B), which extends from the caudal face of the trochanter femoris to the caput femoris. Ridge (B) occurs at an angle of about 45 degrees from the lateral shaft margin. In specimen QM F45056, ridge (B) trends at an angle of about 75 degrees from the lateral shaft margin. It joins to a broad, proximodistally trending ridge that may be interpreted as the impressiones obturatoriae (Fig. 1B). The length of the impressiones obturatoriae, seen in specimens QM F45056 and QM F40231, is less than half, but slightly more than one-third, of the total shaft length.

The shaft is shallow, craniocaudally compressed, and slender with respect to its length. In the holotype specimen CPC7341 the minimum width of the shaft is about 40 per cent of the distal end width. In CPC7341 and the new specimens the minimum shaft width is slightly proximad of its midpoint, with the exception of QM F40231—it is slightly distad. The cross-sectional shape of the shaft is roughly trapezoidal to elliptical. Viewed caudally, the medial shaft margin is slightly to moderately curved. The lateral shaft margin is more or less straight. In specimen QM F45056 the impressiones iliotrochantericae are prominent and broad, terminating proximad of the midpoint of the shaft long axis. The linea intermuscularis cranialis is prominent over the proximal one-third of the femur. It trends proximolaterally and forms an angle of about 5–10 degrees with the long axis of the shaft. The linea intermuscularis caudalis is prominent over the distal half of the femur, appearing narrower and sharper in the new specimens than in the holotype. It trends proximomedially and forms an angle of about 20–25 degrees with the shaft's long axis.

There is no linea intermusculus caudalis present in specimen QM F30352, but a small protuberance on the caudomedial margin. Lack of the linea intermusculus caudalis, unfused condyles, undeveloped popliteal fossa and porosity of the bone may indicate that this femur belonged to a young bird.

The condyli medialis et lateralis are not well preserved together in the new specimens. Although the condylus medialis is incomplete in specimen QM F40231, it appears to have a sharper caudal margin than that in the holotype.

Specimen QMF45420 bears a circular puncture hole of about 5 mm diameter on the cranial surface, mediad of the midline of the shaft (Fig. 4A). This unhealed puncture is associated with several greenstick fractures. Distal to the puncture are two smaller compression marks and a 2 mm long transverse gouge. These injuries indicate that they were formed at or near the time of death, possibly by a predator such as species of *Baru*; large, extinct freshwater crocodiles found at Riversleigh (see Geological Setting). Many fossil specimens of the dromornithid *Bullockornis planei* from the Bullock Creek locality in the Northern Territory bear tooth punctures and point fractures thought to be evidence of crocodile predation (Murray & Vickers-Rich, 2004).

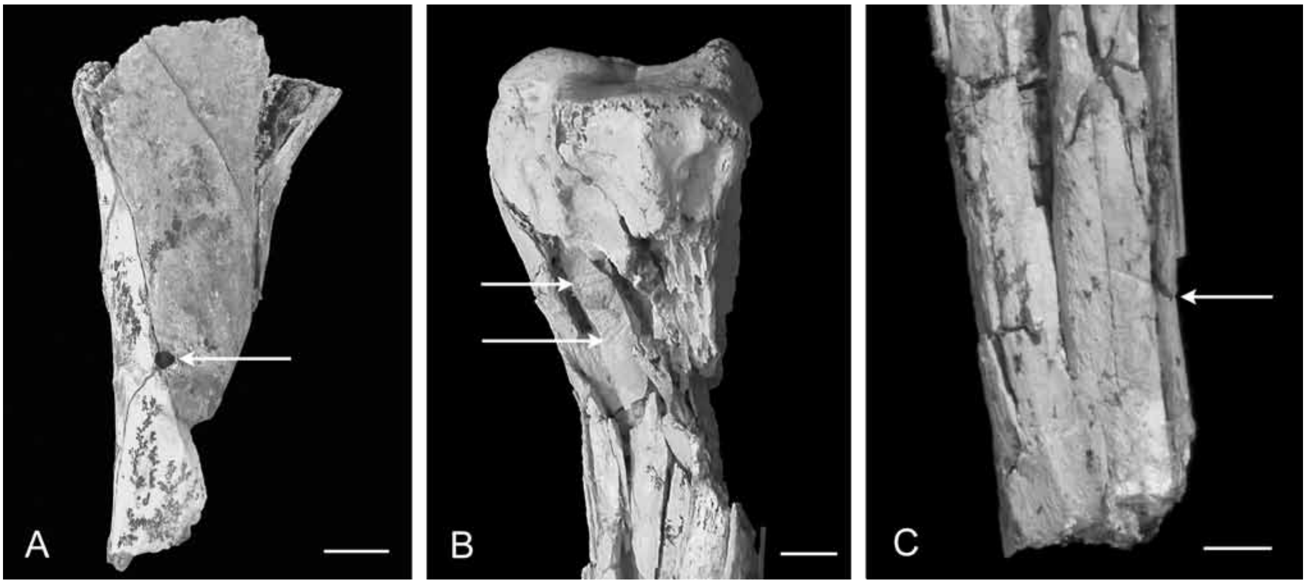

Figure 4. Specimens of *Barawertornis tedfordi*. (*A*) QM F45420, shaft of right femur, cranial view; (*B–C*) QM F45419, right tarsometatarsus; (*B*) caudal view of proximal end; (*C*) caudal view of distal third. Scale = 10 mm.

Tibiotarsus. In proximal view, the incisura tibialis lateralis is shallowly concave. The facies articularis lateralis is shallow and dome-like proximally. It extends slightly laterad and is semicircular in outline. The major axis of the facies articularis lateralis trends caudomedially. The facies articularis medialis is broadly convex, semicircular in outline and nearly flat proximally. From what is preserved, the eminentia intercondylaris appears to extend further proximally than the facies articularis lateralis. The fossa retropatellaris is circular and deep. The area interarticularis is moderately broad and concave proximolaterally. This entire surface slants distolaterally. The crista cnemialis lateralis is partially preserved. It is broad and triangular in cranial view, but is missing the proximal section of the crista. Only the base of the crista cnemialis cranialis is preserved. In proximal view the internal angle formed by the cristae cnemialis lateralis et cranialis is acute, approaching 90 degrees. The fossa flexoria is large and pneumatic. The impressio lig. collateralis medialis is distinct, large and elevated. It is deep and triangular in medial aspect.

The shaft is slightly curved mediolaterally. In caudal view, the medial margin of the shaft is more curved than the lateral margin. The caudal shaft surface is nearly planar but is slightly convex at the distal end. Over the proximal one-third, the cranial shaft surface is nearly planar and curves into the medial shaft surface. It smoothly grades into the lateral shaft surface that lies at about 90 degrees to the cranial shaft surface. The cranial and caudal shaft surfaces meet laterally along the crista fibularis at an angle of about 70 degrees in specimen QM F52257. In specimen QM F45416, these shaft surfaces meet laterally at about 110 degrees. In lateral view, the linea externa musculi peronei is broad and indistinct. Its proximal end is caudad to the crista fibularis. The linea externa musculi peronei trends distocranially and terminates proximad of the condylus lateralis. The linea extensoria is distinct; it trends distomedially away from the long axis of the shaft and intersects the medial shaft margin at about two-thirds down the shaft length. At the proximal and distal ends, the medial shaft surface is slightly convex. The remaining medial surface is nearly planar.

The distal end of the tibiotarsus is broad with respect to shaft width. The trochlea cartilaginis tibialis is moderately deep. The cristae trochleae are near vertical and do not converge proximally. Viewed cranially, the pons supratendineus forms an angle of about 75–85 degrees with the long axis of the shaft. The sulcus extensorius is deep. The distal opening of the canalis extensorius is slightly medial to the mediolateral midpoint of the distal end. The proximal margin of the area intercondylica is concave and forms a broad U-shape. The incisura intercondylaris is very shallow and broadly concave. It does not have an apex and is not V-shaped.

The condyli medialis et lateralis are moderately deep craniocaudally. Viewed cranially, the condyli are about equal in proximal extent. However, the condylus medialis is broader than the condylus lateralis. The proximal and distal margins of the condyli medialis et lateralis are slightly convex. In distal view the condyli appear to slightly diverge cranially, with the condylus medialis projecting further cranially than the condylus lateralis. It also projects further caudally than the condylus lateralis. From what is preserved, the condylus lateralis is roughly parallel with the shaft, whereas the condylus medialis is slightly inclined medially.

Viewed cranially, the condylus lateralis is relatively flat over its proximal half, but convex over its distal half. Its lateral margin is slightly convex and gradually grades into the lateral shaft margin. Viewed laterally, the condylus lateralis is broadly oval in shape. Its cranial margin is semicircular in outline, whereas its caudal margin is almost straight. The condylus lateralis projects a short distance caudad of the shaft but extends much further craniad. The distalmost extension of the condylus lateralis is at or craniad to its craniocaudal midpoint. The depressio epicondylaris lateralis is very shallow. The tuberculum retinaculi m. fibularis is small and slightly raised.

The condylus medialis is very convex over its cranial surface. Although its caudal and medial margins are damaged, the condylus medialis appears broadly oval in medial aspect. Its cranial margin is semicircular in outline. Viewed medially, there is a distinct distal protrusion from the distal margin of the condylus medialis (Fig. 2G), which is apparently absent in published specimens of other dromornithid species. This distal protrusion in *Barawertornis*, however, may be an artefact of the specimen's preservation. The depressio epicondylaris medialis is moderately deep. The epicondylus medialis is large, broad and circular. In caudal view the epicondylus medialis projects slightly further medially than the condylus medialis.

Tarsometatarsus. The proximal end of the tarsometatarsus appears to be relatively shallow compared to the shaft. Viewed proximally, the dorsal border of the proximal end is slightly convex, interrupted by the low eminentia intercotylaris. There is a shallow depression in the area intercotylaris. The hypotarsus is bulbous with a single poorly defined ridge. It is shaped like a scalene triangle, where the lateral side is more elongate than the medial side, and the dorsal side is the longest. Its proximal-most projection is located dorsally. There is a slight indentation in the lateral margin of the hypotarsus. In medial view, the hypotarsus moderately bulges plantarly beyond the shaft margin. The cotylae medialis et lateralis are narrow and roughly symmetrical. The cotyla medialis is moderately excavated, whereas the cotyla medialis is shallower and almost flat.

In dorsal view, the fossa infracotylaris dorsalis is narrow and moderately excavated. The foramina vascularia proximalia are large, deep and adjacent to each other. Distal to these foramina are two low, elongate tuberosities with a broad shallow groove between them; these are perhaps the insertions of the musculus tibialis cranialis. The impressiones retinaculi extensorii is shallow.

In all of the specimens under study, the proximal and middle shaft is not preserved or is heavily damaged. The medial shaft surface on the proximal half is discernable though; it is planar and meets the dorsal surface at about 90 degrees. Over the distal part of the shaft preserved, the dorsal shaft surface reveals a shallow sulcus extensorius extending from the damaged area. The sulcus extensorius appears to trend laterally, before terminating proximad of or level with the foramen vasculare distale. The medial and lateral margins of the sulcus flexorius are more prominent in the new specimens than in the paratype specimen CPC7346, described by Rich (1979). It is narrow and terminates proximad of or level with the foramen vasculare distale. In CPC7346, the cross-section of the shaft is teardrop-shaped, with the medial section of the shaft more circular in cross-section than the more triangular lateral section. In QM F52259, the cross-sectional shape of the shaft is oval, with the shaft dorso-plantarly compressed.

Viewed plantarly, the flare of the distal end is moderate to broad with respect to the shaft width. There is no distinct fossa metatarsi I. The foramen vasculare distale is absent in some specimens of *Dromornis stirtoni*, and its state is uncertain in *Bullockornis planei* (Rich, 1979). In *Barawertornis* it is present in specimens QM F40239 and QM F45419 but, due to damage, is not preserved in other specimens. This foramen is small and does not open into the incisura intertrochlearis lateralis. The incisura intertrochlearis lateralis is narrow and extends further proximad than incisura intertrochlearis medialis. The surface within the incisura intertrochlearis medialis slopes gradually to a shelf that forms about midway between the dorsal and plantar shaft surfaces.

Trochlea metatarsi II is nearly planar dorsally. Its dorso-plantar plane is tilted plantarly towards the lateral border. In medial view, the dorsal, distal and plantar margins of this trochlea are smoothly rounded and approach a semicircular outline. Its medial face is moderately to deeply excavated. Viewed distally, the medial and lateral margins of trochlea metatarsi II diverge plantarly. The dorsal margin of trochlea metatarsi II is about three-quarters the width of the plantar margin.

Dorsal projection of trochlea metatarsi III with respect to the other two trochleae is moderate to great. The central axis of trochlea metatarsi III is slightly mediad to that of the shaft. Only trochlea metatarsi III bears a trochlear groove on the articular surface. This groove is shallow, and is of same depth dorsally and plantarly. In lateral view, the trochlea metatarsi III is circular in outline and has a large, moderately deep depression on its lateral face. In medial view, this trochlea is oval-shaped and has a small and moderately deep depression. The plantar margin of trochlea metatarsi III projects further beyond the shaft than its dorsal margin. Viewed distally, the medial and lateral margins of this trochlea diverge plantarly, and its plantar margin is about three-quarters of the width of the dorsal margin.

In dorsal view, the articular surface of trochlea metatarsi IV is nearly planar, with its plane tilted plantarly towards the lateral border. The dorsal, distal and planar margins of the trochlea form a semicircle in lateral view. Its most plantar projection is distad of the proximal end of the plantar margin.

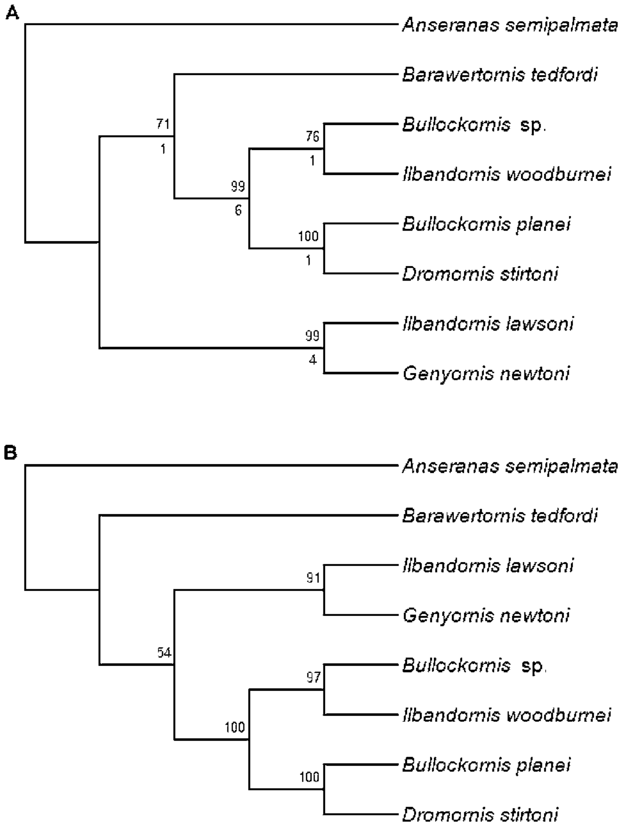

Figure 5. Phylogenetic hypotheses of intrafamilial relationships within the Dromornithidae. (*A*) Single most parsimonious tree resulting from unordered analysis. Bootstrap values are indicated above branches; Bremer support values are indicated below branches. This tree topology was also derived in ordered analysis. (*B*) One of two equally parsimonious trees resulting from ordered analysis. Bootstrap values are indicated above branches.

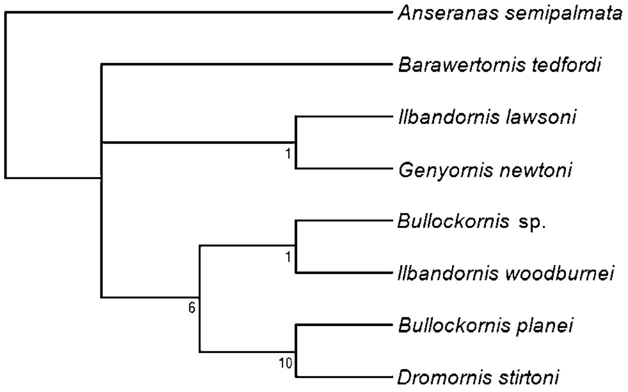

Figure 6. Strict consensus tree of two equally parsimonious trees resulting from ordered analysis. Bremer support values are indicated below branches.

There is a deep depression in the lateral surface of trochlea metatarsi IV. Viewed distally, the dorsal and plantar margins of this trochlea converge laterally. The medial margin is slightly convex and the lateral margin is highly concave.

There is a series of diagonal gouges present on the posterior surface of a heavily damaged right tarsometatarsus (QMF45419, Fig. 4B). Distad to these gouges, another transverse gouge is present (Fig. 4C). These markings may have been inflicted by a predator or a scavenger post-mortem, or animals trampling on the bone.

Results and phylogenetic analysis

Analysis of unordered characters. Analysis of 40 unordered characters resulted in one most-parsimonious tree (Fig. 5A; L = 60, CI = 0.92, RI = 0.93). This tree is consistent with that produced by Murray & Vickers-Rich (2004) in that it supports the monophyly of a group comprising *Bullockornis* sp., *Ilbandornis woodburnei, Bullockornis planei* and *Dromornis stirtoni*, and the clades identified within it. The *Ilbandornis lawsoni-Genyornis newtoni* clade is also proposed in this tree. Species of *Ilbandornis* and *Bullockornis* are divided between different clades.

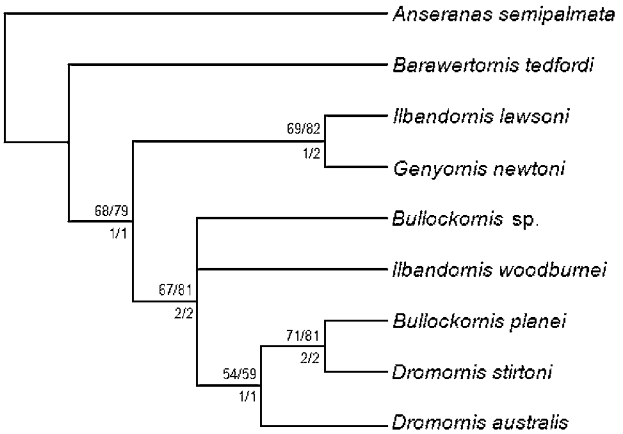

Figure 7. Phylogenetic hypothesis of dromornithid relationships resulting from analysis of femoral characters only. Bootstrap values are indicated above branches; Bremer support values are indicated below branches. Support values to the left are from unordered analysis; values to the right are from ordered analysis.

The position of *Barawertornis tedfordi* in this tree, however, differs from that proposed in previous studies. Here, *B. tedfordi* is the sister group to the clade comprising *Bu.* sp., *I. woodburnei, B. planei* and *D. stirtoni*. Together, these five species form a clade to the exclusion of *I. lawsoni* and *G. newtoni*. However, this clade receives relatively weak bootstrap and Bremer support (Fig. 5A).

The clade comprising of *B. tedfordi, Bu.* sp., *I. woodburnei, B. planei* and *D. stirtoni* is supported by the following synapomorphies: strongly convex culmen and deep and compressed beak (unknown for *B. tedfordi, Bu.* sp., *I. woodburnei*); deep ramus mandibulae (unknown in *B. tedfordi, Bu.* sp.); derived states of the ventral crests and median surface of synsacrum (varies within group, unknown in *Bu. planei*); derived states of crista patellaris of tibiotarsus (varies within group); transversely wider proximal articular surface of tarsometatarsus (plesiomorphic in *Bu.* sp., *I. woodburnei*). All of these character states are not homoplasious relative to large body size.

Analysis of ordered characters. Analysis of nine ordered and 31 unordered characters (see Appendix) resulted in two equally parsimonious trees (L = 65; CI = 0.85; RI = 0.87). The topology of the first tree, tree A, is the same as that derived in the unordered analysis (Fig. 5A). The topology of the second tree, tree B, (Fig. 5B) is identical to the original tree proposed by Murray & Vickers-Rich (2004), in which *B. tedfordi* is sister group to all other dromornithids. The bootstrap consensus tree generated also had the latter topology.

The two topologies resulting from the ordered analysis agree on the monophyly of *Bu.* sp., *I. woodburnei, Bu. planei* and *D. stirtoni*, and the relationships within this clade. They also agree on the grouping of *I. lawsoni* and *G. newtoni*. However, they disagree on the phylogenetic position of *B. tedfordi* relative to the other dromornithid species (Fig. 5A–B).

The synapomorphies that unite *B. tedfordi* with *Bu.* sp., *I. woodburnei, Bu. planei* and *D. stirtoni* in tree A are identical to those that unite the same group in the unordered analysis. The synapomorphies that unite the other dromornithids to the exclusion of *B. tedfordi* in tree B are as follows: sulcus intercondylaris of femur a wide right angle or obtuse angle (varies within group, plesiomorphic in *I. lawsoni*); large fossa poplitea; constricted eminentia cnemialis (extent varies within group); incisura tibialis lateralis is deep open notch; shallow, concave incisura tibialis medialis; very asymmetrical trochlea cartilaginis tibialis. These features, however, appear to correlate with large body size. This clade receives low bootstrap support (Fig. 5B).

A strict consensus tree based on the results of the ordered analysis is given in Fig. 6, with *B. tedfordi* forming an unresolved trichotomy with the *I. lawsoni–G. newtoni* clade and that of the other dromornithid species.

Analysis of femoral characters only. Analysis of this matrix recovered the same single most-parsimonious tree, irrespective of whether characters were unordered or ordered (unordered: L = 15, CI = 0.83, RI = 0.85; ordered: L = 16, CI = 0.80, RI = 0.83) (Fig. 7). This tree topology is identical to that derived by Murray & Vickers-Rich (2004), except that the branches leading to *Bu.* sp. and *I. woodburnei* are collapsed. These two species do not form a clade because they have identical femoral character states but there are no synapomorphies linking them. *Barawertornis tedfordi* remains the sister group to the other dromornithid species. *Dromornis australis* appears to be more closely related to *D. stirtoni* and *Bu. planei* than the other dromornithids.

Diagnoses of clades excluding *Barawertornis tedfordi*. In the following, synapomorphies that diagnose clades excluding *Barawertornis tedfordi* are listed. These only include synapomorphies exhibited in all clade members and in all analyses.

The clade consisting of *Bu.* sp., *I. woodburnei, Bu. planei* and *D. stirtoni* is diagnosed by the following synapomorphies: deep ramus mandibulae (unknown in *Bu.* sp.); deep and bulky condylus lateralis of femur; condylus medialis much deeper craniocaudally than condylus lateralis of tibiotarsus; deep, hatchet-shaped and near vertical crista cnemialis lateralis; deep, open incisura tibialis lateralis; shallow, concave incisura tibialis medialis; depressio epicondylaris medialis of tibiotarsus depressed by tuberosity; very asymmetrical trochleae cartilaginis tibialis.

The *Bu.* sp.–*I. woodburnei* clade is diagnosed by the following synapomorphies: very constricted eminentia cnemialis; acute angle between cristae cnemialis cranialis et lateralis; narrow, elongated proximal surface of tibiotarsus; proximal margin of condylus lateralis of tibiotarsus is broad, low and moderately prominent laterally; cristae trochleae of tibiotarsus are shallow and deviated laterally.

The *Bu. planei*–*D. stirtoni* clade is diagnosed by the following synapomorphies: strongly convex culmen, deep and compressed beak; fused atlas-axis complex; wider than long vertebrae cervicales; wide, obtuse sulcus intercondylaris of femur; slightly constricted eminentia cnemialis; crista patellaris is thick triangular tuberosity; broad, oval proximal surface of tibiotarsus; incisura intercondylaris is wide V-shape with acute apex; obliquely oval and elongated distal condylus lateralis of tibiotarsus; oblique, flange-like cristae trochleae; trochlea metatarsi II longer than IV; foramen vasculare distale low, within trochlear notch; wide incisurae intertrochlearis; deep and dorsally prominent trochlea metatarsi III.

The *I. lawsoni*–*G. newtoni* clade is diagnosed by the following synapomorphies: trochanter femoris considerably higher than the caput femoris; moderately constricted eminentia cnemialis; deep, almost circular incisura tibialis lateralis; marked reduction of trochlea metatarsi II; trochlea metatarsi II shorter than IV.

The *Bu. planei*–*D. stirtoni*–*D. australis* clade is diagnosed by oblique cristae sulci patellaris and wide sulcus patellaris of femur.

Body mass and hind limb proportions

Body mass estimates. The estimated body masses of dromornithids and other large flightless birds are presented as an order of magnitude in Tables 4–5. *Barawertornis tedfordi* was the lightest known dromornithid species. Its estimated body mass, using Campbell & Marcus's (1992) regression equations, is about 59–64 kg. Using Anderson *et al.*'s (1985) equation, the estimated mass range for *B. tedfordi* is about 27–79 kg, and the mean mass 46 kg. The maximum body mass estimated for *B. tedfordi* is within the minimum range of *D. australis. Barawertornis tedfordi* weighed approximately half that estimated for *I. lawsoni* and *Bu.* sp. The other dromornithid species were more heavily built, similar to the Elephant Bird *Aepyornis maximus* Geoffroy Saint-Hilaire, 1851, and moa *Pachyornis elephantopus* (Owen, 1856). *Dromornis, B. planei, G. newtoni* and *I. woodburnei* are within the mass range calculated for moa species *Dinornis giganteus* (*sensu* Jennings, 1990) and *Dinornis maximus* (*sensu* Stirling & Zietz, 1900; Alexander, 1983). The specimens of the latter species, however, are now known to represent the largest female South Island Giant Moa *Dinornis robustus*, the only member of the genus on the South Island of New Zealand (Bunce *et al.*, 2003; Worthy *et al.*, 2005). The largest of the dromornithid species, *D. stirtoni*, weighed almost ten times more than *B. tedfordi*.

The estimated body masses of the extant ratites we obtained (Tables 4–5) are mostly within the observed ranges recorded in Davies (2002) and Dunning (2008). The minimum and maximum mass estimates for the Ostrich *Struthio camelus* Linnaeus, 1758, Emu *Dromaius novaehollandiae* (Latham, 1790), and Southern Cassowary *Casuarius casuarius* are slightly outside the observed ranges. The estimated body mass range for the Dwarf Cassowary *Casuarius bennetti* Gould, 1857 is below the observed mass recorded in Diamond *et al.* (1999).

In comparison to extant flightless birds, *B. tedfordi* was lighter than *S. camelus*. The lower body mass estimates for *B. tedfordi* are within the ranges observed in the Greater Rhea *Rhea americana* (Linnaeus, 1758), *D. novaehollandiae, C. bennetti* and *C. casuarius*. Its mean mass estimates are closest to the maximum mass recorded for *C. casuarius*.

Murray & Vickers-Rich (2004) estimated the body masses of dromornithid species and other birds using a regression equation from Anderson *et al.* (1985) for bipedal dinosaurs rather than birds (equation 1 in Methods). It appears that they inadvertently used least shaft circumferences, not mid-shaft circumferences, to obtain their estimates from Anderson *et al.*'s (1985) equation. They also estimated masses using Campbell & Marcus's (1992) regression equation based on femur circumference. However, they unintentionally converted the original log 10 equation (equation 2 in Methods) to the following non-log equation:

$$\text{Weight} = -\,0.065 \times (\text{femur circumference})^{2.411}$$

The correct non-log equation is:

$$\text{Weight} = 10^{-0.065} \times (\text{femur circumference})^{2.411}$$

After substituting Murray & Vickers-Rich's (2004) circumference measurements in their non-log equation and Campbell & Marcus's (1992) original log equation, different body mass estimations were obtained. It is uncertain how Murray & Vickers-Rich (2004) obtained their estimations from this equation, but their values overestimate the body masses of dromornithids, especially for the heavier birds. Using the correct equation from Campbell & Marcus (1992) and Anderson *et al.*'s (1985) equation for birds, we recalculated body mass estimates for the other dromornithids (Tables 4–5).

Hind limb proportions. Unfortunately, none of the new specimens of *Barawertornis tedfordi* preserves the complete lengths of the femur, tibiotarsus and tarsometatarsus. To estimate its hind limb bone ratio, we used the maximum length of the tarsometatarsus (QM F45419) and the internal length (caput femoris to condylus medialis) of the femur

Table 4. Body mass estimates of *Barawertornis tedfordi* based on femora (holotype CPC7341 and QM F 45056) compared to estimates for other dromornithids and flightless birds. Nomenclature of moa species follows source authors. Mass estimates were calculated using the mid-shaft circumference (MC_f) equation from Anderson *et al.* (1985) [a], and the least shaft circumference (LC_f) equation from Campbell & Marcus (1992)[b]. See Methods for regression equations. Circumference measurements are given as mean (minimum-maximum) values. N/A = not available.

species	source	MC_f (mm)	mass based on MC_f (kg)	LC_f (mm)	mass based on LC_f (kg)
Barawertornis tedfordi	this study	107.3 (104–110.6), n = 2	x = 46 (28.8–73.5) min = 42.9 (26.9–68.2) max = 49.3 (30.8–79)	101.6, n = 1	59.4
Bullockornis sp.	Murray & Vickers-Rich (2004)	N/A	N/A	140 (139–141), n = 2	x = 128.6 min = 126.4 max = 130.8
Bullockornis planei	Murray & Vickers-Rich (2004)	N/A	N/A	207.3 (186–220), n = 6	x = 331.4 min = 255.2 max = 382.5
Dromornis australis	Stirling & Zietz (1900)	171, n = 1	133.2 (79.7–222.8)	N/A	N/A
Dromornis stirtoni	Jennings (1990); Murray & Vickers-Rich (2004)	N/A	N/A	249.8 (210–285), n = 17	x = 519.5 min = 341.9 max = 713.9
Genyornis newtoni	Stirling & Zietz (1900)	228.7 (218–234), n = 3	x = 258.6 (150.2–445.1) min = 231.8 (135.3–397.1) max = 272.4 (157.9–470.1)	N/A	N/A
Ilbandornis lawsoni	Murray & Vickers-Rich (2004)	N/A	N/A	142 (134–155), n = 3	x = 133.1 min = 115.7 max = 164.4
Ilbandornis woodburnei	Murray & Vickers-Rich (2004)	N/A	N/A	176.5 (160–193), n = 2	x = 224.9 min = 177.5 max = 278.9
Dinornis maximus [c]	Stirling & Zietz (1900)	240, n = 1	288.6 (166.8–499.3)	N/A	N/A
Pachyornis elephantopus	Stirling & Zietz (1900); Jennings (1990)	196, n = 1	181.9 (107.3–308.3)	167.5 (160–175), n = 2	x = 198.2 min = 177.5 max = 220.3
Aepyornis maximus	Stirling & Zietz (1900)	270, n = 1	377.5 (215.7–660.8)	N/A	N/A
Struthio camelus	this study	143 (133–145), n = 3	x = 88.6 (54–145.6) min = 75.1 (46.1–122.5) max = 91.5 (55.6–150.5)	137.3 (133–143), n =3	x = 122.7 min = 113.7 max = 135.4
Dromaius novaehollandiae	this study	93.8 (92–95), n = 5	x = 33.9 (21.5–53.4) min = 32.4 (20.6–51) max = 34.9 (22.1–55)	92.2 (91–93.5), n = 5	x = 47 min = 45.5 max = 48.6
Rhea americana	this study	74 (73–75), n = 2	x = 19.7 (12.8–30.4) min = 19.1 (12.5–29.4) max = 20.3 (13.2–31.3)	73.5 (73–74), n = 2	x = 27.2 min = 26.8 max = 27.7
Casuarius bennetti	this study	76, n = 1	21 (13.6–32.3)	73, n = 1	26.8
Casuarius casuarius	Anderson *et al.* (1985); W. Longmore (pers. comm.); R. Palmer (pers. comm.)	94, n = 1	34.1 (21.6–53.6)	92.3 (78–103), n = 4	x = 47.1 min = 31.4 max = 61.4

[a] Anderson *et al.* (1985) regression equation gives estimate ranges of body mass. Presented here are the calculated mass and estimate range based on the mean (x), minimum and maximum circumference values.

[b] Campbell & Marcus's (1992) regression equation gives single-figure estimates of body mass. Here we present the mean (x), minimum and maximum mass values calculated from the mean, minimum and maximum circumference values.

[c] *Dinornis maximus* is synonymized under *Dinornis robustus* in current nomenclature (Bunce *et al.*, 2003).

Table 5. Body mass estimates of *Barawertornis tedfordi* based on the tibiotarsus (QM F45416) compared to estimates for other dromornithids and flightless birds. Nomenclature of moa species follows source authors. Body mass estimates were calculated using the least shaft circumference (LC$_t$) equation from Campbell & Marcus (1992)[a] (equation 3 in Methods). Measurements are presented as mean (minimum–maximum).

species	source	LC$_t$ (mm)	mass based on LC$_t$ (kg)
Barawertornis tedfordi	this study	89.3 n = 1	63.8
Dromornis stirtoni	Jennings (1990)	207.3 (200–220) n = 4	x = 491.4 min = 450.5 max = 567.6
Ilbandornis lawsoni	Jennings (1990)	110 n = 2	105.8
Ilbandornis woodburnei	Jennings (1990)	113.3 (108–120) n = 4	x = 113.6 min = 101.2 max = 130.6
Dinornis giganteus [b]	Jennings (1990)	150 n = 1	224.3
Pachyornis elephantopus	Stirling & Zietz (1900); Jennings (1990)	146 (125–162) n = 5	x = 210.1 min = 144.2 max = 270.3
Aepyornis maximus	Stirling & Zietz (1900)	155 n = 1	242.9
Struthio camelus	this study	107 (98–113) n = 3	x = 98.9 min = 79.9 max = 112.9
Dromaius novaehollandiae	this study	75.6 (71–81) n = 5	x = 42.6 min = 36.6 max = 50.4
Rhea americana	this study	64 (63.5–64.5) n = 2	x = 28.5 min = 27.9 max = 29
Casuarius casuarius	R. Palmer (pers. comm.); this study	87.7 (86–91) n = 3	x = 61.1 min = 58.2 max = 66.8

[a] Campbell & Marcus's (1992) regression equation gives single-figure estimates of body mass. Here we present the mean (x), minimum and maximum mass values calculated from the mean, minimum and maximum circumference values.

[b] Jennings (1990) measured specimens of *Dinornis giganteus* from the South Australian Museum collection. All of the *D. giganteus* specimens in the South Australian collection were found on the South Island of New Zealand (T.H. Worthy, pers comm.), and would therefore be synonymized under *Dinornis robustus* in current nomenclature (Bunce *et al*., 2003).

(holotype CPC7341). The tibiotarsal length was calculated by adding the maximum length of QM F45416, a left tibiotarsus missing the proximal end, and the maximum length of QM F45417, proximal end of a left tibiotarsus. QM F45416 and QM F45417 were recovered from the same limestone block and are probably fragments of the one tibiotarsus.

The hind limb bone ratio derived for *B. tedfordi* was about 1:1.9:1.2. A ratio of approximately 1:2:1 is also seen in *Bu. planei, D. stirtoni, G. newtoni* and *Dinornis. Pachyornis elephantopus*, and all other non-dinornithid moa, and *A. maximus* had relatively shorter tarsometatarsi in comparison to the femur. *Ilbandornis lawsoni* had a relatively long tarsometatarsus, with a hind limb bone ratio of about 1:2:2, like in *S. camelus, D. novaehollandiae* and *R. americana* (Table 6).

Discussion

Phylogenetic relationships. Two phylogenetic hypotheses of the intrafamilial relationships within the Dromornithidae have been produced in our analyses. In both, the relative phylogenetic positions of *I. lawsoni, G. newtoni, Bu.* sp., *I. woodburnei, Bu. planei* and *D. stirtoni* remain the same. In all analyses, a monophyletic group comprising *Bu.* sp., *I. woodburnei, Bu. planei* and *D. stirtoni* is present. Within this group the pairs of *Bu.* sp. and *I. woodburnei*, and *Bu. planei* and *D. stirtoni* form subclades. The phylogeny based on only femoral characters suggests that *D. australis* is most closely related to *Bu. planei* and *D. stirtoni*. Outside this monophyletic group, *I. lawsoni* and *G. newtoni* also form a clade. These relationships are consistent with those proposed by Murray & Vickers-Rich (2004).

However, our results provide conflicting data about the relative position of *B. tedfordi* within the Dromornithidae. One hypothesis suggests that *B. tedfordi* is the sister taxon to all other dromornithids (Fig. 5B), as initially proposed by Rich (1979) and supported by Murray & Vickers-Rich (2004). This is driven by retention of plesiomorphic features in *B. tedfordi* including a small fossa poplitea, no constriction of the eminentia cnemialis, a shallow incisura tibialis lateralis, and absence of an incisura tibialis medialis.

The alternative hypothesis suggests that *B. tedfordi* is the sister group to the monophyletic group comprising *Bu.* sp., *I. woodburnei, Bu. planei* and *D. stirtoni,* to the exclusion of *I. lawsoni* and *G. newtoni* (Fig. 5A). This relationship has not been suggested before, and is based on information provided by the new fossil material of *B. tedfordi* described here. The synapomorphies linking these taxa (see Results) do not appear to be homoplasious with respect to large body size, and hence are likely to be of great phylogenetic significance.

However, both hypotheses regarding the position of *B. tedfordi* are weakly supported, as indicated by the relatively low bootstrap and Bremer support values (Figs 5A,B). Thus

Table 6. Hind limb bone ratios (lengths of femur: tibiotarsus: tarsometatarsus) for *Barawertornis tedfordi* and other dromornithids. Ratios of other flightless birds are also shown for comparison. Nomenclature of moa species follows authors. It is uncertain in the literature if the given bone lengths of fossil birds are from articulated or isolated bones. Here we treated bone lengths of fossil birds as measurements of isolated bones, and calculated ratios using the minimum and maximum known lengths.

species	source		bone length (mm)			ratio
			F	TBT	TMT	
Barawertornis tedfordi	this study		226.2	>430.5	>269.4	1:1.9:1.2
Bullockornis planei	Murray & Vickers-Rich (2004)		350	600 [a]	390	1:1.7:1.1
Dromornis stirtoni	Jennings (1990);	min	330	750	406	1:2.3:1.2
	Murray & Vickers-Rich (2004)	max	470	830	465	1:1.8:1
Genyornis newtoni	Stirling & Zietz (1900);	min	322	602 [b]	320	1:1.9:1
	Rich (1979)	max	345	602 [b]	379	1:1.7:1.1
Ilbandornis lawsoni	Jennings (1990);	min	290	425	475 [b]	1:1.5:1.6
	Murray & Vickers-Rich (2004)	max	325	540	475 [b]	1:1.7:1.5
Ilbandornis woodburnei	Murray & Vickers-Rich (2004)	min	260	570 [b]	340	1:2.2:1.3
		max	290	570 [b]	360	1:2:1.2
Dinornis giganteus [c]	Jennings (1990)		406	889	495	1:2.2:1.2
Dinornis maximus [c]	Alexander (1983)		404.9	859	451.9	1:2.1:1.1
Pachyornis elephantopus	Jennings (1990)		317.9	545.6	233.6	1:1.7:0.7
Aepyornis maximus	Jennings (1990)		480	640	330	1:1.3:0.7
Struthio camelus	this study		317	525	447	1:1.7:1.4
Struthio camelus	Gatesy & Biewener (1991)		294	524	474	1:1.8:1.6
Dromaius novaehollandiae	this study		229	455	381	1:2:1.7
Dromaius novaehollandiae	this study		230	437	403	1:1.9:1.8
Dromaius novaehollandiae	this study		242	464	413	1:1.9:1.7
Dromaius novaehollandiae	Jennings (1990)		203	401	383	1:2:1.9
Rhea americana	Jennings (1990)		220	330	324	1:1.5:1.5
Rhea americana	Gatesy & Biewener (1991)		210	319	306	1 :1.5:1.5
Casuarius casuarius	R. Palmer (pers. comm.)		261	421	331	1:1.6:1.2
Casuarius casuarius	Jennings (1990)		264	443	323	1:1.7:1.2

[a] Length is estimated from specimens of similar sized individuals.

[b] The same value is used to calculate both minimum and maximum ratios. This is because only one specimen is known for the species, or only one measurement is noted in the literature (though there may be more than one specimen described).

[c] See footnotes for Tables 4–5 for explanation of current *Dinornis* nomenclature.

the strict consensus tree based on these two hypotheses represents our preferred summary of dromornithid intrafamilial relationships (Fig. 6) based on current material, with a trichotomous relationship between *B. tedfordi*, the *I. lawsoni–G. newtoni* clade and all other dromornithids. This tree confirms the repeatedly recovered inter-relationships among all other dromornithids found in the other trees, but reflects the uncertain position of *B. tedfordi* within the family.

Resolution of conflict about the intrafamilial position of *B. tedfordi* is impeded by the limited characters available for phylogenetic analyses. At present, the hind limb is the only complete character system available for comparison across all dromornithid taxa. The discovery of more complete fossil material from different morphological (character) systems is needed to further understand the relationships between *B. tedfordi* and other dromornithids, and/or definition of new characters of the known skeletal elements.

Recommended changes to taxonomy. The current analyses support data presented by Murray & Vickers-Rich (2004), and indicate that a formal revision of dromornithid nomenclature is required to reflect the phylogeny. *Bullockornis* sp. and *Ilbandornis lawsoni* were provisionally allocated to these genera by Rich (1979) based on the very little material known at the time, but the current study shows that they appear to be more closely related to other genera. A close relationship between *I. lawsoni* and *G. newtoni* is supported by a number of shared derived states and high bootstrap and Bremer support values (Figs 5 and 7). This suggests that these species are congeneric and hence *Ilbandornis lawsoni* should be renamed *Genyornis lawsoni*, as that generic name has priority.

There is also strong evidence that *Bu.* sp. and *I. woodburnei* belong to the same genus, based on high bootstrap and Bremer support values and several synapomorphies of the tibiotarsus (Fig. 5). The femoral character states for *Bu.* sp. and *I. woodburnei* are identical and do not vary from the states of the node shared with *Bu. planei, D. stirtoni* and *D. australis*. These could therefore be interpreted as ancestral states for the *Bu. planei–D. stirtoni–D. australis* group in which derived states occur (Fig. 7). In order to indicate the close relationship between *Bu.* sp. and *I. woodburnei, Bu.* sp. should be assigned to *Ilbandornis*. It has no specific name because it has not been formally described.

Table 7. List of all dromornithid taxa and their revised names, in accordance to phylogenetic relationships evident in analyses.

dromornithid species	revised name
Barawertornis tedfordi	—
"?*Bullockornis*" sp.	*Ilbandornis* sp.
Bullockornis planei	*Dromornis planei*
Dromornis australis	—
Dromornis stirtoni	—
Genyornis newtoni	—
"*Ilbandornis*?" *lawsoni*	*Genyornis lawsoni*
Ilbandornis woodburnei	—

Bullockornis planei appears to be more closely related to *D. stirtoni* than to *Bu.* sp. The two species share many synapomorphies of the cranial and postcranial skeleton, and their relationship is strongly supported by significantly high bootstrap and Bremer support values (Figs 5–7). We argue that *Bu. planei* and *D. stirtoni* are probably part of a temporal series and should be considered as congeneric; thus *Bullockornis planei* should be renamed *Dromornis planei*.

However, the genus *Dromornis* is problematic because of the paucity of material representing its type species, *D. australis*. The lack of representation for this species makes it uncertain that *D. stirtoni* is correctly assigned to this genus. This can only be confirmed with discovery of more fossil material for *D. australis* and consequent reanalysis of dromornithid intrafamilial relationships.

Although the above relationships were also found by Murray & Vickers-Rich (2004), these dromornithid species were still maintained in separate genera. We consider that the taxonomic revision presented here, which reflects the phylogenetic relationships within the Dromornithidae, is necessary to improve our understanding of the taxonomy of the group; hereafter in this paper, dromornithid taxa are referred to by their revised names (following Table 7).

Paleobiology. *Barawertornis tedfordi* was the smallest of the known dromornithids, with an estimated body mass range of 26.9–79 kg, and mean mass of 46–63.8 kg. This bird was smaller than *S. camelus*, and is within the higher mass ranges observed in *D. novaehollandiae, R. americana*, and *C. bennetti*. It is most similar in size to *C. casuarius*. Its femur is proportionately short and stout relative to that of *S. camelus* and *D. novaehollandiae*, but is gracile in comparison to the more robust femora of other dromornithids, dinornithiforms and *A. maximus*.

Cursoriality in animals is associated with an increase in lengths of the distal limb elements relative to the proximal ones (Howell, 1944; Storer, 1960; Gray, 1968). This overall increase of the distal limb elements, as well as elongation of the tarsometatarsus relative to the tibiotarsus, is exhibited in cursorial ground birds such as *S. camelus, D. novaehollandiae* and *R. americana* (Gatesy & Biewener, 1991; Boles, 1997, 2001; Christiansen & Bonde, 2002). The hind limb proportions of *Genyornis lawsoni* are very similar to those of these birds, suggesting that this species was also capable of running at rapid speed over long distances. Relative proportions of the hind limb bones in *B. tedfordi*, however, are most similar to that of *C. casuarius. Casuarius casuarius* is less cursorial than *S. camelus, D. novaehollandiae* and *R. americana*, but has powerful legs capable of sustaining a reasonable degree of speed if required (Boles, 1997). This suggests that *B. tedfordi* exhibited similar cursorial abilities.

The hind limb bone ratios obtained for dromornithid and other fossil taxa are derived from bones of different individuals. Inferences of their locomotory mode are based on observations of living, unrelated animals. As such, these inferences are speculative and should be treated with caution.

ACKNOWLEDGMENTS. We thank the following people: M. Archer (UNSW) and H. Godthelp (UNSW) as co-leaders of the Riversleigh Fossil Project; K. Black (UNSW), A. Gillespie (UNSW) and J. Scanlon (Riversleigh Fossil Interpretive Centre, Mount Isa) for preparation and loans of specimens; R. Beck for assistance with phylogenetics; W. Longmore (Museum of Victoria) and R. Palmer (Australian National Wildlife Collection, CSIRO Sustainable Ecosystems) for additional osteological measurements; T.H. Worthy (UNSW) for assistance with moa nomenclature; and C. Bento for photographs. The Riversleigh Fossil Project is supported by the Australian Research Council (DP043262, LP453664, 0989969), Environment Australia, Queensland Parks and Wildlife Service, the University of New South Wales, the Queensland Museum, the Australian Museum, Xstrata Copper (North Queensland) and the Riversleigh Society. We are also grateful to R. Beck, P. Vickers-Rich and T. Worthy for constructive criticism of the manuscript.

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Appendix

Character state scores for *Barawertornis tedfordi* in the matrix of Murray & Vickers-Rich (2004).

	1	1111111112	2222222223	3333333334
	1234567890	1234567890	1234567890	1234567890
Barawertornis tedfordi	??00???010	0000000000	0000100?00	0000000100

Characters 13, 16–17, 21–22, 25, 27, 30 and 32 were ordered in the second phylogenetic analysis (see Methods). The femoral matrix was derived from scores for characters 10–18.

Notes. In their analysis, Murray & Vickers-Rich (2004) scored the hind limb bone ratio (character 11) and the proximal articular surface of the tarsometatarsus (character 38) of *B. tedfordi* as 0 (plesiomorphic). However, it is not clear whether this scoring was based on observations of fossil material (rather than assumed), because there is no indication in their descriptions that the tibiotarsal length or proximal tarsometatarsus were known for *B. tedfordi* at the time. We scored character 38 as 1 for *B. tedfordi* based on observations of specimen QM F45419; however, this state may be exaggerated by the distortion and poor preservation of the bone. Because the complete lengths of the tibiotarsus and tarsometatarsus are unknown for *B. tedfordi*, we used the minimum lengths of these bones and the internal length of the femur to score character 11. This character was scored as 0 for *B. tedfordi*.