A RE-EXAMINATION OF THE MOA GENUS *MEGALAPTERYX*

By T. H. WORTHY

ABSTRACT

A re-examination of the moa genus *Megalapteryx* reveals that the two currently accepted species, *M. didinus* (Owen) and *M. benhami* Archey, do not differ in the shape of the bones. They represent small and large specimens in an unbroken size continuum. Specimens from northwest Nelson have a larger mean size than those in a sample from Takahe Valley, Fiordland. A series of ^{14}C dates indicates that the largest '*M. benhami*' are all of Otiran derivation, whereas *M. didinus* bones are from Otiran and Holocene deposits. Therefore *M. benhami* is synonymised with the Upland Moa, *M. didinus* (Owen).

Out of all the New Zealand birds, the moa, or more specifically the group of species included under this name, have the greatest record of taxonomic confusion. This was caused in part by all members of the group being extinct, but mainly by their being much larger than most other birds, resulting in too much emphasis being placed on relatively small size differences between specimens. Thus, many size groups within one 'form' have been considered to represent species and as many as 37 moa species have been recognised (Rothschild 1907). Archey (1941) and Oliver (1949) perpetrated this trend and not until Cracraft (1976) examined moa taxonomy by statistical techniques was this problem adequately tackled. Using covariant statistics Cracraft reduced the observed variation to comparable figures and proposed the synonymy of several pairs of species, leaving just 13. By invalidating *Anomalopteryx oweni* (Haast), Millener (1981) reduced the 13 to 12.

Cracraft had not been able to assess the validity of *Megalapteryx benhami* Archey (1941) because the three specimens available did not allow adequate comparison with *M. didinus.* Thus he retained these two species in his classification.

M. benhami was described by Archey (1941) from a femur and a tibiotarsus from a cave on the Mt Arthur Tablelands, northwest Nelson. Oliver (1949) referred a femur to this species from Wairanga, also in northwest Nelson. In 1980, staff from the Canterbury Museum collected several bones of a moa of this species from Hives Passage in Honeycomb Hill Cave, Karamea. Several bones in the size range of this species were recovered from Honeycomb Hill Cave by P. R. Millener in 1983: a femur, tibiotarsus and tarsometarsus of an individual from Enduro Passage and a tarsometatarsus from Eagle's Roost. In 1987, during further research on the subfossil fauna of this cave, I recovered a great deal of *Megalapteryx* material, including four partial skeletons and odd bones of six more birds, all in the size range of *M. benhami.* This new material contained all skeletal elements of *M. benhami*, including the previously unknown sternum, pelvis, vertebrae and cranial elements. In January 1987, further *Megalapteryx* material was collected from a cave in Poverty Basin, Mt Owen, north-west Nelson. With this new material I could re-examine the *M. didinus* versus *M. benhami* problem. In this paper, I compare the bones from each size range, examine the size range of *Megalapteryx* in different sites, and discuss associated faunas and the relative ages of deposits. In Appendix 1, I give a brief morphological description of *Megalapteryx*, comparing it with *Anomalopteryx didiformis* (the most similar species).

Material for the morphological comparision was as follows. For *M. didinus*: National Museum of New Zealand (NMNZ) DM 435-440, 443-449 — Takahe Valley; NMNZ S 23527-23567 — Poverty Basin, Mt Owen; NMNZ S 23700 — Honeycomb Hill; Canterbury Museum (CM) AV 8505, 8507, 8513, 10335, 10336, 10338, 10339 — Takahe Valley; Otago Museum (OM) A52.1-.14 — Takahe Valley; NMNZ S 22689, 22721, 22889-22890, 23027, 23032, 23062, 23086, 23645-7, 23686, 23733, 23736-9, 23740, 23802-807, 23809, 23813, 23824, — Honeycomb Hill Cave.

For *M. benhami*: NMNZ S 22710, 23425-23430, 23575, 23618-23622, Honeycomb Hill.

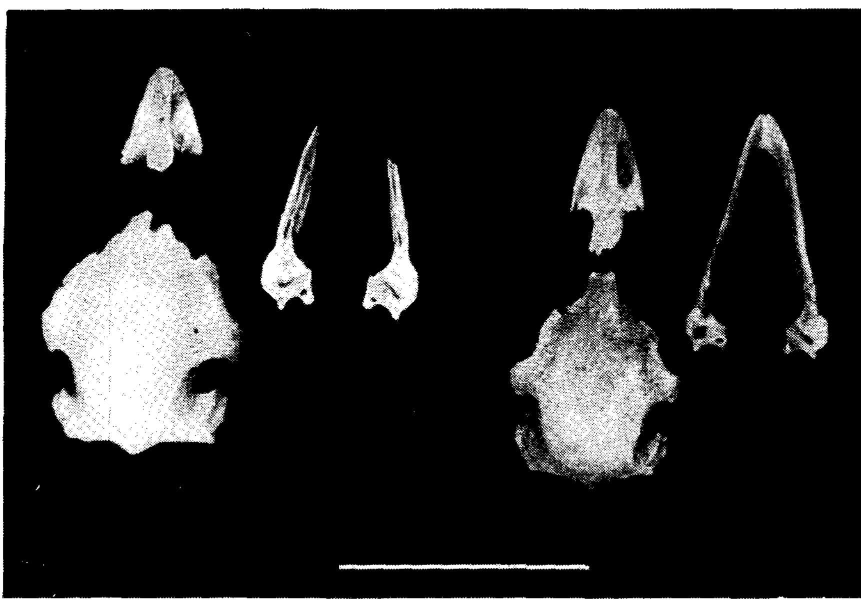

FIGURE 1 — Dorsal views of crania, premaxillae and mandibles of *Megalapteryx*. Left group (NMNZ S23575) typical of *M. benhami*, right group (NMNZ S23700) typical of *M. didinus*. Scale bar = 10 cm

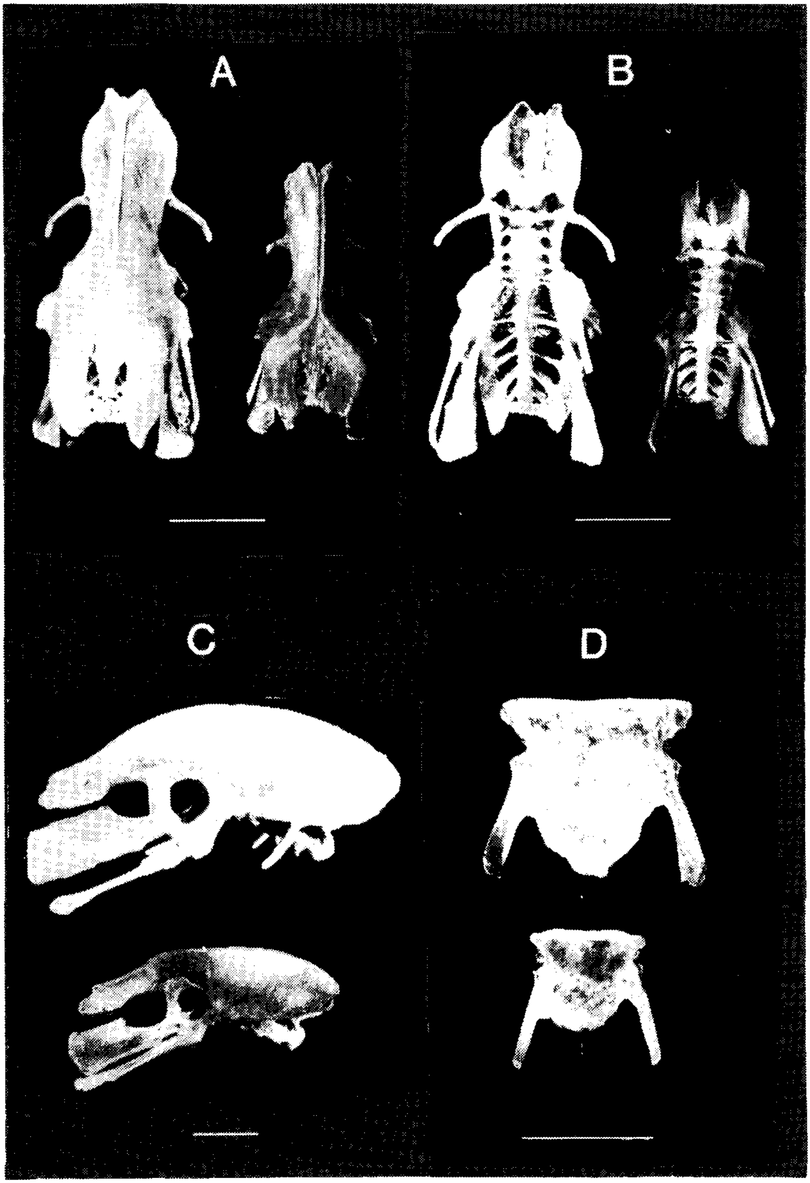

FIGURE 2 — Pelves of *Megalapteryx* in dorsal (A), ventral (B), right lateral (C) views and dorsal view of sterna (D). Larger specimens (NMNZ S23575) typical of *M. benhami*; smaller pelvis (NMNZ S23700) and sterna (NMNZ S443) typical of *M. didinus*. Scale bars= 10 cm

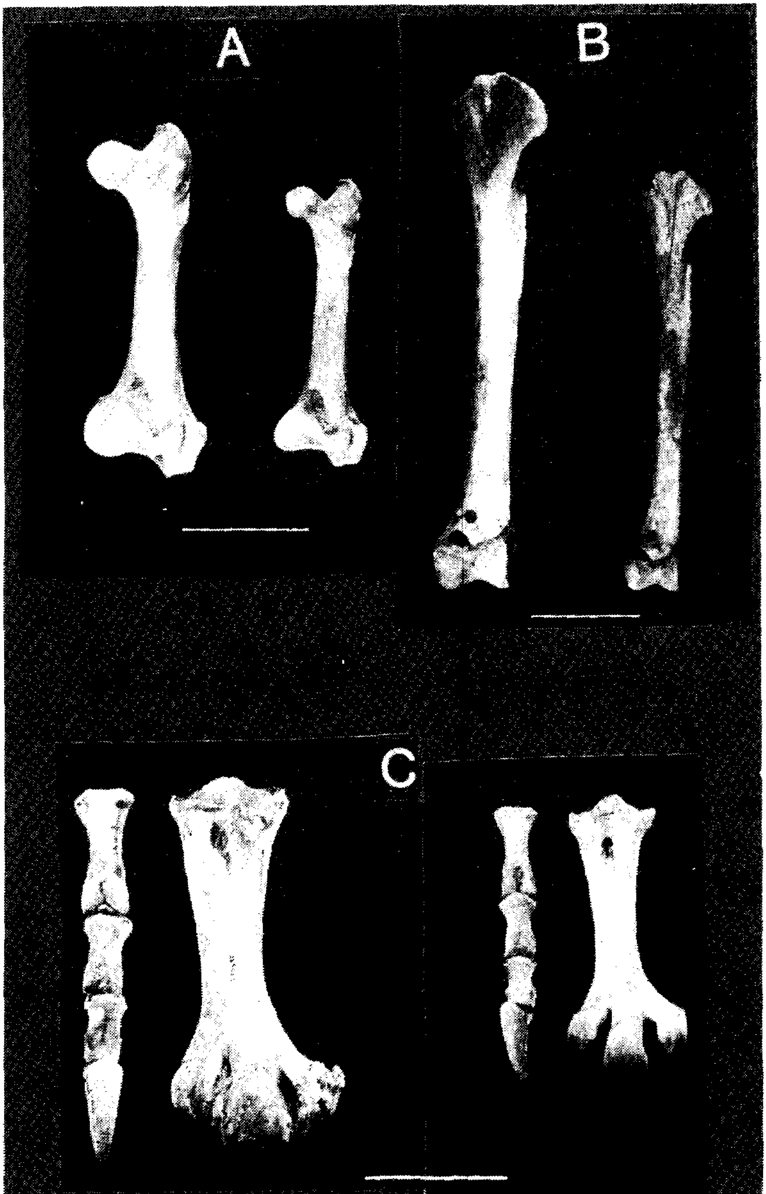

FIGURE 3 — Right femora — ventral view (A), left tibiotarsi — anterior view (B), (larger of each pair NMNZ S23575, smaller NMNZ S23700), right tarsometatarsi and phalanges of digit 3 (larger specimen NMNZ S23430, smaller NMNZ S23700) of *Megalapteryx*. Scale bars = 10 cm

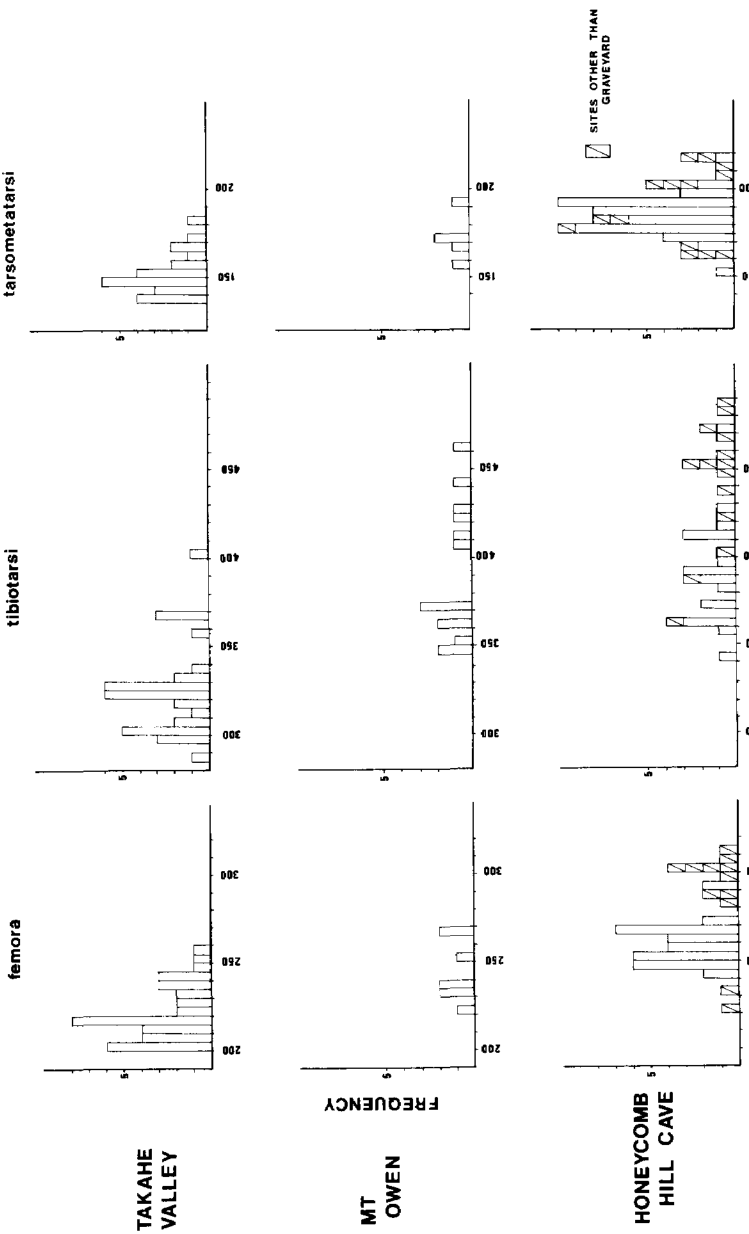

FIGURE 4 — Length frequency histograms of femora, tibiotarsi and tarsometatarsi of *Megalapteryx didinus* at Takahe Valley, Mt Owen and Honeycomb Hill Cave

Morphological comparison of *Megalapteryx* material

A detailed comparison of bones in the size range usually associated with *M. didinus* was made with the larger bones of *M. benhami*. Skeletal elements compared included complete skulls, sterna, coracoid-scapulae, pelves, femora, tibiotarsi, tarsometatarsi and phalanges. In all comparisons, the bones of *M. benhami* were only a larger version of those in *M. didinus*. I could discern no differences in shape or form. (Fig. 1, 2, & 3).

Size range of *Megalapteryx*: The range in absolute size is similar for femora, tibiotarsi and tarsometatarsi from Takahe Valley, Mt Owen and Honeycomb Hill, but it is significant that the bones from Takahe Valley are from smaller birds than those in the northern sites of Mt Owen and Honeycomb Hill Cave (Table 1, Fig 4.). Tibial length appears more variable than femoral or metatarsal length, but the coefficients of variation show that they are similar. These data strongly suggest regional variation of populations, which may be clinal but without examining material from other sites with large numbers of bones I cannot be sure. The data show that to distinguish a species from another solely because of apparent discrete size ranges is inadvisable until the nature of regional variation is well documanted and understood.

TABLE 1 Values of the mean, standard deviation, and number for long bones in various populations of *Megalapteryx*

	Femora	Tibiotarsi	Tarsometatarsi
Takahe Valley-Te Anau	220.6, 14.74 (37)	322.8, 24.06 (34)	150.7, 11.08 (24)
Mt Owen	246.2, 16.15 (9)	388.9, 35.70 (14)	172.0, 10.61 (5)
Graveyard (total)	257.6, 10.72 (36)	392.0, 27.32 (19)	184.5, 10.86 (46)
Honeycomb (total)	264.1, 20.58 (47)	409.7, 40.47 (32)	185.7, 14.07 (60)

When there are enough data for a site, e.g. Takahe Valley, only one mode is discernable within the size range of a bone (Fig. 4). Thus there is no suggestion of either a sexually dimorphic population or two species separated by size, Specimens in the size range of *M. benhami* (Oliver 1949), notably from Honeycomb Hill Cave but also from Mt Owen, represent only individuals in the upper size range of *Megalapteryx* in northwest Nelson.

Faunas associated with material in the size range of *M. benhami*

I collected an associated avifauna from five sites in Honeycomb Hill Cave where material the size of *M. benhami* was found. Other moa species represented were Upland Moa *M. didinus* (5 sites), Little Bush Moa *Anomalopteryx didiformis* (3 sites), Heavy-footed Moa *Pachyornis elephantopus* (2 sites), and Large Bush Moa *Dinornis novaezealandiae* (4 sites). Other birds included Kokako *Callaeas cinerea*, Robin *Petroica australis*, Saddleback *Creadion carunculatus*, Tui *Prosthemadera novaeseelandiae*, and various wrens, kiwis, rails, and parrots. It is notable that

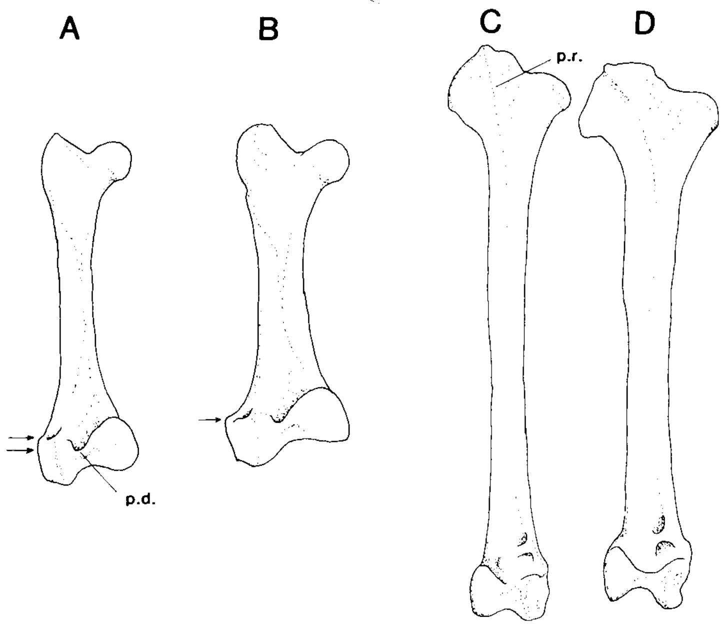

FIGURE 5 — Femora (AB) and tibiotarsi (CD) of *M. didinus* (left of each pair) and *A. didiformis* (right of each pair) from Archey (1941). p.d. = popliteal depression, p.r. = procnemial ridge.

material in the size range of the Upland Moa *M. didinus* and of *M. benhami* was found sympatrically and in the case of the Graveyard at Honeycomb Hill Cave temporal sympatry was also demonstrated. In general these associated species indicate the presence of at least a partially forested habitat. Pollen and faunal analyses show it is probable that, when the Graveyard was being deposited between 20 000 and 14 000 years BP, there was montane forest and subalpine scrubland in the area of the cave (Worthy, unpublished data).

A sizable sample of *Megalapteryx* has now been dated, either directly (Table 2, excluding L27/f108) or indirectly (a minimum number of 73 *Megalapteryx* were excavated from L3 of the Graveyard). Material in the size range of *M. benhami* is found only in the Otiran deposits, where *M. didinus* is found in both the Otiran (Graveyard L3, His and Hers Cave) and Holocene deposits (Graveyard L2, Eagle's Roost).

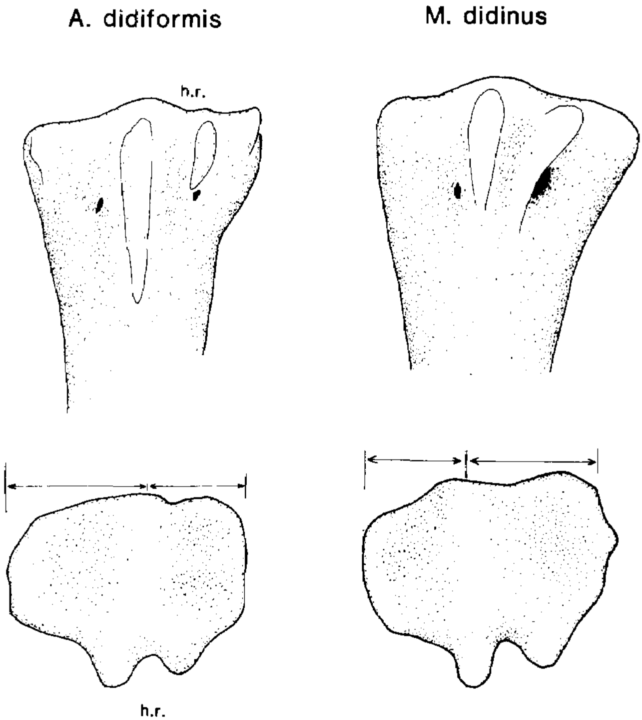

FIGURE 6 — Proximal left tarsometatarsi of *Anomalopteryx didiformis* (NMNZ S23571) and *Megalapteryx didinus* (NMNZ S23575) in posterior view (upper) and proximal view (lower). h.r. = hypotarsal ridges

The faunas from Mt Owen and Takahe Valley must both be post-glacial and probably less than 10 000 years old because the collection sites were ice covered during the Otiran.

It is possible to interpret the data thus: *M. benhami* represents the largest birds in the Otiran population in the northern South Island, and with the transition to the Holocene, the mean size of birds in the population became smaller so that all specimens fell in the size range of *M. didinus.* Such a temporal change has been demonstrated to have occurred in the North Island *Pachyornis mappini* (Worthy, 1987). Even in layer 3 of the Graveyard, dated between 20 000 amd 14 00 years old, material in the size range of *M. benhami* was rare. Of the 73 *Megalapteryx* represented, only 3 were in the size range of *M. benhami.* Therefore the rarity of *M. benhami* in the Graveyard exemplifies the collecting bias towards *M. benhami* in Honeycomb Hill Cave.

TABLE 2 — List of dates for *Megalapteryx* material from Honeycomb Hill Cave. L27/f108 is for a *Dinornis* bone which was associated with the *Megalapteryx* bones by stratigraphy. All other dates were determined by radiocarbon dating of bone collagen calculated using Libby 7½ (5568 yr).

Species	Fossil Record No.	INS Ref.No.	Age ^{14}C Yrs BP
M. didinus (Eagles Roost)	L27/f93		11,250±150
M. didinus (L2, Graveyard)	L27/f100	R11411/1	11,200±150
M. didinus (L3, Graveyard)	L27/f101	R11411/2	19,300±400
M. didinus (Graveyard, lag)	L27/f102	R11411/3	10,980±140
M. benhami (Enduro)	L27/f104	R11410/1	14,385±433
M. benhami (Aven)	L27/f105	R11410/2	15,580±702
M. benhami (Eagles Roost)	L27/f106	R11410/3	14,335±351
M. benhami (Wren Wrecker)	L27/f107	R11410/4	14,694±681
M. benhami/didinus (His & Hers)	L27/f108	R11411/5	15,900±240

CONCLUSION

M. benhami Archey is synonymised with *M. didinus* (Owen) because the bones of both share all essential shape characters. Size differences can be explained by a north-south cline combined with temporal variation such that specimens were larger in the north during the Otiran. Similar temporal variation is known for the North Island *Pachyornis mappini* (Worthy 1987). Some of the other 'large' ranges in variation for moa species can probably be explained by similar geographic and temporal analyses.

ACKNOWLEDGMENTS

This study would not have been possible if it were not for the co-operation and assistance of the Department of Conservation (formerly NZ Forest Service), for which I am most grateful. This co-operation resulted in the joint research project between the Department of Conservation and the National Museum of which this study forms a part. I thank Mark Strange for the photography.

LITERATURE CITED

ARCHEY, G. 1941. The moa: a study of the Dinornithiformes. Bull. Auck. Inst. Mus. No. 12. 145 pp.

CRACRAFT, J. 1976. The species of moa (Aves: Dinornithidae). Smithsonian Contributions to Paleobiology No. 27. pp. 189-205.

MILLENER, P. R. 1981. The Quaternary avifauna of the North Island, New Zealand. Unpubl. PhD Thesis. University of Auckland. 2 vol. 897 pp.

MILLENER, P. R. 1982. And then there were twelve: the taxonomic status of *Anomalopteryx oweni* (Aves: Dinornithidae). Notornis 29: 165-170.

OLIVER, W. R. B. 1949. The Moas of New Zealand and Australia. Dom. Mus. Bull. No. 15. 206 pp.
ROTHSCHILD, W. 1907. Extinct Birds. pp.185-220. London: Hutchinson & Co.
WORTHY, T. H. 1987. Sexual dimorphism and temporal variation in the North Island moa species *Euryapteryx curtus* (Owen) and *Pachyornis mappini* Archey. National Museum of New Zealand Records 3: 59-70.

T. H. WORTHY, *National Museum, P.O. Box 467, Wellington*

APPENDIX 1

Morphological description of *Megalapteryx didinus* with comparative notes on *Anomalopteryx didiformis*

A. didiformis and *M. didinus* can be confused because both species have leg bones of similar size and relative proportions, and together they differ from the rest of the Anomalopterygidae. Notes in brackets describe the state in *A. didiformis*.

Skull: Premaxilla narrow, pointed; post-orbital width greater than width across zygomatic processes (equal); temporal fossa narrow (very wide), not excavated ventrally on anterior margin (ventrally excavated), temporal ridge nearly meets lambdoidal (always meeting); orbital margins of nasal convergent towards premaxilla (parallel); preorbital plate arising from inferior aliethymoid at wide angle; maxillary antrum nearly collapsed (expanded, robust); Fig 1.

Sternum: Anterior margin straight; anterior width slightly greater than length; lateral processes not longer than xiphoid process, diverging, tips further apart than distance between coracoid articular facets; coracoid depressions shallow, indistinct (prominent); precostal processes tapering, blunt; pneumatic foramina in shallow depressions each side of midline; Fig. 2.

Scapulocoracoid: Very reduced, coracoidal segment longer than scapular.

Pelvis: Narrow, ilia meeting anterior to acetabulum in curved arch, arch continuous to posterior of acetabulum; base of ischium and pubis forming ventral part of acetabulum, meeting with synsacra at abrupt, square angle (rounded in *A. didiformis*); Fig. 2.

Femur: Length 64% tibiotarsus length; rotular depression narrow (wide); popliteal depression and fossa superior to fibular articular surface at unequal levels (level); lateral and medial distal condyles parallel to each other, together, not diverging widely from shaft (subparallel to shaft); Fig. 3, 5.

Tibiotarsus: Shaft straight, slender; proximal and distal ends not much expanded (more so); procnemial ridge straight (curved); medullarterial orifice usually proximal to distal end of fibular articular surface (distal to); Fig. 3, 5.

Tarsometatarsus: Length 45% tibial length; in proximal aspect medial and articular surface wider than lateral (lateral wider); lateral hypotarsal ridge more prominent than medial in proximal view, but of equal length (lateral more prominent and longer than medial); foramen adjacent to medial hypotarsal ridge in distinct, sharply angled depression (on sloping surface at base of hypotarsal ridge); shaft variably robust, less robust in small individuals, more in large; Fig. 2, 6.

Digits: Phalanx formula 3:3:4:5; third digit longer than metatarsus (shorter), ungual phalanx long, slender, width 0.3 x length (distinctly broader, width 0.45 x length).