THE CARPOMETACARPUS OF *APTERORNIS*

By BRADLEY C. LIVEZEY

ABSTRACT

The carpometacarpus of the extinct, flightless gruiform *Apterornis* is described and illustrated, based on one specimen from the North Island form (*A. otidiformis*) and two specimens from the larger South Island form (*A. defossor*). The element is uniquely truncated distally, resulting in the loss of the distal portions of ossa metacarpalia majus and minus, the entire extremitas distalis carpometacarpi, and the spatium intermetacarpale. Although a few features of the extremitas proximalis carpometacarpi are variably discernable (e.g., trochlea carpalis, fovea carpalis cranialis, and fossa supratrochlearis), most features typical of the element in other Gruiformes are lacking. In both specimens for *A. defossor*, phalanx digiti alulae is synostotic with processus extensorius of the carpometacarpus, whereas in the single specimen for *A. otidiformis* the phalanx is absent. The absence of facies articularis of phalanges digiti majoris and digiti minoris indicates the loss of both digits in *Apterornis*. The qualitative, flightlessness-related apomorphies of the carpometacarpus of *Apterornis* are unique among birds, and indicate a degree of alar reduction unequalled among carinate birds.

INTRODUCTION

The genus *Apterornis* (Owen 1848a) (=*Aptornis* Owen 1848b, auct.), comprises two extraordinary species of extinct, flightless Gruiformes endemic to New Zealand: *A. otidiformis* (Owen 1844) of the North Island, and the larger *A. defossor* (Owen 1871) of the South Island (Turbott 1990). Bones of *Apterornis*, associated with those of moas (Dinornithiformes: *Euryapteryx, Emeus,* and *Pachyornis*) and the extinct, flightless *Cnemiornis* (Anseriformes), were found in a Maori midden at Waimataitai, South Island (Trotter 1965), a site dated at 626 ± 30 years BP (Trotter & McCulloch 1984), but the genus evidently was extirpated prior to the arrival of Europeans. Formerly considered to be allied with the Rallidae (e.g., Fürbringer 1888; Oliver 1945, 1955), but in recent years inferred to be more closely related to the Kagu (Rhynochetidae: *Rhynochetos jubatus*) of New Caledonia (Olson 1975, 1985; Livezey, in prep.), the genus *Apterornis* has been classified as a member of the Gruiformes by most taxonomists (Lydekker 1891, Lambrecht 1933, Brodkorb 1967, Cracraft 1983, Turbott 1990; but see Hesse 1990).

The first skeletal element ultimately referred to *Apterornis* was a tibiotarsus, attributed originally by Owen (1844) to a new species of moa, which Owen likened in size to a bustard (Otididae) and named *Dinornis otidiformis*. Most other elements of the skelton of *Apterornis* were collected during the following decades, some of which were misassigned initially to *Dinornis, Notornis* (Gruiformes: Rallidae), or *Cnemiornis,* and these provided a satisfactory osteological knowledge of both species of *Apterornis* (Owen 1846, 1848b, 1851, 1866, 1871, 1872, 1875, 1879; Fürbringer 1888; Forbes 1890; Hamilton 1892). These collections not only included the comparatively abundant elements of the large pelvic limb, major elements of the diminutive pectoral limb, well preserved specimens of the cranium, maxilla, and mandibula, and mounted, largely complete skeletons (Hamilton 1892; Andrews 1896; Lambrecht 1933; Oliver 1955), but also such minor elements as the ossa palatinum, quadratum, entoglossum, and cricoideum (Owen, 1871, Lowe 1926, Worthy 1989). However, I know of no published record, description, or figure of any of the ossa manus (ossa carpi radiale, carpi ulnare, carpometacarpus, or phalanges digitorum) of the genus, the hypothetical skeletal reconstruction by Owen (1872: Plate XVI, Fig. 1) notwithstanding. I describe here three carpometacarpi of *Apteromis* and discuss the morphological and developmental implications of the unique features of these elements.

SPECIMENS AND METHODS

Two carpometacarpi of *Apteromis* were catalogued in the collections of the Canterbury Museum, both from the South Island and referable to *A. defossor:* CM Av. 14181, left carpometacarpus, from Pyramid Valley; and CM Av. 32388, right carpometacarpus, from Spring Hills, Central Southland (Fig. 1A). At the National Museum of New Zealand, I found one right carpometacarpus of *A. otidiformis:* NMNZ S. 24648, collected from fissure 1A, Ruakokopatuna, North Island (Fig. 1B).

All measurements were made using dial calipers to within 0.2 mm. Anatomical nomenclature follows Baumel (1979a,b), Lucas (1979), and Vanden Berge (1979). Illustrations of the elements of *Apteromis* were made from photographs; comparative illustrations of those of *Rhynochetos* were prepared using a Wild dissecting microscope equipped with reducing lens and drawing tube.

OSTEOLOGICAL DESCRIPTIONS

The single carpometacarpus of *A. otidiformis* (NMNZ S. 24648) measured (mm) 18.1 in total length and 9.9 in maximal proximal (trochlear) width. These dimensions for the two carpometacarpi of *A. defossor* were, respectively: 22.4, 9.6 (CM Av. 14181); and 20.0, 9.1 (CM Av. 32388).

Diagnostic features shared by all three specimens were the diminutive facies articularis ulnocarpalis and radiocarpalis of the trochlea carpalis, relatively distal processus extensorius, and variably distinct foveae carpalis cranialis and caudalis, and at least a shallow fossa infratrochlearis (Figs. 1,2). All three elements shared several characteristics, apparently unique to the genus, most notably a truncation of the distal portions of ossa metacarpale majus and metacarpale minus and the complete loss of the extremitas proximalis carpometacarpi. Although the gross appearance of the corpus carpometacarpi of *Apteromis* might suggest that os metacarpale minus may be lacking entirely, the bilobate transverse profile and the suggestion of an intermetacarpal sulcus distally indicate that vestiges of both ossa metacarpalia majus and minus remain (Fig. 2). The spatium intermetacarpale – typically an elongate, semi-elliptical space bounded cranially by os metacarpale majus, caudally by os metacarpale minus, proximally by sysostosis metacarpalis proximalis, and distally by synostosis metacarpalis distalis – is lacking in *Apteromis;* the shallow incisura at the distal end of the corpus carpometacarpi may be a vestige of the synostosis metacarpalis proximalis (Figs. 1,2).

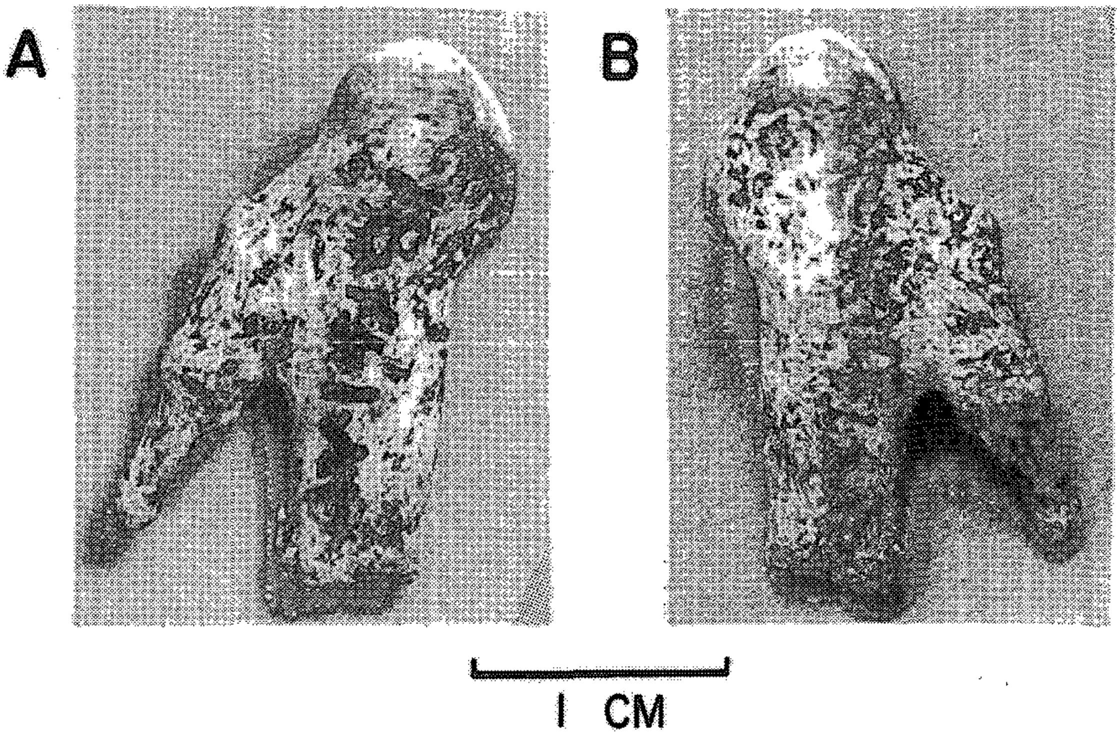

FIGURE 1 — Photographs of the left carpometacarpus of *Apterornis defossor* (CM Av. 14181), (A) dorsal and (B) ventral surfaces.

Associated with the loss of the extremitas distalis is the absence of the facies articularis digitalis major and facies articularis digitalis minor, thereby indicating the loss of phalanges digiti majoris and phalanx digiti minoris. The restricted trochlea carpalis of *Apterornis*, in particular the restricted facies articularis ulnocarpalis and obsolete facies articularis radiocarpalis, suggests that ossa carpi ulnare and radiale were minute. Also, the carpometacarpus of *Apterornis* also lacked a processus pisiformis, and the fossa supratrochlearis is indistinct (Figs. 1,2).

Several characters varied somewhat among the three carpometacarpi. Phalanx digiti alulae was synostotic with processus alularis in the two specimens of *A. defossor*, approximating in distal extent the corpus carpometacarpi in one specimen (CM Av. 14181; Figs. 1,2) and terminating 9 mm proximad to the distal end of the corpus carpometacarpi in the other (CM Av. 32388). However, phalanx digiti alulae evidently was not synostotic in the specimen of *A. otidiformis;* in the latter specimen, the processus alularis was truncate, terminating 7 mm proximad to the distal end of the corpus carpometacarpi. No consistent interspecific difference can be inferred with presently available specimens, however, particularly given the variation within *A. defossor* and the possibility of sexual dimorphism in both species. Fovea carpalis caudalis was indistinct in one specimen of *A. defossor* (CM Av. 14181; Figs. 1,2) but very deep and distinct in the other specimen of *A. defossor* (CM Av. 32388). The fovea carpalis caudalis in the single element of *A. otidiformis* (NMNZ S. 24648) was very deep and enclosed a dorsoventral

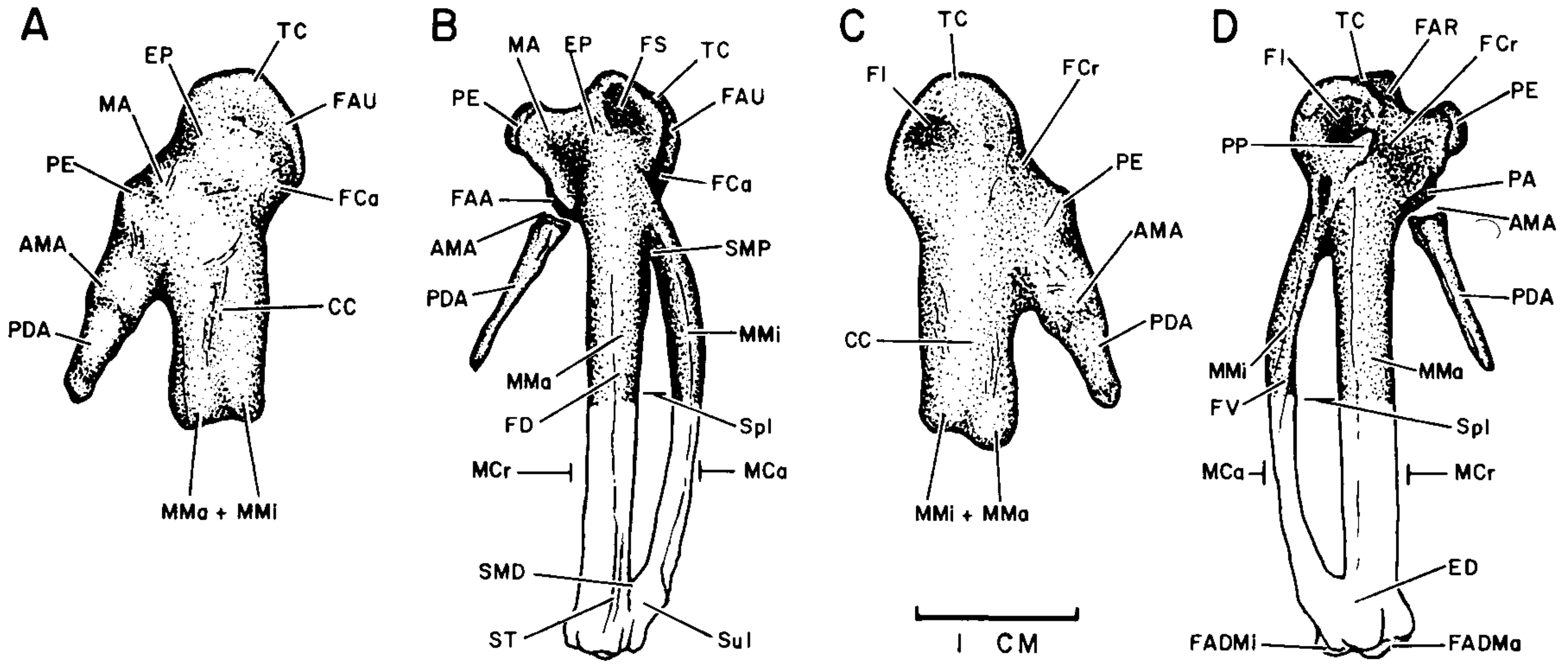

FIGURE 2 — Illustrations of the left carpometacarpus and phalanx digiti alulae (moderately extended) of *Apterornis defossor* (CM Av. 14181), dorsal (A) and ventral (C) surfaces; and *Rhynochetos jubatus* (USNM 612087), dorsal (B) and ventral (D) surfaces. Abbreviations: AMA, articulatio metacarpophalangealis alulae (synostotic in *A. defossor*); CC, corpus carpometacarpi; ED, extremitas distalis carpometacarpi; EP, extremitas proximalis carpometacarpi; FAA, facies articularis alularis; FADMa, facies articularis digitalis major, FADMi, facies articularis digitalis minor, FAR, facies articularis radiocarpalis; FAU, facies articularis ulnocarpalis; FCa, fovea carpalis caudalis; FCr, fovea carpalis cranialis; FD, facies dorsalis of corpus; FI, fossa infratrochlearis; FS, fossa supratrochlearis; FV, facies ventralis of corpus; MA, os metacarpale alulare; MCa, margo caudalis of corpus; MCr, margo cranialis of corpus; MMa, os metacarpale majus; MMi, os metacarpale minus; PA, processus alularis; PDA, phalanx digiti alulae; PE, processus extensorius; PP, processus pisiformis; SI, spatium intermetacarpale; SMD, synostosis metacarpalis distalis; SMP, synostosis metacarpalis proximalis; Sul, sulcus interosseus; SuT, sulcus tendineus; TC, trochlea carpalis.

perforation of the element; the latter evidently was produced by foramina neurovascularia between the fovea carpalis caudalis dorsally and fossa infratrochlearis ventrally.

Truncation of the carpometacarpus in *Apterornis*, compared to *Rhynochetos*, is particularly evident in comparisons with relative lengths of pelvic elements. Lengths of carpometacarpi of *A. otidiformis* and *A. defossor* were only 53% and 61%, respectively, of those of *R. jubatus* ($\bar{x}$ = 34.5 mm, s = 1.8, n = 14); whereas mean lengths of femora of *A. otidiformis* ($\bar{x}$ = 153.5, s = 5.8, n = 72) and *A defossor* ($\bar{x}$ = 172.2, s = 6.6, n = 17) were 231% and 259%, respectively, of those of *R. jubatus* ($\bar{x}$ = 66.4, s = 3.2, n = 19). Intra-alar proportions further underscore the disproportionate shortening of the antebrachium and two segments of the manus in *Apterornis*. Based on a modest sample for *A. defossor*, the humerus (n = 3), ulna (n = 4), carpometacarpus (n = 2), and major digit (absent) composed roughly 64%, 25%, 11%, and 0% of mean skeletal wing length. These proportions contrast with the means for 10 associated skeletons of *R. jubatus* (34%, 35%, 18%, and 13%) and those of all other flightless carinates heretofore studied quantitatively (Livezey & Humphrey 1986; Livezey 1988, 1989a-c, 1990, 1992a-b, 1993a-b).

DISCUSSION

Compared to the carpometacarpus of *Rhynochetos* (Fig. 2) or any other gruiform (including the flightless Phorusrhacoidea and flightless Rallidae), the carpometacarpus of *Apterornis* is extraordinarily reduced (Parker 1869; Andrews 1899; Sinclair & Farr 1932; Olson 1973, 1975, 1977). Given that flightlessness is not always associated with large body size among Gruiformes (e.g., the rails *Porzana* and *Atlantisia*; Olson 1977, Olson & James 1991), the diminutive carpometacarpus of *Apterornis* is particularly noteworthy relative to the body size of the species; Atkinson & Millener (1991) listed estimates of 10-11 kg and 12-13 kg for *A. otidiformis* and *A. defossor*, respectively.

Moreover, the unique truncation of the distal segments of the ossa metacarpalia majus and minus, as well as the reduction or loss of most of the features typical of the proximal portion of the element, represent structural reduction of a greater magnitude than that described for flightless members of any other order of carinates, including grebes (Podicipediformes), cormorants (Pelecaniformes), waterfowl (Anseriformes), ibises (Ciconiiformes), parrots (Psittaciformes), raphids (Columbiformes), and acanthisittid wrens (Passeriformes) (Owen 1875; Sinclair & Farr 1932; Olson & Wetmore 1976; Livezey & Humphrey 1986; Livezey 1989a-b, 1990, 1992a-b, 1993a-b; Millener 1988; Millener & Worthy 1991; Olson & James 1991). Of these, only the extinct, flightless anseriforms of Hawaii (*Thambetochen, Ptaiochen, Chelychelynechen*) possessed carpometacarpi in which the spatium intermetacarpale is absent (Olson & Wetmore 1976, Olson & James 1991). Flightless carinates that are wing-propelled diving birds – the penguins (Sphenisciformes), plotopterids (Pelecaniformes), and flightless alcids (Charadriiformes) – also retain complete, but variably derived elements of the manus (Olson & Hasegawa 1979; Livezey 1988, 1989c). Among the ratites (flightless Palaeognathiformes), the carpometacarpi of adult ostriches (Struthionidae), rheas (Rheidae), casuaries (Casuariidae), and Dromornithidae retain complete, distinguishable ossa metacarpalia (although variably synostotic for some of their lengths), whereas those of emus (Dromaiidae), kiwis (Apterygidae), and elephant birds (Aepyornithidae) are variably synostotic with the distal antebrachium and lack distinct ossa metacarpalia and the spatium intermetacarpale (Owen 1841, Parker 1892, Pycraft 1900, Rich 1979, McGowan 1982). The moas (Dinornithiformes) showed the greatest pectoral reduction in the Class Aves, apparently lacking all skeletal elements distal to the scapulocoracoideum (Anderson 1989; but see Forbes 1892). There is no indication that the variably synostotic phalanx digiti alulae of *Apterornis* functioned as a combative "spur;" there are no examples of a true "spur" derived from the phalanx digiti alulae among birds, and the element in *Apterornis* shows none of the distal rugosity or thickening typical of the "spurs" derived from os metacarpale alulare or os carpi radiale (Rand 1954).

Probable reduction of the ossa carpi indicates that muscles which typically insert (at least in part) on these small bones (M. tensor propatagialis pars longus, M. flexor carpi ulnaris; Raikow 1985, McGowan 1986) would have been reduced, shortened, or lost as well. Muscles typically inserting or (especially) originating on the carpometacarpus or ossa digitorum manus would have undergone profound shortening or loss; diminution, tendinal fusion, or loss of distal musculi alae have been documented for some ratites (e.g., Mm. interossea) and the ligaments of joints within the manus had been lost completely in *Apterornis*.

Corresponding losses in distal structures of the alar integument in *Apterornis* also are indicated, most importantly the primary remiges and the associated coverts, which arise from the manus. Based on the length of the vestigial carpometacarpus and apparent absence of the ossa digiti majoris of *Apterornis*, a maximum of 1-3 (probably diminutive) remiges primarii could have been retained; this contrasts with the 10 remiges primarii (excluding the remicle) found in *Rhynochetos* and most other Gruiformes (Murie 1871; unpubl. data).

The importance of heterochrony, shifts in ontogenetic schedules, as a source of evolutionary novelties has become increasingly recognized (Raff & Wray 1989, McKinney & McNamara 1991). This recognition extends to the morphological bases of avian flightlessness, e.g., the inference that comparative underdevelopment of the pectoral appendage in flightless carinates is attributable to paedomorphosis (e.g., Olson 1973; Livezey 1989a, 1990, 1992a-b, 1993b). The reduced pectoral skeleton of *Apterornis*, especially the disproportionate shortening of the distal wing elements, is consistent with a hypothesis of paedomorphosis of the pectoral limb (Steiner 1922, Böker 1927, Marples 1930, Montagna 1945, Sullivan 1962). The specific mechanism that produced the pectoral paedomorphosis of *Apterornis* (McKinney & McNamara 1991 – post-displacement (late initiation of growth), neoteny (slowed rate of growth), or progenesis (early terminus of growth) – is not determinable, but the radical underdevelopment of the carpometacarpus indicates that the ontogenetic shift involved was profound.

The avian carpometacarpus represents the ankylosis of certain fetal ossa carpi centralia and ossa carpi distalia with the proximal termina of the ossa metacarpalia during early postnatal ontogeny (Shubin & Alberch 1986). During this process the carpometacarpus passes through a stage in which a poorly defined proximal complex and three distal cartilaginous elements are discernible (Seiglbauer 1911, Holmgren 1955). With the exception of the synostosis of ossa metacarpalia majus and minus and the variable synostosis of os metacarpale aluluare with the phalanx digiti alulae, the form of the vestigial carpometacarpus of *Apterornis* (Figs, 1,2) resembles the homologous structures of the domestic fowl (*Gallus gallus*) during stages 27-29 (Sullivan 1962); these stages correspond to embryonic development at 5-6 days of incubation (Hamburger & Hamilton 1951). At this stage the distal portions of ossa metacarpale majus and metacarpale minus and distal ossa digitorum manus are not yet formed, and the developing carpometacarpus comprises (Hinchliffe 1977, Hinchliffe & Griffiths 1983): (1) a proximal, progressively fused complex of the cartilaginous distal carpals and pisiform (corresponding to the extremitas proximalis carpometacarpi); (2) a cranial cartilaginous mass (precursor of phalanx digiti alulae); (3) a distocranial cartilaginous splint (giving rise to os metacarpale majus); and (4) a slightly smaller, distocaudal cartilaginous splint (homologous to os metacarpale minus). Based on this correspondence, development of the manus of *Apterornis* was terminated at a very early stage, and this significant paedomorphosis of the pectoral limb (especially the manus) in *Apterornis*, together with a notable "overdevelopment" (peramorphosis) of the pelvic appendage and cranium, contributed in large part to the unique appendicular proportions of the genus.

ACKNOWLEDGEMENTS

My visits to the Canterbury Museum, Christchurch (CM) and National Museum of New Zealand, Wellington (NMNZ) during December 1992 were made possible by grant BSR-9120545 from the Systematic Biology Program of the National Science Foundation (USA). I thank B. McCulloch and P.R. Millener for their many kindnesses during this time. N. Heke (NMNZ) and C. Jacomb (CM) prepared photographs (Fig. 1) of the three elements described herein. I am grateful to R. L. Zusi for sharing his many insights on avian anatomy and the osteology of *Apterornis*, and for arranging the loan of a skeletal specimen of *Rhynochetos jubatus*. P. S. Humphrey, P. R. Millener, and R. N. Holdaway provided helpful comments on the manuscript.

LITERATURE CITED

ANDERSON, A. 1989. Prodigious birds: moas and moa-hunting in prehistoric New Zealand. Cambridge: Cambridge Univ. Press. 238pp.

ANDREWS, C.W. 1896. Note on a nearly complete skeleton of *Aptornis defossor* (Owen). Geol. Mag. (New Ser.) 3:241-242.

ANDREWS, C.W. 1899. On the extinct birds of Patagonia. – I. The skull and skeleton of *Phororhacos inflatus* Ameghino. Trans. Zool. Soc. London 15: 55-86.

ATKINSON, I.A.E.; MILLENER, P.R. 1991. An ornithological glimpse into New Zealand's pre-human past. Pp. 127-192 *in* Acta XX Congressus Internationalis Ornithologici, vol I. Wellington: New Zealand Ornithol. Congr. Trust Board. 650pp.

BAUMEL, J.J. 1979a. Osteologia. Pp. 53-122 *in* Baumel, J.J,; King, A.S.; Lucas, A.M.; Breazile, J.E.; Evans, H.E. Nomina anatomica avium. London: Academic Press. 637pp.

BAUMEL, J.J. 1979b. Arthrologia, Pp. 123-174 *in* Baumel, J.J.; King, A.S.; Lucas, A.M.; Breazile, J.E.; Evans, H.E. Nomina anatormica avium London: Academic Press. 637pp.

BÖKER, H. 1927. Die biologische Anatomie der Flugarten der Vögel und ihre Phylogenie. J. Ornithol. 75: 304-371.

BRODKORB, P. 1967. Catalogue of fossil birds: Part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). Bull. Florida State Mus. (Biol. Sci.) 2: 99-220.

CRACRAFT, J. 1982. Phylogenetic relationships and transantarctic biogeography of some gruiform birds. Pp. 393-402 *in* Buffetaut, E.; Janvier, P.; Rage, J. C.; Tassy, P. Phylogenie et paleobiogeographie: livre jubilaire en l'honneur de Robert Hoffstetter. Geobios, Mém Spéc. No. 6. 492pp.

FORBES, H.O. 1890. [Announcement of a paper given on 3 October 1889 at the meeting of the Philosophical Institute of Canterbury, New Zealand.] Nature 41: 209.

FORBES,H.O. 1892. Evidence of a wing in *Dinornis*. Nature 45: 257.

FÜRBRINGER,M. 1888. Untersuchungen zur Morphologie und Systematik der Vögel, zugleich ein Beitrag zur Anatomie der Stütz- und Bewegungsorgane. 2 vol. Amsterdam: T.J. Van Holkema.1751pp.

HAMBURGER, V.; HAMILTON, H.L. 1951 A series of normal stages in the development of the chick embryo. J Morphol. 88: 49-92.

HAMILTON, A. 1892. On the genus *Aptornis*, with more especial reference to *Aptornis defossor*, Owen. Trans. New Zealand Inst. 24:175-184.

HESSE, A. 1990. Die Beschreibung der Messelornithidae (Aves: Gruiformes: Rhynocheti) aus dem Alttertiär Europas und Nordamerikas. Cour. Forsch.-Inst. Senckenberg 128: 1-176.

HINCHLIFFE, J.R. 1977. The chondrogenic pattern in chick limb morphogenesis: a problem of development *and* evolution. Pp. 293-309 *in* Ede, D.A.; Hinchliffe, J.R.; Balls, M. Vertebrate limb and somite morphogenesis. Cambridge: Cambridge Univ. Press. 498pp.

HINCHLIFFE, J.R.; GRIFFITHS, P.J. 1983. The prechondrogenic patterns in tetrapod limb development and their phylogenetic significance. Pp. 99-121 *in* Goodwin, B.C.; Holder, N.; Wylie, C.C. Development and evolution. Cambridge: Cambridge Univ. Press. 437pp.

HOLMGREN, N. 1955. Studies on the phylogeny of birds. Acta Zool. 36: 243-328.

LAMBRECHT, K. 1933. Handbuch der Palaeornithologie. Berlin: Gebruder Borntraeger. 1024pp.

LIVEZEY, B.C. 1988. Morphometrics of flightlessness in the Alcidae. Auk 105: 681-698.

LIVEZEY, B.C. 1989a. Flightlessness in grebes (Aves, Podicipedidae): its independent evolution in three genera. Evolution 43: 29-54.

LIVEZEY, B.C. 1989b. Phylogenetic relationships and incipient flightlessness in the extinct Auckland Islands Merganser. Wilson Bull. 101: 410-435.

LIVEZEY, B.C. 1989c. Morphometric patterns in Recent and fossil penguins (Aves, Sphenisciformes). J. Zool . (London) 219: 269-307.

LIVEZEY, B.C. 1990. Evolutionary morphology of flightlessness in the Auckland Islands Teal. Condor 92: 639-673.

LIVEZEY, B.C. 1992a. Flightlessness in the Galápagos Cormorant (*Compsohalieus* [*Nannopterum*] *harrisi*): heterochrony, giantism, and specialization. Zool. J. Linnean Soc. 105: 155-224.

LIVEZEY, B.C. 1992b. Morphological corollaries and ecological implications of flightlessness in the Kakapo (Psittaciformes: *Strigops habroptilus*). J. Morphol. 213: 105-145.

LIVEZEY, B.C. 1993a. Morphology of flightlessness in *Chendytes*, fossil seaducks (Anatidae: Mergini) of coastal California. J. Vert. Paleontol. 13:185-199.

LIVEZEY, B.C. 1993b. An ecomorphological review of the Dodo (*Raphus cucullatus*) and Solitaire (*Pezophaps solitaria*), flightless Columbiformes of the Mascarene Islands, J. Zool. (London) 230:247-292.

LIVEZEY, B.C.; HUMPHREY, P.S. 1986. Flightlessness in steamer-ducks (Anatidae: *Tachyeres)*: its morphological bases and probable evolution. Evolution 40: 540-558.

LOWE, P.R. 1926. More notes on the quadrate as a factor in avian classification. Ibis 68: 152-188.

LUCAS, A.M. 1979. Integumentum commune. Pp. 7-51 *in* Baumel, J.J.; King, A.S.; Lucas, A.M.; Breazile, J.E.; Evans, H.E. Nomina anatomica avium. London: Academic Press. 637pp.

LYDEKKER, R. 1891. Catalogue of the fossil birds in the British Museum (Natural History). London: Brit. Mus. (Natur. Hist.). 368pp.

MARPLES, B.J. 1930. The proportions of birds' wings and their changes during development. Proc. Zool. Soc. London 1930: 997-1008.

McGOWAN, C. 1982. The wing musculature of the Brown Kiwi *Apteryx australis mantelli* and its bearing on ratite affinities. J. Zool. (London) 197: 173-219.

McGOWAN, C. 1986. The wing musculature of the Weka (*Gallirallus australis*), a flightless rail endemic to New Zealand. J. Zool. (London) 210: 305-346.

McKINNEY, M.L.; McNAMARA, K.J. 1991. Heterochrony: the evolution of ontogeny. New York: Plenum Press. 437pp.

MILLENER, P.R. 1988. Contributions to New Zealand's Late Quaternary avifauna. I: *Pachyplichas*, a new genus of wren (Aves: Acanthisittidae), with two new species. J. Royal Soc. New Zealand 18: 383-406.

MILLENER, P.R.; WORTHY, T.H. 1991. Contributions to New Zealand's Late Quaternary avifauna. II *Dendroscansor decurvirostris*, a new genus and species of wren (Aves: Acanthisittidae). J. Royal Soc. New Zealand 21: 179-200.

MONTAGNA, W. 1945. A re-investigation of the development of the wing of the fowl. J. Morphol. 76: 87-113.

MURIE, J. 1871. On the dermal and visceral structures of the Kagu, Sun-bittern, and Boatbill. Trans. Zool. Soc. London 7: 465-492.

OLIVER, W.R.B. 1945. Avian evolution in New Zealand and Australia. Emu 45: 119-152.

OLIVER, W.R.B. 1955. New Zealand birds, 2nd ed. Wellington: A.H. & A.W. Reed. 661pp.

OLSON , S.L. 1973. Evolution of the rails of the South Atlantic islands (Aves: Rallidae). Smithsonian Inst. Contr. Zool. 152: 1-53.

OLSON, S.L. 1975. A review of the extinct rails of the New Zealand region (Aves: Rallidae). Nat. Mus. New Zealand Rec. 1: 63-79.

OLSON, S.L. 1977. A synopsis of the fossil Rallidae. Pp. 339-373 *in* Ripley, S.D. Rails of the world. Boston: D.R. Godine. 406pp.

OLSON, S.L. 1985. The fossil record of birds. Pp. 79-252 *in* Farner, D.S.; King, J.R.; Parkes, K.C. Avian biology, vol 8. New York: Academic Press. 252pp.

OLSON, S.L.; HASEGAWA, Y. 1979. Fossil counterparts of giant penguins from the North Pacific. Science 206: 688-689.

OLSON, S.L.; JAMES, H.F. 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part I. Non-Passeriformes. Ornithol. Monogr. 45. Washington, D.C.: Am. Ornithol. Union. 88pp.

OLSON, S.L.; WETMORE, A. 1976. Preliminary diagnoses of two extraordinary new genera of birds from Pleistocene deposits in the Hawaiian Islands. Proc. Biol. Soc. Washington 89: 247-258.

OWEN, R. 1841. On the anatomy of the southern Apteryx (*Apteryx australis*, Shaw). Trans. Zool. Soc. London 2: 257-302.

OWEN, R. 1844. On *Dinornis*, an extinct genus of tridactyle struthious birds, with descriptions of portions of the skeleton of five species which formerly existed in New Zealand. Trans. Zool. Soc. London 3: 243-276.

OWEN, R. 1846. On *Dinornis* (Part II.): containing descriptions of portions of the skull, the sternum and other parts of the skeleton of the species previously determined, with osteological evidences of three additional species, and of a new genus, *Palapteryx*. Trans. Zool. Soc. London 3: 307-330.

OWEN, R. 1848a. On the reamins of the gigantic and presumed extinct wingless or terrestrial birds of New Zealand (*Dinornis* and *Palapteryx*), with indications of two other genera (*Notornis* and *Nestor*). Proc. Zool. Soc. London 1848: 1-10.

OWEN, R. 1848b. On *Dinornis* (Part III.): containing a description of the skull and beak of that genus, and of the same characteristic parts of *Palapteryx*, and of two other genera of birds, *Notornis* and *Nestor;* forming part of an extensive series of ornithic remains discovered by Mr. Walter Mantell at Waingongoro, North Island of New Zealand. Trans. Zool. Soc. London 3: 345-378.

OWEN, R. 1851. On *Dinornis* (Part IV.): containing the restoration of the feet of that genus, and of *Palapteryx*, with a descrption of the sternum in *Palapteryx* and *Aptornis*. Trans. Zool. Soc. London 4: 1-20.

OWEN, R. 1866. On *Dinornis* (Part X.): containing a description of the skull, femur, tibia, fibula, and metatarsus of *Aptornis defossor*, Owen, from near Oamaru, Middle Island, New Zealand, with additional observations on *Aptornis otidiformis*, on *Notornis mantellii* [sic], and on *Dinornis curtus*. Trans. Zool. Soc. London 7: 353-380.

OWEN, R. 1872. On *Dinornis* (Part XVII.): containing a description of the sternum and pelvis, with an attempted restoration, of *Aptornis defossor*, Ow. Trans. Zool. Soc. London 8: 119-26.

OWEN, R. 1875. On *Dinornis* (Part XX.): containing a restoration of the skeleton of *Cnemiornis calcitrans*, Ow., with remarks on its affinities in the lamellirostral group. Trans. Soc. London 9: 253-292.

OWEN, R. 1879. Memoirs on the extinct wingless birds of New Zealand with an appendix on those of England, Australia, Newfoundland, Mauritius, and Rodriguez. 2 vol. London: John van Voorst. 550pp.

PARKER, T.J. 1892. Observations on the anatomy and development of *Apteryx*. Philos. Trans. Royal Soc. London 182: 25-134.

PARKER, W.K. 1869. On the osteology of the Kagu (*Rhinochetus jubatus*). Trans. Zool. Soc. London 8: 501-521.

PYCRAFT, W.P. 1900. On the morphology and phylogeny of the Palaeognathae (Ratitae and Crypturi) and Neognathae (Carinatae). Trans. Zool. Soc. London 15: 149-290.

RAFF, R.A.; WRAY, G.A. 1989. Heterochrony: developmental mechanisms and evolutionary results. J. Evol. Biol. 2: 409-434.

RAIKOW, R.J. 1985. Locomotor system. Pp. 57-147 in King, A.S.; McLellund, J. Form and function in birds, vol 3. London: Academic Press. 522pp.

RAND, A.L. 1954. The spurs on birds' wings. Wilson Bull. 66: 127-134.

RICH, P.V. 1979. The Dromornithidae, an extinct family of large ground birds endemic to Australia. Bull. 184, Bur. Nat. Resour., Geol. and Geophys. Canberra: Dept. Nat. Develop. 196pp.

SHUBIN, N.H.; ALBERCH, P. 1986. A morphogenetic approach to the origin and basic organization of the tetrapod limb. Pp. 319-387 *in* Hecht, M. K.; Wallace, B.; Prance, G,T, Evolutionary biology, vol 20. New York: Plenum Press. 472pp.

SIEGLBAUER, F. 1911. Zur Entwicklung der Vogelextremität. Zeit. Wiss. Zool. 97: 262-313.

SINCLAIR, W.J.; FARR, M.S. 1932. Part II, Aves of the Santa Cruz beds. Pp. 157-191 *in* Scott, W.B. Reports of the Princeton University Expeditions to Patagonia, 1896-1899. Vol. VII – Palaeontology IV. Princeton, New Jersey: Univ. Press. 238pp.

STEINER, H. 1922. Die ontogenetische und phylogenetische Entwicklung des Vogelflügelskelettes. Acta Zool. 3: 307-359.

SULLIVAN, G.E. 1962. Anatomy and embryology of the wing musculature of the domestic fowl (*Gallus*). Australian J. Zool. 10: 458-518.

TROTTER, M.M. 1965. Avian remains from North Otago archaelogical sites. Notornis 12: 176-178.

TROTTER, M.M.; McCULLOCH, B. 1984. Moas, men, and middens. Pp. 708-727 *in* Martin, P.S.; Klein, R.G. Quarternary extinctions: a prehistoric revolution. Tucson: Univ. Arizona Press. 892pp.

TURBOTT, E.G. (Convener, Checklist Committee). 1990. Checklist of the birds of New Zealand and the Ross Dependency, Antarctica, 3rd ed. Wellington: Ornithol. Soc. New Zealand. 247pp.

VANDEN BERGE, J.C. 1979. Myologia. Pp. 175-220 *in* Baumel, J.J,; King, A.S.; Lucas, A.M.; Breazile, J.E.; Evans, H.E. Nomina anatomica avium. London: Academic Press. 637pp.

WORTHY, T.H. 1989. The glossohyal and thyroid bone of *Aptornis otidiformes* [*sic*]. Notornis 36: 248.

BRADLEY C LIVEZEY, *Museum of Natural History, University of Kansas, Lawrence, KS 66045-2454, U.S.A.* Present address: *Section of Birds, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, PA 15213-4080. U.S.A.*