

**Description of the first complete skeleton of the extinct
New Zealand goose *Cnemiornis calcitrans* (Aves: Anatidae),
and a reassessment of the relationships of *Cnemiornis***

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The discovery of the first essentially complete *Cnemiornis calcitrans* skeleton is reported. This has facilitated a description of features of the skeleton not previously described and a reassessment of the phylogenetic relationships of *Cnemiornis*. A morphological comparison is supported by a cladistic analysis to show that *Cnemiornis* is the sister taxon of *Cereopsis novaehollandiae*. The data set based on morphological characters was insufficient to resolve the issue of whether the *Cnemiornis/Cereopsis* clade was the sister taxon of the rest of the Anserines or more primitive than them. The anserines (geese and swans) are the sister group to *Dendrocygna*, *Thalassornis*, and all other anatids. A 96 base pair sequence of mitochondrial DNA is reported for *Cnemiornis calcitrans* which shows much similarity with the equivalent section in *Cereopsis*, and is considerably different from other anserines. The DNA sequence supports the inclusion of the *Cnemiornis/Cereopsis* clade within the Anserinae.

Introduction

Taxonomic history of Cnemiornis

Owen (1866) erected the genus and species *Cnemiornis calcitrans* on a partial skeleton from a fissure near Timaru, South Island, New Zealand. The tibiotarsus BMNH 46587 was the first bone described, and so is nominated as the lectotype. Owen next described and figured a femur and tarsometatarsus of the same individual, and other bones, to form the type series of *Cnemiornis calcitrans*, which was listed by Lydekker (1891) as BMNH 46584 pelvis, 46585 sternum, 46586 L fem, 46587 L tib, 46588 R fibula, 46589 L tmt, 46581 mid-dorsal vert, 46582 post-dorsal vert. The correctly referred pelvis and sternum were fragmentary. Associated with these bones were 27 others, including some from a smaller second individual. Some of these were later figured by Owen (1875) as detailed by Lydekker (1891: 99–102), e.g. the cranium 46575. Owen (1866) also described some additional vertebrae and a humerus that belong, however, to *Aptornis defossor* (see below). This error was partly rectified when the correct humerus was described (Owen, 1875), but Owen still erred in his

referral of *Aptornis* cervical vertebra and coracoids to *Cnemiornis*. Owen considered that *Cnemiornis* was most similar to *Cereopsis novaehollandiae*, the Australian Cape Barren Goose.

Hector (1874) described a more complete skeleton of *Cnemiornis* from Earnsclough Cave, Central Otago. The specimen was sent to the British Museum (now BMNH A226), but a cast (MNZ S964) was made of the specimen before it was sent. Hector's was the first description of a skull, but he noted that the quadrate, jugal, pterygoid, and lacrymal bones had been lost. Owen (1875) described the skull of *Cnemiornis calcitrans* in greater detail from a more perfect specimen (BMNH 46575) from the type locality, but he still lacked jugals, quadrates, or pterygoids.

A smaller fossil species of *Cnemiornis* (*C. gracilis* Forbes, 1892) is found in the North Island. The osteology of the two species differ in several important ways that are referred to below.

Shufeldt (1913) studied the osteology of *Cereopsis* and concluded that the skeletal differences warranted a separate subfamily from that of other geese. However, he was not able to compare *Cnemiornis* to *Cereopsis* so did not comment on their relationships. Oliver (1955) agreed with Owen that *Cnemiornis* was similar to *Cereopsis*, as did others (e.g. Woolfenden, 1961; Brodkorb, 1964; Howard, 1964). However, generic comparisons were made with reference to *C. calcitrans* as little material of *C. gracilis* was available. Woolfenden (1961) removed *Cereopsis* from the Tadornini to a monophyletic tribe of the Anserinae, so allying *Cnemiornis* with geese, which was supported by Livezey's (1986) morphological analysis.

More recently, Livezey (1989) studied the phylogenetic relationships of *Cnemiornis* based on the coded states of 41 of 62 skeletal characters, and concluded that *Cnemiornis* was not a goose, and was not closely related to *Cereopsis*, but instead represented a very early branch of the Anseriformes, the next after *Anseranas*. He therefore proposed that *Cnemiornis* be placed in its own family Cnemiornithidae, prior to the Anatidae.

Discovery of present specimen

The previous taxonomic studies were all based on the incomplete material available at the time. *Cnemiornis* bones are relatively rare in fossil deposits in New Zealand (Worthy & Holdaway, 1993, 1994), and most are isolated limb bones. The discovery of a nearly complete specimen is therefore important, especially for the opportunity it presents for further phylogenetic studies. In this paper, this skeleton is described and the phylogenetic hypothesis proposed by Livezey (1989) is examined using its data as well as other material of *Cnemiornis*.

THW found the specimen MNZ S35266 semi-articulated in very finely laminated silts at Site 3, Chatto Creek, (NZMS 260, 1:50,000 series map, grid reference G42 353573; Lat. 45° 8' 28.5", Long. 169° 30' 25.5") near Alexandra in Central Otago, South Island, New Zealand, while prospecting alluvial sediments (Worthy, In prep.). It was found on the 14 December 1994, and excavated by THW and S. Watkin. The site was visited again on 21 September 1995, and the previously missed furcula and vertebra 17 were recovered.

Bones present

Skull, near perfect—cranium, articulated premaxilla, complete maxillopalatine complex (slight crushing and ventral displacement of right maxilla), pterygoids, quadratojugals, quadrates, mandible (damaged during excavation).

Vertebrae—atlas, axis, cervicals 3–18, and 5 thoracic vertebrae (19–23). Six rib-bearing presacral vertebrae are present. The first has small ribs that do not articulate with sternal ribs, it is therefore

assumed to be cervical #18. Only the anterior third of #11 is preserved, and the neural spine of #22 is missing. Three caudal vertebrae are preserved.

Pectoral elements—sternum (complete but imperfectly preserved on right side), furcula (tip of right side damaged), coracoids, scapulae, humeri, ulnae, radii, carpometacarpi, L major digit phalanges 1 and 2, R major digit phalanges 1 to 3 (found articulated with rest of right manus), radiales, R ulnare. There was no sign of phalanges of either the alulae (phalanges digiti alulae) or the minor digit (phalanx digiti minoris), despite both mani being excavated with all bones apparently in articulation. Ribs—6L6R presacral and 2L2R sacral; 7 sternal ribs (mainly left side).

Pelvic elements—near-perfect pelvis found in articulation with the rib cage and sternum, and legs—the vertebrae having fallen down anteriorly to lie more or less articulated on a level with the base of the rib cage, femora, tibiotarsi (L more weathered and broken in two pieces), fibulae, tarsometatarsi (R more weathered and partly crushed). Phalanges—Left side—2.1–2.3, 3.1–3.4, 4.1–4.5; right side—2.1–2.3, 3.1–3.4, 4.1–4.4. R 4.5 is missing. No phalanges for digit 1 were found.

Geological age

MNZ S35266 was found in alluvial silts which are exposed elsewhere on the valley sides of Chatto Ck. Fossil bones are rare in the alluvial beds, but moa eggshell is relatively common. Moa eggshell from an alluvial bed of approximately similar stratigraphic level and only 500 m distant to that containing the *Cnemiornis* skeleton was dated by radiocarbon Accelerator Mass Spectrometry, and gave a conventional radiocarbon age of $13,500 \pm 110$ yrs BP (NZA 6062). This confirms the age of deposition of the sediments as late-Otiran (last glacial) period. From previous environmental reconstructions (e.g. McGlone, Mark & Bell, 1995), the date suggests *Cnemiornis* was living in an open landscape near retreating glaciers. Vast amounts of sediment were being deposited in the valley floors at that time.

Methods

We made a detailed analysis of skeletal characters chosen for their phylogenetic significance, and as used by Livezey (1986). This enabled us to use and extend Livezey's (1989) data matrix, with modifications as described below, to re-examine the phylogenetic relationships of *Cnemiornis*. For this reason, the comparative material includes the same species Livezey used. They are mainly basal anseriforms chosen as they are probably more closely related to *Cnemiornis* than more derived species.

Comparisons are particularly drawn with *Cereopsis novaehollandiae*, the Australian Cape Barren goose, with which *Cnemiornis* has been allied (Owen, 1875; Oliver, 1955), although their close relationship was disputed by Livezey (1989). Similarities with other anseriforms are identified as appropriate. Specimens used are as follows: *Cereopsis novaehollandiae*: CM Av21198, Av3350, MNZ 8686 (skull only), AM O4435, ANSS 738; *Cnemiornis gracilis*: CM Av 25366, Av25367, Av24967, Av25001, Av18035, the unreg. Wheturau colln in MNZ; *Cnemiornis calcitrans*: CM Av21286, 21285, 21284, 25366, 36013, 3318, 5404; *Cygnus atratus*: CM Av31540, 31541; MNZ 15267, 17250; *Cygnus melanocoriphus*: MNZ 1492 (skull); *Cygnus columbianus*: MNZ 1453; *Cygnus olor*: MNZ 16454; *Tadorna variegata*: CM Av16588; MNZ 16471, 16472; *Plectropterus gambensis*: CM Av33451; *Biziura lobata*: CM Av7116; *Anas superciliosa*: MNZ 16476; *Anas chlorotis*: MNZ 15628; *Hymenolaimus malacorhynchus*: MNZ 24586, 24587; *Anser anser*: MNZ 20812, 24519, 23745; *Branta sandvicensis*: MNZ 618; *Dendrocygna arcuata*: AM O64697 male; *Dendrocygna eytoni*: AM O64729 female; *Stictonetta naevosa*: AM O60224 female, AM O60386 male juv., AM O56967 female, AM O60382 female, AM O60385 male; *Anseranas semipalmata*: AM O58033 female, AM O60523, AM O59362, AM O65705, AM O67706; *Chauna torquata*: CM Av21208.

Anatomical terminology follows that advocated by Baumel *et al.* (1993). Measurements were made with dial callipers to 0.01 mm and rounded to 0.1 mm.

A cladistic analysis was performed using Livezey's (1989) matrix with the addition of new data from the more complete material at our disposal. The modifications and additions are detailed in **Appendix 2**. The 62 characters employed by Livezey were augmented by 7 others, making a total of 69. Only 6 characters—2 of the integument (char. 2), trachea (6), and 4 the sternum (81, 85, 87, 88)—were coded as missing because they are unknown (first 2) or are not codable because of modifications to the element related to flightlessness. The new data matrix was analysed using PAUP version 2.4.0, (Swofford, 1985) using the mulpars, global branch swapping, and branch and bound options. A consensus tree was produced using CONTREE (Swofford, 1985).

A 96 base pair fragment of mitochondrial DNA, including the 3' end of the control region and part of tRNA-phenylalanine, was extracted from a fossil bone of *C. calcitrans* (MNZ S23220) by ACC and compared to the same sequence in other anseriforms by MDS as detailed in **Appendix 3**. The phylogenetic relationship of *Cnemiornis* derived from this analysis of DNA is compared to that derived from the morphological analyses.

Skeletal description

Skull (Plate I)

The skull of MNZ S35266 was excavated with all bones in articulation, and prepared as found with no restoration. The only damage is to the anterior right palatine where some bone is lost. Measurements are given in **Appendix 1**. It differs from those depicted by Hector (1874) and Owen (1875) in some minor features: the temporal fossae are less defined dorsally, and the lacrymal is much more extensive with a large, posteriorly-directed ventral extension which reaches nearly to the post-frontal, so the eye is completely ringed by bone as in *Cereopsis*.

Cnemiornis has large *fossae glandulae nasalis* (salt glands) which occupy the entire area above the orbit and are bounded medially by a sharp ridge. Several foramina perforate this fossa, opening into the orbit. A rim of solid bone about 2 mm wide forms the orbital margin and the lateral edge to each fossa. Anteriorly, the rim widens into a weakly developed supraorbital process which is formed from part of the lacrymal. However, the rim above the orbit is not a posterior extension of the supraorbital process, as shown by the cranium from Enfield (CM Av5404) in which the lacrymals are unfused and missing. The Enfield specimen clearly shows that the salt glands have deformed the frontal, displacing them laterally. In *Cereopsis*, the salt glands are relatively larger, and the orbital rim is not continuous. The anterior part of this rim is a posterior extension of the lacrymal, as shown by CM Av21128 and ANSS 738. No other waterfowl have similar salt gland impressions.

In the tympanic cavity, immediately distal to the *cotyla quadratica otici*, a vertical bar of bone, perhaps a modified *processus zygomaticus*, descends parallel to the *processus paroccipitalis* and links the *os squamosum* with an outgrowth of bone from the *ala parasphenoidalis* across the anterior of the *recessus tympanicus rostralis*. This structure is present in *Cereopsis*, but is not seen in *Anas* spp., *Anseranas*, *Stictonetta*, *Dendrocygna*, *Euryanas*, *Cygnus*, *Anser*, *Plectropterus*, *Tadorna* or *Biziura*. The anhimid *Chauna torquata* and the extinct duck *Malacorhynchus scarletti* have similar structures.

The premaxilla is not fused to the cranium, enabling dorsoventral flexion about the articulation. The lacrymal occupies part of the dorsal surface of the premaxilla-cranial articulation. In *Chauna*, *Dendrocygna*, *Cereopsis* and *Anser*, the lacrymal extends over the dorsal surface of the premaxilla—cranial articulation to some extent, and the naso-frontal hinge is unfused: fusion is restricted to the frontals with the nasal processes of the premaxillary. In *Anseranas*, *Stictonetta*, *Cygnus*, *Plectropterus*, *Tadorna*, *Hymenolaimus*, *Anas* spp. and *Euryanas*, the lacrymal-premaxilla junction is restricted to the

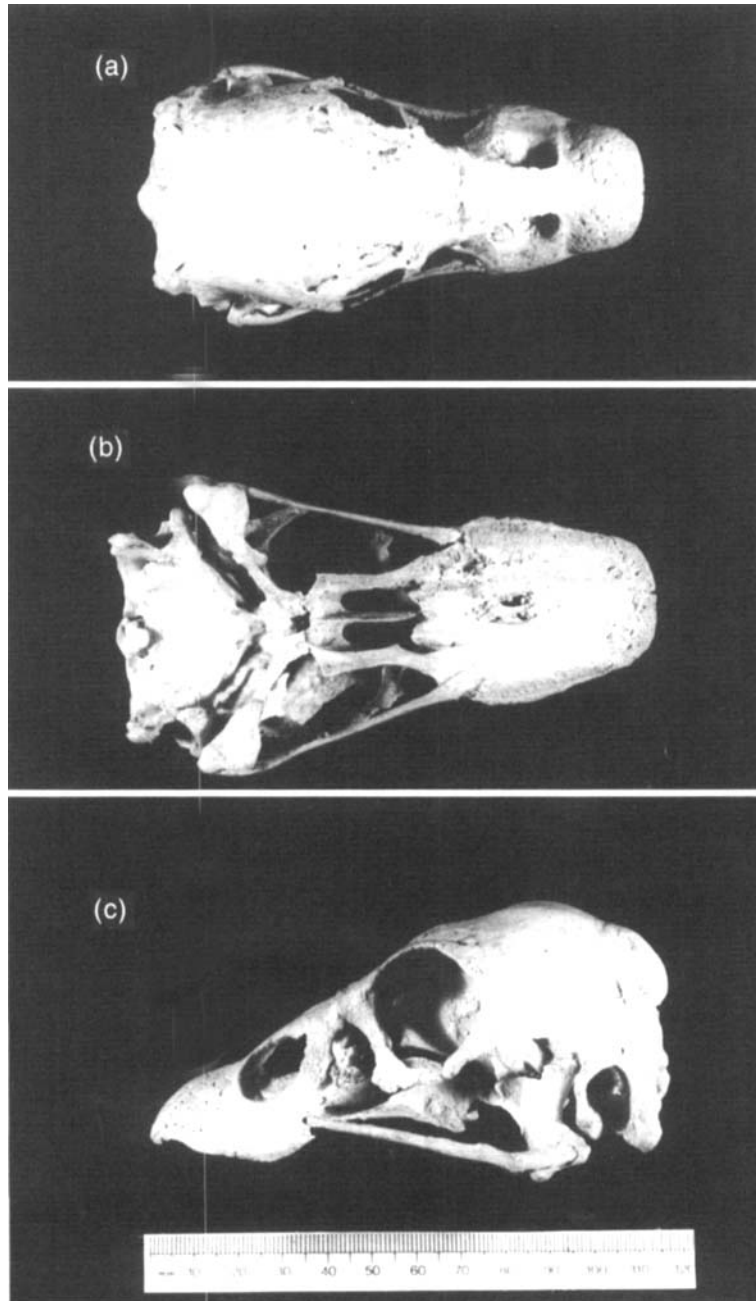


PLATE 1. The skull of *Cnemiornis calcitrans* MNZ S35266 in (a) dorsal view, (b) ventral view and (c) left lateral view.

lateral surface, and dorsally the naso-frontal hinge is fused across the whole of its width. The premaxilla has no posterior extension under the jugal, as in *Chauna* and *Cereopsis*, but differing from *Anseranas*, *Stictonetta*, *Dendrocygna*, *Cygnus*, *Anser*, *Branta* and all anatid spp. which all have a pronounced caudal process. On MNZ S35266, the internal left side of the premaxilla just anterior to the palatine has seven parallel lines which probably represent weakly defined osteological impressions of mandibular lamellae. Livezey (1989) stated that these structures were present, although they were not depicted or described by Owen (1875) or Hector (1874).

The crania, as for other specimens of *Cnemiornis calcitrans*, lack occipital fontanelles. In contrast, in most crania of *C. gracilis*, occipital fontanelles are present, although they are nearly occluded by bone. In *Cereopsis*, they are variably present, e.g. CM Av21128 has none, but CM Av3350 has small, partly occluded ones. Livezey (1989) coded both taxa as having fontanelles, having argued that they were secondarily closed, which is supported here. Fontanelles are usually present in waterfowl, but in some, especially those that graze terrestrially, they are absent (e.g. *Cygnus atratus*) or can be small and partly occluded (e.g. *Biziura lobata*).

The *arcus jugalis* is a straight slender bone linking the premaxilla and the quadrate in the same manner as shown for *Cereopsis* (Owen, 1875). It joins to the premaxilla by a 6.7 mm wide sliver of bone that is overlapped dorsally by the palatine on its medial half. It is perfectly straight caudally until it overlaps the quadrate, at which point it is bent dorsally slightly for the last 12.5 mm.

The *os quadrati* have a very similar form to those of *Cereopsis*. The *processus orbitalis* is long, terminating in a point level with, and at mid-length to, the *processus basipterygoideus*. The orbital process has a lateral protuberance at mid-length as in *Cereopsis*. The medial pneumatic foramen is small, and is at the base of the *processus otica* above the divergence with the orbital process as in *Cereopsis*. The *condylus medialis* and the *condylus caudalis* form a single complex articular surface with the mandible. The *cotylo quadratojugalis* is on a distal expansion of the *processus mandibularis*, that extends distad of a line drawn down the rear of the otic process to the caudal condyle.

The *os pterygoideum* are about 18 mm long between the *facies articularis quadratica* and the *facies articularis palatina*. The *facies articularis basipterygoidea* are robust oval processes nearly 8 mm long and 4.5 mm wide.

The *os palatinum* is convex laterally, as in *Cereopsis*; it is concave in *Anseranas*, *Stictonetta*, *Dendrocygna*, *Anser*, *Cygnus*, and all anatines. The palatines are robust and fused centrally, from which point a large anteriorly directed process, possibly a modified vomer, arises and divides the *fossa choanalis*. There is a similar but much smaller structure in *Cereopsis*. The palatines have widely flaring *anguli caudolaterali*, but in neither *Cnemiornis* nor *Cereopsis* do they extend rearward of the pterygoid junction.

The mandible was described by Owen (1875). The main differences between the mandibles of *Cnemiornis* and *Cereopsis* are that, in the former, it is much more robust, and relatively shorter. The truncation of the bill in *Cnemiornis* has been accompanied by its becoming square. *Cereopsis* bills are rounded, and the mandible has a distinct ventral deflection anteriorly.

Pelvis, sternum (Plate II)

Previous descriptions of the pelvis and sternum are in Owen (1866) and in Hector (1874). In MNZ S35266, the pelvis is almost complete. The only imperfections are peri-mortem damage to the ilia: large notches extend back from their anterior border several centimetres. Because the skeleton was essentially in a position of articulation, erosion by fluvial action or similar can be discounted. Similar damage has been observed on moa pelvises from swamp deposits and it seems best explained as the

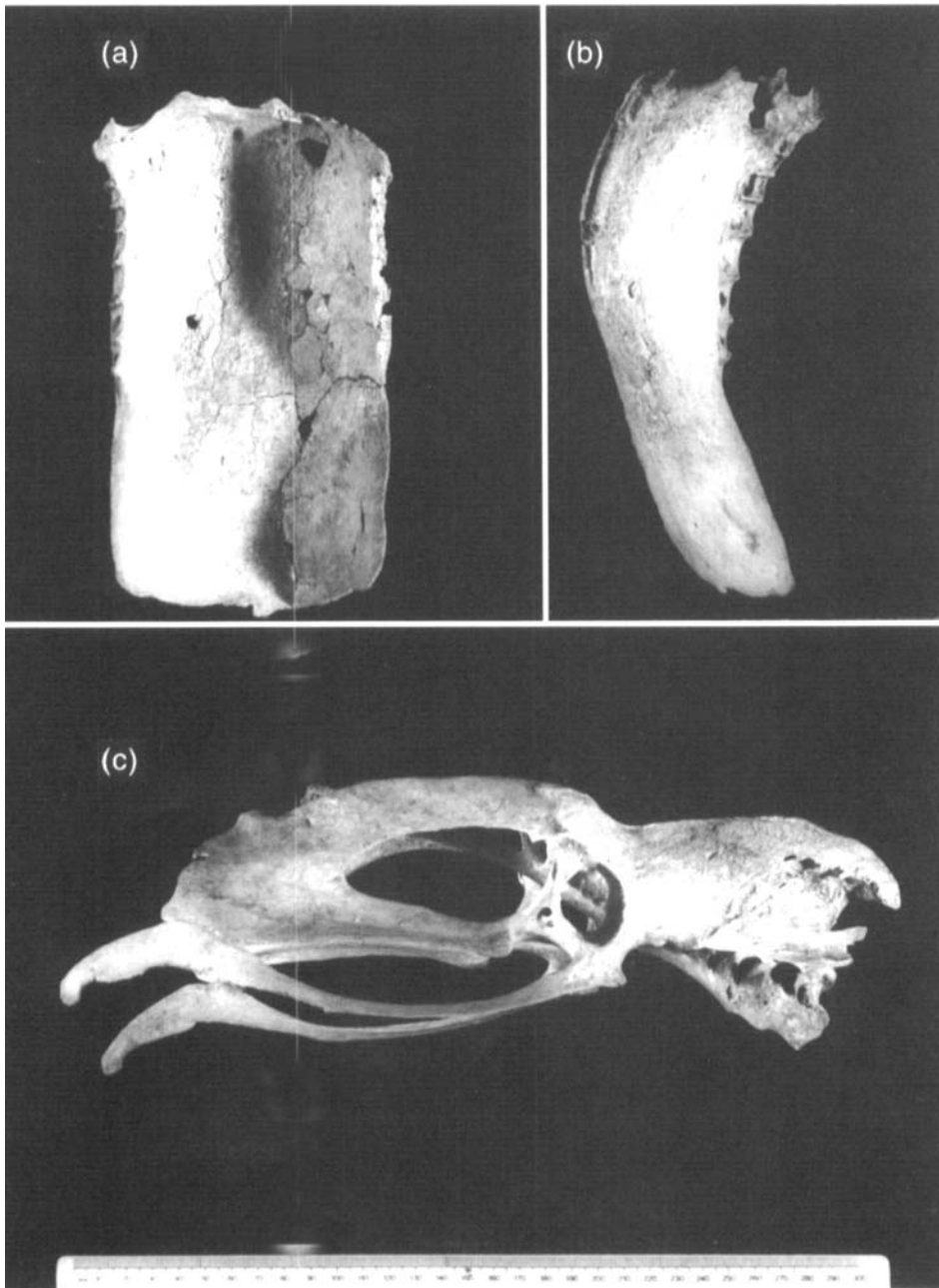


PLATE II. Sternum (a, b) and pelvis (c) of *Cnemiornis calcitrans* MNZ S35266. Scale is a 300 mm rule. Note scavenging damage to ilium.

result of scavenging activities of a bird like a kea (*Nestor notabilis*) seeking the kidneys which lie beneath this region of the ilia in birds.

The pubes are entire, and when found were not fused to the posterior margin of the ischia although an articulation facet is present. The caudal terminations of the pubes, past the articulation with the ischia, are oriented posteroventrally, and have slightly expanded, rounded, terminal knobs similar to those of swans and geese. The pelvis has unfused ribs articulating with the first two sacral vertebrae; there are no fused ribs. Large foramina perforate the ilia above the antitrochanters, and others at the base of the ischia on the lateral surface. In other *C. calcitrans* pelvises, the foramina above the antitrochanters are often very small, but the ischiadic foramen is always large. In *Cereopsis*, there are no foramina above the antitrochanters, but there are large ones in the base of the ischium. No similar antitrochanteric or ischiadic foramina were seen in any other anatid, nor in *Anseranas* or *Chauna*.

In MNZ S35266, the sternal costal margin is about 80 mm long and so is slightly less than half the length along the basin (177 mm); there are seven costal facets. In *C. gracilis*, the costal margin contributes 65 mm to a total length of 143 mm in a near-perfect unlocalized, unregistered, MNZ specimen (probably from Te Aute, by its preservation). Woolfenden (1961) noted that the length of the costal margin was always less than 50% of the length of the sternal body in anserines. He also noted six or seven costal facets for *Cereopsis*, but CM Av21198 has only five. In MNZ S35266, there is no dorsal central foramen, but a single foramen opens from the dorsal surface into the left side of the keel, suggesting that a larger central one has been occluded by a medial bar. Large, complex foramina open dorsally above the coracoidal sulci. There is a manubrial notch, but no spine or other projection. In *Cereopsis*, there is a large central foramen on the dorsal surface, and laterad of this, above the coracoidal sulci, is an area with numerous small foramina.

Femur, tibiotarsus, tarsometatarsus, fibulae

Owen (1866) and Hector (1874) adequately described these bones. Of note in MNZ S35266, is that both femora have the anterior part of the trochanter missing. The femora were articulated in the sockets on the pelvis, so erosion or weathering can be discounted. The cause of this damage, as in that to the ilia described above, is probably some scavenging bird.

The femora have the anterior edge of the external condyle elevated from the shaft as in all anserines, but not anatines (Woolfenden, 1961). *Cnemiornis* shares with *Cereopsis* the unique feature of the fibular condyle extending farther distally than its point of junction with the external condyle (Woolfenden, 1961).

On the better preserved left tarsometatarsus, there is a shallow facet about 9 mm long for the articulation of metatarsal 1 on the posterior surface. The distal foramen is open distally, however, protuberances from the trochlea for digits III and IV suggest a former enclosing bridge. While this foramen is large and can be sighted through in a plane at right angles to the shaft (cranio-caudal), the proximal side of the foramen (which reflects the alignment of the tendon) slopes distoposteriorly, not strictly craniocaudally. If the two protuberances were extended so as to close the foramen distally, the posterior exit of this foramen would be recessed in a depression, as in *Euryanas* or *Anas* spp. That is, the posterior opening of this foramen, even allowing for the loss of the distal enclosing strut (often lost in larger flightless birds such as kiwi or moa), does not open flush with the surface of the shaft, as in *Anseranas*. In some *C. gracilis* tarsometatarsi, the distal foramen is closed distally. In *Cereopsis*, the foramen is aligned distoposteriorly, and the bone enclosing the foramen distally is recessed relative to the anterior rim.

The proximal width of the tarsometatarsus is 37 mm. The hypotarsus is 22 mm wide, and so

occupies about 60% of this width. This is more than Livezey's fig. 2 (1989) indicates, as evidently that figure was from a somewhat medial viewpoint. The medial hypotarsal ridge is 37 mm long, and is centred behind the *area intercotylaris* at the lateral edge of the *cotyla medialis*. It grades evenly into the shaft distally, unlike in most waterfowl, where it ends abruptly. Laterad of the medial hypotarsal ridge is a large enclosed tendinal canal overlain (caudally) by a smaller open canal. Laterad to these are two other open canals. There are therefore four hypotarsal ridges. The proximal lateral vascular foramen opens posteriorly immediately distad of the most laterally placed tendinal canal. In *Cereopsis*, the structure differs only in that the groove adjacent to the main canal is deeper and nearly enclosed.

The trochlea for digits II and IV extend distally to a near equal extent, unlike in most anatids, where that for digit II is relatively much shorter. As Owen (1866) noted, the conformation in *Cereopsis* is nearer to that of *Cnemiornis* than other anatids, as while trochlea II is shorter than trochlea IV, it extends past the base of the intertrochlear notch between trochlea III and IV: in most anatids, trochlea II does not extend past that intertrochlear notch.

Digital phalanges (Plate III)

The skeleton MNZ S35266 affords the first description of these elements. There are three phalanges in digit II, four in digit III, and five in digit IV. Despite the care taken during the excavation, there was no sign of any metatarsal or bones of digit I, therefore the phalanges of digit I are unknown and the formula is ?:3:4:5. Phalanges (except unguals) are higher than wide in digits II and IV.3 and IV.4, slightly wider than high in digit III, and markedly wider than high in IV.1 and IV.2 (**Appendix 1**). The unguinal phalanx of digit II is a straight spur, that of digit III shorter and somewhat curved, that of digit IV is the smallest and most curved.

Cnemiornis gracilis has the same spur-like unguinal for digit II. The phalanges of *Cereopsis* have the formula 2:3:4:5. The unguinal for digit II is the longest, and is slightly curved and stout; that of digit III is relatively narrow, deep and more curved; that of digit IV smaller again, and curved; that of digit I is the smallest, but is still distinctly curved. The unguinal of digit II supports a long, curved horny sheath.

Humerus, ulna, radius, carpometacarpus (Plates IV & V)

The humerus described by Owen (1866) was that of *Aptornis defossor*, a fact he realised following Hector's (1874) description of the Earnsclough material (Owen, 1875: 266). The further descriptions by Owen (1875, plate XXXVIII) adequately described this bone, and the ulna and carpometacarpus as well. Noteworthy features of the humerus include: a prominent capital shaft ridge *margo caudalis* that is not directed towards the *tuberculum dorsale* (external tuberosity), but grades into a flat area between the base of the external tuberosity and the pneumatic foramen; the external tuberosity is raised on a platform above the plane of the surrounding bone; the capital groove is short and does not undercut the head much; the *fossa pneumaticipitalis* (bicipital fossa of some authors) is open and visible in anconal view; the *crista deltopectoralis* (deltoid crest) is evenly rounded along its length and grades smoothly into the shaft distally, and is concave anconally. The humerus of *Cereopsis* is longer and more sigmoid, and the capital shaft ridge extends up to the head, but otherwise has all the above features that define the Anserinae (Woolfenden, 1961). The humerus of *Cnemiornis* differs further from that of *Cereopsis* in having a very squared proximal end, virtually no *sulcus transversus*, and a deeper *impressio coracobrachialis*. The differences may relate to reductions following flightlessness; *Cereopsis* flies well.

On the carpometacarpus, the *processus alularis* is very small and no alular phalanx or pollex was found, which suggests that it may be absent. The *processus extensorius* is short, and is not formed into a prominent spur-like process as it is in many waterfowl. The facets for the phalanges of the minor and major digits extend about equally, as in *Cereopsis*. The distal metacarpal symphysis is long, as in *Cereopsis*, in which it is longer than other geese (Woolfenden, 1961). The external trochlea has a shallow notch in its lower portion, but one which is less distinct than in other anseriforms except *Anseranas* (Woolfenden, 1961). There is a prominent tuberosity at the anterior end of metacarpal III.

The radius shaft is triangular in cross-section, and the distal end is a little expanded or flattened.

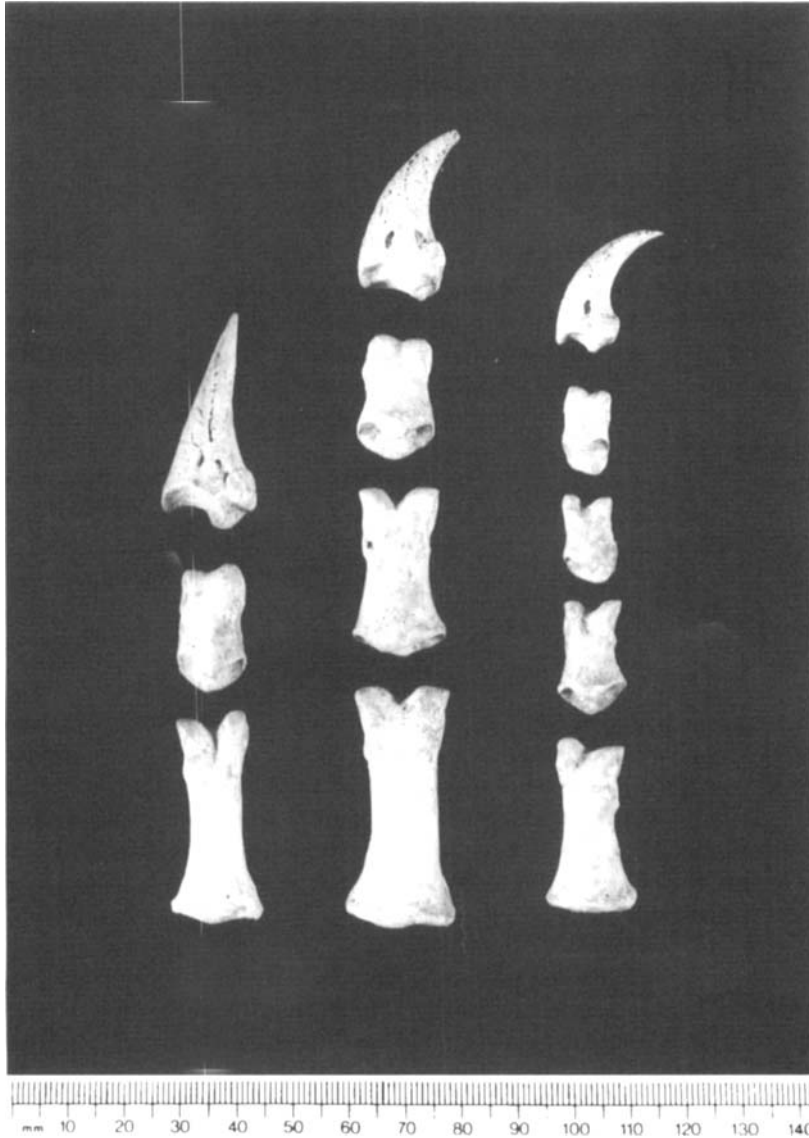


PLATE III. Phalanges of the right pes of *Cnemiornis calcitrans* MNZ S35266.

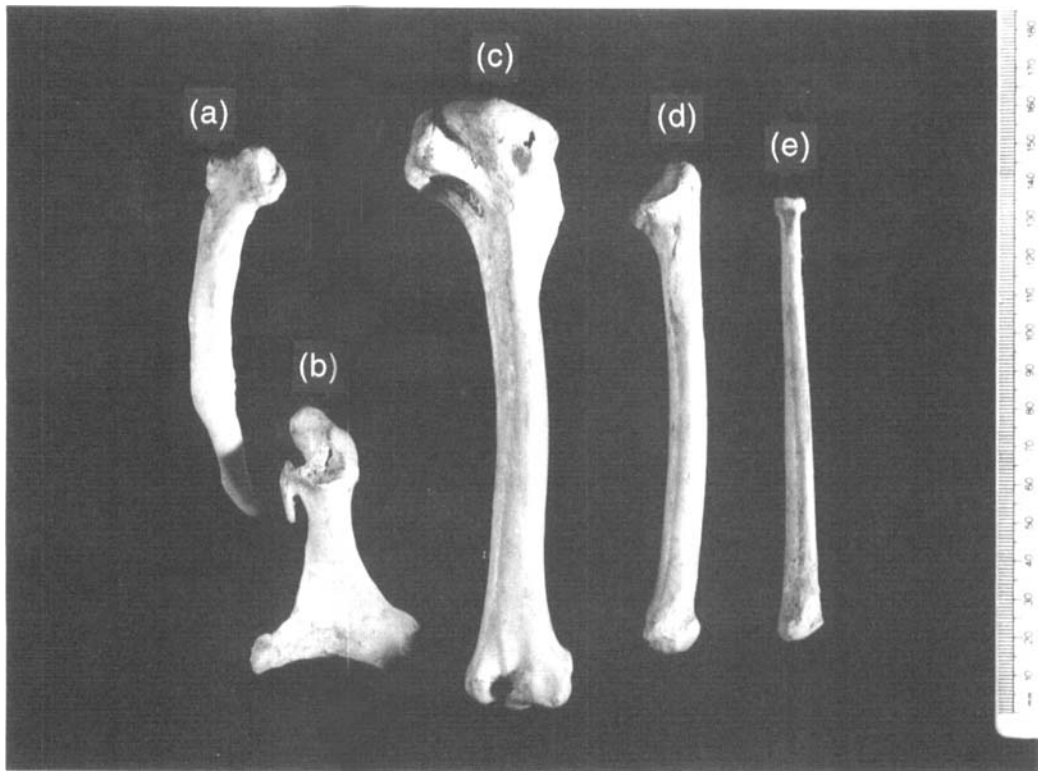


PLATE IV. Right pectoral elements of *Cnemiornis calcitrans* MNZ S35266: (a) scapula, (b) coracoid, (c) humerus, (d) ulna, (e) radius.

Wing phalanges (Plate V)

MNZ S35266 includes previously unknown distal wing elements. No phalanges of the alulae or minor digits were found, despite both wings having been excavated in a position of articulation, and three phalanges being found on the major digit. In addition to the usual phalanges 1 and 2 of the major digit, a small triangular third phalanx is present. Considering the general reduction in the wing and the exceptional preservation, it is possible that the alulae and minor digit lacked phalanges. These are, however, present in *Cereopsis*, which also has three phalanges in its major digit.

Vertebrae (Plate VI)

Hector (1874) was the first to comment on *Cnemiornis* vertebrae, but the Earnsclough specimen was incomplete with only 12 cervicals. Owen (1875) did not know what the full complement of vertebrae was—"but the precise sum of cervicals waits a better opportunity of obtaining the skeleton of the same individual." (Owen, 1875: 260). However, a more serious problem was which bones Owen attributed to *Cnemiornis*. In the type series, Owen (1866) correctly included two thoracic vertebrae (plate LXIV figs 3, 4), but he wrongly attributed some vertebrae of *Aptornis defossor* to *Cnemiornis* as Hamilton (1892) and Lydekker (1891) noted. The correct geese vertebrae were attributed to *Aptornis* as indicated in plate 16 (Owen, 1872).

MNZ S35266 has a nearly complete complement of vertebrae. The atlas, axis and cervicals 3–10 are well preserved, 11 is fragmentary with only its posterior portion remaining, and 12–23 are in good condition. Vertebra 17 is the last cervical vertebra without ribs; the next six vertebrae have freely-articulating ribs. There are six pairs of presacral dorsal ribs. The ribs on vertebra 18 do not articulate with sternal ribs, so 18 is not part of the thoracic series (*sensu* Woolfenden, 1961; Baumel *et al.*, 1993). Five vertebrae (19–23) form the thoracic series. Hence, there are 18 cervical and 5 thoracic vertebrae.

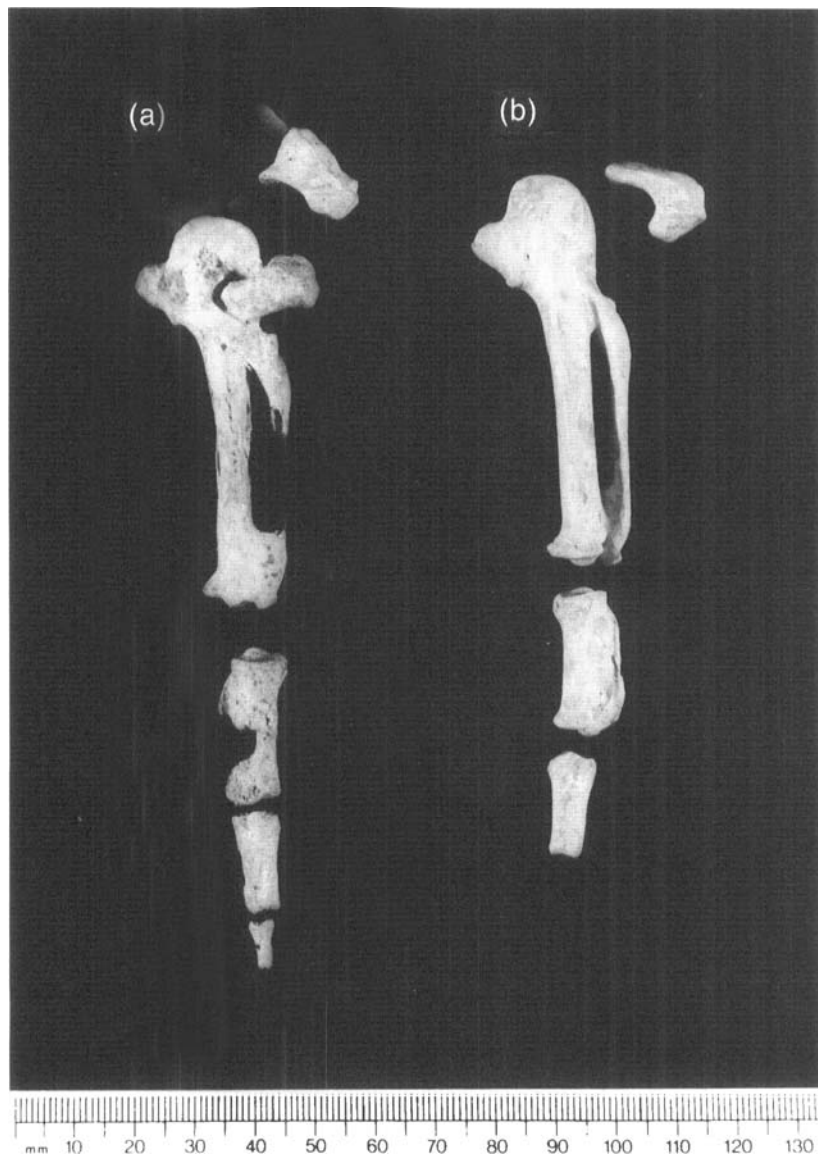


PLATE V. Distal wing elements of *Cnemidornis calcitrans* MNZ S35266: (a) right carpometacarpus with articulated radiale and associated ulnare, and distally M2.1, M2.2, M2.3; (b) left distal wing elements.

The axis has a low neural spine; by the third vertebra the spine is bifid. By vertebra 7 there are two distinct crests, which develop between 8 and 14 into prominent transverse ridges (*crista transverso-obliqua*). In 15 these are shortened, are higher, and form a pair of prominences that form the beginnings of the neural spine as properly developed in 16. The thoracic vertebrae all have stout neural spines, with anterior and posterior surfaces parallel, and which are not sloped either anteriorly or posteriorly. There is no evidence of ossified ligaments on these neural spines or along the transverse processes. Vertebrae 17–21 have ventral spines. Vertebra 17 has a small ventrally-directed, stubby, *processus ventralis* (Owen's hypapophysis). By vertebrae 19 this ventral process is stouter, with its base including the whole length of the centrum, and it has lateral tubercles. The ventral process in vertebra 20 is the longest and also has significant lateral expansion. Vertebra 21 has a much reduced (from 20) ventral process that is directed anteriorly. There is no ventral process on vertebrae 22 or 23. The last six dorsals (18–23) have relatively narrow centra, ranging from 11 mm high by 19.4 mm wide in vertebra 18 (widest), to 14.7 by 13.4 mm in vertebra 23.

There are two ribs freely articulating with the pelvis. Three caudal vertebrae were recovered. The loss of the rest may be attributed to the scavenger that damaged the ilia and femora.

Cereopsis usually has 19 cervical and four dorsal vertebrae, for a total of 23 presacral vertebrae (e.g. ANSS 738, CM Av3350; Woolfenden, 1961). In CM Av21198 only vertebrae 21–23 have ribs

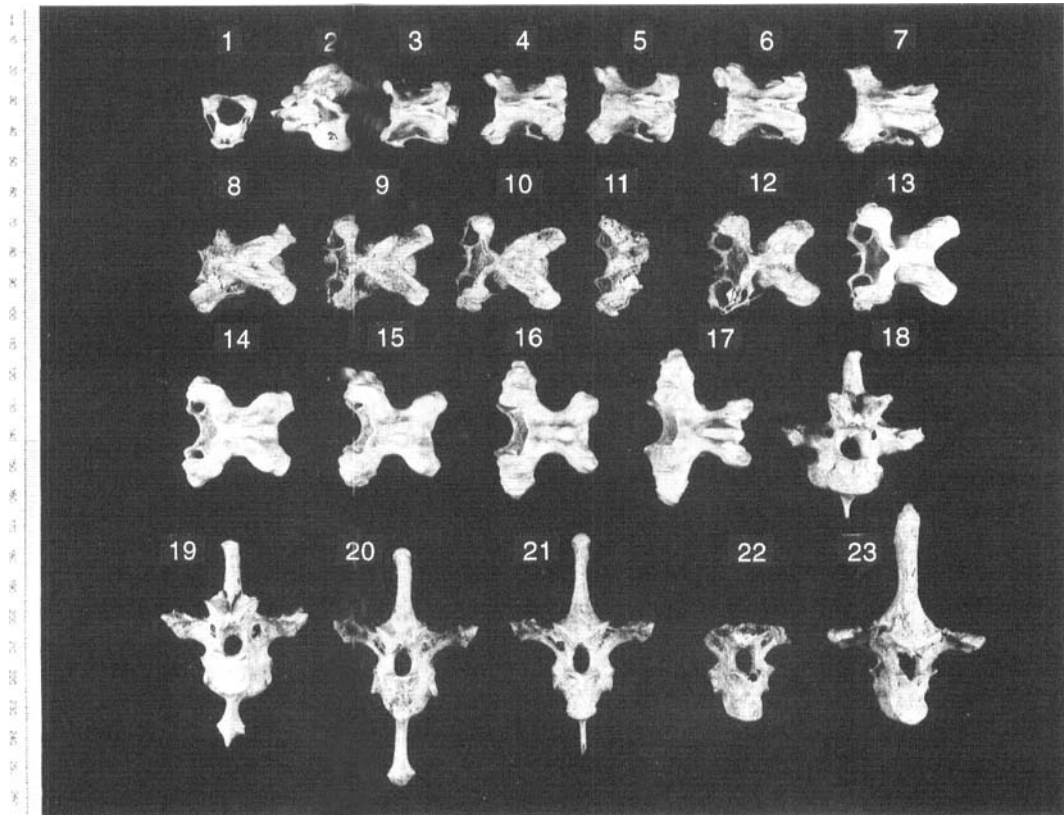


PLATE VI. Vertebral series of *Cnemiornis calcitrans* MNZ S35266 in numerical sequence.

articulating with sternal ribs, resulting in 20 cervical and three thoracic vertebrae (this specimen had an unusually low count of five costal facets on the sternum). In Av21198, the neural spine of vertebra 18 is small, and the ribs are vestigial and fused to the zygapophyses; vertebrae 19–23 have small ossified ligaments dorsally; ventral spines are present only on 21 and 22. Also, in Av21198, the first thoracic vertebra (21) has a flattened and laterally expanded ventral spine similar to the first thoracic vertebrae (19) of MNZ S35266. In both *Cereopsis* and *Cnemiornis*, there are seven sacral vertebrae anterior to the acetabulum. But, in *Cereopsis*, the first three of these articulate with detachable ribs that articulate with sternal ribs, rather than two in MNZ S35266. However, a third isolated sternal rib is fused to the second sacral rib of MNZ S35266, suggesting the former presence of a third dorsal sacral rib that is now lost.

Ribs

In MNZ S35266, there are eight pairs of dorsal ribs, six of which articulate with presacral vertebrae. Uncinate processes articulate with the ribs associated with vertebrae 19–22. Sternal ribs articulated with all but the first pair. All presacral dorsal ribs have large pneumatic foramina opening from the posterior surface below the *tuberculum costae*. Owen (1875) wrongly associated the ribs of *Aptornis* with the *Cnemiornis* bones.

Coracoids (Plate IV)

There is a large procoracoidal foramen or *incisura nervosum supracoracoidei* that is not enclosed medially. There is no foramen opening from its caudal, medial margin into the *processus procoracoideus*. The *facies articularis sternalis* is concave in ventral or dorsal profile, and the facet is poorly developed. The *processus lateralis* is broad and squarish with its cranial margin parallel to the sternal facet. The process extends slightly beyond the sternal facet as a wide and rounded projection. The *angulus medialis* is not acute, being broadened by a flange cranially. The *impressio ligamentosa acrocoracohumeralis* is shallow. There is no deep fossa in the *sulcus supracoracoideus* undercutting the *facies articularis humeralis* (as in some anatids), so the ridge between the *facies articularis humeralis* and the *processus acrocoracoideus* (brachial tuberosity) is rounded. A small pneumatic foramen is present in the supracoracoidal sulcus of the left coracoid only. Most coracoids of *C. calcitrans* have no pneumatic foramina in the supracoracoidal sulcus. In contrast, most coracoids of *C. gracilis* have such a pneumatic foramen, which may be large (e.g. CM Av25366, 6.3 × 3.3 mm; Av25367, 8.9 × 4.2 mm), or small (e.g. CM Av25001, 2.7 × 1.1 mm). The very reduced state of, or the apparent absence of, this pneumatic foramen in *C. calcitrans* is therefore not a generic character, but another feature associated with flightlessness. The ventral surface of the coracoid is convex above the sternal facet, and there are no ridges. While slightly flattened, it has no marked depression on it. There is no pneumatic foramen dorsally above the sternal facet, as seen in *Anseranas* (Woolfenden, 1961).

Owen (1875) described a coracoid along with the vertebrae in 1875 but, unfortunately, it too was of *Aptornis*, as Lydekker (1891) and Livezey (1989) pointed out. Owen compared it to a coracoid of *Cereopsis* (plate XXXVII, fig. 8), whose identification Livezey (1989) disputed, contending that the coracoid in Owen's fig. 8 was that of *Cnemiornis*, citing as evidence the form of the procoracoidal foramen. This cannot be so, as although the bone figured by Owen apparently had a damaged lateral process, the shaft is aligned acutely and medial to the sternal facet rather than at right angles as in *Cnemiornis*. Owen's figure shows a prominent ridge on the bone's ventral surface which extends towards the sternal facet. The ridge is not present on the *Cnemiornis* coracoid, but is in *Cereopsis*. Finally, the head appears to be angled more mesad in Owen's figure than it is in *Cnemiornis* coracoids.

The form of the procoracoidal foramen is variable (open or closed) in *Cereopsis*, and CM Av21198 is as in Owen's figure. Clearly, fig. 8 in Owen (1875) is of a coracoid of *Cereopsis*, and not that of *Cnemiornis*.

Livezey (1989) dwelt at length on the 'presence of a conspicuous procoracoidal foramen' and considered it primitive in anatids. He considered that *Cnemiornis* coracoids always had a procoracoidal foramen which was enclosed medially, and that *Cereopsis* did not, except 'infrequently ... (perhaps only in captive birds)'. The skeleton described here does not have medially enclosed procoracoidal foramina, neither do several others in collections: four coracoids from the Prydes Gully site, North Otago (M. Denny colln) have the fenestra open, and all those seen of *C. gracilis* (CM Av25366, 25367, 25001, 18035, several unreg. MNZ specimens), were also open. The condition is variable, because the left and right coracoids from a site at Three Mile Bush Road (J38 482652), J. Fisher collection, have both fenestra closed. There are no coracoids of *C. calcitrans* in MNZ or CM. Among other anserines, the coracoids of *Branta sandvicensis* (e.g. MNZ 618) have an enclosed procoracoidal foramen, so the feature is not unique to *Cnemiornis* and *Cereopsis*.

Livezey also stated that *Cnemiornis* coracoids had an enclosed pneumatic foramen to the interior of the element at the cranial end of the procoracoidal foramen, and that such foramina were lacking in the coracoids of most *Cereopsis*. MNZ S35266, and all other *Cnemiornis* coracoids examined, including those of *C. gracilis*, do not have such a foramen. We found such foramina only in the coracoids of *Cereopsis* in ANSS 738, which also had closed procoracoidal foramina and was a young specimen. However, such foramina were obvious in *Anseranas*. These observations show that the distinction drawn between *Cereopsis* and *Cnemiornis* by Livezey (1989) using these characters have little basis.

The Anserinae, especially swans and geese, have large and/or numerous pneumatic foramina in the supracoracoidal sulcus below the brachial tuberosity and/or furcular head (Woolfenden, 1961), and this was taken by Livezey (1989) to be a synapomorphy of geese and swans. Foramina are present in *Cnemiornis gracilis*, *Cereopsis*, *Cygnus*, *Anser*, *Branta* and other true geese, but are also present in the shelduck genera *Chloephaga*, *Neochen* and *Alopochen* (Woolfenden, 1961), and in *Plectropterus* (pers. obs.).

Scapulae (Plate IV)

The main feature of this bone is the very reduced acromion, so much so that the *tuberculum coracoideum* projects farther cranial. The acromion is more prominent in all waterfowl except *Anseranas* (Woolfenden, 1961), but it seems more prominent among volant birds in general, so the reduction could be related to the reduced flight ability. In MNZ S35266, there is no pneumatic foramen behind the coracoid tubercle on the lateral surface. However, in another *C. calcitrans* specimen MNZ S23481, and in most scapulae of *C. gracilis*, which are of similar shape to those of *C. calcitrans*, there is a large pneumatic foramen at this point e.g. CM Av24967, 25001. The variable absence of this foramen in *C. calcitrans* mirrors the loss of the pneumatic foramen in the coracoid, and again is no doubt associated with flightlessness and subsequent reduction of vestigial organs. This foramen occurs in other waterfowl only in *Anseranas*, true geese and *Coscoroba* (Woolfenden, 1961). In *Cereopsis*, the acromion is longer, and a prominent pneumatic fossa is present.

Furculae

The furcula of MNZ S35266 is broadly U-shaped, with a length of 77 mm from the symphysis *apophysis furculae* to the scapular end. The symphysis area is flattened, with no foramina, and with no furcula process *synostosis interclavicularis*. There is no coracoidal facet *facies articularis*

acrocoracoidea. There are large complex pneumatic foramina below the *processus acromialis*. Furculae of the volant *Cereopsis* are much more robust than those of the larger but flightless *Cnemiornis* but share the following features: they are broadly U-shaped, lack a furcular process, have only a slight rugose area in place of the coracoidal facet, and have pneumatic foramina in the area between the coracoidal and scapular tuberosities.

Results

Livezey's (1989) phylogenetic analysis of *Cnemiornis* was based on 62 characters for which he listed 21 as missing. Of the total, only 11 were cranial characters, but of these he did not have data for three and we disagree with his assessment of one, the supraoccipital. Although the supraorbital processes appear large in *Cereopsis*, we contend that this is an artefact of the anterior extent of the salt glands that are excavated mesad of the lacrymals. Also, the dorsal rim of the orbit is not developed in *Cereopsis* as compared to *Cnemiornis*, because of the much greater extent of the salt gland impressions. Therefore, we do not consider the apparently large supraorbital processes of *Cereopsis* to be homologous with those of other waterfowl. If one 'completes' the orbital frontal border as in *Cnemiornis*, then only a small supraorbital process need be present.

There are several other characters which would seem to be significant but which Livezey (1989) does not mention. These include: presence or absence of salt glands (not of this extent or form in any other anatid); anterior closure (or not) of the tympanic cavity (not seen in any other waterfowl except *Malacorhynchus scarletti*); palatines that are concave or convex laterally (concave in all anatids except *Cereopsis*); presence or absence of posterior process to premaxilla (present in all except *Cereopsis*), and the form of the premaxilla-cranial hinge.

Significant postcranial characters not scored for other taxa by Livezey (1989) include, in particular, the presence of a foramen at the base of the ischium or above the antitrochanter, and the sloping versus abrupt termination of the medial hypotarsal ridge. Contrary to Livezey (1989), we found the distal foramen on the tarsometatarsus to be aligned distoposteriorly, the presence of a distinct buttress on the anterior margin of the ventral sternal facet of the coracoid, and on the pelvis the post-ischiadic pubis terminated in a circular flange.

Assessment of synapomorphies for the Anatidae

Livezey (1989) listed the derived states of the following characters as synapomorphies of the Anatidae (including Anserinae) that excluded *Cnemiornis*.

1. The femoral head is aligned perpendicular to the exterior surface of the shaft, or the caudal or ventral surface below the proximal end is at right angles to the adjacent lateral surface. While in *Cnemiornis*, the femoral head is aligned caudal to the exterior surface of the shaft, or at about 110–120° to the lateral surface, this angle is about 110° in *Cereopsis* femora, and *Cygnus olor* has femora very like those of *Cnemiornis*, especially *C. gracilis*. Femora of *Cygnus olor* are nearly the same size as those of *Cnemiornis gracilis*, which suggests that the conformation of femora may relate to body size. In both, the head is angled cranially rather than approximately at right angles to the shaft, and the proximal ventro-lateral angle is about 120°. The first results in the femora being able to be splayed wider from the pelvis (necessary in these large-bodied birds), and the second results in an effective twist of the femoral–tibiotarsal joint so that distally the tibiotarsus is angled medially, placing the feet under the body. Together, these aspects of femora shape appear to be responses to large body size. Even if they are not, *Cnemiornis* shares the feature with *Cygnus olor*, and to a lesser extent with *Cereopsis*, so the perpendicular orientation of the femoral head is not a synapomorphy for Anatidae.

2. The approximately equal distal extent of trochlea II and trochlea IV was taken to be primitive. In other anatids, trochlea II is markedly more proximal than trochlea IV, that is except in *Cereopsis* where trochlea IV is only slightly more distal, as Owen (1875) noted. To code *Cereopsis* as being identical to all other anatids in this respect is certainly incorrect as it has an intermediate condition.
3. *Cnemiornis* has a moderate lateral displacement of the hypotarsus on the tarsometatarsus. Livezey (1989) defined the primitive state of this character as two ridges lateral to the midline of the shaft and bordered by a deep depression medially; derived as three or four ridges situated on the midline (char. 72). The hypotarsus of *Cnemiornis* has four hypotarsal ridges. Interpretation of ‘lateral displacement of the calcaneum’ is impossible in plantar view in *Cnemiornis*. In *Cnemiornis* and, for example, *Anas* or *Euryanas*, the principal hypotarsal ridge is immediately posterior to the *area intercotylaris*. That the calcaneum is apparently shifted to the lateral edge is caused by an expansion of the *cotyla medialis*, which also generates the medial hollow. So the ‘character’ appears to be comprised of two discrete elements: *a*, the number of hypotarsal ridges; *b*, the expansion of the medial cotyla. Assuming that *a* is more phylogenetically significant and that *b* is a function of large size and a cursorial lifestyle, the condition in *Cnemiornis* is derived, with more than two ridges.
4. *Cnemiornis* has a strictly cranio-caudal orientation of the distal foramen of the tarsometatarsus (77a) rather than it being directed distoposteriorly, and that the posterior opening was flush with the surface rather than deeply recessed. While we acknowledge that the modified vestigial nature of the foramen makes interpretation difficult, as described above, the foramen of *Cnemiornis* is best considered to be oriented distoposteriorly with the posterior opening recessed, therefore *Cnemiornis* is derived in this respect.
5. The presence of a large, densely-margined foramen at the base of the *processus procoracoideus* was taken to be primitive but, as described above, this feature is shared by *Cereopsis*, and the foramen may be open or closed in both species of *Cnemiornis*.
6. The wide, long, and rounded shape of the sternocoracoidal process was taken to be primitive, but is also shared with *Cereopsis*.
7. The coracoidal process on the scapula is equal to the acromion in proximal extent. It seems to us that the acromion is largest in flighted species, and because *Cnemiornis* has markedly reduced wings and could not have flown, the reduced acromion is probably related to flightlessness.
8. The costal margin of the sternum occupies less than half the basin length. This is also so for *C. gracilis*. Woolfenden (1961) stated that only *Anseranas* among anseriforms had a costal margin >50% of basin (midline) length, and that, in Anserinae, it is always less than 50%. *Cnemiornis* therefore agrees with the Anserinae in this respect. Since reductions in the pectoral girdle associated with flightlessness would result in a shortening of the anterior edge in the region of the coracoidal sulci, the immediate ancestor of *Cnemiornis* would have been characterized by even shorter costal margins relative to basin length.

In summary, of the eight characters for which *Cnemiornis* was reported to be plesiomorphic and the rest of the anatidae derived, six were shared with or approached in *Cereopsis* (1, 2, 3, 4, 5, 6), three we interpret to be derived in *Cnemiornis* (*contra* Livezey, 3, 4, 8), and three are of doubtful value because of morphological changes associated with flightlessness (1, 7, 8). These characters do not, therefore, support *Cnemiornis* being a clade that branches from the anatids after *Anseranas* but discrete from the rest of the anatids.

Assessment of synapomorphies for the Anserinae

Livezey (1989) listed the following features as diagnostic synapomorphies of true geese: more than

17 cervical vertebrae, spur-like elaboration of the metacarpal, pneumatic foramina under the brachial tuberosity of the coracoid, and pubes with caudal flanges. MNZ S35266, the only almost complete skeleton of *Cnemiornis*, has 18 cervical vertebrae and 5 thoracic vertebrae. *Cereopsis* typically has 19 cervical and 4 dorsal vertebrae, but vertebrae 18–19 bear ribs in addition to the true thoracics. So, in both *Cnemiornis* and *Cereopsis*, there are 23 presacral vertebrae and 18–23 bear ribs.

The modifications associated with flightlessness include reductions that are most pronounced in distal wing elements, so the absence of a spur-like metacarpal on the carpometacarpus of *Cnemiornis* is not significant phylogenetically. Also, the presence of a metacarpal spur may be related to the behaviour of using wings for fighting (Woolfenden, 1961). *Anas chlorotis* has a rugose metacarpal spur and is not a goose. *Cereopsis*, which has a metacarpal spur, uses its wings for fighting (Marchant & Higgins, 1990). The markedly reduced wings of *Cnemiornis* would make the use of wings for fighting ineffective. It is therefore significant that the unguis in pedal digit 2 is developed as a large spur which would presumably have had similar functional significance and could have replaced the metacarpal spur.

The presence of pneumatic foramina under the brachial tuberosity of the coracoid and on the scapulae in *C. gracilis* indicates they have been secondarily lost in *C. calcitrans*. Their absence is not a generic character. MNZ S35266 has weakly developed caudal flanges to the pubes. *Cnemiornis* therefore does not lack the four diagnostic synapomorphies of true geese listed by Livezey (1989), and so is a goose.

Assessment of characters unique to Cereopsis

Livezey (1989) maintained that *Cnemiornis* did not share what he considered to be the autapomorphic supraorbital process, nor the pneumatic swelling of the nasofrontal region or dorsal bowing of the upper bill characteristic of *Cereopsis*. We contend that the structure of the supraorbital process is not comparable in *Cereopsis* with that in other anatids lacking large salt gland impressions. Moreover, the apparent differences between *Cereopsis* and *Cnemiornis* in this feature may relate entirely to the greater excavation of the salt gland impressions, both anteriorly and laterally, in the former. The structures allow *Cereopsis* to subsist in areas where there is no available fresh water (Marchant & Higgins, 1990). The swelling of the nasofrontal region in *Cereopsis* is associated with a much larger *os mesethmoidale*, *os ectethmoidale* and *concha nasalis caudalis* than in *Cnemiornis*. These features, combined with the bowed upper bill, accommodate relatively larger olfactory structures in *Cereopsis* than in *Cnemiornis*, probably indicating greater olfactory ability in the Cape Barren goose.

Although the olfactory and salt excretion abilities of *Cnemiornis* are reduced in comparison to *Cereopsis*, its eyesight may have been better. If the height of the orbit is taken to be related to eye size and body size to cranial length, then *Cnemiornis* has a relatively bigger eye than *Cereopsis*. These differences are related to function and have corollaries among the moas (Aves; Dinornithiformes) where the olfactory structures are very large and expanded in some species and reduced in others. Baumel *et al.* (1993) stated that the size of the nasal cavity and of the olfactory lobes of the brain show marked interspecific variation, which is probably correlated with olfactory ability. Such differences could be present at generic level, but do not preclude familial relationships.

Owen (1875) stated that *Cnemiornis* differed from *Cereopsis* in “the greater breadth of the cerebellar prominence..., and in the greater slope forward as it rises from the foramen magnum”. This apparent difference in slope is caused primarily by the robust posteriorly-directed paroccipital processes in *Cnemiornis* which are undoubtedly developed to support bigger muscles to manoeuvre the larger head. As part of the same musculature development the mamillar tuberosities have become robust posteriorly-directed structures. So these gross differences between *Cnemiornis* and *Cereopsis*

crania relate primarily to functional requirements of associated musculature. Both genera have a similar, unique structure to the tympanic cavity, similar quadrates, long posteriorly-directed lacrymals that nearly reach the post-orbital process, large sharply delineated impressions for salt glands, closed or often-closed occipital fontanelles, and short premaxillae weakly fused to the frontals with no posterior extension under the jugal.

The palate of *Cereopsis* differs from that of *Cnemiornis* primarily in the reduced sizes of the large central 'vomer' and the caudolateral palatine processes. In both genera, the palatines are convex laterally as against concave in *Anser*, *Branta*, *Cygnus* and anatines.

In summary, *Cereopsis* and *Cnemiornis* have very similar skulls. The main difference is in the rounded rather than square, somewhat more down-turned premaxilla in *Cereopsis*, and the domed nasal region associated with greater development of the olfactory structures.

Postcranially, *Cereopsis* and *Cnemiornis* are similar in both having a similar vertebral formula; a large procoracoidal foramen; pneumatic foramina in the supracoracoidal sulcus under the brachial tuberosity and laterally on the scapula (both secondly lost in *C. calcitrans*); a large foramen at the base of the ischia; an approximately equal extent of trochlea II and trochlea IV; four hypotarsal ridges with the first long and grading gradually into shaft rather than abruptly; a similarly shaped sternocoracoidal process; a fibular condyle that extends farther distad of the junction with the external condyle; and the ungual on digit II developed into a spur. No other anatids share this suite of characters.

Cladistic analysis of morphological characters

To test the sister group relationship of *Cnemiornis* and *Cereopsis* suggested by the above analysis, we adapted Livezey's (1989) data matrix by adding new data derived from the more complete material at our disposal, and otherwise modified it as detailed (**Appendix 2**). Three equally short trees (branch

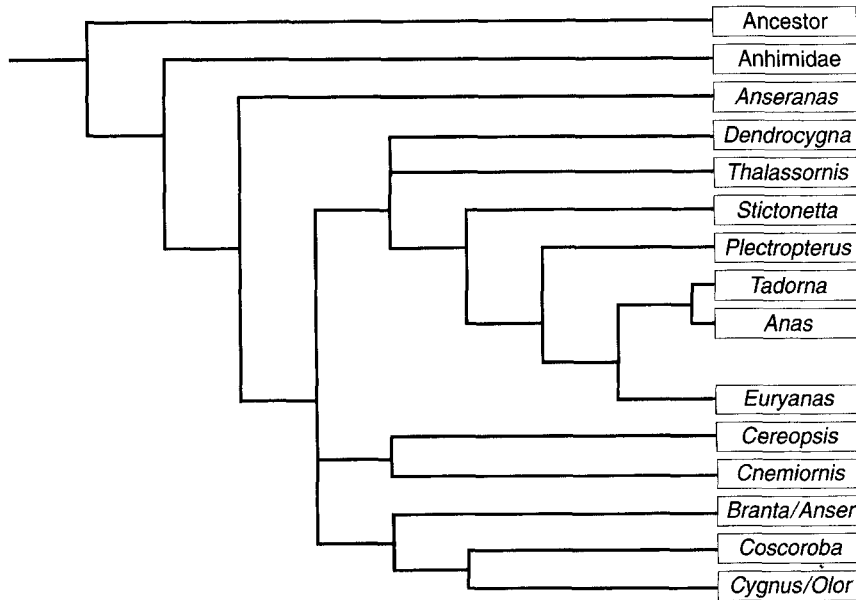
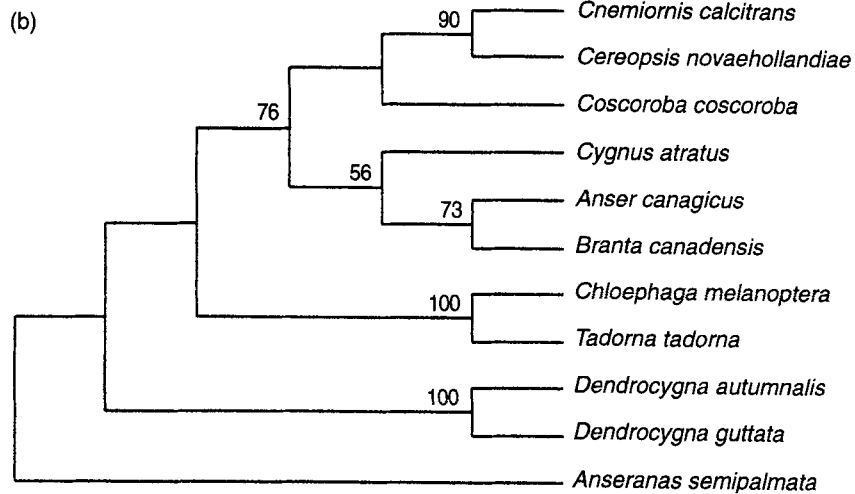


FIG. 1. A strict consensus tree for the three shortest phylogenetic trees obtained from the morphological analysis.

(a) *Cnemiornis*
TAAACA-AAGGT--TACAAACGCAAATCTTATATACTTTA-CTTACA-C-C-
CACCCTC
Cereopsis
.....--T.....C.C.-C...-T-T...G...
Coscoroba
.....ACAAA.....AAC..T.C.....C.-.C.TT...-C.G.C.
Anser
....A.-T.TAAAC..G.AAT..T.C.....C.-.CT...-T-.....
Branta
....A.-TGATAAAC...G.AAC..T.C.....C.-.CCA...-G.C.
Cygnus
.....GT.A.AAC..T.AAC..T.C.C.C.T.CGC..CC..C.GTC..T..TC.
Chloephaga
...GA.C..CACAAC-TCG..AAC...-C.-.....-ACCC...-A-A..TG...
Tadorna
...GA.C..CA.AA.-TCG..AAC...-C.-.....G-ACCC...-AA-AT.AC.C.
D. autumnalis
....A.CG.ATA-A.-.....ATC...T..C-CTAACC.-A.CTTTTT-CTCT..ACT
D. guttata
....A.CG.ATA--A..G...ATC...T..C..TAAC...-A.CCAT-T..CGCTA.A..
Anseranas
C.....GCAA--T.TCAAACG.-ACA.-CCA..C.-TCC.TT-TA.T.TG.A..

Cnemiornis AATTACCAGCTAATCCCTTCT-CGTCCACATAGCTTAACACAAA
CereopsisTA..CA.....
Coscoroba ..C.....A.C.C-.....
Anser ..C..T.....C.A.A..CC.....
BrantaT.....A.AC.CA.....
Cygnus ..CC.T...GGC..ACTCC..T.....
Chloephaga CCCC-.....C.-.AC.C-.....CAC...
Tadorna ..C.CC...C.-CT-.AATCAT.....CACT...
D. autumnalis CCCAG.T.A.CC.AAA.CAAATT.....C...
D. guttata CCCAG.T..TCT.AATAC.AACT.....C...
Anseranas CTC..G.ATC-.AA.GA..AAA..C.....C...



length of 142.00, and consistency indices of 0.732) all grouped *Cnemiornis* and *Cereopsis* as sister taxa. The variation in tree topology was in the location of two branches: 1, whether *Dendrocygna* is the sister group of *Thalassornis*, or a clade before *Thalassornis* as the sister taxon to it and all successive anatids on that branch; and 2, whether the *Cereopsis/Cnemiornis* clade branched off after *Anseranas* and before the geese/swan clade, or was the sister taxon to the geese/swan clade.

The *Cereopsis/Cnemiornis* clade is supported by eight synapomorphies: two synapomorphies support the monophyly of the Anserinae. The strict consensus tree included two trichotomies (Fig. 1), indicating non-resolution of: 1, the placement of *Dendrocygna* and *Thalassornis* in relation to other anatines; and 2, the placement of the *Cnemiornis/Cereopsis* clade relative to other 'anserines' and anatines (consensus fork index = 11; CF (normalized) = 0.846; term information = 56; total information = 67; Mickevich's consensus information (CI) = 0.531).

Livezey (1989) was unable to resolve the placement of the Anserinae within his tree: equally parsimonious topologies placed this group after *Anseranas* but before *Dendrocygna*, or between *Dendrocygna* and *Thalassornis*, or between *Thalassornis* and *Stictonetta*. The position of the anserines as derived with respect to *Anseranas*, and the sister group to *Dendrocygna*, *Thalassornis* and other anatids was resolved in our analysis.

The failure of our analysis to resolve the relationships of *Dendrocygna* and *Thalassornis* in relation to other anatines partly supports Livezey (1989) who placed them in separate subfamilies, rather than as sister taxa in a clade which is the sister taxon of other anatines, e.g. Marchant & Higgins (1990).

Significantly, our results support a sistergroup relationship between *Cnemiornis* and *Cereopsis* as Owen (1875) originally inferred. Whether this clade is the sister taxon of other anserines or an earlier branch is unresolved. Most workers this century have supported a close relationship between *Cnemiornis* and *Cereopsis* (e.g. Oliver, 1955; Howard, 1964). The arrangement is followed in the New Zealand Checklist where they are included in the Anserinae (Turbott, 1990).

Analysis of mitochondrial DNA from Cnemiornis

The 96 base pair fragment of mitochondrial DNA from *Cnemiornis* that was sequenced was clearly similar to that of *Cereopsis* (Fig. 2a), although alignment of the sequences is complicated by length variation. Aligning the sequences using MALIGN (Wheeler & Gladstein, 1992) with a 2:1 transversion/transition cost ratio and a 2:1 gap/transversion cost ratio yielded a single alignment. Parsimony analysis based on this alignment yielded a single tree (Fig. 2b) which is highly congruent with our tree based on morphological data. Using different cost ratios in MALIGN resulted in alternative alignments and some variation in tree topology, but the sister relationship of *Cnemiornis* and *Cereopsis* and monophyly of the Anserinae (including *Cnemiornis*, *Cereopsis*, *Branta*, *Anser*, *Cygnus* and *Coscoroba*) were found in most analyses (Appendix 3).

Phylogenetic relationships of Cnemiornis

The morphological and DNA analyses clearly supports the sister group relationship of *Cnemiornis*

FIG. 2. (a) Alignment of control region sequences generated by MALIGN using a 2:1 transversion/transition cost ratio and a 2:1 gap/transversion cost ratio. (b) Single most parsimonious tree of length 370 based on the alignment in (a). Parsimony analysis done in PAUP 3.1 (Swofford, 1993) using a stepmatrix specifying transition, transversion, and gap costs of 1, 2 and 4, respectively. *Anseranas* was designated as the outgroup. Consistency index is not calculable with stepmatrix characters. Numbers above branches designate the proportion of trees that included the adjacent node among 124 trees resulting from alignments generated by MALIGN under 20 different parameter combinations (see Appendix 3).

and *Cereopsis* as previously advocated (e.g. Owen, 1866; Oliver, 1955). We suggest the DNA data resolves the more basal trichotomy in Fig. 1 within the Anatidae. Thus, the *Cnemiornis/Cereopsis* clade plus all other anseriforms constitute the Anserinae, which from the morphological studies of Livezey (1989) and data herein is shown to be the sister taxon of the Anatinae, which includes all other anatids except *Anseranas*. The higher trichotomy in Fig. 1 remains unresolved, and taxa so affected must be listed using the convention of *sedis mutabilis* as suggested by Wiley (1981). We suggest the following classification is appropriate.

Family Anseranatidae Stejneger, 1885

Genus *Anseranas* Latham, 1798

Family Anatidae Vigors, 1825

Subfamily Anserinae, (swans and geese)

Tribe Cereopsini, (Australasian geese)

Genus *Cereopsis* Latham, 1801

C. novaehollandiae Latham, 1801

Genus *Cnemiornis* Owen, 1865

C. calcitrans Owen, 1865

C. gracilis Forbes, 1892 (not 1891, as incorrectly cited by Livezey, 1989)

Tribe Anserini (Geese and swans)

Subtribe **Anserae** (*Branta/Anser*)

Subtribe **Cygneae** (swans)

Subfamily Anatinae, *sedis mutabilis* (all other anatids)

Tribe Dendrocygnini, *sedis mutabilis*

Tribe Thalassornithini, *sedis mutabilis*

Tribe Anatini, *sedis mutabilis*

All other anatines

Discussion

The New Zealand extinct anseriforms in *Cnemiornis* are shown here to be geese, and to be the sister taxa of the Australian Cape Barren goose (*Cereopsis novaehollandiae*). A sister taxon relationship with an Australian species is not unusual in New Zealand faunas. Within anatids alone there are the following Australian/New Zealand pairs: *Anas castanea/A. chlorotis*; *Malacorhynchus membranaceus/M. scarletti*; *Cygnus atratus/C. sumnerensis*; *Tadorna tadornoides/T. variegata*; *Biziura lobata/B. delautouri*. Another potential pair is *Aythya australis* and *A. novaeseelandiae* but Livezey (1996) suggested that these were independently derived from northern hemisphere ancestors. Of the prehuman New Zealand anatid fauna, only *Hymenolaimus malacorhynchus* appears not to have an Australian analogue.

Cnemiornis had two species in New Zealand, one in the North Island (*C. gracilis*), and one in the South Island (*C. calcitrans*). While both were larger than the Cape Barren goose, the North Island species was significantly smaller and differed in details of its skeletal morphology than the South Island goose. Both were flightless and lived in the more open environments afforded by mosaics of grassland, shrublands, and forest that were present in the drier eastern regions of either island during the Holocene (Worthy & Holdaway, 1993, 1994). During the last glacial period their range was extended to include western regions—grasslands prevailed. Like its nearest relative the Cape Barren goose, *Cnemiornis* was, therefore, probably a grazer. It had developed a more robust bill with a squarer

end which would be more effective for grazing. The Australian bird lives in very arid and salty environments, and has evolved salt excretion mechanisms (large salt glands) to cope with this. In New Zealand, this was not as necessary, and the glands became reduced. At the same time its eyes became relatively larger which, if correlated with better eyesight, would have facilitated detection of predators, e.g. Haast's eagle (*Harpagornis moorei*). The New Zealand extinct geese both became extinct following the arrival of Polynesians—the remains of both are found in archaeological middens.

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Abbreviations used in the text

CM Canterbury Museum, Christchurch, New Zealand
 BMNH Palaeontology Department, The Natural History Museum, London, U.K.
 MNZ Museum of New Zealand Te Papa Tongarewa, Wellington, N.Z.
 AM Australian Museum, Sydney, Australia
 ANSS Australian National Wildlife Collection, CSIRO, Australia
 When describing bones, L = left, R = right.

Appendix 1

Measurements of MNZ S35266, a Cnemiornis calcitrans skeleton from Chatto Creek, Otago, New Zealand

Sternum	Length midline	177 mm
	Mid-length width	102 mm
Mandible	Length ramus	97.6 mm
	Maximum depth	23.1 mm
	Width of tip	25.6 mm
Skull	Length to occipital condyle	108 mm
	Squamosal (zygomatic) width	50.1 mm
	Temporal fossae width	40.7 mm
	Post-orbital width	45.6 mm
	Interorbital width	28.2 mm
	Premaxillae hinge width	21.0 mm
	Maximum length	51.3 mm
	Maximum width	37.8 mm
	Length nares	16.8 mm
	Height of nares	11.6 mm
	Height × Length orbit	22 × 25.5 mm
	Height × width of foramen magnum	13.1 × 8.8 mm

Phalanges

The left elements were measured: (element) – length × max. width × height posterior (mm);

(II.1) – 37 × 15.4 × 15.7; (II.2) – 22.5 × 12.2 × 14.3; (II.3) – 38.7 × 12.6 × 16.8; (III.1) – 42.7 × 19.1 × 18.5; (III.2) – 30.0 × 16.5 × 14.7; (III.3) – 21.6 × 13.7 × 13.2; (III.4) – 31.2 × 14.0 × 15.0; (IV.1) –