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PHYLOGENETIC RELATIONSHIPS OF SEVERAL SUBFOSSIL ANSERIFORMES OF NEW ZEALAND

By

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Three genera of waterfowl (Anseriformes) are known only from subfossil remains from New Zealand (Oliver 1955, Howard 1964): *Cnemiornis* Owen 1866, *Euryanas* Oliver 1930, and *Pachyanas* Oliver 1955. The first two are represented by numerous well-preserved elements, and *Cnemiornis* is renowned for its radical morphological modifications related to flightlessness. *Pachyanas chathamica* is represented by relatively few skeletal elements (Oliver, 1955) and is not discussed here; the genus currently is under study independently by R. J. Scarlett (pers. comm.) and P. R. Millener (pers. comm.). With the exception of *Cnemiornis*, which has a comparatively long history of taxonomic reclassification and description, these subfossil endemics have received little attention from avian systematists since their original description.

A phylogenetic analysis of Recent anseriform genera (Livezey, 1986), based largely on comparative osteology, permitted a reappraisal of the relationships and classification of these endemic waterfowl. In this paper I: (1) present analyses of characters of *Cnemiornis*, *Euryanas*, and the extinct New Zealand swan *Cygnus sumnerensis*; (2) construct phylogenetic trees for these groups based on these characters; (3) propose a revised classification of these taxa; and (4) discuss selected evolutionary and biogeographic implications of these findings.

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MATERIALS AND METHODS

I examined specimens of *Cnemiornis calcitrans* and *C. gracilis* (= *septentrionalis*) at the British Museum (South Kensington), Canterbury Museum (Christchurch), Otago Museum (Dunedin), and the National Museum of New Zealand (Wellington). Elements of *Cnemiornis* illustrated herein were borrowed from the British Museum (BM). *Euryanas finschi* and *Cygnus sumnerensis* were studied using specimens held at the Otago Museum. I endeavored unsuccessfully to borrow specimens of *Euryanas* for purposes of illustration and confirmation of characters; therefore the analysis of this genus must remain preliminary. Skeletal specimens of anhimids, *Anseranas*, *Dendrocygna*, *Cereopsis*, *Branta*, and *Chenonetta* were made available by the Museum of Natural History, University of Kansas (KU) and U. S. National Museum of Natural History (USNM).

Fundamentals of phylogenetic (cladistic) analysis are detailed in Wiley (1981). Characters of available elements were coded as described in Livezey (1986), which in turn was based in large part on the comparative osteology of Woolfenden (1961). Anatomical nomenclature follows Howard (1929), Woolfenden (1961), and Livezey (1986). Characters are discussed in the "phylogenetic order" proposed by Livezey (1986), i.e., from the most inclusive (ordinal) characters to the least inclusive characters (those supporting subfamilial and tribal relationships); characters are coded as in Livezey (1986). Most skeletal elements of the Recent genera relevant to this study were illustrated by Livezey and Martin (1988). Phylogenetic trees were generated using the PAUP program (Swofford, 1985) based on the criterion of maximal parsimony of character change (Wiley, 1981).

ACCOUNTS OF GENERA

Cnemiornis spp.

Taxonomic history. Owen (1866) described and illustrated a variety of postcranial skeletal elements of a previously unknown large, flightless bird, which he named *Cnemiornis calcitrans*, from deposits in a limestone fissure at Timaru, South Island. Owen (1866) compared the elements with those of the moas (Dinornithidae) and the flightless gruiform *Aptornis*, but proposed no systematic placement for the species. Hector (1873a, b, 1874) examined more material for the species, including a skull and a complete sternum, and recognized it as a member of the "Lamellirostrate Natatores" (= Anseriformes). Owen (1875, reprinted in 1879) confirmed this classification and, based on the additional material collected since his earlier work, concluded that the humerus attributed to *Cnemiornis* in the original description (Owen, 1866) was actually that of the flightless gruiform *Aptornis*. Owen (1875) also

presented detailed osteological comparisons of *Cnemiornis* with the modern Cape Barren Goose (*Cereopsis novaehollandiae*) of Australia and a flightless steamer-duck (*Tachyeres cf. pteneres*) of South America, and, finding that *Cnemiornis* was more similar to the former, inferred that *Cnemiornis* was of anserine affinity. This decision was to influence profoundly the subsequent classifications of the genus.

Forbes (1890) discovered that the coracoids illustrated by Owen (1875, 1879) as those of *Cnemiornis* were instead those of the unique flightless gruiform *Aptornis*, and stated that the coracoid of *Cnemiornis* closely resembled that of *Cereopsis*. Forbes (1891) contributed to this perception of close relationship with his report of a *Cereopsis* from New Zealand, to which, on the basis of a subfossil cranial fragment, he gave the name *novaezealandiae*. Lydekker (1891) listed *Cnemiornis calcitrans* within the Cereopsinae, and noted several small specimens that (p. 102) "...indicate a distinct species;" he also illustrated a coracoid of *Cnemiornis*. Forbes (1891, 1892a, b) distinguished a smaller species of *Cnemiornis* of the North Island (*C. gracilis*) from the larger South Island form (*calcitrans*); he (1891) also proposed a third species, *C. minor*, on the basis of several tibiotarsi from the South Island.

Oliver (1930, 1945, 1955) followed Owen in his placement of *Cnemiornis* with *Cereopsis*, and he considered both to be "geese." Oliver justified this classification using comparisons (mostly cranial) between the two genera, but acknowledged a number of conspicuous dissimilarities in osteology and did not discuss comparisons with any other genera. Oliver (1930, 1955) also proposed the name *C. septentrionalis* for the North Island form. Lambrecht (1933) listed three species (*calcitrans*, *gracilis*, *minor*) of *Cnemiornis*, also under the subfamily Cereopsinae, after the typical geese. Delacour (1954:199) endorsed this practice with the comment: "...the genus *Cereopsis* has no very close living relative, although the extinct *Cnemiornis calcitrans* from New Zealand was probably similar."

Dawson (1958) re-evaluated several of the taxonomic decisions based on the types designated by Forbes and found that: (1) the supposed Quaternary record of *Cereopsis "novaezealandiae"* from New Zealand was based on the misidentification of a fragmentary specimen of *Cnemiornis calcitrans*, and (2) that *C. septentrionalis* Oliver is a junior synonym of *C. gracilis* Forbes.

Both Brodkorb (1964) and Howard (1964) adhered to the tradition of listing *Cnemiornis* with *Cereopsis* but, in accordance with the re-assignment of *Cereopsis* to the shelducks (Tadorninae) by Delacour and Mayr (1945), placed both genera in or next to this subfamily. Delacour (1964) dismissed the osteologically based conclusion of Woolfenden (1961) and the ethological inference of Johnsgard (1961a) that *Cereopsis* should be returned to the Anserinae.

Character analysis. I examined virtually all major skeletal elements of *Cnemiornis*, including the skull, humerus, radius, ulna, carpometacarpus,

femur, tibiotarsus, tarsometatarsus, sternum, coracoid, scapula, furcula, and pelvis. Most were represented by several specimens. The quadrate, pterygoid-palatine complex, and trachea were not available for study. The northern and southern "species" of *Cnemiornis* differed in size but were identical in the characters discussed below, and are considered together under the generic taxon in descriptions and phylogenetic analyses. The skull and a variety of postcranial elements of *Cnemiornis* were illustrated in Owen (1866, 1875, 1879) and Hector (1893a, b).

Cnemiornis shared several derived characters with all others of the Anseriformes, including bill lamellae (13b, indicated on the ventral surfaces of the premaxillae), recurved and pointed retroarticular processes of the mandible (14b), pedicellate basipterygoid processes (20b), and reduced furcular process of the furcula (102b). Several synapomorphies support the membership of *Cnemiornis* in the suborder Anseres (anseriforms exclusive of the Anhimidae): occipital fontanelles are indicated in outline, although (secondarily) closed, as they are in some specimens of large Anserinae (9b, see fig. 3 in Hector 1873a); and the caudal terminus of the pubis shows some ventral orientation (116b, although more slight than in *Anseranas*; Fig. 1).

Several characters indicate that *Cnemiornis* represents a branch after *Anseranas* (i.e., appears to be synapomorphic with the Anatidae, *sensu stricto*). One of these is the rounded cranial terminus of the upper bill (12c). Another is the lack of an iliac recess in the pelvis (120b, illustrated in plate XIV of Hector 1893a). Two others are of questionable reliability because of the radical morphological changes associated with flightlessness: the approximately equal distal extent of the facets for digits II and III of the carpometacarpus (45b) and the absence of a pneumatic foramen in the dorsal surface of the coracoid cranial to the sternal facet (93b). The third synapomorphy uniting *Cnemiornis* with the Anatidae is the absence of a facet for metatarsal I on the caudal surface of the tarsometatarsus (71b).

A number of osteological characters show that *Cnemiornis* was more primitive than *Dendrocygna* and the rest of the Anatidae, i.e., was sympleiomorphic with *Anseranas* and indicate that *Cnemiornis* diverged from other Anseres prior to the Dendrocygnines. These characters include: the relatively caudal orientation of the femoral head (51a); the approximately equal distal extent of the tarsometatarsal trochleae for digits II and IV (68a; illustrated in Owen, 1866, plate 67, and described by Owen, 1875, pp. 269-270), a condition coincident with the lack of caudal rotation of the inner trochlea; a moderate lateral displacement of the calcaneum on the tarsometatarsus (72a; Fig. 2); the strictly cranio-caudal orientation of the (incompletely ossified) distal foramen of the tarsometatarsus (77a; Fig. 3); the presence of a large, densely margined foramen at the base of the procoracoid (92a, see below); the long, wide, and rounded conformation of the sternocoracoidal process of the coracoid (99a, shared also with *Cereopsis*); and the equal proximal extent of

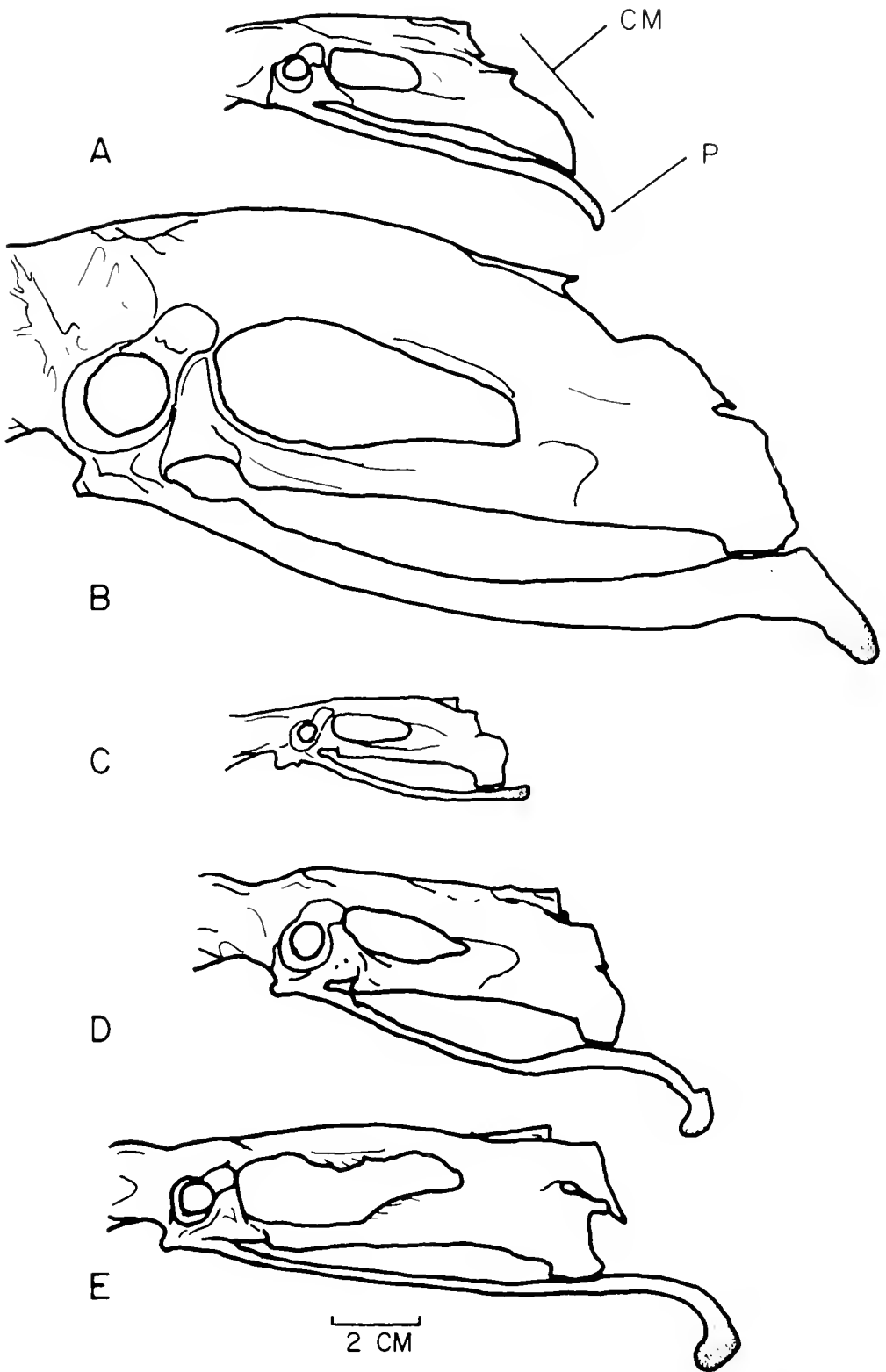


Fig. 1. Postacetabular portions of the pelvis, lateral surfaces: (A) *Anseranas semipalmata* (KU 80620); (B) *Cnemiornis calcitrans* (BM 75.12.15.4); (C) *Dendrocygna autumnalis* (KU 37725); (D) *Cereopsis novaehollandiae* (USNM 430244); and (E) *Branta canadensis* (KU 23403). Caudal margins of illium and ischium (CM) and caudal terminus of pubis (P) are indicated on *Anseranas*.

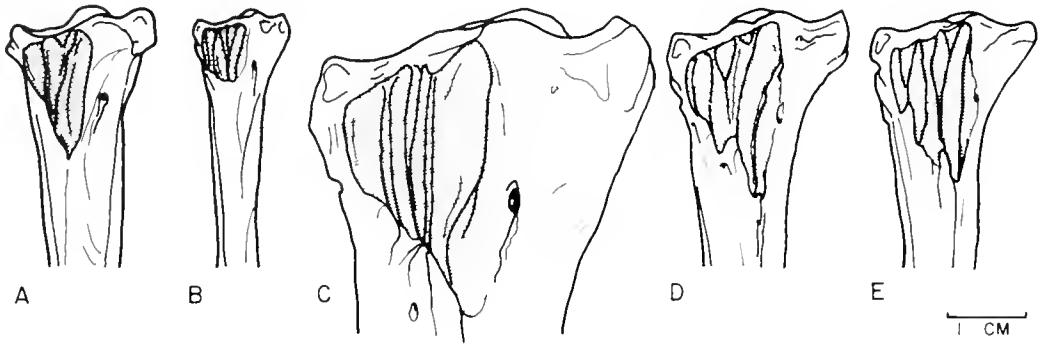


Fig. 2. Proximal ends of the left tarsometatarsus, caudal surfaces: (A) *Anseranas semipalmata* (KU 80620); (B) *Dendrocygna autumnalis* (KU 37725); (C) *Cnemiornis calcitrans* (BM 75.12.15.32); (D) *Cereopsis novaehollandiae* (USNM 429730); and (E) *Branta canadensis* (KU 23403). Calcaneum is shown in stipple.

the coracoidal process and acromion of the scapula (109a). Also, the costal margin of the extremely modified sternum of *Cnemiornis* occupies slightly less than half of the basin length (86a), a primitive proportionality found only in anhimids and *Anseranas* among Recent anseriforms. *Cnemiornis* lacks, however, all of the diagnostic autapomorphies of *Anseranas* (Livezey, 1986). Three subordinal characters (88, 100, 104) were problematic because of the dubious homologies of states related to flightlessness; for example, the reduced furcula of *Cnemiornis* shows moderate flattening of the clavicles, reminiscent of that in the Anhimidae (104b), but the state was coded as “missing” for *Cnemiornis*.

The presence of a conspicuous procoracoidal foramen (92a) in *Cnemiornis* is especially compelling evidence of its primitiveness; this character typically occurs among modern Anseriformes only in the Anhimidae and *Anseranas* (Woolfenden, 1961; Livezey, 1986). This primitive character is variable in conformational detail, however, and deserves more detailed description. A densely margined foramen is characteristic of the anhimids (*Chauna* and

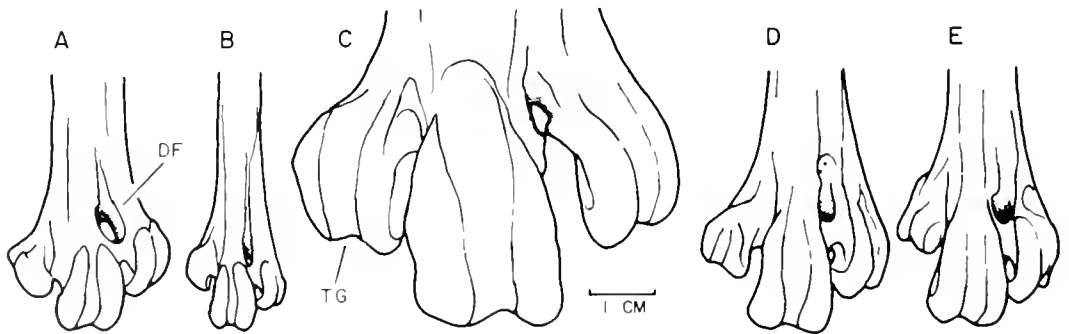


Fig. 3. Distal ends of the left tarsometatarsus, cranial surfaces: (A) *Anseranas semipalmata* (KU 80620); (B) *Dendrocygna autumnalis* (KU 37725); (C) *Cnemiornis calcitrans* (BM 75.12.15.32); (D) *Cereopsis novaehollandiae* (USNM 429738); and (E) *Branta canadensis* (KU 23403). Distal foramen (DF) and trochlear groove (TG) are indicated; note also the relative distal extent of lateral and medial trochleae in A through C vs. that in D and E.

Anhima), *Anseranas*, and *Cnemiornis* (Fig. 4), although considerable variation occurs in at least *Chauna* (Livezey, 1986). A superficially similar structure is found infrequently in *Cereopsis* (perhaps only in captive birds), but is distinguishable (when present) by its thin medial margin, evidently an ossified ligament. The "foramina" of most *Cereopsis* also differ from those of *Anseranas* and *Cnemiornis* in lacking an enclosed pneumatic foramen to the interior of the element in their caudal margins. Variation of this character in *Cereopsis* is indicated by the range of variation seen in a series of skeletons of captive birds held in the U. S. National Museum (Fig. 4). This structure varies considerably in *Cereopsis*, and differences occur even within individuals; the specimen with a completely closed foramen in its right coracoid (Fig. 4g) lacked the suggestion of closure in its left coracoid (i.e., resembled Fig. 4e).

Unfortunately, the early descriptions of the coracoid of *Cnemiornis* were largely erroneous. Owen (1875, 1879) figured coracoids which he attributed to *Cnemiornis* and *Cereopsis*, but those labelled as *Cnemiornis* are instead those of the gruiform *Aptornis* (Forbes 1890; pers. obs.), whereas the coracoid attributed to *Cereopsis* also is assigned incorrectly. The latter (plate XXXVII in Owen [1875]) is a coracoid with a prominent procoracoidal foramen and appears to be identical to the coracoid of *Cnemiornis* and almost certainly pertains to that genus. Lydekker (1891) illustrated a genuine coracoid of *Cnemiornis*, but stated (p. 100) without supporting details that "This specimen (fig. 26) agrees very closely with the coracoid of *Cereopsis*." The notion that a procoracoidal foramen occurs in some Anserinae was perpetuated by the statement of Howard (1964:250) that "...this foramen is rarely found in the *Anatidae* [*sic*] except in *Anseranas* and occasionally in certain swans." Although no details were given, this observation by Howard probably stemmed from the traditional assignment of certain primitive fossil anseriforms (e.g., *Cygnopterus*) to the Anserinae (Livezey, 1986) or to the infrequent foramen-like structures seen in procoracoidal processes of some anserines (Fig. 4).

Several synapomorphies unite *Cnemiornis* with the Anatidae exclusive of the Dendrocygninae: the caudal margins of the ilium and ischium present an obliquely sloping aspect (114b; Fig. 1); the inner cnemial crest of the tibiotarsus shows slight, perhaps equivocal lateral deflection (63b); and the tarsometatarsal trochlea for digit II is grooved (74b, Fig. 3; see discussion of homoplasy by Livezey and Martin, 1988).

Numerous characters of the wing and pectoral girdle, elements that were modified substantially in association with the loss of flight in *Cnemiornis*, were not comparable to the states defined for Recent anseriforms (Livezey, 1986). These characters, several of which present difficulties in comparisons even among some flighted waterfowl, include features of the carpometacarpus (37, 38, 43, 44), sternum (78, 79, 81, 88, 89), coracoid (96, 100), furcula

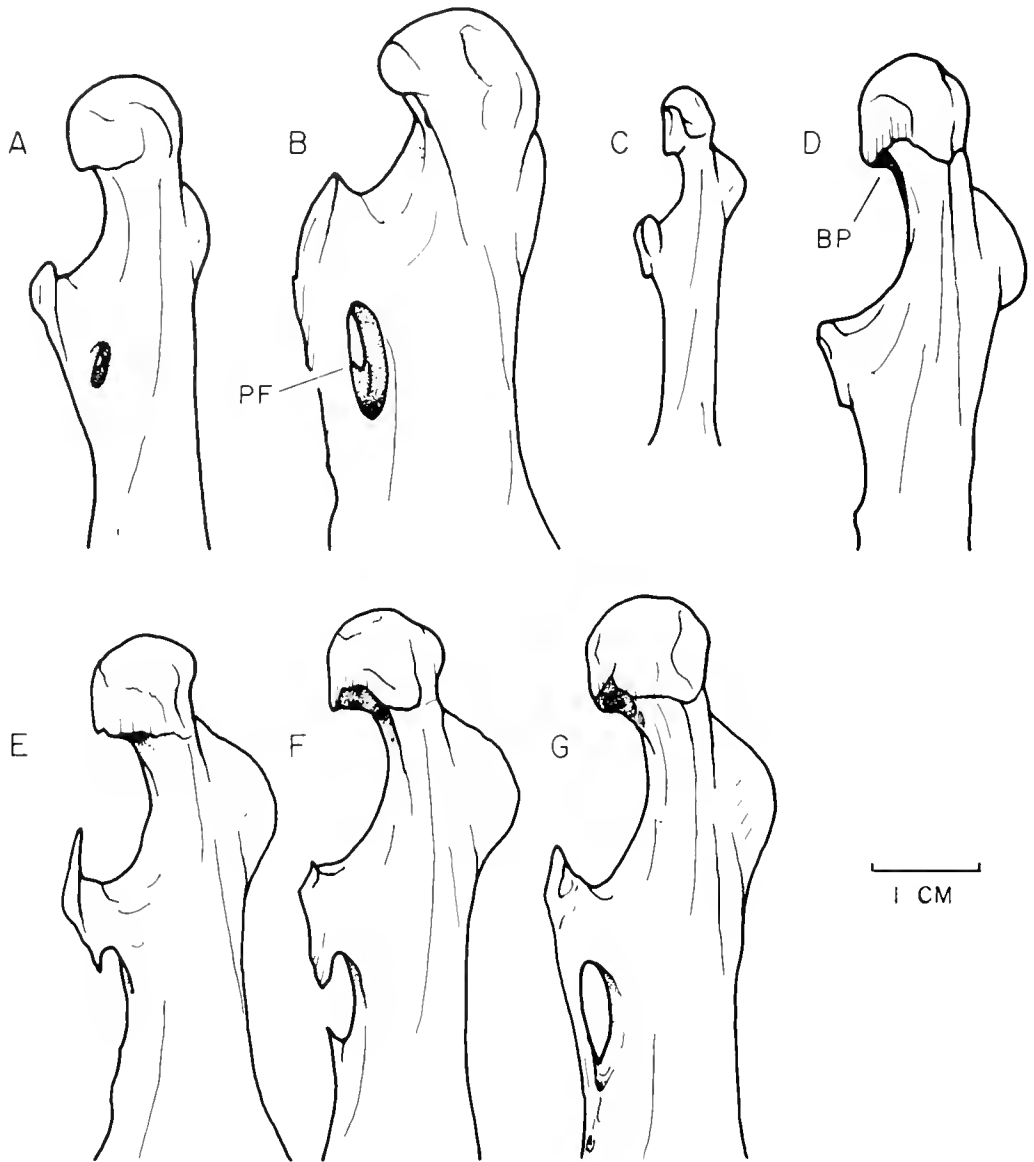


Fig. 4. Cranial portions of the left coracoid, ventral surfaces: (A) *Anseranas semipalmata* (KU 80620); (B) *Cnemiornis calcitrans* (BM A.1521); (C) *Dendrocygna autumnalis* (KU 37725); (D) *Branta canadensis* (KU 23403); (E-G) *Cereopsis novaehollandiae* (USNM 420244, 429738, 318044, respectively). Procoracoidal foramen (PF) and pneumatic area under brachial tuberosity (BP) are indicated.

(101, 105), and scapula (108, 112).

Cnemiornis lacks the diagnostic synapomorphies of the true geese (Anserini): it evidently retained the primitive number of 17 cervical vertebrae, including the axis and atlas (21a; cf. partial counts in Hector [1873a, b], reconstruction in Owen [1875], and mounted skeleton BM 75.12.15.4); it shows no spur-like elaboration of metacarpal I (42a); there are no pneumatic foramina under the brachial tuberosity of the coracoid (95a; Fig. 1); and its pubes lack caudal flanges (117a; Fig. 1). *Cnemiornis* does not share the autapomorphic supraorbital process (11a), pneumatic swelling of the fronto-

nasal region (16a), or dorsal bowing of the upper bill (19a) characteristic of *Cereopsis*.

Neither Brodkorb (1964) nor Howard (1964) offered osteological support for their placement of *Cnemiornis* with the shelducks (Tadorninae); this assignment evidently resulted from its traditional association with *Cereopsis*, itself not tadornine (Woolfenden, 1961; Livezey, 1986). However, it seems prudent to review the skeletal evidence against a close relationship between *Cnemiornis* and the Tadorninae. In addition to the symplesiomorphies of *Cnemiornis* and *Anseranas* discussed above, several character states of *Cnemiornis* are primitive relative to those of the larger clade including *Stictonetta*, *Plectropterus*, the Tadorninae and the Anatinae: the retention of the primitive number of cervical vertebrae (21a); the orientation of the humeral capital shaft ridge toward the head (22a); the short capital groove of the humerus (23a); the unelevated humeral facet of the anterior articular ligament (26a); the proximally rotated internal tuberosity of the humerus (27a); the dorsal surface of metacarpal II is flattened proximally (39a); the attachment site of *M. extensor metacarpi ulnaris* on the carpometacarpus is completely proximad to the proximal fornx (43a); and the lack of a medial protuberance in the ventral manubrial region of the sternum (79c). In addition, *Cnemiornis* is more primitive than the Tadorninae *sensu stricto* in the unenlarged process of metacarpal I (42a) and the tibiotarsus without torsion about its long axis (61a).

Euryanas finschi

Taxonomic history. Van Beneden (1875) described a small duck from subfossil remains found in Earnsclough Cave, New Zealand, and named it *Anas finschi*. This paper, in French, was followed by a report in English (Van Beneden, 1876). In both papers, Van Beneden compared elements of *finschi* variously with those of the Recent *Dendrocygna eytoni*, *Anas gibberifrons*, *Aythya fuligula*, and *Bucephala clangula*, as well as to the Miocene fossil *Mionetta* (“*Anas*”) *blanchardi* (Livezey and Martin, 1988). Hamilton (1892) reported the discovery of more specimens of *finschi* in the fissures at Castle Rocks.

Oliver (1930) placed the species in its own genus *Euryanas*, which he (1930, 1945, 1955) believed compared favorably (using skull characters) with the Maned Duck (*Chenonetta jubata*), a morphologically and behaviorally unique endemic of Australia (Delacour, 1959). Lambrecht (1933) placed *E. finschi* within the Anatinae. Howard (1964), following the assignment of *Chenonetta* to the “perching ducks” (“Tribe Cairinini”) by Delacour and Mayr (1945) and Delacour (1956), placed *Euryanas* in this tribe. Without comment, however, Brodkorb (1964) listed *Euryanas* within the “spur-winged geese” (his Plectropterinae).

Character analysis. I examined specimens of the skull (lacking quadrates and pterygoid-palatine complex), humerus, ulna, carpometacarpus, femur, tibiotarsus, tarsometatarsus, sternum, costae, coracoid, furcula, scapula, and pelvis of *Euryanas*. S. L. Olson (*in litt.*) described the syringeal bulla of *Euryanas* as being of typical anatine form (*sensu Anas, Chenonetta*; 6c). The skull and a number of the postcranial elements of *Euryanas finschi* were figured by Van Beneden (1875, 1876).

Inclusion of *Euryanas* within the suborder Anseres is supported by all available characters listed by Livezey (1986), including its typically "duck-like" bill. Synapomorphies uniting *Euryanas* with other Anatidae (*sensu stricto*, excluding *Anseranas*) are equally numerous, including: the craniomedial orientation of the femoral head (51b), the lateral deflection of the inner cnemial crest of the tibiotarsus (63b), the proximal position of the tarsometatarsal trochlea for digit II (68b), the orientation of the distal foramen of the tarsometatarsus (77b), the absence of a procoracoidal foramen (92b) or an iliac recess in the pelvis (120b). Two synapomorphies show *Euryanas* to be derived with respect to *Dendrocygna*—a grooved tarsometatarsal trochlea for digit II (74b) and the obliquely sloping caudal margins of the ilium and ischium (114b).

Additional synapomorphies support a closer relationship of *Euryanas* with *Stictonetta* + *Plectropterus* + Tadorninae + Anatinae than with *Thalassornis* or the Anserinae: the orientation of the capital shaft ridge (22b) and capital groove (23b) of the humerus; and the presence of a notch (although weak) in the external rim of the carpal trochlea (38b), the rounded dorsum of metacarpal II (39b), and the position of the scar of *M. extensor metacarpi ulnaris* (43b) of the carpometacarpus. With the exception of a widening of the scapular blade (108b), *Euryanas* lacks the synapomorphies characteristic of the Anserinae (e.g., characters 85a, 95a; Livezey, 1986).

Compared with the shelducks, *Euryanas* is primitive in the unelevated facet for the anterior articular ligament (26a) and proximally oriented internal tuberosity (27a) of the humerus, and lacks the tadornine synapomorphies of a carpometacarpal spur (42a) and tibiotarsal torsion (61a). *Euryanas* is plesiomorphic with respect to the Anatinae in a number of characters, notably in the rounded, anconally concave deltoid crest (25a) and prominent, buttressed external tuberosity (32a) of its humerus.

These characters indicate that *Euryanas* diverged from modern anatid lineages after the basal anatid grade of *Dendrocygna*, *Thalassornis*, and the Anserinae, but before the Tadorninae (Livezey, 1986). *Euryanas* lacks the somewhat convergent features indicative of diving specialization found in *Thalassornis*, pochards (Aythyini), sea ducks (Mergini), and stiff-tailed ducks (Oxyurini), especially characters of the femur (52a, 54a, 55a, 56a), tibiotarsus (64a, 65a), tarsometatarsus (69a, 75a), sternum (78a), and pelvis (119a).

Both *Euryanas* and *Stictonetta* have long, peg-like ventral manubrial spines (79d), a character shared also by the more derived genus *Anas*; this feature, however, is variable and its transformational pattern is inadequately resolved (Livezey, 1986). *Euryanas* differs from *Stictonetta* in two characters of the coracoid, both of problematic polarity and transformation: the ventral surface is without a deep depression (96b) and the ventral sternal facet is without a buttress (100a).

The presence of an asymmetrically enlarged, unfenestrated syringeal bulla in *Euryanas* (6a; S. L. Olson, *in litt.*) supports, however, a closer relationship between *Euryanas* and the terminal clade of *Plectropterus* + Tadorninae + Anatinae than with *Stictonetta*.

Cygnus sumnerensis

Taxonomic history. Forbes (1890a, b) and Sclater (1890) announced the discovery of three coracoids and a partial humerus of a large, extinct swan from a cave near Christchurch, which Forbes (1890a) named *Chenopsis sumnerensis*. Forbes (1891) reported the collection of more material for the species, and speculated that more than one species might be represented. Forbes (1893a, b) later reported numerous specimens of the swan from the Chatham Islands.

Oliver (1930) and Lambrecht (1933) listed *Chenopsis sumnerensis* as a typical swan. Oliver (1955) later reassigned the fossil swan to *Cygnus* in accordance with current generic taxonomy; he also proposed a new species name, *C. chathamicus*, arguing that the earlier name should be abandoned because the types for the species described by Forbes (1890a, b) could not be identified. Dawson (1958) reported the rediscovery of this type material and relegated *chathamicus* to junior synonymy of *C. sumnerensis*, a restoration followed by Brodkorb (1964) and Howard (1964).

Character analysis. I examined all important skeletal elements of *C. sumnerensis* except the quadrate, pterygoid-palatine complex, and syrinx. Oliver (1955:603) figured a mounted, presumably composite skeleton of this species.

C. sumnerensis is synapomorphic with modern geese and swans (Anserinae) in the presence of foramina on the midline and cranial margin of the dorsal surface of the sternal basin (89a), the presence of foramina under the brachial tuberosity of the coracoid (95b–c), the lack of a ventral depression on the coracoid (96b), reduced coracoidal tuberosities on the furcula (101a–b), and a caudal widening of the pubis (117b). The species is united with extant swans (Cygnini) by the caudomedial extension of the xiphial region of the sternal basin (85b), the presence of a small foramen in the cranial edge of its uninflated sternal carina (87b), and the comparatively medial orientation of the sternal intermuscular line (88a). Two apparent synapomorphies are shared

with the modern geese (Anserini): an enlarged process of metacarpal I (42c) and the diverse foramina present under the brachial tuberosity of the coracoid (95c). The moderately low consistency and sexual variation of the first (Livezey, 1986), the intermediate condition of the second, and the limited material available for characterization of *C. sumnerensis* support the interpretation that these similarities are convergent. *C. sumnerensis* lacks the derived, trachea-related modifications of the sternal carina and furcula found in *Olor* (87c, 106b).

CONSTRUCTION OF TREES

Methodological Considerations

For derivation of phylogenetic trees, I used the characters described in Livezey (1986), but excluded from analyses those characters which were not informative for inferences concerning relationships among subfamilies. Excluded characters were unique autapomorphies (particularly of Anhimidae, *Anseranas*, and *Plectropterus*), diving-related autapomorphies of *Thalassornis* (several convergent with some members of the Tadorninae and Anatinae), and characters which were invariant among the Anseriformes exclusive of the Tadorninae and Anatinae. This reduced the characters analyzed to 62 which were useful for inferences in the basal segment of the order (Figs. 2 and part of Fig. 3 in Livezey, 1986), the segment which, on the basis of the foregoing character analyses, included the subfossil genera to be placed. As in Livezey (1986), several characters were analyzed as unordered (Table 1). In all analyses, two primary weighting schemes were employed: the "standard" weighting scheme of Livezey (1986), in which the syringeal bulla (character 6) was given a weight of two and all other characters were given unit weight; and the "unit" weighting scheme in which all characters were given unit weight.

A further simplification was made through the reduction of the taxonomic units considered in construction of trees. Recent taxa analyzed were reduced to 12 taxonomic units, in addition to the hypothetical ancestor proposed by Livezey (1986): the Anhimidae, seven single-genus lineages (*Anseranas*, *Cereopsis*, *Coscoroba*, *Dendrocygna*, *Thalassornis*, *Stictonetta*, and *Plectropterus*), and four taxa representing well-established monophyletic groups of genera (*Branta-Anser*, *Cygnus-Olor*, Tadorninae, and Anatinae). This streamlined set of Recent taxa was used for separate (14-taxon, 62-character) phylogenetic analyses of *Cnemiornis* and *Euryanas* using the exhaustive branch-and-bound algorithm in the PAUP program, a time-consuming technique for finding all possible shortest trees which is practical only with small numbers of taxa (Swofford, 1985). The body of evidence confirming the systematic position of *Cygnus sumnerensis* among the moderately derived

TABLE 1. Character-state matrix for basal extant lineages and two subfossil genera of Anseriformes. Character numbers and state codings follow Livezey (1986). Characters analyzed as unordered are indicated by asterisks and "missing" data are shown as an "x." Problematic states for *Cnemionis*, alternatively treated as "missing," are enclosed by brackets.

Taxon	Character																																		
	2	6*	9	10*	11	12	13	14	15	16*	18	19	20	21*	22	23	25	26	27	32	33	38	39	42*	43	44	45*	51	61	63	68	71	72	74	
Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	
Anhimidae	a	a	a	b	a	a	a	a	a	a	a	a	a	b	a	a	a	a	a	a	a	a	a	b	a	a	a	a	a	a	a	a	a	a	
<i>Anseranas</i>	a	b	a	b	a	b	a	a	a	a	a	a	a	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	
<i>Dendrocygna</i>	a	b	d	a	a	b	a	a	a	a	a	a	a	b	a	a	a	a	a	a	a	a	a	a	a	a	b	a	b	a	b	a	b	a	
<i>Thalassornis</i>	a	a	b	c	a	c	b	b	a	b	a	a	a	b	a	a	a	a	a	a	a	a	a	a	a	a	b	b	a	b	b	b	b	b	
<i>Cereopsis</i>	a	a	b	e	b	c	b	b	a	c	b	a	a	b	a	a	a	a	a	a	a	a	a	a	a	a	b	b	a	b	b	b	b	b	
<i>Branta/Anser</i>	a	a	b	e	a	c	b	b	a	a	b	a	a	b	a	a	a	a	a	a	a	a	a	a	a	a	b	b	a	b	b	b	b	b	
<i>Coscoroba</i>	a	a	b	e	a	c	b	b	a	a	b	a	a	b	c	a	a	a	a	a	a	a	a	a	a	a	b	b	a	b	b	b	b	b	b
<i>Cygnus/Olor</i>	a	a	b	e	a	c	b	b	a	a	b	a	a	b	d	a	a	a	a	a	a	a	a	a	a	a	a	a	b	a	b	b	b	b	b
<i>Stictonetta</i>	a	a	b	e	a	c	b	b	a	a	b	a	a	b	a	b	a	a	a	a	a	a	a	a	a	a	b	b	a	b	b	b	b	b	b
<i>Plectropterus</i>	b	c	b	e	b	c	b	b	a	a	b	a	a	b	a	b	b	a	a	a	a	a	a	a	a	a	a	b	b	a	b	b	b	b	b
Tadorninae	b	c	b	e	b	c	b	b	a	a	b	a	b	e	b	b	a	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b
Anatinae	b	c	b	e	a	c	b	b	a	a	b	a	b	e	c	b	a	b	b	b	b	b	b	b	b	b	b	b	b	a	b	b	b	b	b
<i>Cnemionis</i>	x	x	b	x	a	c	b	b	x	a	x	a	a	b	a	a	x	a	a	a	x	x	[a]	a	a	[a]	x	b	a	a	b	a	b	a	b
<i>Euryanas</i>	x	c	b	e	x	c	b	b	x	x	x	x	a	b	x	b	a	a	a	a	x	x	a	b	a	b	x	b	a	b	a	b	b	b	b

TABLE 1. Continued

Taxon	Characters																												
	77	78*	79*	81*	85	87	88	89*	92	93	95*	96*	99	100	101*	102	104	105	108	109	111*	112	114	115	116	117	118	120	
Ancestor	a	x	x	x	a	a	a	x	a	a	a	x	a	a	a	a	a	a	a	a	x	a	a	a	a	a	a	a	
Anhimidae	a	b	b	a	a	a	c	a	a	a	a	b	a	a	a	b	b	a	a	a	a	a	a	a	a	a	a	a	
<i>Anseranas</i>	a	b	b	a	a	a	b	c	a	a	a	b	a	a	a	a	a	a	a	a	a	a	a	a	b	a	a	a	
<i>Dendrocygna</i>	b	a	c	a	a	a	b	a	b	a	b	a	b	b	a	a	a	a	a	a	b	a	a	a	b	a	b	b	
<i>Thalassornis</i>	b	c	c	a	a	a	b	b	b	b	a	a	b	b	a	a	a	a	a	a	b	a	a	a	b	a	b	b	
<i>Cereopsis</i>	b	a	c	a	a	a	b	a	b	b	c	b	a	b	b	a	a	a	b	b	a	b	a	a	b	b	b	b	
<i>Branta/Anser</i>	b	a	a	a	a	a	b	a	b	b	c	b	b	b	b	a	a	a	b	b	a	a	a	b	a	b	b	b	
<i>Coscoroba</i>	b	a	a	a	b	b	a	a	b	b	b	b	b	b	b	b	a	a	b	b	a	a	a	b	b	b	b	b	
<i>Cygnus/Olor</i>	b	a	a	a	b	b	a	a	b	b	b	b	b	b	b	b	a	c	b	b	b	a	b	b	b	b	b	b	
<i>Stictonetta</i>	b	a	d	b	a	a	b	a	b	b	a	a	b	b	a	a	a	a	a	b	a	a	b	a	b	a	b	b	
<i>Plectropterus</i>	b	a	c	b	a	a	b	b	b	b	a	b	b	b	b	a	a	a	a	b	a	a	b	a	b	a	b	b	
Tadorninae	b	a	e	b	a	a	b	b	b	b	a	b	b	a	a	a	a	a	a	b	a	a	b	a	b	a	b	b	
Anatinae	b	a	e	b	a	a	b	b	b	b	a	b	b	a	a	a	a	a	a	b	a	a	b	a	b	a	b	b	
<i>Chenionornis</i>	a	x	[c]	x	x	x	x	x	a	b	a	x	a	[a]	x	b	[b]	[a]	x	a	a	x	b	x	b	a	a	[a]	b
<i>Eurynas</i>	b	a	d	x	a	a	b	b	b	b	a	b	b	a	a	b	x	a	b	b	b	b	x	a	b	b	a	b	b

members of the modern genus *Cygnus* rendered unnecessary a numerical analysis of the species; a species-level analysis of *Cygnus* is not possible at present.

Cnemiornis spp.

The phylogenetic relationships of this genus were analyzed under a variety of alternative character codings and weights. An initial analysis was based on all 62 characters, for which 41 were determined for *Cnemiornis* (Table 1); all other character states were coded as "missing." A series of subsequent, progressively "conservative" analyses were performed in which an additional 1–7 characters considered to be problematic for *Cnemiornis*—two of the carpometacarpus (38, 43), one of the sternum (79), one of the coracoid (100), two of the furcula (104, 105), and one of the pelvis (118) were coded as "missing" as well. Both the "standard" and "unit" weighting schemes were employed. In addition, each of these analyses was performed with another somewhat problematic character, the procoracoidal foramen (92), assigned a unit weight (like all other characters) or with weight zero (i.e., it did not affect the derivation of trees); the latter treatment seems justified in light of intrageneric variation in this character and the possibility that the foramen typical of *Cnemiornis* is homologous to those found infrequently in *Cereopsis* (Fig. 4). None of these analytical variants altered the position of *Cnemiornis* in the resultant trees or the number of equally short trees found, but these modifications of data did produce minor differences in tree lengths and consistency indices. Consequently, the trees depicted in Fig. 5 are based on the most conservative analysis of *Cnemiornis*, in which 34 character states were specified for the genus.

In all analyses, *Cnemiornis* was inferred to be a lineage which diverged after *Anseranas* but before the divergence of the Recent taxa included in the Anatidae by Livezey (1986); i.e., *Cnemiornis* was found to be the sister-group of the suborder Anseres exclusive of *Anseranas* (Fig. 5). The position of *Cnemiornis* was supported by 15 character changes, between *Anseranas* and *Cnemiornis*, and seven character changes supportive of monophyly of the other Anseres. Two characters which were retained in all analyses and which were derived in *Cnemiornis* but primitive in *Dendrocygna* (characters 74, 114) were inferred to be reversals in the latter.

An unexpected finding of the branch-and-bound analyses of the reduced data set for extant taxa was that several, equally parsimonious permutations of *Dendrocygna*, *Thalassornis*, and the *Anserinae* are possible (Fig. 6). Only one of these is most parsimonious if *Cnemiornis* is included in the analysis (Fig. 5); this arrangement, in which the *Anserinae* are inferred to be the sister-group to the rest of the (Recent) Anatidae, differs from both of the two topologies described by Livezey (1986).

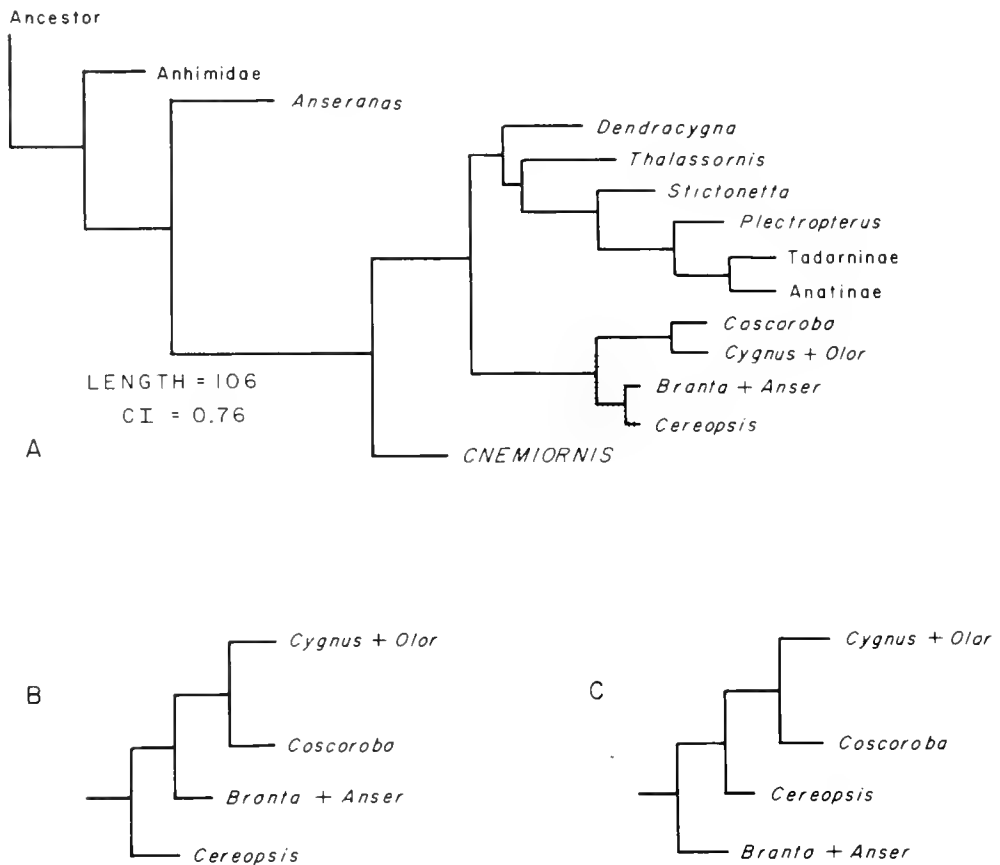


Fig. 5. Phylogenetic trees for *Cnemiornis* and basal lineages of Anseriformes: (A) Complete tree with one of three equally parsimonious topologies (for branches overlaid with stipple) for the geese (*Cereopsis*, *Anser*, and *Branta*); (B, C) Alternative topologies for the geese.

There also were three equally parsimonious topologies *within* the Anserinae, alternatives which were possible whether *Cnemiornis* was included in the analysis or not (Fig. 5). These topological variants are not directly relevant to the position of *Cnemiornis* in the tree, but one of these topologies—in which *Cereopsis* is hypothesized to be the sister-group to the rest of the subfamily (Fig. 5b)—would be favored in the event that symplesiomorphies between *Cnemiornis* and *Cereopsis* (not shared by other anserines) were to be documented. A strict consensus tree for the analysis of *Cnemiornis* depicts the Anserinae as a trichotomy involving *Cereopsis*, *Branta + Anser*, and the Cygnini.

Euryanas finschi

Of the 62 characters employed in the analyses of subfossil taxa, 50 were determined for *Euryanas* (Table 1); the other 12 were coded as “missing.” An exhaustive search for all most-parsimonious trees using the “standard” weighting scheme found nine equally parsimonious topologies, but in each *Euryanas* was the sister-group to the clade Tadorninae + Anatinae (Fig. 7a).

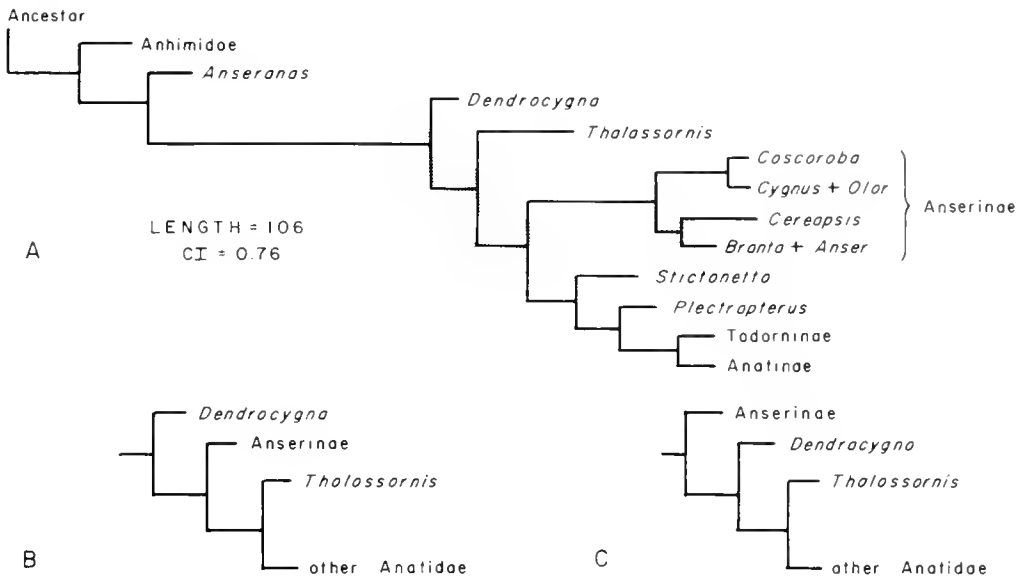


Fig. 6. Phylogenetic trees for extant basal lineages of Anseriformes: (A) Complete tree with one of three equally parsimonious topologies (for branches overlaid with stipple) for *Dendrocygna*, *Thalassornis*, and Anserinae (the last taxon shows three topologies depicted in Fig. 5); (B–C) Alternative topologies for the grade including *Dendrocygna*, *Thalassornis*, and Anserinae.

The topological variants resulted from two previously discussed, unresolved segments: (a) three alternative positions of *Dendrocygnus*, *Thalassornis*, and Anserinae; and (b) the three arrangements of *Cereopsis*, *Branta + Anser*, and the Cygnini within the Anserinae. Using the “unit” weighting scheme, 12 equally parsimonious trees were found, but once again *Euryanas* was the sister-group to the clade composed of Tadorninae and Anatinae in each. The majority of the topological variants resulted from combinations of arrangements within the unresolved grade and geese (discussed above); reduced weight of the syringeal bulla, however, permitted an additional sequence for the grade composed of *Stictonetta* and *Plectropterus* (three of 12 trees; Fig. 7b).

PROPOSED CLASSIFICATION

Based on the trees discussed above, I conclude that:

- (1) *Cnemiornis* is the sister-group to the Anatidae (*sensu* Livezey, 1986).
- (2) Inclusion of *Cnemiornis* in the phylogenetic analysis indicated that the subfamily Anserinae (true geese and swans, including *Cereopsis*) may be the sister-group to the rest of the family Anatidae (including Dendrocygninae).
- (3) *Euryanas* appears to be a moderately derived “proto-duck,” a member of a lineage that arose after the Anserinae, Dendrocygninae, and Thalassornithinae but before the divergence of the Tadorninae from the Anatinae; it appears to be the sister-group to the clade composed of the Tadorninae and Anatinae.

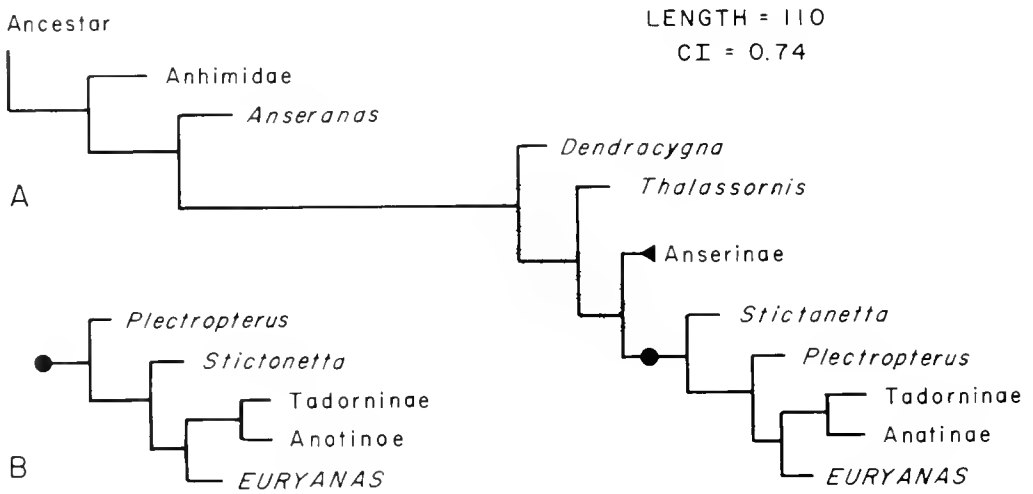


Fig. 7. Phylogenetic trees for *Euryanas* and basal lineages of Anseriformes: (A) Complete tree using weighting scheme of Livezey (1986), unresolved grade overlaid in stipple; (B) Alternative topology for terminal clade involving *Euryanas* if syringeal bulla (character 6) is given unit weight.

(4) *Cygnus sumnerensis* is a true swan (Cygnini), more derived than *Coscoroba* but less so than *Olor*; it agrees in its characters with those of the possibly paraphyletic genus *Cygnus* (*sensu stricto*; Livezey, 1986), which includes *C. atratus* of Australia.

Accordingly, I propose the following classification, based on the relevant section of the schemes presented by Livezey (1986) and Livezey and Martin (1988), and annotational conventions of Wiley (1981). Taxa analyzed herein are shown in boldface. *Sedis mutabilis* indicates that the phylogenetic sequences of associated sections are unresolved.

Order Anseriformes

Suborder Anseres

Family Anseranatidae

Family Cnemiornithidae Stejneger, 1885

Genus *Cnemiornis* Owen, 1865

C. calcitrans Owen, 1865

C. gracilis Forbes, 1891

Family Anatidae

Subfamily Dendrocygninae¹

Subfamily Dendrocheninae¹

Subfamily Thalassornithinae¹

Subfamily Anserinae¹

Tribe Anserini (possibly paraphyletic)

Tribe Cygnini

¹*sedis mutabilis*

Genus *Coscoroba*

Genus *Cygnus* (possibly paraphyletic)

C. sumnerensis (Forbes, 1890)

Genus *Olor*

Subfamily Stictonettinae

Genus *Stictonetta*

Subfamily Plectropterinae

Subfamily Euryanatinae, subfam. nov.

Genus *Euryanas* Oliver, 1930

E. finschi (Van Beneden, 1875)

Subfamily Tadorninae

Subfamily Anatinae

Diagnoses for Cnemiornithidae and Euryanatinae are as for the included genera (see character analyses above). The Cnemiornithidae can be characterized additionally by large size and reduced pectoral elements, both of which were illustrated and described previously (Owen, 1866, 1875; Hector, 1873a, b; Howard, 1964); representative measurements were given by Howard (1964). Note that in the foregoing partial classification the subfamily name Thalassornithinae is used instead of the incorrectly derived taxon Thalassorninae given in Livezey (1986).

DISCUSSION

This reappraisal indicates that *Cnemiornis* and *Euryanas* represent two variably primitive lineages endemic to New Zealand. The earlier classifications of these taxa were based largely on comparisons that were influenced profoundly by biogeographic preconceptions; classifications of *Cnemiornis*, *Euryanas*, and *Cygnus sumnerensis* were based largely on comparisons with *Cereopsis*, *Chenonetta*, and *Cygnus atratus* of Australia, respectively. This was a strangely parochial approach to the study of waterfowl, an ancient group in which several modern genera have cosmopolitan distributions (e.g., *Cygnus*, *Tadorna*, *Anas*). The early systematic analyses of these endemics also were limited by the taxa compared (e.g., Owen, 1875) and the virtual exclusion of postcranial characters from the pioneering work of Oliver (1930, 1945, 1955). The failure of previous workers to distinguish between primitive and derived characters undoubtedly contributed to these classificatory problems, as has been the case for many paleornithological investigations (Craft, 1980). The methodological and philosophical justification for cladistic analysis in paleontological study was reviewed by Schoch (1986).

The early perception of an "alliance" between *Cnemiornis* and *Cereopsis* evidently was based on very limited phenetic comparisons and the comparatively large body size of both genera. *Cnemiornis* was extremely derived

osteologically and of immense size (by anseriform standards); both characteristics were related to its obvious flightlessness, and reductions of wing elements and the sternal carina in this genus are among the most extreme in the Anseriformes (Livezey, in prep.). However, in virtually all other characters the genus is very primitive. The unique skeletal characters of *Cnemiornis* led Oliver (1945) to conclude the genus deserved subfamilial rank, while paradoxically maintaining the view that *Cnemiornis* "is a close ally of *Cereopsis*" (p. 125). The traditional view of such an "alliance" was so profound that, following the re-classification of *Cereopsis* to the Tadorninae (largely on behavioral grounds) by Delacour and Mayr (1945), *Cnemiornis* was similarly reclassified by Howard (1964) and Brodkorb (1964). Ironically, Howard (1964) herself had warned against such taxonomic revisions (in the context of the classification of a fossil anserine), indicating (pp. 268–269) "...the need for caution in attempting to trace an evolutionary line based on the names of fossils without careful review of the characteristics of the fossils themselves in the light of accumulating knowledge of existing forms."

Wetmore (1943) described the fragmentary tibiotarsus of a goose from Hawaii, *Geochen rhuax*, which he felt resembled *Cereopsis* (and by association of traditional taxonomy, *Cnemiornis*) most closely. As with *Cnemiornis*, *Geochen* followed the later movement of *Cereopsis* to the shelducks in both Brodkorb (1964) and Howard (1964). In contrast, the present study indicates that: (1) *Cnemiornis* is not a goose and is not closely related to *Cereopsis* (a true goose, Anserini) but instead represents a very early branch of the Anseriformes (i.e., is the sister-group to the Anatidae, *sensu stricto*); and (2) neither *Cnemiornis* nor *Cereopsis* belongs in the shelducks (Tadorninae). The finding that *Cereopsis* is anserine and not tadornine in relationship was inferred by several earlier investigations of osteology (Shufeldt, 1913; Verheyen, 1953; Woolfenden, 1961; Livezey, 1986). Furthermore, preliminary examinations of *Geochen* and flightless *Thambetochen* of Hawaii (Olson and Wetmore, 1976; Olson and James, 1982) indicate that these genera are probably anserine and not tadornine in relationship.

It has been suggested to me that several of the "primitive," non-gooselike characters found in *Cnemiornis* (especially of the pelvic limb) may be reversals associated with the terrestrial specialization, a condition related in turn to the evident flightlessness of the genus. Unfortunately, no compelling evidence for such functional relationships or for the occurrence of such reversals in other anseriforms has been demonstrated. Lacking such support, and given that several other "terrestrial" waterfowl (e.g., *Thambetochen*, *Branta sandvicensis*, *Chloephaga*) show none of these putative reversals (cf. Miller, 1937), the parsimonious inference remains that these characters reflect an early divergence for *Cnemiornis*. "Adaptive" rationalizations to retain *Cnemiornis* in the Anserini, and in particular to suggest that *Cnemiornis* is the sister-group of *Cereopsis*, not only assume synapomorphies not in

evidence, but also imply additional homoplasy in the associated phylogenetic hypothesis and are based on unsupported *ad hoc* arguments concerning presumed evolutionary change. A similar suite of “adaptational” rationalizations was suggested by Davies and Frith (1964) to conserve the classification of *Anseranas* within the Anserinae in the face of growing morphological evidence of its extreme primitiveness (cf. Delacour, 1954; Johnsgard, 1961b; Woolfenden, 1961).

Based on my studies of the osteology of waterfowl and the limited comparisons involving *Cnemiornis*, I suggest that the following structures may prove useful for further testing of the systematic position of the genus: the conformational details of the palate; patterns of cranial canals, including the morphology of foramina in the cranioventral floor of the cranium; the fine structure of vertebrae, especially the cervical vertebrae and those composing the synsacrum; and anatomical details of the calcaneum of the tarsometatarsus. Furthermore, I predict that the determination of homologous states and transformation series of such fine-grained characters may prove problematic if attempted for the entire order Anseriformes; study of a more restricted subgroup of taxa (e.g., *Anseranas*, *Cnemiornis*, *Dendrocygna*, *Cereopsis*, *Anser*, and *Stictonetta*) probably would be adequate for inferences regarding *Cnemiornis*. At least one of these character complexes—the morphology of the vertebral column—would provide insights into the augmentation of cervical vertebrae in *Anseranas* and the Anserinae and thereby also shed light on the relationships within the Anserinae.

Euryanas finschi also deserves continued study. The unfortunately limited material available for this study notwithstanding, there is substantial evidence that *Euryanas* is not anatine or tadornine (*sensu* Livezey, 1986); this lends some support to the observation by Oliver (1945:124) that *Euryanas* “...seem[s] to be more primitive than the typical ducks.” However, I am not persuaded by Oliver (1945) that *Chenonetta* and the New Zealand teal (*Anas chlorotis* and *A. aucklandica*) are similarly plesiomorphic, although *Chenonetta* is osteologically unusual in several respects (Woolfenden, 1961; Livezey, 1986). Skeletal elements deserving of particular attention in *Euryanas* are the skull, carpometacarpus, and tibiotarsus; the (modal) number of cervical vertebrae would be particularly useful for phylogenetic inference. Worthy (1988) inferred that there has been modest shortening of wing elements in *Euryanas* during recent millenia; whether this trend has modified any of the osteological characters considered here is not known. Two humeral characters which I found to be problematic in *Euryanas* (characters 22 and 33) seem likely candidates for such evolutionarily modified features; the capital shaft ridge (22) also may be similarly modified in *Chenonetta*, which shows a reversal in this character (Livezey, 1986).

Inclusion of *Cnemiornis* in the analysis indicated that, of the three alternative sequences of the extant taxa *Dendrocygna*, *Thalassornis*, and

Anserinae (Fig. 6), placement of the Anserinae as the sister-group of the rest of the Anatidae is most parsimonious (Fig. 5). The relatively poor resolution of the phylogenetic sequence of the Anserinae and Thalassorninae was indicated previously by Livezey (1986) and also by an analysis of the Miocene fossil *Mionetta blanchardi* (Livezey and Martin, 1988). The importance of fossils in the (cladistic) inference of phylogenetic relationships of extant taxa was demonstrated by Panchen and Smithson (1987) and Gauthier et al. (1988). In practice, however, this advantage must be weighed against the disadvantages associated with incomplete data, worn material, uncertain association, and unknown sex of many specimens of fossil and subfossil taxa.

The phylogenetic hypotheses proposed here add to the growing evidence of the diversity and probable origin of the Anseriformes in the Southern Hemisphere (Livezey, 1986). The very early divergence of *Cnemiornis* is concordant with the numerous flightlessness-related autapomorphies in the genus, in that it provides a much greater period of time for the accumulation of these evolutionary novelties. A parallel example of morphologically radical flightlessness in an ancient carinate lineage is the gruiform *Aptornis* (also endemic to New Zealand); formerly thought to be a rail (Oliver, 1945), *Aptornis* instead probably represents a separate family related to the Rallidae (cf. Olson, 1975).

The finding that *Euryanas* is not a member of the Anatinae underscores the diversity of the more primitive "proto-ducks" in the Southern Hemisphere in the past. Moreover, *Euryanas*, the extant *Thalassornis* of Africa and *Stictonetta* of Australia (Livezey, 1986), and several Miocene forms from the Northern Hemisphere (Livezey and Martin, 1988) indicate that there was a more widespread radiation of these "duck-like" anseriforms in the late Tertiary.

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SUMMARY

The phylogenetic relationships of several endemic subfossil Anseriformes of New Zealand—*Cnemiornis* spp., *Euryanas finschi*, and *Cygnus sumnerensis*—are re-examined using the osteological characters analysed in an earlier study of anseriform systematics (Livezey, 1986). Flightless *Cnemiornis*, traditionally considered to be a “goose” and closely related to the extant Australian genus *Cereopsis*, is shown to be a very primitive anseriform representing a branch shortly after that of *Anseranas* of Australia. *Euryanas finschi* is found to be a moderately derived “proto-duck,” most probably representing the sister-group to the clade including Tadorninae and Anatinae. *Cygnus sumnerensis* is confirmed to be a true swan (Cygnini), more derived than *Coscoroba* but less so than *Olor*. A revised classification is presented and selected biogeographic, analytical, and evolutionary implications are discussed.

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