A PHYLOGENETIC ANALYSIS OF POSTCRANIAL SKELETAL CHARACTERS OF THE RATITE BIRDS

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Abstract

A numerical cladistic analysis of 83 skeletal characters of the ratite birds produced a minimum-length tree in which: the ostriches (*Struthio*) and rheas (*Rhea*) form the sister group of the elephant-birds (*Aepyornis*); the cassowaries (*Casuarius*) are the sister group of the emus (*Dromaius*) are the sister group of the kiwis (*Apteryx*); and the *Struthio-Rhea-Aepyornis* and *Casuarius-Dromaius-Apteryx* clades are sister groups, together forming the sister group of the moas (Dinornithidae). The positions of the moas and elephant-birds varied among longer alternative topologies, in part because many of their character states are not known. In contrast, the pattern of branching among the extant ratites was insensitive to small increases in tree length and broadly congruent with the results of molecular comparisons.

Introduction

Although the living species of ostriches, rheas, cassowaries, emus and kiwis were described over 100 years ago, are few in number, and have been studied in considerable detail, avian systematists have been unable to reach a consensus about their phylogenetic relationships. The wide interest in flightless paleognaths and the regularity with which systematists have commented on them, however, belie the lack of adequate studies of the degree to which various sets of characters support alternative phylogenetic reconstructions. For instance, since Merrem (1813) united the large ratites because they lack keeled sterna, systematists have frequently invoked osteological characters to support their phylogenetic contentions, with important contributions by Huxley (1867), Mivart (1877), Fürbringer (1888, 1902), Pycraft (1900), McDowell (1948), Zavattari and Cellini (1956), Bock (1963), Cracraft (1974, 1987), and Rich (1979). However, despite the large amount of information produced by these studies, the osteological variation among the ostriches, rheas, cassowaries, emus and kiwis has not been rigorously analyzed.

Cracraft (1974), in an effort to provide such an analysis, studied the taxonomic distribution of 25 postcranial osteological characters. However, the set of characters employed by Cracraft contained virtually no homoplasy, a surprising result given that sets of postcranial skeletal characters in other groups (e.g., Alcidae, Strauch, 1985; Pelecaniformes, Cracraft, 1985) typically exhibit high levels of parallelism and reversal. In 1980, I began comparisons of ratite skeletons and observed additional characters not noted by Cracraft (1974), as well as variation that made it difficult to determine the ancestral state of several characters he employed. Subsequently, I became aware that a monograph by Rich (1979) on the Dromornithidae, a family of flightless birds known from fossils from the Miocene to Pleistocene of Australia, provided a large compilation of postcranial skeletal characters of the ratites. Rich's analysis included the characters I had observed and several others as well, and excluded the problematic characters used

by Cracraft. It became evident that Rich's compilation included most of the useful characters of the postcranial skeletons of the living and recently extinct ratites.

This paper presents a phylogenetic analysis of Rich's (1979) characters. The goal of the analysis was to estimate the phylogeny of the ratities with numerical cladistic methods, using a larger set of characters than that used by Cracraft (1974). I then compared the results of the cladistic analysis with those obtained from molecular and other morphological studies of the ratite birds.

I assumed initially that the ostriches (*Struthio*), rheas (*Rhea*), elephant-birds (*Aepyornis*), cassowaries (*Casuarius*), emus (*Dromaius*), kiwis (*Apteryx*) and moas (Dinornithidae): (1) are derived from flying birds; and (2) form a monophyletic group (termed the ratites) that is the sister group of the tinamous (Tinamidae). Although some workers (e.g., McGowan, 1986) continue to maintain that none of the ancestors of the ratites was volant, most avian systematists accept the derivation of the ratites from flying ancestors because the anatomical evidence for such a derivation (DeBeer, 1956) is extensive. The hypothesis of monophyly, however, remains controversial. The results of molecular (Prager et al., 1976; Sibley and Ahlquist *in* Diamond, 1983; Stapel et al., 1984), behavioral (Meise, 1963) and morphological (Parkes and Clark, 1966; Cracraft, 1987) studies support the monophyly of the ratites and a sister-group relationship between them and the tinamous. The initial assumption of monophyly thus rests on the congruence of these lines of evidence.

TAXA, CHARACTERS AND CLADISTIC METHODS

Taxa.—The following taxa formed the operational units for the cladistic analysis: Tinamidae, *Struthio, Rhea, Apteryx, Casuarius, Dromaius, Aepyornis,* Dinornithidae and Dromornithidae. I assumed that *Apteryx* (three species, Mayr, 1979), *Casuarius* (three species, Mayr, 1979), *Dromaius* (two species, Mayr, 1979), and the Dinornithidae (*sensu* Cracraft, 1976) are each monophyletic (see Appendix for a list of the species examined). *Struthio* and *Rhea* (*sensu* Mayr, 1979) are monotypic, as *Aepyornis* is also considered here. Neither I nor Rich (1979) examined specimens of the Lesser Rhea (*Pterocnemia pennata*), and *Pterocnemia* was not included in the analysis. (See the section on cladistic analysis for a discussion of the treatment of the Dromornithidae, which may not be ratites.)

Characters.—I compared skeletal specimens of ratites, tinamous and selected species of Galliformes and Anseriformes to define the characters and character states for cladistic analysis (see Appendix for description of the characters and a list of examined specimens). The distribution of character states among ratite taxa is tabulated in Table 1 in the Appendix. In most instances, the definitions were similar to those of Rich (1979). I excluded characters that were highly variable within a taxon (e.g., length of the costal margin of the sternum in *Apteryx*) or difficult to define unambiguously. The anatomical nomenclature of Baumel et al. (1979) is used throughout.

Cladistic analysis.—Character states were coded for the numerical cladistic analysis. The ancestral state of each character was considered to be the state found uniformly among tinamous and also present in other carinate birds (e.g., Galliformes). This particular "outgroup" method relies on the initial assumptions discussed above. Because the evolutionary transformations between multiple derived states of a single character are not known, I did not impose *a priori* assumptions of transformation between such states. For characters with a single derived state, the ancestral state was coded "0" and the derived state "1." Each

character with multiple derived states was divided into several characters, one for each derived state (see Table 2 in the Appendix). With this method, clades were based on evident synapomorphy rather than synapomorphy presumed from transformations for which there is no evidence. I performed a second analysis using a different method of coding characters with more than one derived state. The ancestral state was designated "0" and each derived state was coded with a separate number (e.g., "1," "2," "3"). The transformation series requiring the fewest steps were then found using the UNORDERED option of the computer program PAUP (see below). For both methods of coding, characters that varied within an operational taxonomic unit and the character states not known in the Dinornithidae and Aepyornithidae were coded as "unknown," which for the purposes of numerical cladistic analysis was interpreted as "any possible state."

The coded character states were analyzed with the computer program PAUP (Phylogenetic Analysis using Parsimony, version 2.4, by D. L. Swofford), using the ALLTREES option and Farris' (1970) method of assigning character states to internal nodes. The ALLTREES option seeks the shortest tree among all possible topologies for nine or fewer taxa. (See Cracraft, 1985 for a discussion of numerical cladistics.) The shortest tree was rooted at a hypothetical ancestor with the ancestral state for all characters.

The idea of the minimum-length criterion (often equated with "parsimony") is that it requires the fewest *ad hoc* hypotheses and provides an objective basis for choosing among several hypotheses. A minimum-length tree has minimum homoplasy (parallel and reverse character-state changes) and maximum character congruence (Cracraft, 1985). Thus, although the evolution of characters might in reality be more complex than implied by the minimum-length criterion, the choice among trees is based on the simplest hypothesis for which evidence is available.

The consistency index (CI) is a measure of the amount of homoplasy and was calculated for each tree and for the sets of character states delimiting each group of taxa (CI = the minimum number of possible character-state changes divided by the actual number of character-state changes). I ignored autapomorphic characters in calculating CI and tree lengths to avoid inflating CI values artificially.

To determine how stable clades were under different character-state distributions, the BANDB option of PAUP was used to construct trees that were several steps longer than the shortest tree. The CONTREE program of PAUP was used to produce strict (Rohlf, 1982) and Adams (1972) consensus trees from the set of slightly longer phylogenies.

The Dromornithidae were not included in the main cladistic analysis because the palatal and rhamphothecal evidence for their inclusion with the ratites is fragmentary (Olson 1985). I included the Dromornithidae with the other taxa in a separate cladistic analysis.

RESULTS

Fig. 1 depicts the minimum-length tree (length = 130, CI = 0.61) and character-state distribution based on the method of coding that treated each derived state as a separate character (see "Taxa, Characters and Cladistic Methods"). Of 79 non-autapomorphic derived character states, 36 (46%) were derived only once, 24 (30%) were independently derived twice, 11 (14%) were derived once and lost once, seven (9%) were derived once and lost independently twice, and one (1%) was independently derived twice and lost once. In five instances, the loss of a derived state was associated with a gain of another derived state of the same

Dinornithidae Aepyornis Struthio   Rhea   Apteryx Casuarius Dromaius
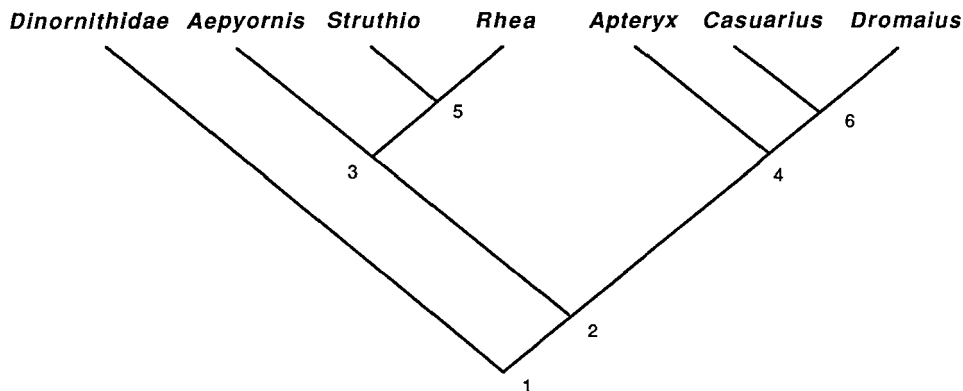

Fig. 1.—Phylogeny of the ratite birds estimated from numerical cladistic analysis of postcranial skeletal characters. The tree is rooted to a hypothetical ancestor (not shown) with the ancestral state for all characters, which corresponds to the Tinamidae (see text). The character-state changes (including autapomorphies) are listed below for the non-terminal clades (designated by numbers next to the nodes of the tree) and for the terminal taxa. Unless otherwise indicated, changes are from the ancestral condition (a) to the listed derived state. See Appendix for characters and character states. *Clade 1*: 5d, 6b, 12b, 13b, 18b, 28b, 29b, 33b, 46b, 52b, 63b, 67c, 68b, 71b, 72b, 78b. *Clade 2*: 2c, 35b, 49b, 57b, 69b, 70b, 73b. *Clade 3*: 7b, 8b, 9b, 19b, 21c, 22b, 51c, 53b, 59b, 60b, 64c, 72b. *Clade 4*: 19c, 26b, 30c, 31b, 32b, 34b, 44b, 48b, 56b, 64b, 71b→a. *Clade 5*: 5d→c, 11b, 14c, 15b, 37c, 38b, 42b, 43b, 45b, 46b→c, 47c, 50c, 52b→c, 61b, 62c, 66c, 68b→a. *Clade 6*: 3c, 4b, 5d→c, 6b→a, 13b→a, 14b, 18b→a, 21b, 22c, 27b, 37b, 38c, 40c, 41b, 45b, 47c, 50b, 52b→c, 53c, 54b, 55b, 66c, 70b→c, 74b. Dinornithidae: 3b, 38b, 43b, 65b, 76b, 80b. *Aepyornis*: 1c, 11c, 14b, 15c, 27b, 35b→a, 37b, 38b, 40c, 44c, 49b→a, 54b, 55b, 62b, 65b, 66c, 72c. *Struthio*: 3c, 4c, 6b→a, 19b→a, 28b→a, 39b, 44d, 75b, 79c, 80b, 82b. *Rhea*: 2c→a, 4b, 5b, 8b→a, 41b, 44b, 48b, 59b→a, 71b→a, 74b, 80c. *Apteryx*: 1b, 2c→a, 9c, 14c, 16b, 21d, 22d, 24b, 25b, 40b, 43c, 46b→a, 47b, 73b→a, 80d. *Casuarius*: 11c, 28b→a, 30c→b. *Dromaius*: 8b, 11d, 15b.

character, constituting evidence for a linear transformation series (5d→c→b, 30c→b, 46b→c, 52b→c, and 70b→c).

The descriptions of the character suites below are based on Fig. 1.

All Ratites

Sixteen derived character states delimit this clade, of which six showed no homoplasy, four were lost once, and six were lost twice (CI = 0.62).

The ventral surface of the sternum is flattened (5d) and its articular coracoidal sulci are restricted to the lateral margins (6b). On the humerus, the transverse ligamental sulcus is shallow (12b), the pneumatic foramen is lacking (13b), and a ridge is present at the base of the pectoral crest (18b). The radius is broad (28b), the ulna and radius are longer than the humerus (29b), and os metacarpale majus is compressed dorsoventrally (33b). The lateral condyle of the femur is elongated (46b). On the tibiotarsus, the articular surface of the head is expanded (52b), and the lateral epicondylar depression is deep (63b). On the tarsometatarsus, only one hypotarsal sulcus is present (67c), the hypotarsus is shifted toward the midline of the shaft (68b), the depression between the hypotarsus and intercotylar area is absent (71b), the medial cotyla is enlarged (72b), and the margins of trochlea III are straightened (78b).

The conditions of several character states coded as unknown are hypothesized to be derived in the Dinornithidae (12b, 18b, 28b, 29b, 33b, 78b) and *Aepyornis* (28b, 33b), based on the PAUP analysis.

All Taxa but Dinornithidae

The Dinornithidae form the sister group of the other ratites, which are delimited by seven derived character states, of which two showed no homoplasy, four were lost once, and one was lost twice (CI = 0.54).

The craniolateral process of the sternum is very short (2c), the synsacrum is narrow (35b), the muscle impression near the popliteal fossa of the femur is reduced (49b), and the supratendinal bridge of the tibiotarsus is lacking (57b). On the tarsometatarsus, the medial margin of the medial condyle is smooth (69b), the hypotarsus is expanded distally (70b), and the number of subhypotarsal ridges is reduced to one (73b).

In *Aepyornis,* the condition of one character state coded as missing is hypothesized to be derived (70b), based on the PAUP analysis.

Aepyornis-Struthio-Rhea

This clade is delimited by 12 derived states, of which eight exhibited no homoplasy, three were subsequently lost once in this clade, and one was lost once in this clade and independently evolved once elsewhere in the tree (CI = 0.71).

The glenoid facet of the scapulocoracoid is shifted dorsally (7b), a groove medial of the glenoid cavity is present (8b), and the surface between the cranial surface of the glenoid cavity and the medial margin of the scapulocoracoid is knob-like (9b). On the humerus, the dorsal epicondyle is reduced (19b), the shaft is triangular in cross-section (21c), and the distal end is widened caudally (22b). On the tibiotarsus, the cnemial crests are substantially compressed (51c), the cranial cnemial crest is shortened (53b), the ridge extending laterally from the extensor canal is lacking (59b), the craniodistal edge of the lateral condyle is elliptical (60b), and the medial condyle is very wide and very short (64c). The medial condyle of the tarsometatarsus is enlarged (72b).

In *Aepyornis,* the conditions of three character states coded as missing are hypothesized to be derived (7b, 21c, 22b), based on the PAUP analysis.

Struthio-Rhea

This clade forms the sister group of *Aepyornis* and is delimited by 15 derived states (seven with no homoplasy and eight evolved independently elsewhere in the tree), two of which were acquired by concomitant loss of a separate derived state for the same character, and by two reacquired ancestral states (CI = 0.56).

The ventral surface of the sternum is curved (5d→c). The humerus is slender and elongate (11b), its ventral tuberculum is expanded (14c), and the head is shifted dorsally away from the dorsoventral midline (15b). On the synsacrum, the trochanter is shifted cranially (37c) and the pubis is elongated relative to the ilium and ischium (38b) and is widened (42b). On the femur, the caudal margin of the antitrochanteric articular surface is straightened (43b), the axes of the medial and lateral condyles are divergent (45b), the lateral condyle is even further elongated distally (46b→c), the cranial margin of the lateral condyle is highly concave (47c), and the distal margin of the medial condyle is flattened (50c). On the tibiotarsus, the cranial cnemial crest is expanded relative to the rest of the articular surface (52b→c), the cranial-most extension of the lateral condyle lies proximal of the condyle's proximodistal midpoint (61b), and the lateral condyle is extended caudally (62c). The hypotarsus of the tarsometatarsus is formed into a narrow ridge (66c) and is shifted toward the proximodistal midline of the shaft's axis (68b→a).

Casuarius-Dromaius-Apteryx

·· This clade forms the sister group of the *Aepyornis-Struthio-Rhea* lineage and is delimited by ten derived states, including seven with no homoplasy, two independently gained once elsewhere in the tree, and one lost once in this clade, and by a single reacquired ancestral state (CI = 0.69).

The dorsal epicondyle of the humerus is highly reduced (19c). On the ulna and radius, the proximal end is narrowed (26b), the carpal trochlea is flattened (30c), the phalangeal articulation of os metacarpale alulare is lacking (31b), os metacarpale majus and minus are fused completely (32b), and only one metacarpal has a phalangeal articulation (34b). The trochanteric crest of the femur is shortened (44b), as is the fibular trochlea (48b). On the tibiotarsus, the intercondylar eminence is lacking (56b), and the medial condyle is shortened (64b). The depression between the intercotylar area and the hypotarsus of the tarsometatarsus is present (71b→a).

Casuarius-Dromaius

This clade, the sister group of *Apteryx,* is delimited by 21 derived states, including six with no homoplasy and 15 acquired independently elsewhere in the tree, and by six reacquired ancestral states, three of which were re-evolved only in this clade, and three of which were also re-evolved elsewhere in the tree (CI = 0.53).

On the sternum, the cranial margin is convex (3c), the incisures are lacking (4b), the ventral surface is curved (5d→c), and the articular coracoidal sulci is located medially (6b→a). On the humerus, a pneumatic foramen is present (13b→a), the ventral tuberculum is lengthened (14b), the ridge at the base of the pectoral crest is absent (18b→a), the shaft is circular in cross-section (21b), and the margins of the distal end are straightened (22c). The ulna and radius are fused (27b). On the synsacrum, the trochanter is shifted cranially (37b), the pubis, ilium and ischium are nearly equal in caudal extension (38c), the postacetabular ilium is widened (40c), and the preacetabular tuberculum is shortened (41b). On the femur, the margins of the medial and lateral condyles are tilted relative to the shaft (45b), the lateral condyle is highly concave cranially (47c), and the distal margin of the medial condyle is slightly flattened (50b). On the tibiotarsus, the cranial cnemial crest is expanded (52b→c) and extended (53c), the lateral margin of the proximal end is deeply concave (54b), and the channels at the margins of the intercondylar eminence are absent (55b). On the tibiotarsus, the hypotarsus is formed into a narrow ridge (66c) and extends beyond the intercotylar area (70b→c), and the plantar surface is deeply grooved (74b).

The condition of one character state (27b) coded as unknown (polymorphic) in *Casuarius* is considered to be derived, based on the PAUP analysis.

Alternative Trees

There were 16 trees longer than the shortest tree by 1–3 steps (lengths 131–133). One tree united the cassowary-emu and rhea-ostrich clades as sister groups, forming the sister group of the kiwis, with the moas and elephant-birds forming a clade and the sister group of the other ratites. The remaining 15 topologies differed from the tree in Fig. 1 only in the positions of elephant-birds and moas. Of these, five united the moas and elephant-birds as sister groups, this clade being the sister group either of the ostriches and rheas, of the cassowary-emu-kiwi
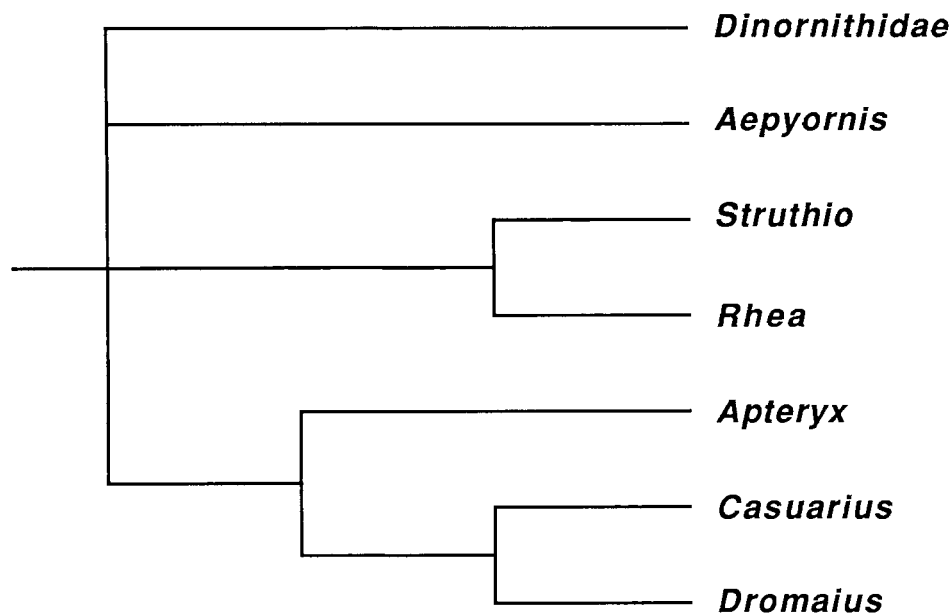
Fig. 2.—Consensus tree constructed from the set of alternative trees (see text) using the method of Adams (1972) for trees with unlabeled internal nodes. This method seeks the intersection of the inclusive sets of the alternative trees.

lineage, of the cassowaries and emus, of the kiwis, or of all of the other living ratites. Four trees placed the elephant-birds as the sister group of the cassowaries and emus; in these, the moas were the sister group either of the kiwis, of the cassowary-emu-*Aepyornis* clade, of the lineage including the kiwis, emus, cassowaries and elephant-birds, or of all of the other ratites. Of the other remaining six alternatives, one was identical to Fig. 1 in topology but not in character-state distribution, while three were identical to Fig. 1 except in the position of the moas, which were the sister group either of the ostriches and rheas, of the ostrich-rhea-*Aepyornis* clade, or of the Australo-New Zealand ratites. In one tree, the moas were the sister group of the kiwi-cassowary-emu clade, forming an assemblage that was the sister group of the elephant-birds, while in another these positions of the elephant-birds and moas were reversed. Fig. 2 and 3 present consensus phylogenies based on the set of trees of length 130–133.

Analysis of the data set based on the alternative method of coding produced a tree identical in topology to Fig. 1 except in placing the elephant-birds as the sister group of the cassowary-emu lineage (length = 137, CI = 0.68).

Analysis Including the Dromornithidae

This analysis produced a tree that for the living ratites was identical in topology to Fig. 1 but that placed the mihirung-birds as the sister group of the cassowary-emu lineage, the elephant-birds as the sister group of the cassowary-emu-Dromornithidae clade, and the moas as the next successive sister group (length = 162, CI = 0.54). The pattern of character states changed when the mihirung-birds were included. In the suite of states uniting the ratites, the Dromornithidae ex-
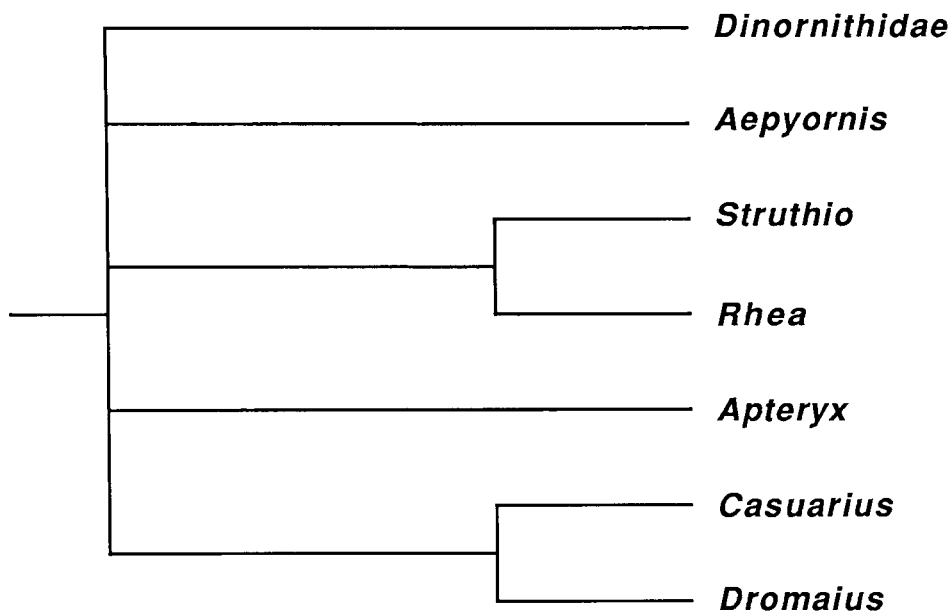
Fig. 3.—Consensus tree constructed from the set of alternative trees (see text) using the method of Rohlf (1982). This method produces a "strict" consensus tree including only the identical sets of taxa among the alternative trees.

hibited none of the six non-homoplastic derived states in the analysis excluding the Dromornithidae.

DISCUSSION

The phylogenies in Fig. 1–3 corroborate the initial hypothesis of monophyly of the ratites and add to the behavioral (Meise, 1963), molecular (Prager et al., 1976; Sibley and Ahlquist *in* Diamond, 1983), and morphological (Mivart, 1877; Cracraft, 1974, 1987) data in support of ratite monophyly. The pattern of branching among the living ratites was essentially stable as tree length increased, being the same as in Fig. 1 in 15 of 16 alternative trees and in the analysis employing an alternate method of character-coding. The results of the numerical cladistic analysis thus also supplement the substantial body of evidence supporting the monophyly of the ostriches and rheas (Mivart, 1877; Meise, 1963; Cracraft, 1974; Sibley and Ahlquist *in* Diamond, 1983), and of the cassowaries and emus (Mivart, 1877; Meise, 1963; Cracraft, 1974; Prager et al., 1976; Sibley and Ahlquist *in* Diamond, 1983).

The clade consisting of the cassowaries, emus, and kiwis has also been proposed previously on morphological (Mivart, 1877) and biochemical (Sibley and Ahlquist *in* Diamond, 1983) grounds. However, the cassowary-emu-kiwi clade is at odds in two respects with Cracraft's (1974) analysis. First, Cracraft surmised that the cassowaries and emus are the sister group of the ostriches and rheas. Second, like nearly all previous workers, Cracraft allied the kiwis with the moas rather than with the Australian-New Guinea ratites.

The discrepancies between the views of Cracraft (1974) and the phylogeny in Fig. 1 are probably best explained by differences in the size of the data sets and

the extent of the comparisons. Cracraft used a smaller set of characters (25) that did not encompass the taxonomic variation of the forelimb elements. In addition, several of the characters he used were not included here because they vary among Tinamidae and other outgroup taxa. For instance, cassowaries, emus, ostriches, rheas and elephant-birds possess a long, deep cranial metatarsal groove, but some tinamou specimens (e.g., *Tinamus major*, AMNH 3675; *Crypturellus noctivagus*, AMNH 10443) exhibit the same condition, so that its apomorphy is uncertain. For other characters, Cracraft's assessment of taxonomic occurrence was incomplete. For example, Cracraft used (among other characters) the loss of the supratendinal bridge in cassowaries, emus, ostriches, rheas and elephant-birds to unite them, yet the kiwis lack a supratendinal bridge as well. That Cracraft identified only a single homoplastic character, the width of the pelvis, when homoplasy is so extensive in the data set analyzed here, suggests that Cracraft's comparisons were less detailed than those used in the present study.

Thus, the phylogeny in Fig. 1 is more informative and probably a better estimate of phylogeny than Cracraft's (1974) arrangement. His analysis nonetheless showed that nearly all previous workers failed to consider the plesiomorphy and apomorphy of characters. This is particularly true for characters traditionally used (e.g., Oliver, 1949) to ally the moas and kiwis, as Cracraft (1974) noted. Cracraft (1974) observed four derived character states allying the moas and kiwis, of which three were not used in the current study. The projection of trochlea III distally beyond trochleae II and IV occurs in some tinamids, as Cracraft noted, and its apomorphy is thus unclear. The location of the coracoidal process of the scapulocoracoid adjacent to the glenoid cavity is indeed shared only among moas and kiwis, but its ancestral state is difficult to infer because no strictly comparable character occurs among the outgroups. The presence of a single deep hypotarsal sulcus hinges on the apomorphy of the number of sulci rather than their depth, because the ancestral condition is for each sulcus to be deep. The other ratites possess a single sulcus (67c), although the Dromornithidae have two sulci (67b). A fourth character used by Cracraft to ally the moas and kiwis—the relative projections of the medial and lateral condyles of the tibiotarsus—is defined somewhat differently in this study (character 65) and as a result *Apteryx* shows the ancestral state while the moas and elephant-birds possess the derived condition. However, even if Cracraft's definition of this character is admitted in placed of character 65, the topology of Fig. 1 is not altered.

Thus, the results of this study support Cracraft's contention (1974) that it is difficult to recognize characters confirming the monophyly of the moas and kiwis. However, even though the moas and kiwis are not sister groups in Fig. 1 nor in 15 of 16 alternative trees, the absence of wings from moas might compromise the ability to infer the frequently proposed sister-group relationship between moas and kiwis (and the one with the simplest biogeographic interpretation) even if that arrangement were indeed correct. Wing bones of moas have never been found (Oliver, 1949), and the absence of a glenoid facet on the scapulocoracoid indicates that the moas probably lacked them.

An analogous situation applies to the elephant-birds, for which 12 character states are not known because several of the wing elements are poorly preserved. The lack of such information does not weaken the conclusion of ratite monophyly because the extinct taxa exhibit other character states delimiting the ratites (Fig. 1), as well as the rhamphothecal structure described by Parkes and Clark (1966) and the derived palatal characters discussed by Cracraft (1987). However, because

the PAUP program allows missing character states to vary among all possible conditions, the lack of knowledge of many character states in the moas and elephant-birds creates a situation in which these taxa may assume almost any position on an otherwise stable tree. Thus, additional information will be required to determine if Fig. 1 provides a good estimate of the relationships of the moas and elephant-birds.

The relationships of the extinct mihirung-birds (Dromornithidae) of Australia are even more difficult to infer. Their possession of the ancestral state of the six non-homoplastic character states delimiting the ratite clade is consistent with the hypothesis that they are not members of that clade, but they share the derived state of several other characters with the ratites. The remains of the palate and rhamphotheca of the mihirung-birds are so fragmentary and poorly preserved (see Olson, 1985:104–105) that they do not clarify the situation. The phylogenetic relationships of the mihirung-birds are thus not resolved by this study.

Since Cracraft's study, several analyses of ratite phylogeny have been published. Some (e.g., Feduccia, 1980:133; Olson, 1985) were based on a few, incompletely surveyed morphological characters of uncertain apomorphy, and on the idea that differences argue against monophyly of taxa. For instance, Olson (1985:102) stated that "the great diversity in . . . morphology within the large ratites favors their having evolved their ratite grade of morphology independently of one another." There is no doubt that the ratites are diverse morphologically, but without evidence of a relationship to other groups of birds (in the form of derived character states, macromolecular evidence, etc.), the hypothesis of independent evolution of the morphological similarities among the ratites receives no phylogenetic support. It makes no sense to suppose that morphological diversity alone is indicative of non-monophyly (Raikow and Cracraft, 1983).

Houde (1986) maintained that several "paleognathous" volant fossil taxa known from the Paleocene and Eocene of North America and Europe "gave rise to the various lineages of ratite birds." However, of the ratites, Houde included only the kiwis and ostriches, and like Olson (1985) and Feduccia (1980), did not present a complete character-set for the diagram of relationships he depicted. Although the phylogeny presented by Houde is fully consistent with Fig. 1, it is difficult to assess the validity of his results or of the opinions of Olson (1985) and Feduccia (1980) without a more complete study.

Rich (1979) employed a tally of shared derived states among each pairwise combination of ratite taxa to infer three possible phylogenies of the ratites. Even though the derived states she observed form the basis for the current study, each of the alternatives she proposed differs from the topology in Fig. 1 except in grouping the cassowaries with the emus and the ostriches with the rheas. The alternative she proposed on the basis of an outgroup method of determining polarity placed the moas and kiwis as sister groups, together forming the sister group of the other ratites; the elephant-birds were the sister group of a clade in which the Dromornithidae and Casuariidae formed the sister group of the ostriches and rheas. However, a PAUP analysis of the character states of the present study indicated that this topology is longer (length = 176, CI = 0.52) than the comparable tree presented here, that which included the Dromornithidae (length = 162, CI = 0.54). Thus, the "tally" method of Rich (1979) did not identify the shortest possible tree.

Prager et al. (1976) used immunological comparisons of transferrins to propose a tree linking cassowaries and emus as sister groups, with a trifurcation between

the cassowary-emu clade, the kiwis and the rheas, and another trifurcation between these taxa and the ostriches and tinamous. Although these trifurcations reduce the resolution of the tree, its topology is nonetheless consistent with that of Fig. 1, except in the position of *Rhea*, which is not the sister group of *Struthio* in the phylogeny proposed by Prager et al. (1976).

Sibley and Ahlquist (*in* Diamond 1983) used DNA-DNA hybridization comparisons to construct a tree identical to Fig. 1 in its branching pattern among the living ratites. However, the thermal dissociation curves and distances reported in an earlier study (Sibley and Ahlquist 1981, Figs. 5–10, Table 1) indicated that the ostriches and rheas are farther from each other than either is from the cassowaries, emus and kiwis. If the later phylogeny of Sibley and Ahlquist is taken as the definitive DNA phylogeny, then congruence between it and Fig. 1 would argue for the validity of both as estimates of the phylogeny of the ratites.

The most serious potential objection to the present study is that the characters are primarily qualitative and thus are difficult to partition into discrete states. Such character states also might have evolved concomitantly through neoteny and an increase in body size, which may have occurred independently in the various groups (Raikow 1985:91). The high level of homoplasy in Fig. 1, which is characteristic of avian phylogenies employing osteological traits (Strauch, 1985, Livezey, 1986), reflects an inability to recognize the nonhomology that, at some level, must exist to explain such discordant distributions among character states. Yet the suggestion of congruence between the morphological and molecular approaches implies that, in this instance, each provides a good estimate of phylogeny, and by implication that qualitative osteological characters carry substantial phylogenetic information. If this is correct, a more quantitative analysis of osteological variation should yield results congruent with the results presented here and with other lines of phylogenetic evidence, both molecular and morphological.

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APPENDIX

Specimens. — Skeletal specimens of the following taxa were compared (AMNH = American Museum of Natural History; YPM = Peabody Museum of Natural History, Yale University). Tinamidae: *Tinamus solitarius* (YPM 2085), *T. major* (AMNH 3675, 5283; YPM 374), *Crypturellus undulatus* (AMNH 6479, 6481; YPM 11564), *C. noctivagus* (AMNH 10443, 10444, 10445; YPM 2120, 2121), *Rhynchotus rufescens* (YPM 2041), *Nothoprocta perdicaria* (YPM 2040, 6696), *N. cinerascens* (AMNH 6505, 6507, 6509), *Nothura darwinii* (YPM 6697), *N. maculosa* (AMNH 2325, 2864, 3540; YPM 2086), *Eudromia elegans* (AMNH 8565, 8678, 9152, 11395; YPM 2086). Struthionidae: *Struthio camelus* (YPM 560, 561, 2116, 2117, 2124, 4236, 4347, 4382, 4799). Rheidae: *Rhea americana* (AMNH 1500, 1673; YPM 2234, 6503, 11524). Casuariidae: *Casuarius* sp. (AMNH 1517; YPM 2123, 4351, 6208), *Dromaius novaehollandiae* (YPM 567, 2127, 2128, 2129). Apterygidae: *Apteryx australis* (YPM 4383, one uncatalogued specimen), *A. owenii* (YPM 2118), *Apteryx* sp. (AMNH 3738, 3739, 4437, 5372). Dinornithidae: *Pachyornis elephantopus* (YPM Vertebrate Paleontology [VP], uncatalogued material), *Euryapteryx* sp. (YPM VP, uncatalogued material), *Dinornis* "*maximus*" (=*giganteus*, YPM VP 9206), *D.* "*gracilis*" (YPM VP 9207), *D. struthoides* (YPM VP, uncatalogued material). I also examined a large series of skeletal specimens of *Bonasa umbellus* and single specimens of selected species of Galliformes and Anseriformes for analysis of character polarity. I was unable to study specimens of the Lesser Rhea (*Pterocnemia pennata*), *Aepyornis maximus*, and the Dromornithidae. For *Aepyornis* and the Dromornithidae, I thus used the character descriptions provided by Rich (1979).

Characters. — The characters used for numerical cladistic analysis are listed and numbered below, grouped by skeletal element. The character is described first, followed by the ancestral and derived states, designated alphabetically beginning with the ancestral state (a). The alphabetical order of the character states does not imply a linear transformation series among multiple derived states of a single character. The terminology follows Baumel et al. (1979).

Sternum

1. Proportions: (a) longer (craniocaudally) than wide (mediolaterally); (b) length and width equal; (c) wider than long.

2. Craniolateral process: (a) elongate; (b) shortened; (c) very short.

3. Cranial margin: (a) concave cranially; (b) straight; (c) convex cranially.

4. Number of incisures: (a) two; (b) none; (c) four.

5. Ventral surface: (a) highly curved, carina present; (b) highly curved, low medial ridge present; (c) moderately curved, no distinct medial ridge; (d) flattened.

6. Articular coracoidal sulci: (a) meet or nearly meet medially; (b) restricted to lateral margins.

Scapulocoracoid

7. Orientation of glenoid facet: (a) lateral; (b) dorsolateral.

8. Groove medial of glenoid cavity: (a) absent; (b) present.

9. Cranial surface between glenoid cavity and medial margin: (a) smooth; (b) knobbed; (c) ridged.

10. Scapular body: (a) lateral facet concave; (b) medial facet concave.

Humerus

11. Proportions: (a) slender, length moderate; (b) slender, elongate; (c) stout, short; (d) slender, short.

12. Transverse ligamental sulcus: (a) deep; (b) shallow; (c) absent.

13. Pneumatic foramen: (a) present; (b) absent.

14. Proximal protrusion of ventral tuberculum and head: (a) head protrudes beyond tuberculum; (b) subequal; (c) tuberculum protrudes beyond head.

15. Position of head: (a) near midline; (b) shifted dorsally; (c) shifted ventrally.

16. Ligamental impression on ventral surface of shaft near its midpoint: (a) absent; (b) present.

17. Fossa of m. brachialis: (a) small, shallow; (b) large, deep.

18. Ridge at base of pectoral crest: (a) absent; (b) present.

19. Dorsal epicondyle: (a) well developed; (b) moderately developed; (c) highly reduced.

20. Articular surfaces: (a) sharply defined; (b) poorly defined.

21. Shape of shaft in cross-section: (a) elliptical proximally and distally; (b) circular proximally and distally; (c) triangular proximally and distally; (d) triangular proximally, elliptical distally.

22. Distal end: (a) widest cranially; (b) widest caudally; (c) cranial, medial and caudal widths subequal; (d) widest medially.

23. Olecranal fossa: (a) absent or very shallow; (b) well developed.

Ulna-radius

24. Proximal articular surface of ulna: (a) well developed; (b) poorly defined.

25. Olecranon: (a) large; (b) reduced.

26. Proximal end of ulna: (a) broad in proximal view; (b) narrow in proximal view.

27. Ulna and radius: (a) unfused; (b) fused.

28. Width of shafts of ulna and radius: (a) ulna broader; (b) subequal.

29. Lengths of ulna-radius and humerus: (a) subequal; (b) ulna-radius longer than humerus; (c) humerus longer than ulna-radius.

30. Carpal trochlea: (a) highly curved; (b) moderately curved; (c) flattened.

31. Phalangeal articulation on os metacarpale alulare: (a) present; (b) absent.

32. Fusion of os metacarpale majus and os metacarpale minus: (a) incomplete; (b) complete.

33. Os metacarpale majus: (a) wide dorsoventrally; (b) compressed dorsoventrally.

34. Number of metacarpals with phalangeal articulation: (a) three; (b) one.

Synsacrum

35. Dorsal surface of synsacrum caudal of the antitrochanter: (a) broad; (b) narrow.

36. Dorsal surface of synsacrum caudal of the antitrochanter: (a) decreases in width posteriorly; (b) does not narrow substantially caudally.

37. Position of trochanter (craniocaudal axis): (a) cranial of midpoint; (b) at midpoint; (c) caudal of midpoint.

38. Caudal protrusion of ilium, ischium and pubis: (a) pubis and ischium extend beyond ilium; (b) pubis extends beyond ischium, which extends beyond ilium; (c) protrusion subequal; (d) ischium protrudes beyond subequal pubis and ilium.

39. Fusion of pubes: (a) unfused; (b) fused.

40. Dorsoventral width of postacetabular ilium: (a) narrow; (b) moderately wide; (c) very wide.

41. Preacetabular tuberculum: (a) elongate; (b) short; (c) absent.

42. Dorsoventral width of pubis and ischial bar: (a) ischial bar markedly wider than pubis; (b) subequal.

Femur

43. Caudal margin of proximal antitrochanteric articular surface: (a) highly concave; (b) moderately concave; (c) straight or nearly so.

44. Proximal extension of trochanteric crest and acetabular articular surface: (a) trochanteric crest extends moderately beyond acetabular articular surface; (b) subequal; (c) trochanteric crest extends far beyond acetabular articular surface; (d) acetabular articular surface extends beyond trochanteric crest.

45. Relationship of longest axis of shaft to longest axes of medial and lateral condyles: (a) parallel or nearly so; (b) divergent by 15 degrees or greater.

46. Extension of medial and lateral condyles: (a) subequal distally; (b) lateral condyle extends slightly distally beyond medial condyle; (c) lateral condyle extends distally far beyond medial condyle.

47. Dorsal margin of lateral condyle: (a) straight or nearly so; (b) moderately concave dorsally; (c) highly concave dorsally.

48. Distal extension of lateral condyle and fibular trochlea: (a) subequal or nearly so; (b) fibular trochlea extends ¾ or less of the distal extension of the lateral condyle.

49. Muscle impression near popliteal fossa: (a) well-developed; (b) absent or reduced.

50. Distal margin of medial condyle: (a) semicircular; (b) triangular or elliptical; (c) flattened.

Tibiotarsus

51. Mediolateral compression of cranial and lateral cnemial crests: (a) slight or no compression; (b) moderate compression; (c) substantial compression.

52. Extent of cranial cnemial crest and remaining articular surface in proximal view: (a) cnemial crest equal in extent to remaining articular surface; (b) cnemial crest less extensive than remaining articular surface; (c) cnemial crest more extensive than remaining articular surface.

53. Proximal extension of cranial cnemial crest: (a) moderately beyond articular surface; (b) slightly beyond articular surface; (c) far beyond articular surface.

54. Lateral margin between lateral cnemial crest and lateral articular surface: (a) shallowly concave; (b) deeply concave.

55. Channeling at margins of intercondylar eminence: (a) present; (b) absent.

56. Intercondylar eminence: (a) present; (b) absent.

57. Supratendinal pons: (a) present; (b) absent.

58. Location of area of extensor canal: (a) medial of the midline of the shaft; (b) at the midline of the shaft.

59. Ridge extending laterally from extensor canal: (a) present; (b) absent.

60. Craniodistal margin of lateral condyle: (a) semicircular; (b) elliptical.

61. Most cranial extension of lateral condyle: (a) at or near proximodistal midpoint of condyle; (b) markedly proximal of midpoint.

62. Caudal extension of lateral condyle: (a) moderate; (b) short; (c) long.

63. Lateral epicondylar depression: (a) shallow; (b) deep.

64. Width and length of medial condyle: (a) moderate; (b) moderate in width, short in length; (c) very wide, very short.

65. Comparative size of medial and lateral condyles in distal view: (a) subequal or nearly so; (b) medial condyle larger than lateral condyle.

Tarsometatarsus

66. Hypotarsus: (a) rectangular; (b) triangular; (c) narrow ridge.

67. Number of hypotarsal sulci: (a) three; (b) two; (c) one.

68. Location of hypotarsus: (a) lateral of midline of shaft; (b) at or very near midline.

69. Medial margin of proximal end: (a) ridged; (b) unridged.

70. Extension of hypotarsus and intercotylar eminence: (a) intercotylar area extends further proximally; (b) subequal; (c) hypotarsus projects further proximally.

71. Depression between intercotylar area and hypotarsus: (a) present; (b) absent.

72. Depths of medial and lateral cotylae: (a) subequal; (b) medial deeper than lateral; (c) lateral deeper than medial.

73. Number of subhypotarsal ridges: (a) three or two; (b) one.

74. Plantar surface: (a) slightly grooved or ungrooved; (b) deeply grooved.

75. Number of trochlea: (a) three; (b) two.

76. Distal extension of trochleae IV and II: (a) IV extends beyond II; (b) subequal; (c) II extends beyond IV.

77. Depths of trochleae: (a) moderate; (b) deep.

78. Medial and lateral margins of trochlea III: (a) not parallel; (b) parallel.

Pes

79. Number of phalanges of digits II, III and IV: (a) three-four-five; (b) three-four-four; (c) zero-four-five.

80. Proximodistal lengths of proximal phalanges: (a) III longest, IV shortest or III and IV subequal; (b) III longest, II shortest; (c) II longest; (d) II and III subequal, IV shortest.

81. Proximal margins of phalanges: (a) v-shaped; (b) straight.

82. Surface of articular cotylae of basal phalanges: (a) deep, curved; (b) shallow, flattened.

83. Distal phalanges: (a) claw-shaped; (b) straightened.

Table 1.–Character states of each taxon. The letters "a," "b," "c," and "d" refer to the character states described in the Appendix for each character. The letter "m" stands for "missing" and indicates either that the element showing a character has not been found (e.g., forelimb elements of the Dinornithidae), or that one of the structures used in defining the character is absent (e.g., intercotylar eminence of the tarsometatarsus in Aepyornis). The letter "u" stands for "unclear" and indicates that the state of a character is uncertain in Aepyornis because the skeletal element is poorly preserved. The letter "p" stands for "polymorphic" and indicates that the taxon exhibits several states of a given character.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
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
Dinornithidae	a	a	b	a	d	b	m	a	m	a	m	m	b	m	m	m	m	m	m	m	m	m	m	m	m	m	m	m	m	m
Apteryx	b	a	a	a	d	b	a	a	a	c	a	a	b	b	c	a	b	a	b	c	a	d	d	a	b	b	b	a	b	c
Casuarius	a	c	c	b	c	a	a	a	a	c	b	a	b	a	a	a	a	c	a	b	c	a	a	a	b	p	a	b	b	b
Dromaius	a	c	c	b	c	a	a	b	a	a	d	b	a	b	b	a	a	a	c	a	b	c	a	a	a	b	b	b	b	c
Rhea	a	a	a	b	b	b	b	a	b	a	b	b	b	c	b	a	a	b	b	a	c	b	a	a	a	a	a	b	b	a
Struthio	a	c	c	c	c	a	b	b	b	a	b	b	b	c	b	a	a	b	a	a	c	b	a	a	a	a	a	a	b	a
Aepyornis	c	c	a	a	d	b	p	b	b	a	c	b	b	b	c	u	a	b	b	a	u	u	a	u	u	u	b	u	b	u
Dromornithidae	a	b	a	b	c	b	a	b	a	b	c	c	a	p	a	b	b	a	a	b	a	c	b	b	b	a	b	b	p	c

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
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
Dinornithidae	m	m	m	m	a	a	p	b	a	p	p	a	b	a	p	b	a	a	a	a	b	a	a	a	a	a	a	a
Apteryx	b	b	b	b	b	a	a	a	a	b	a	a	c	b	a	a	b	b	b	a	a	b	a	a	a	b	b	a
Casuarius	b	b	b	b	b	a	b	c	a	c	b	a	a	b	b	b	c	b	b	b	a	c	c	b	b	b	b	a
Dromaius	b	b	b	b	b	a	b	c	a	c	b	a	a	b	b	b	c	b	b	b	a	c	c	b	b	b	b	a
Rhea	a	a	b	a	b	a	c	b	a	a	b	b	b	b	c	c	b	b	c	c	c	b	a	a	a	b	a	a
Struthio	a	a	b	a	b	a	c	b	b	a	a	b	b	d	b	c	c	a	b	c	c	c	b	a	a	a	b	m
Aepyornis	u	u	u	u	a	a	b	d	a	c	u	a	a	c	a	b	a	a	a	a	c	b	b	b	b	a	b	a
Dromornithidae	b	b	a	b	b	b	b	c	a	a	c	b	c	b	b	b	a	b	b	b	b	a	c	b	b	a	a	b

	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83
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
Dinornithidae	a	a	a	a	b	a	b	a	c	b	a	a	a	b	b	a	a	a	c	p	p	p	b	a	a
Apteryx	a	a	a	a	b	b	a	a	c	b	b	b	a	b	a	a	a	a	b	a	d	a	a	a	a
Casuarius	a	a	a	a	b	b	a	c	c	b	b	c	a	b	b	b	a	a	a	b	a	a	a	a	a
Dromaius	a	a	a	a	b	b	a	c	c	b	b	c	a	b	b	b	a	a	a	b	a	a	a	a	a
Rhea	a	b	b	c	b	c	a	c	c	a	b	b	a	a	b	b	a	a	a	b	a	c	a	a	a
Struthio	b	b	b	c	b	c	a	c	c	a	b	b	b	a	b	a	b	m	a	b	c	b	a	b	a
Aepyornis	b	b	a	b	b	c	b	b	c	b	b	m	b	c	b	a	a	b	a	b	a	a	a	a	a
Dromornithidae	b	a	a	b	a	a	b	b	b	b	a	c	a	b	b	a	a	a	b	a	b	c	b	b	b

Table 2.—*Character coding. The sample below indicates the method for subdividing a character with multiple derived states (in this instance character 21) into several characters. A separate character is constructed for each derived state. Note that the coded characters retain the pattern of the uncoded shared derived character states. The character states "m" (missing), "u" (unclear), and "p" (polymorphic) were coded as unknown and are indicated by a question mark.*

Taxon	Uncoded state	Subdivided coded characters		
		1	2	3
Hypothetical ancestor	a	0	0	0
Dinornithidae	m	?	?	?
Apteryx	d	0	0	1
Casuarius	b	1	0	0
Dromaius	b	1	0	0
Rhea	c	0	1	0
Struthio	c	0	1	0
Aepyornis	u	?	?	?
Dromornithidae	a	0	0	0