



# A new Transantarctic relationship: morphological evidence for a Rheidae–Dromaiidae–Casuariidae clade (Aves, Palaeognathae, Ratitae)

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Although ratites have been studied in considerable detail, avian systematists have been unable to reach a consensus regarding their relationships. Morphological studies indicate a basal split separating Apterygidae from all other extant ratites, and a sister-group relationship between Rheidae and Struthionidae. Molecular studies have provided evidence for the paraphyly of the Struthionidae and Rheidae, with respect to a clade of Australasian extant ratites. The position of the extinct Dinornithidae and Aepyornithidae also remains hotly debated. A novel pattern of diversification of ratites is presented herein. The phylogenetic analysis is based on 17 taxa and 129 morphological characters, including 77 new characters. The resultant tree yields a sister-group relationship between New Zealand ratites (Apterygidae plus Dinornithidae) and all other ratites. Within this clade, the Aepyornithidae and Struthionidae are successive sister taxa to a new, strongly supported clade comprising the Rheidae, Dromaiidae, and Casuariidae. The link between South American and Australian biotas proposed here is congruent with numerous studies that have evidenced closely related taxa on opposite sides of the Southern Pacific. These repeated patterns of area relationships agree with current knowledge on Gondwana break-up, which indicates that Australia and South America remained in contact across Antarctica until the earliest Tertiary. © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, 156, 641–663.

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## INTRODUCTION

Living ratites include five species of kiwis (*Apteryx*, Apterygidae, New Zealand), three species of casuaries (*Casuarius*, Casuariidae, northeastern Australia and New Guinea), the emu (*Dromaius*, Dromaiidae, Australia), two species of rheas (*Pterocnemia* and *Rhea*, Rheidae, South America), and the ostrich (*Struthio*, Struthionidae, Africa) (del Hoyo, Elliott & Sargatal, 1992; Davis, 2002; Heather & Robertson, 2005). Furthermore, two remarkable ratite groups lived in the Pleistocene, and persisted in Holocene times until a few centuries ago: the New Zealand moas (Dinornithidae) that comprised ten

species in six genera, including *Anomalopteryx*, *Dinornis*, *Emeus*, *Euryapteryx*, *Megalapteryx*, and *Pachyornis* (Worthy & Holdaway, 2002; Bunce *et al.*, 2003; Huynen *et al.*, 2003), and the elephantbirds from Madagascar (Aepyornithidae) that possibly include seven species in two genera (Milne-Edwards & Grandidier, 1894; Monnier, 1913), namely *Aepyornis* and *Mullerornis*. All of these birds are flightless and lack a keel on the sternum.

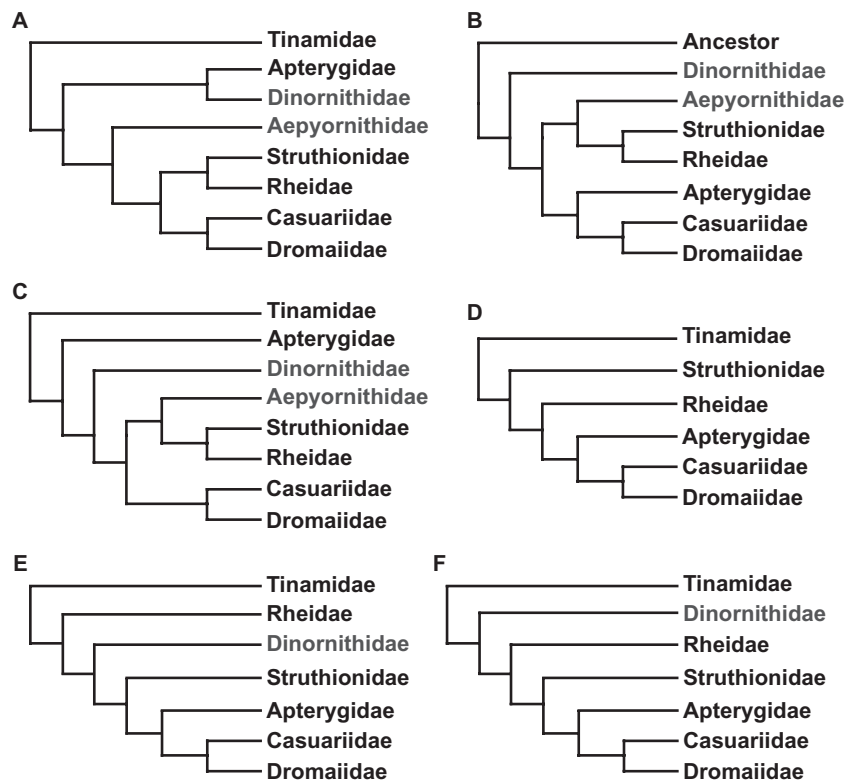
Relationships of ratite birds have perplexed avian systematists for well over a century (see Sibley & Ahlquist, 1990). Over the last four decades, numerous molecular and morphological studies have dealt with ratite relationships. There is general agreement that living ratites are monophyletic, and that the weakly flying tinamous are their closest living relatives (Meise, 1963; Cracraft, 1974; Prager *et al.*, 1976;

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de Boer, 1980; Sibley & Ahlquist, 1981, 1990; Stapel *et al.*, 1984; Caspers, Wattel & de Jong, 1994; Lee, Feinstein & Cracraft, 1997; Van Tuinen, Sibley & Hedges, 1998, 2000; Haddrath & Baker, 2001; Paton, Haddrath & Baker, 2002; García-Moreno, Sorenson & Mindell, 2003; Mayr & Clarke, 2003; Cracraft *et al.*, 2004; Harrison *et al.*, 2004; Pereira & Baker, 2006; Slack *et al.*, 2006; Harshman, 2007; Livezey & Zusi, 2007).

Phylogenetic relationships within ratites remain controversial, however. Most phylogenetic analyses based on morphology show that the kiwis are the sister taxon of a clade of large living ratites, which splits into the emu plus the cassowaries on the one hand, and the rheas plus the ostrich on the other (Cracraft, 1974; Lee *et al.*, 1997; Zelenitsky & Modesto, 2003; Livezey & Zusi, 2007) (Fig. 1A, C). In most molecular works, the rheas and the ostrich are paraphyletic with respect to a clade comprising the kiwis, the emu, and the cassowaries (Prager *et al.*, 1976; Sibley & Ahlquist, 1990; Cooper *et al.*, 1992, 2001; Cooper, 1997; Lee *et al.*, 1997; Haddrath & Baker, 2001; Paton *et al.*, 2002; Harrison *et al.*, 2004;

Slack *et al.*, 2006) (Fig. 1D–F). The phylogenetic placement of the extinct New Zealand moas still remains hotly debated (Fig. 1A–C, E, F). Several morphological studies (Cracraft, 1974; Lee *et al.*, 1997; see also Zelenitsky & Modesto, 2003), and one ethological study (Meise, 1963), advocated a close relationship between moas and kiwis; other morphological (Bledsoe, 1988; Zelenitsky & Modesto, 2003; Grellet-Tinner, 2006; Livezey & Zusi, 2007) and all molecular (Cooper *et al.*, 1992, 2001; Cooper, 1997; Haddrath & Baker, 2001; Paton *et al.*, 2002) studies suggested that moas and kiwis are not sister taxa, but failed to propose a well-supported alternative hypothesis. Likewise, the position of the poorly known elephantbirds from Madagascar is not solidly established (Fig. 1A–C). Cracraft (1974) proposed that elephantbirds are sister to a clade of large living ratites; more recent studies found a sister-group relationship between elephantbirds and an ostrich-rhea clade (Bledsoe, 1988; Livezey & Zusi, 2007); finally, one oological study suggested a close relationship between *Aepyornis* and *Struthio* (Grellet-Tinner, 2006).



**Figure 1.** Phylogenetic relationships between ratites proposed in previous studies. A, Cracraft (1974) and Lee *et al.* (1997), excluding Aepyornithidae. B, Bledsoe (1988). C, Livezey & Zusi (2007). D, Prager *et al.* (1976), Sibley & Ahlquist (1990), Harrison *et al.* (2004) and Slack *et al.* (2006). E, Cooper *et al.* (1992, 2001), Cooper (1997) and Lee *et al.* (1997), excluding Dinornithidae. F, Lee *et al.* (1997), excluding Dinornithidae, Haddrath & Baker (2001) and Paton *et al.* (2002).

The present study aims to clarify phylogenetic relationships among ratites using a new set of morphological characters. The obtained phylogeny is compared against the vicariance biogeography hypothesis, which proposes that ratites achieved their current distribution pattern via the break-up of Gondwana (Cracraft, 1973, 1974).

## MATERIAL AND METHODS

We assessed the phylogenetic relationships of ratite birds with a matrix of 17 taxa and 129 morphological characters, including 127 skeletal and two integumental characters. A list of characters included in the analysis is provided in Appendix 1, and the character–taxon matrix is shown in Appendix 2.

Outgroup taxa included in the analysis comprise two Mesozoic non-neornithine Ornithurae, *Hesperornis* (Marsh, 1880; Witmer & Martin, 1987; Bühler, Martin & Witmer, 1988; Witmer, 1990; Elzanowski, 1991) and *Ichthyornis* (Marsh, 1880; Clarke, 2004), plus the palaeognathous Tinamidae, which are widely accepted as the sister taxon of ratites (see above). Ingroup taxa include all extant ratite genera (*Apteryx*, *Casuarius*, *Dromaius*, *Pterocnemia*, *Rhea*, and *Struthio*), plus the extinct Aepyornithidae (*Aepyornis* and *Mullerornis*) and Dinornithidae (*Anomalopteryx*, *Dinornis*, *Emeus*, *Euryapteryx*, *Megalapteryx*, and *Pachyornis*). The following taxa were scored from skeletons deposited in the collections of the American Museum of Natural History (AMNH), New York, Muséum National d'Histoire Naturelle (MNHN), Paris, and the Natural History Museum (NHM), London.

Hesperornithiformes: Hesperornithidae: *Hesperornis*.

Ichthyornithiformes: Ichthyornithidae: *Ichthyornis*.

Tinamiformes: Tinamidae: *Crypturellus*, *Eudromia*, *Nothoprocta*, *Nothura*, *Rhynchotus*, and *Tinamus*.

Struthioniformes: Aepyornithidae: *Aepyornis* and *Mullerornis*. Apterygidae: *Apteryx*. Casuariidae: *Casuarius*. Dinornithidae: *Anomalopteryx*, *Dinornis*, *Emeus*, *Euryapteryx*, *Megalapteryx*, and *Pachyornis*. Dromaiidae: *Dromaius*. Rheidae: *Pterocnemia* and *Rhea*. Struthionidae: *Struthio*.

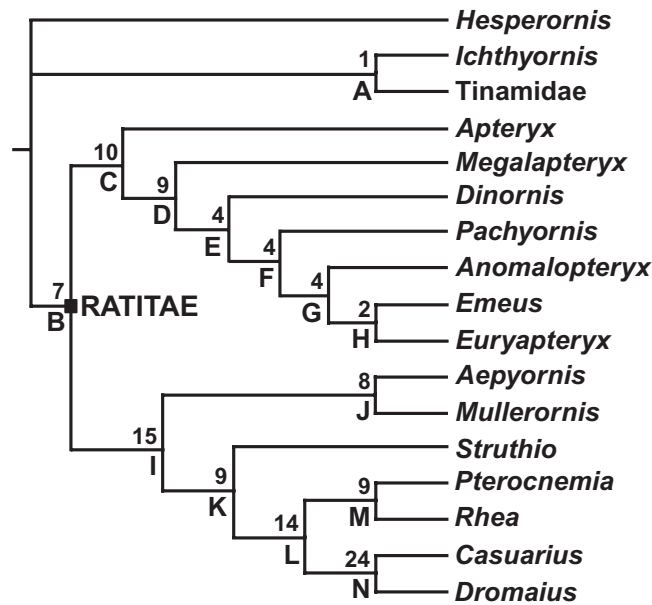
In addition, we consulted the literature for complementary anatomical information concerning fossil taxa, namely *Hesperornis* (see references above), *Ichthyornis* (see above), Aepyornithidae (Milne-Edwards & Grandidier, 1894, 1895; Andrews, 1896, 1897, 1904; Monnier, 1913; Lamberton, 1930, 1934, 1946a, b; Lowe, 1930; Wiman, 1935, 1937a, b; Wiman & Edinger, 1941; Balanoff & Rowe, 2007), and Dinornithidae (Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).

Fifty-two skeletal characters were completely or partially taken from previous phylogenetic analyses (Cracraft, 1974; Bledsoe, 1988; Lee *et al.*, 1997; Worthy & Holdaway, 2002; Livezey & Zusi, 2006). These include 33 characters with no, or minor, modifications with respect to the original ones (10, 12, 17, 23, 35, 40, 42, 45, 49, 51, 53, 55, 58, 62, 65–67, 72, 73, 76, 77, 79, 80, 86, 90, 100, 101, 107, 108, 115, 116, 125, and 127), 12 with important modifications in description and/or coding (31, 32, 46, 57, 59, 82, 91, 98, 102, 105, 112, and 121), and seven new multistate characters comprising some character states taken from the literature (21, 43, 44, 88, 93, 114, and 122). A total of 77 characters are completely new, including 75 skeletal (1–9, 11, 13–16, 18–20, 22, 24–30, 33, 34, 36–39, 41, 47, 48, 50, 52, 54, 56, 60, 61, 63, 64, 68–71, 74, 75, 78, 81, 83–85, 87, 89, 92, 94–97, 99, 103, 104, 106, 109–111, 113, 117–120, 123, 124, and 126) and two integumental (128 and 129) characters. Anatomical terminology follows that of Baumel *et al.* (1993), unless stated otherwise.

The parsimony analysis was performed using PAUP v4b10 (Swofford, 1998) and Winclada (Nixon, 1999). The 20 multistate characters (6, 7, 14, 16, 18, 21, 28, 34, 43, 44, 70, 71, 87, 88, 93, 103, 109, 114, 117, and 122) were treated as ordered. The branch-and-bound search option was used for the PAUP program. Node support was assessed using Bremer-support indices (Bremer, 1994), calculated by searching suboptimal trees up to 24 extra steps with the branch-and-bound search option of PAUP.

## RESULTS

Cladistic analysis of the character–taxon matrix in Appendix 2 resulted in one most parsimonious tree (length,  $L = 170$ ; consistency index,  $CI = 0.87$ ; retention index,  $RI = 0.95$ ), which is shown in Figure 2. Only major results are provided in this section. Readers are referred to the caption of Figure 2 for a complete list of unambiguous synapomorphies. The monophyly of the Ratitae is supported by seven strict synapomorphies: (6) processus paroccipitalis flange-like with concave anterior surface (Fig. 3E–I); (17) processus zygomaticus greatly elongated, projecting over two-thirds of corpus ossis quadrati; (51) os scapulo-racoideum present; (58) humerus, tuberculum ventrale knob-like, ventrally prominent, protruding far proximally to and continuous with caput humeri; (67) pelvis, vertebrae synsacrales with poorly developed processus transversi and greatly elongated processus spinosi; ilium high, strongly sloping on either side, with ala preacetabularis ilii forming carina iliaca dorsales; (74) caudal edge of acetabulum elongated, vertical, column-shaped, and perpendicular to



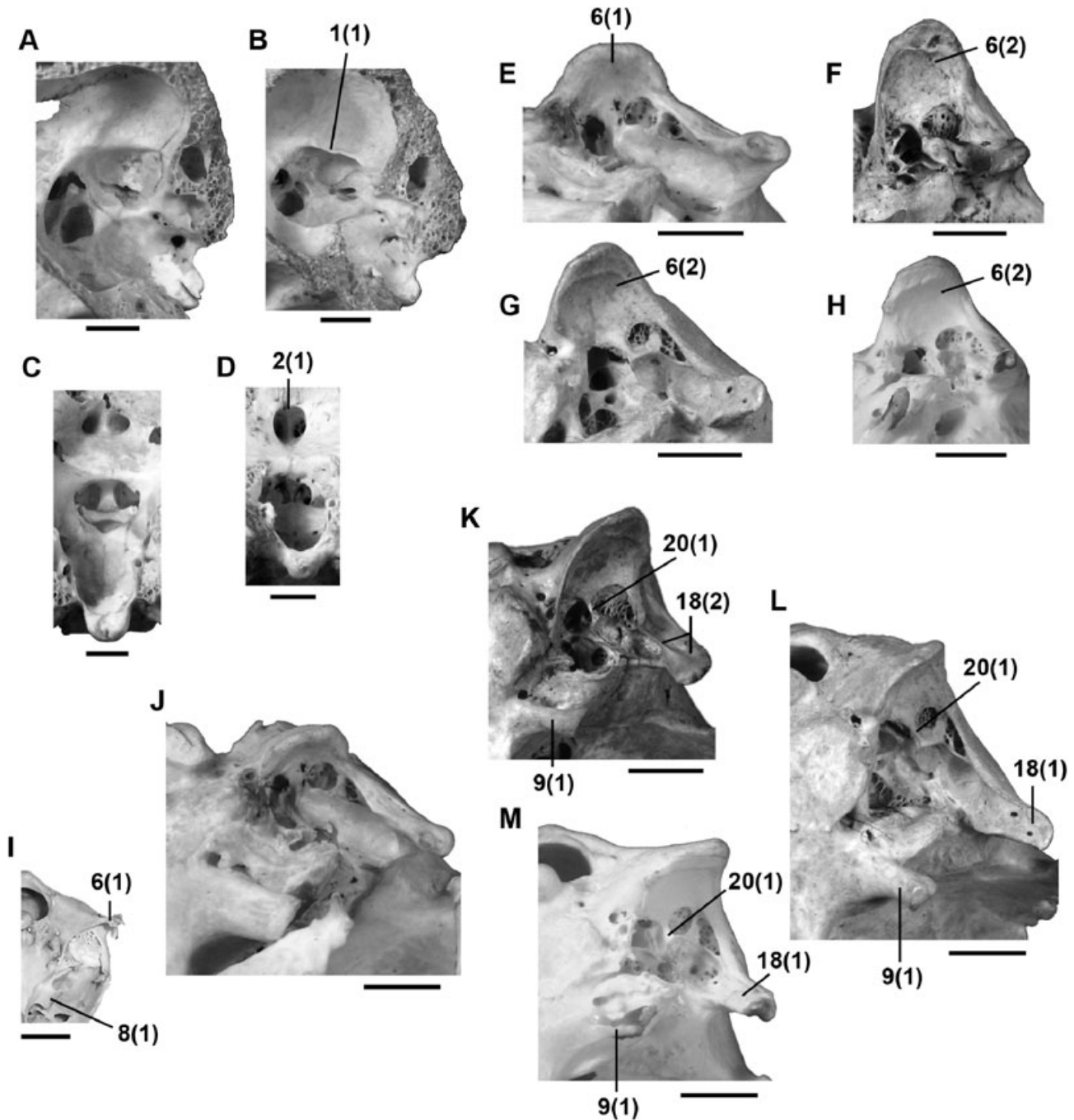
**Figure 2.** Single most parsimonious tree showing the phylogenetic relationships between ratites. Length (L), 170; consistency index (CI), 0.87; retention index (RI), 0.95. Numbers above branches correspond to Bremer-support indices. Unambiguous synapomorphies (with homoplastic ones marked with an asterisk): node A, 42(0); node B, 6(1), 17(1), 51(1), 58(1), 67(1), 74(1), and 111(1); node C, 3(1)\*, 8(1), 12(1), 23(1), 31(1), 35(1), 44(1), 49(1), 81(1), 89(1), 101(1), 115(1), and 118(1); node D, 25(1), 26(1), 33(1), 47(1), 71(1)\*, 87(1), 92(1), 97(1), and 99(1); node E, 79(1)\*, 84(1), 85(1)\*, and 87(2); node F: 7(1), 28(1), 71(2), and 123(1); node G, 7(2), 15(1), 28(2), and 44(2); node H, 27(1) and 127(1); node I, 5(1), 16(1), 29(1), 38(1), 86(1), 91(1), 93(1), 98(1), 102(1)\*, 107(1), 114(2), 116(1), 120(1), 122(1), and 125(1); node J, 11(1), 13(1), 16(2), 61(1), 94(1), 96(1); 113(1), and 119(1); node K, 21(1), 70(1), 72(1)\*, 75(1), 82(1)\*, 103(1), 105(1), 109(1), and 121(1); node L, 1(1), 2(1), 4(1), 6(2), 9(1), 14(1), 18(1), 20(1), 21(2), 34(1), 39(1), 43(1), 48(1), 70(2), 78(1), 83(1), 88(1), 95(1), 104(1), 109(2), 112(1), 117(1), 124(1), and 128(1); node M, 14(2), 18(2), 45(1), 54(1), 60(1), 64(1), 73(1), 76(1), and 100(1); node N, 19(1), 22(1), 24(1), 30(1), 32(1), 34(2), 36(1), 40(1), 41(1), 43(2), 46(1), 50(1), 56(1), 57(1), 66(1)\*, 68(1), 69(1), 77(1), 88(2), 103(2), 110(1), 117(2), 122(2), and 129(1).

ala ischii; (111) cotyla medialis tarsometatarsi dorsoplantarly elongated, protruding far dorsal to cotyla lateralis.

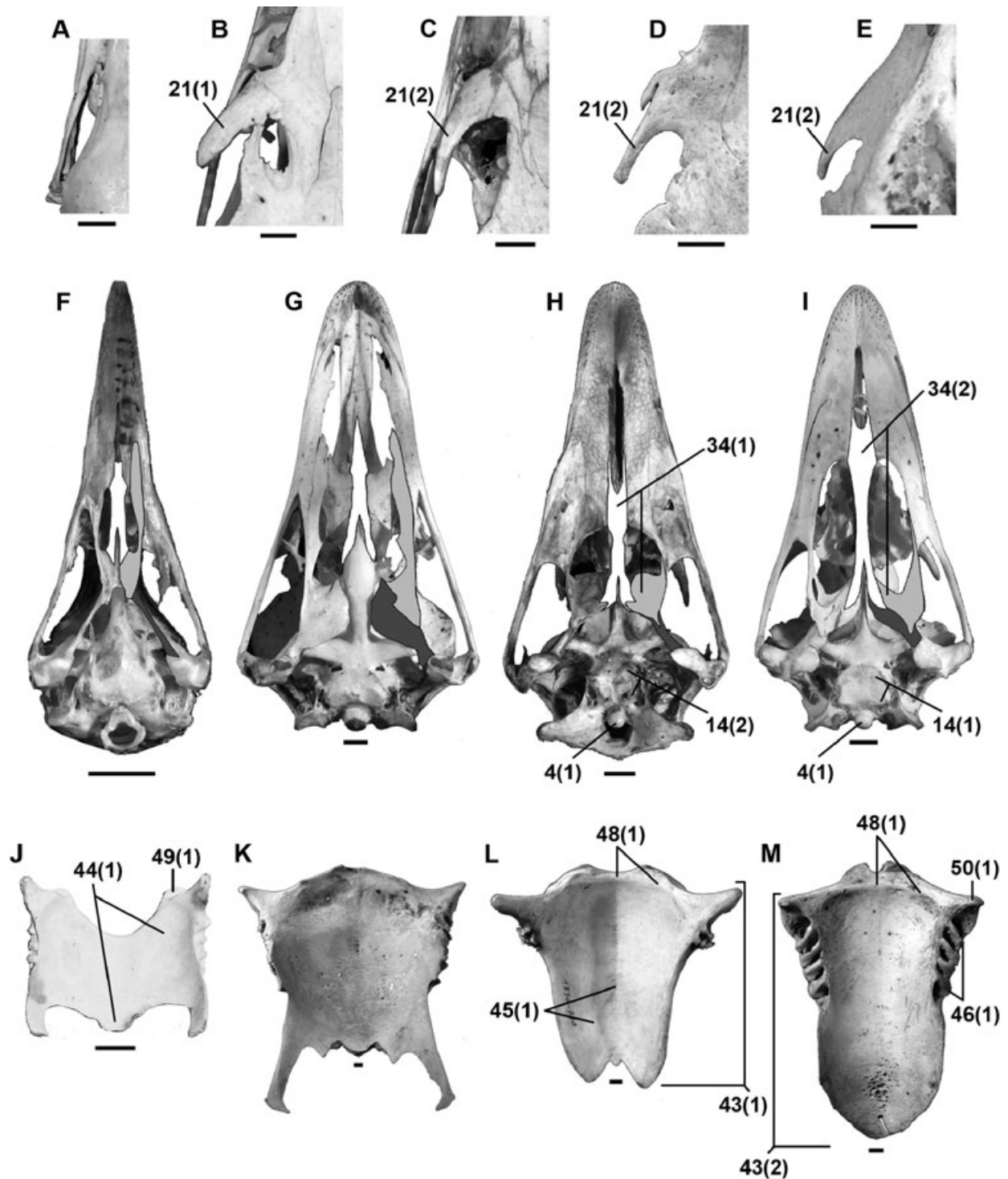
The Ratitae split into a New Zealand clade (Apterygidae plus Dinornithidae) and a clade comprising all other ratites. Monophyly of the New Zealand ratites is based on 13 synapomorphies. A pedicellate condylus occipitalis that is sharply constricted at the base (character 3) is also found in *Aepyornis*. The remaining 12 synapomorphies are strict: (8) processus basiptyergoidei short, lateromedially elongated, and dorsoventrally compressed (Fig. 3I–M); (12) lamina parasphenoidalis triangular, concave, well-defined caudally, with caudolateral corner bearing prominent tuberculum basilare; (23) concha nasalis caudalis of huge size, formed into an olfactory chamber; (31) processus maxillopalatinus of os maxillare forming pocket with tiny caudal aperture; (35) os pterygoideum bearing conspicuous medial fossa, just rostral to facies articularis basiptyergoidea; (44) sternum flattened and wider than long to square in shape, with trabecula mediana a smoothly curved convexity

not exceeding length of corpus sterni (Fig. 4J–M); (49) sulcus articularis coracoideus of sternum lateromedially narrow, widely separated from its counterpart, and located just medial to processus cranio-lateralis (Fig. 4J–M); (81) collum femoris elongated and proximally protruding, separated from oblique plane of facies articularis antitrochanterica by distinct depression; (89) femur with wide, narrow, prominent, and oblique intercondylar ridge; (101) condylus medialis tibiotarsi strongly projecting rostrally and separated from distal end of canalis extensorius by marked depression; (115) hypotarsus composed of two proximodistally short cristae hypotarsi that are widely separated from each other; (118) corpus tarsometatarsi smooth and ovoid in transverse section, with flat facies dorsalis and low cristae plantares.

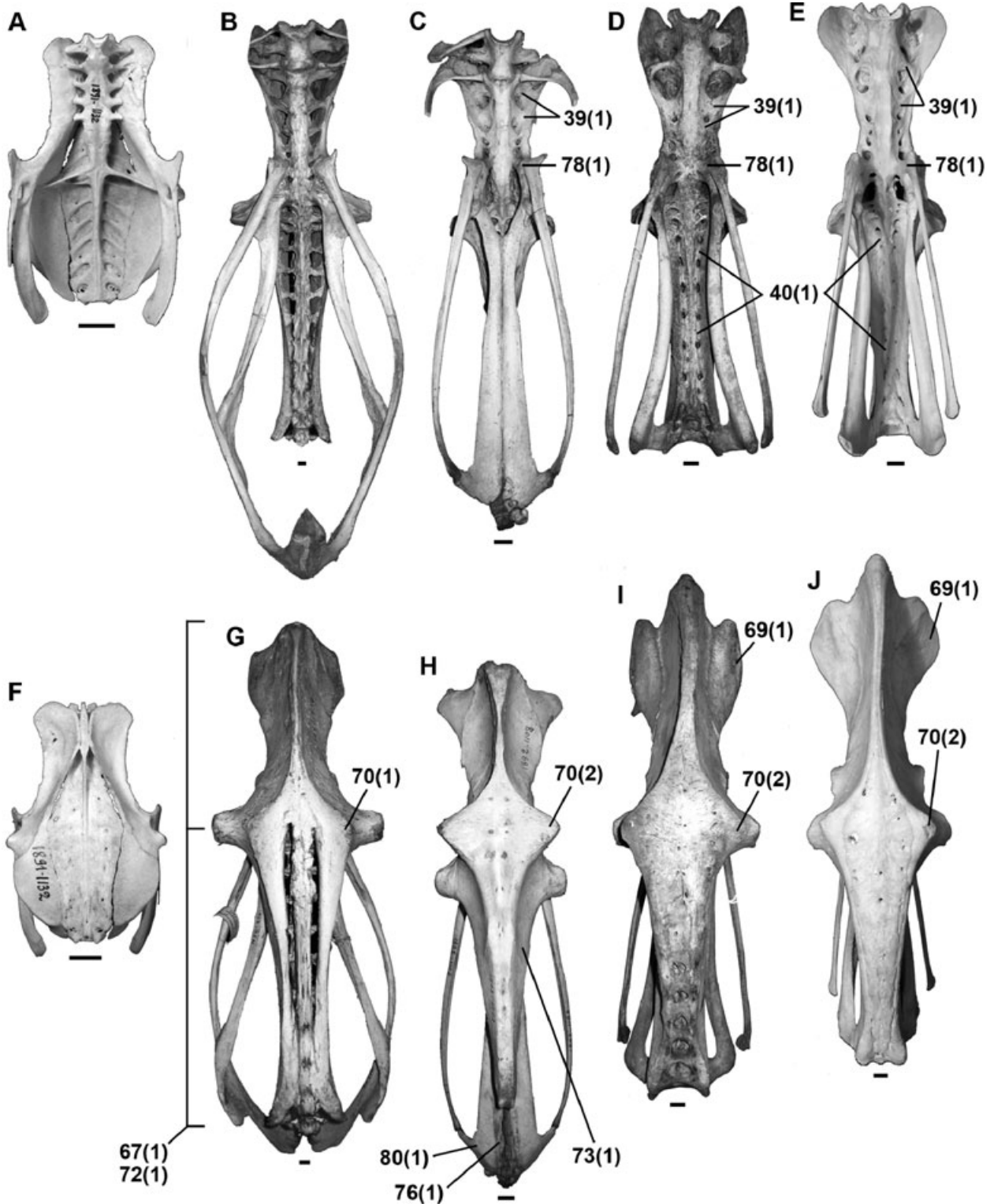
The monophyly of the clade including Aepyornithidae, Struthionidae, Rheidae, Dromaiidae, and Casuariidae is based on 15 synapomorphies. The presence of a very deep ligamental pit on the condylus medialis tibiotarsi (character 102) is also found in *Dinornis*. The remaining 14 synapomorphies are



**Figure 3.** A, B, cava craniorum in left lateral view: (A) *Struthio camelus* Linnaeus, 1758 (MNHN-LAC 1928-15); (B) *Dromaius novaehollandiae* (Latham, 1790) (MNHN-LAC 1900-429). C, D, cava craniorum in caudal view: (C) *S. camelus* (MNHN-LAC 1928-15); (D) *D. novaehollandiae* (MNHN-LAC 1900-429). E–H, cava tympanicorum in rostroventral view: (E) *S. camelus* (MNHN-LAC 1928-15); (F) *Pterocnemia pennata* (D’Orbigny, 1834) (MNHN-LAC 1923-930); (G) *D. novaehollandiae* (MNHN-LAC 1989-89); (H) *Casuarium* sp. (MNHN-LAC 1966-245). I, basis cranii externa and cavum tympanicum of *Apteryx haastii* Potts, 1872 (BMNH 1900-1-4-4) in ventral view. J–M, cava tympanicorum in ventral view: (J) *S. camelus* (MNHN-LAC 1928-15); (K) *P. pennata* (MNHN-LAC 1923-930); (L) *D. novaehollandiae* (MNHN-LAC 1989-89); (M) *Casuarium* sp. (MNHN-LAC 1966-245). Scale bars: 10 mm.



**Figure 4.** A–E, left parietes dorsales orbitarum and ossa lacrimales in dorsal view: (A) *Apteryx australis* Shaw, 1813 (BMNH 1939-12-9-1488); (B) *Struthio camelus* (MNHN-LAC 1923-954); (C) *Rhea americana* (Linnaeus, 1758) (MNHN-LAC 1876-730); (D) *Dromaius novaehollandiae* (MNHN-LAC 1989-89); (E) *Casuarus* sp. (MNHN-LAC 1966-245). F–I, crania, ossa maxillarum and palatorum in ventral view: (F) *Rhynchotus rufescens* (Temminck, 1815) (MNHN-LAC 1877-649); (G) *S. camelus* (MNHN-LAC 1944-69); (H) *R. americana* (MNHN-LAC 1876-730); (I) *D. novaehollandiae* (MNHN-LAC 1900-429). J–M, Sterna in dorsal view: (J) *Apteryx haastii* (BMNH 1900-1-4-4); (K) *S. camelus* (MNHN-LAC, unnumbered); (L) *R. americana* (MNHN-LAC 1876-730); (M) *Casuarus* sp. (MNHN-LAC A-4146). Scale bars: 10 mm.



**Figure 5.** A–E, pelvis in ventral view: (A) *Eudromia elegans* I. Geoffroy Saint-Hilaire, 1832 (MNHN-LAC 1891-1132); (B) *Struthio camelus* (MNHN-LAC 1923-954); (C) *Pterocnemia pennata* (MNHN-LAC 1892-1108); (D) *Dromaius novaehollandiae* (MNHN-LAC 1923-956); (E) *Casuarius casuarius* (Linnaeus, 1758) (MNHN-LAC 1983-18). F–J, pelvis in dorsal view: (F) *E. elegans* (MNHN-LAC 1891-1132); (G) *S. camelus* (MNHN-LAC 1923-954); (H) *P. pennata* (MNHN-LAC 1892-1108); (I) *D. novaehollandiae* (MNHN-LAC 1923-956); (J) *C. casuarius* (MNHN-LAC 1983-18). Scale bars: 10 mm.

**Figure 6.** A–E, right extremitates distales femorum in lateral view: (A) *Rhynchotus rufescens* (MNHN-LAC 1877-649); (B) *Struthio camelus* (MNHN-LAC, unnumbered); (C) *Rhea americana* (MNHN-LAC 1876-730); (D) *Dromaius novaehollandiae* (MNHN-LAC 1900-429); (E) *Casuarius casuarius* (MNHN-LAC 1946-162). F–J, right extremitates distales tibiotarsorum in medial view; (F) *Ry. rufescens* (MNHN-LAC 1877-649); (G) *S. camelus* (MNHN-LAC 1923-954); (H) *Rh. americana* (MNHN-LAC 1876-730); (I) *D. novaehollandiae* (MNHN-LAC 1887-374); (J) *C. casuarius* (MNHN-LAC 1946-162). K–O, left extremitates proximales fibularum in lateral view: (K) *Ry. rufescens* (MNHN-LAC 1877-649); (L) *S. camelus* (MNHN-LAC 1923-954); (M) *Rh. americana* (MNHN-LAC 1876-730); (N) *D. novaehollandiae* (MNHN-LAC 1900-429); (O) *Casuarius* sp. (MNHN-LAC 1966-245). P–T, left extremitates proximales tarsometatarsorum in dorsal view: (P) *Apteryx haastii* (BMNH 1900-1-4-4); (Q) *S. camelus* (MNHN-LAC, unnumbered); (R) *Rh. americana* (MNHN-LAC 1892-1108); (S) *D. novaehollandiae* (MNHN-LAC 1887-374); (T) *C. casuarius* (MNHN-LAC 1946-162). U–Y, left extremitates distales tarsometatarsorum in dorsal view: (U) *A. haastii* (BMNH 1900-1-4-4); (V) *S. camelus* (MNHN-LAC unnumbered); (W) *Rh. americana* (MNHN-LAC 1897-493); (X) *D. novaehollandiae* (MNHN-LAC 1887-374); (Y) *Casuarius* sp. (MNHN-LAC 1966-245). Scale bars: 10 mm.

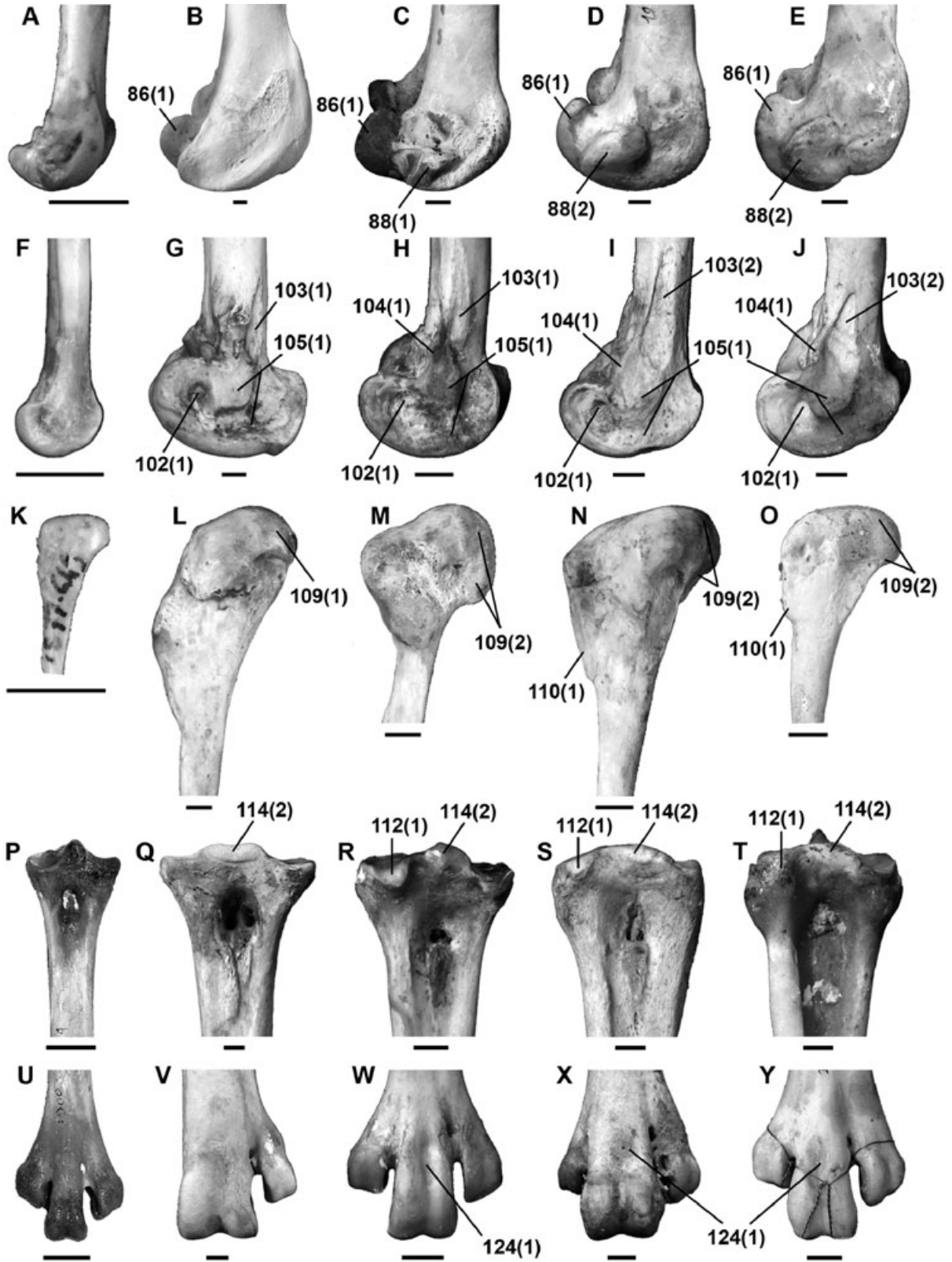
unique to this clade: (5) foramen rami occipitalis ophthalmicae externae located into concavity not far medial to crista nuchalis lateralis, and just dorsal to processus paroccipitalis; ramus occipitalis of arteria ophthalmica externa running into well-defined grooves; (16) origo musculi pseudotemporalis superficialis deep, facing fully laterally (with no dorsal extension), and bounded by distinct crista temporalis; (29) fossa caudalis mandibulae oblique, straight, bounded by sharp crista transversa fossae, and bearing pointed processus retroarticularis plus rostrally protruding processus medialis; (38) vertebrae thoracicae, eminentiae costolaterales forming rostro-laterally projecting peduncle, the rostral border of which is convex; (86) femur, condylus lateralis greatly enlarged and projecting distally beyond the level of condylus medialis; (91) fossa poplitea large and deep, rounded at the bottom, and extending to margo medialis; (93) base of cristae cnemiales tibiotarsi somewhat compressed lateromedially, with crista cnemialis cranialis proximorostrally projecting and evenly curved; (98) distal end of sulcus extensorius tibiotarsi shallow, medially open, with low medial edge (a feature related to the absence of pons supratendineus); (107) incisura intercondylaris tibiotarsi wide and shallow, so that condylus medialis continuous with condylus lateralis, the rostral margin of which tapers proximally; (114) eminentia intercotylaris tarsometatarsi very poorly developed, in median position, dorsally concave; (116) hypotarsus, very large crista lateralis hypotarsi and feebly developed crista medialis hypotarsi; (120) proximal part of corpus tarsometatarsi widening on either side towards extremitas proximalis; (122) corpus tarsometatarsi with well-defined sulcus extensorius that extends in distal half; (125) pes with only three digiti: II, III, and IV.

The clade including Aepyornithidae, Struthionidae, Rheidae, Dromaiidae, and Casuariidae splits into the Malgash aepyornithids and a clade comprising all long-legged ratites, namely Struthionidae, Rheidae,

Dromaiidae, and Casuariidae. Monophyly of the long-legged ratites is based on nine synapomorphies, seven of which are strict: (21) os lacrimale with elongated caudolaterally projecting processus supraorbitalis (Fig. 4A–E); (70) ilium with feebly developed prominence dorsal to acetabulum plus antitrochanter (Fig. 5F–J); (75) ala ischii narrow, slender, laterally concave, parallel with ventral edge of ala postacetabularis ilii, and perpendicular to caudal edge of acetabulum; (103) tibiotarsus with conspicuous scar proximocaudal to epicondylus medialis (Fig. 6F–J); (105) epicondylus medialis tibiotarsi enlarged and plate-like, bounded distally by deep depressio epicondylaris medialis (Fig. 6F–J); (109) caput fibulae roundish and proximocaudally protruding (Fig. 6K–O); (121) greatly elongated corpus tarsometatarsi, with facies subcutanea lateralis strongly flared plantarily. An ala postacetabularis ilii lateromedially compressed and longer than the ala preacetabularis ilii (character 72), is also found in *Hesperornis*; a trochanter femoris bearing feebly developed crista trochanteris and lying perpendicular to facies articularis antitrochanterica (character 82), is found convergently in *Ichthyornis*.

Within this clade, the Struthionidae are sister to a clade comprising the Rheidae and the Dromaiidae plus Casuariidae. The monophyly of the rheamu–cassowary group is based on 24 strict synapomorphies: (1) crista tentorialis very prominent and flange-like (Fig. 3A, B); (2) fossa bulbi olfactorii deep, ovoid, and higher than wide, so that the foramen nervi olfactorii is fairly close to its counterpart (Fig. 3C, D); (4) condylus occipitalis large, sessile, and rounded in shape, with no distinct incisura mediana condyli (Fig. 4G–I); (6) processus paroccipitalis greatly developed, with anterior surface facing fully rostrally, and bearing a curved ridge for the attachment of the membrana tympanica (Fig. 3E–I); (9) processus basipterygoidei elongated and slender (Fig. 3I–M); (14) lamina parasphenoidalis caudorostrally elongated, pentagonal in shape, ventrally





protruding, and well defined caudally and laterally (Fig. 4F–I); (18) ventral side of processus zygomaticus flat with sharp lateral ridge (Fig. 3I–M); (20) pila otica slender, sharply defined medially, and protruding ventrally to foramen pneumaticum caudale (Fig. 3J–M); (21) processus supraorbitalis of os lacrimale elongated, slender, with pointed tip (Fig. 4A–E); (34) vomer extending far caudally, contacting os pterygoideum and wide shallow pars choanalis of os palatinum (Fig. 4F–I); (39) vertebrae synsacrales sectio I, processus transversi short, caudocranially thick, in ventral position, and lying horizontally, so that margo ventralis of ala preacetabularis ilii is level with facies ventralis of corpus vertebrae (Fig. 5A–E); (43) sternum longer than it is wide, with smooth margo caudalis sterni (Fig. 4J–M); (48) margo cranialis sterni dorsal to sulci articulares coracoidei, thick, curved, and smooth, and distinct from depression of facies visceralis sterni (Fig. 4J–M); (70) ilium with well-developed prominence dorsal to acetabulum plus antitrochanter (Fig. 5F–J); (78) pelvis: surface formed by fused proximal ends of ischium and pubis, at caudal end of vertebrae synsacrales sectio I, wide, medially convex, and in a vertical plane (Fig. 5A–E); (83) femur: caudal end of trochanter continuous with well-defined, proximodistally elongated protuberance on facies caudalis; (88) femur: trochlea fibularis laterally prominent, noticeably rostral and distal to crista tibiofibularis (Fig. 6A–E); (95) proximal half of corpus tibiotarsi somewhat compressed lateromedially, exhibiting markedly convex facies rostralis and flattened facies medialis; (104) tibiotarsus with sharp convex ridge continuing proximally to the epicondylus medialis (Fig. 6F–J); (109) caput fibulae roundish, proximocaudally protruding, and with marked caudal extension (Fig. 6K–O); (112) tarsometatarsus: distinct prominence on facies dorsalis, just distal to cotyla medialis, separated from eminentia intercotylaris by depression (Fig. 6P–T); (117) tarsometatarsus with proximally expanded crista lateralis hypotarsi; (124) facies dorsalis of trochlea metatarsi III with distinct depression just proximal to median groove (Fig. 6U–Y); (128) chick covered in a coat of plumae bearing dark stripes at hatching.

## DISCUSSION

### RATITE PHYLOGENETICS

We propose a sister-group relationship between New Zealand ratites (kiwis plus the subfossil moas) and a clade comprising all other ratites (Fig. 2). The latter clade splits into the extinct aepyornithids and a taxon including all large, long-legged living ratites. This result agrees with Cracraft's (1974) hypothesis (Fig. 1A). Lee *et al.* (1997) obtained the same morpho-

logically based topology, except that aepyornithids were not included in their study. Our phylogeny contradicts the recent morphologically based hypothesis, which suggests that Dinornithidae are closer to the clade (elephantbirds/large living ratites) than to *Apteryx* (Zelenitsky & Modesto, 2003; Livezey & Zusi, 2007) (Fig. 1C). A close relationship between Aepyornithidae and either Struthionidae (Grellet-Tinner, 2006) or Struthionidae plus Rheidae (Bledsoe, 1988; Livezey & Zusi, 2007) (Fig. 1B, C) is not retained here.

Although a detailed discussion on moa interrelationships is beyond the scope of this paper, it is worth noting that our phylogeny shows a basal dichotomy separating the small upland moa *Megalapteryx* from all other moa genera, in accordance with previous molecular (Cooper *et al.*, 1992; Cooper, 1997; Baker *et al.*, 2005) and morphological (Worthy & Holdaway, 2002) evidence. This dichotomy is inconsistent with the traditional taxonomy, in which *Dinornis* is assigned to the family Dinornithidae, and the other genera are grouped together in the Emeidae (Worthy & Holdaway, 2002).

We were unable to find new evidence supporting the monophyly of the living Australasian ratites, a hypothesis that has been repeatedly supported by molecular data (Prager *et al.*, 1976; Sibley & Ahlquist, 1981, 1990; Cooper *et al.*, 1992, 2001; Cooper, 1997; Lee *et al.*, 1997; Haddrath & Baker, 2001; Paton *et al.*, 2002; Harrison *et al.*, 2004; Slack *et al.*, 2006) (Fig. 1D–F). Most of these studies, however, have used either phenetical (Prager *et al.*, 1976; Sibley & Ahlquist, 1981, 1990; Cooper, 1997; Haddrath & Baker, 2001) or probabilistic (Cooper *et al.*, 1992, 2001; Cooper, 1997; Haddrath & Baker, 2001; Paton *et al.*, 2002; Harrison *et al.*, 2004; Slack *et al.*, 2006) approaches to infer relationships among taxa, and few of them have performed parsimony analysis (Cooper, 1997; Lee *et al.*, 1997), which aims to refute or validate hypotheses of homology with the test of congruence (e.g. Patterson, 1988; de Pinna, 1991).

Bledsoe (1988) has proposed 11 skeletal synapomorphies (B19, B26, B30, B31, B32, B34, B44, B48, B56, B64, and B71) for the kiwi–emu–cassowary clade. A recent study has shown that five of these characters are either ill-defined or contain coding mistakes (Lee *et al.*, 1997: 210–211, characters B26, B32, B56, B64, and B71). We have included, without modification, the character B34 (Appendix 1, character 66: carpometacarpus with only one os metacarpale bearing facies articularis), which is ambiguous in our resultant tree. Characters B30, B44, and B48 have been greatly modified, and are incorporated in three characters of the present analysis (65, 82, and 88, respectively). Character B31 (no facies articularis alularis on os metacarpale alulare) has not been included in our list,

as it is correlated with character B34 (see above). Character B19 (highly reduced epicondylus dorsalis of humerus) has not been included, because we regard it as ill-defined: the condition of the kiwis is not comparable with that of the emu and the cassowaries. Grellet-Tinner (2006) also obtained a kiwi–emu–cassowary grouping in his cladistic analysis based on oological characters, but this hypothesis is not well supported: only two homoplastic synapomorphies (character 3, eggshell with superficial ornamentation; character 7, spherulites as short, bladed calcite crystals) characterize the kiwi–emu–cassowary clade. In sum, the monophyly of the living Australasian ratites is very poorly supported by cladistic analysis of morphological characters.

The present study strongly supports a clade comprising the rheas, the emu, and the cassowaries (Fig. 2). This new hypothesis is based on 24 uniquely derived characters, including 23 skeletal features plus the striped down of the chicks. To date, none of the above cited works has proposed a rhea–emu–cassowary clade. One study based on mitochondrial DNA sequences (Van Tuinen *et al.*, 1998) proposed a *Dromaius–Rhea* clustering using the neighbour-joining method, which uses global similarity to assess relationships among taxa. Moreover, Van Tuinen *et al.* (1998) did not include *Apteryx* and *Casuarius* in their sampling, because they assumed that the living Australasian ratites were monophyletic, based on previous molecular evidence. Whereas some molecular studies place the rheas as the sister taxon of a clade comprising ostriches plus the living Australasian ratites (Cooper *et al.*, 1992, 2001; Cooper, 1997; Lee *et al.*, 1997; Haddrath & Baker, 2001; Paton *et al.*, 2002) (Fig. 1E, F), some others indicate that the ostrich branches off first, thus only differing from the present topology in the placement of the kiwis (Prager *et al.*, 1976; Sibley & Ahlquist, 1990; Harrison *et al.*, 2004; Slack *et al.*, 2006) (Fig. 1D). Other features concur with a rhea–emu–cassowary clade: the rheas, the emu, and the cassowaries all lack rectrices, in contrast with the ostrich (del Hoyo *et al.*, 1992). In the rheas, the emu, and the cassowaries, the male carries out the tasks of incubation and care of the chick without any help from the female, unlike the kiwis, the ostrich, and most other living birds. Within the Palaeognathae, incubation and parental care exclusively in charge of the male are found convergently in the rhea–emu–cassowary clade and in the tinamous. McKittrick (1992) found that these behavioural features supported palaeognath monophyly, because her palaeognath sampling was limited to Tinamidae and Rheidae.

Within our Rheidae–Dromaiidae–Casuariidae clade, we obtain a close relationship between Dromaiidae and Casuariidae, in accordance with all previous

works (Meise, 1963; Cracraft, 1974; Prager *et al.*, 1976; Sibley & Ahlquist, 1981, 1990; Bledsoe, 1988; Cooper *et al.*, 1992, 2001; Cooper, 1997; Lee *et al.*, 1997; Haddrath & Baker, 2001; Paton *et al.*, 2002; Zelenitsky & Modesto, 2003; Harrison *et al.*, 2004; Grellet-Tinner, 2006; Slack *et al.*, 2006; Livezey & Zusi, 2007) (Figs 1, 2).

Our result contradicts the morphological (Cracraft, 1974; Bledsoe, 1988; Lee *et al.*, 1997; Livezey & Zusi, 2007) and ethological (Meise, 1963) evidence that proposes a sister-group relationship between the ostrich and the rheas (Fig. 1A–C). Lee *et al.* (1997) have defined no less than 16 strict skeletal synapomorphies for the ostrich–rhea grouping (characters L9, L10, L14, L21, L23, L24, L26, L27, L33, L36, L41, L45, L46, L48, L51, and L57). Five of these (L21, L27, L36, L51, and L57) have been incorporated in the present analysis with major modifications (Appendix 1: 73, 115–116, 100, 91, and 31–32, respectively), such that they characterize other nodes in our cladogram. Characters L24 (ischium, processus obturatorius fused to pubis to form a foramen obturatum), L45 (femur, caudal margin of trochlea fibularis rounded, and not extended as far proximally as condylus medialis), and L48 (femur, sulcus patellaris narrow and deep) have not been included in our analysis because we have been unable to recognize the corresponding character states among the specimens examined. The eight remaining synapomorphies of Lee *et al.* (1997) (characters L9, L10, L14, L23 plus L26, L33, L41, and L46) correspond to seven characters of our character list, respectively (see Appendix 1): (53) coracoidal process of os scapulocoracoideum pronounced, knob-like, and projecting toward cavitas glenoidalis; (55) cavitas glenoidalis of os scapulocoracoideum oriented dorsolaterally; (65) carpometacarpus, internal and external margins of trochlea carpalis essentially level with each other and well rounded; (80) sutura ischiopubica distalis present (corresponding to L23 plus L26); (93) tibiotarsus, base of cristae cnemiales sharply compressed lateromedially; crista cnemialis lateralis very poorly developed and knob-like; (108) tibiotarsus, crista trochleae lateralis strongly protruding caudally; (90) femur, condylus medialis distally flattened and continuous, with short, thick, and proximally blunt crista medialis sulci patellaris. Two supplementary characters uniting the ostrich and the rheas come from Livezey & Zusi's (2006) and Bledsoe's (1988) character lists, respectively: (10) rostrum parasphenoidale semicylindrical, ending well rostral to orbita, and incompletely fused to septum interorbitale plus septum nasi osseum; (59) corpus humeri elongated, slender, straight in distal part, ventrally sloping in proximal part, and bearing sharp linea musculi latisimi dorsi. An additional vertebral feature uniting the

ostrich and the rheas has been defined here: (37) third to caudalmost vertebrae cervicales greatly elongated proximodistally. The ten ostrich–rhea hypotheses of homology included in the present study are ambiguous in the resultant cladogram. Our result shows that the ostrich and the rheas have retained the plesiomorphic condition for a number of features within the clade of large living ratites, in particular a fully developed wing skeleton.

#### BIOGEOGRAPHICAL CONSIDERATIONS

Ratites have long been a puzzling problem for biogeographers. All ratites are flightless and are distributed on the southern continents. It is now known that these continents once formed a united land mass, Gondwana, which began to break up in the late Jurassic, between 155 and 150 Mya (Hallam, 1994; Smith, Smith & Funnell, 1994; Scotese, 2001; Jokat *et al.*, 2003). The vicariance biogeography hypothesis proposes that the major ratite clades are descended from a flightless ancestor that was widespread in Gondwanaland: as the landmass fragmented, ratites achieved their current distribution pattern (Cracraft, 1973, 1974, 2001). The oldest ascertained ratite is from the Middle Paleocene of South America (Alvarenga, 1983; Tambussi, 1995). Some workers have postulated the presence of Palaeognathae in the Cretaceous (for a review see Hope, 2002), or at the Cretaceous–Tertiary boundary (Parris & Hope, 2002), but these records remain problematic, largely as a result of their poor preservation and uncertain phylogenetic position (e.g. Chiappe, 2002; Hope, 2002; Dyke & Van Tuinen, 2004). However, it appears that there is now solid evidence for a Cretaceous origin and early diversification of the Neornithes, including at least the initial split between Palaeognathae and Neognathae, and the divergence separating Galloanserae and Neoaves (Cracraft, 2001; Chatterjee, 2002; Parris & Hope, 2002; Dyke & Van Tuinen, 2004; Clarke *et al.*, 2005; Agnolin, Novas & Lio, 2006; Pereira *et al.*, 2007).

Criticisms to the vicariance biogeography hypothesis have rested primarily on the assumption of palaeognath non-monophyly (Olson, 1985, 1989; Feduccia, 1999), which is not supported by any alternative phylogenetic hypothesis (Cracraft, 2001). Detractors of Cracraft's hypothesis also argued that the presence of 'lithornithine' birds in Paleocene–Eocene deposits of Europe and North America (Houde, 1988), and the occurrence of the ostrich-like bird *Palaeotis* in the Middle Eocene of Germany (Houde & Haubold, 1987), indicate a Northern Hemisphere origin for the palaeognaths (Olson, 1989; Feduccia, 1999). Dyke (2003) has placed *Palaeotis* as sister to a clade of large living ratites using character

descriptions presented by Lee *et al.* (1997). Regardless of the weak support of this phylogenetic hypothesis, *Palaeotis* at most demonstrates that some ratites had a European distribution by the Middle Eocene (Cracraft, 2001). A sister-group relationship between *Lithornis* and either Tinamidae (Clarke & Norell, 2002) or Ratitae (Dyke, 2003) has also been proposed. These phylogenetic inferences, however, do not refute the hypotheses that ratites are monophyletic, that they evolved flightlessness once, and that they were primitively Gondwanan (Cracraft, 2001). In a recent paper, Briggs (2003) has suggested an Early Tertiary origin in South America for ratite birds, and a subsequent broad distribution, followed by a decline to their present pattern in the Southern Hemisphere. Regardless of the growing evidence for the presence of palaeognathous birds in the Cretaceous (see above), Briggs's hypothesis takes the fossil record of ratites at face value, and rests on the assumption that flightlessness evolved several times within ratites through neoteny (Briggs, 2003).

The current knowledge on Gondwana break-up states that the Madagascar/Seychelles/India/Sri Lanka landmass separated from the African coastline in the Late Jurassic (Rabinowitz, Coffin & Falvey, 1983; Coffin & Rabinowitz, 1987; Smith *et al.*, 1994; Scotese, 2001). The Madagascar/India block drifted away from East Antarctica in the Early Cretaceous, between 130 and 110 Mya (Powell, Roots & Veevers, 1988; Lawver, Gahagan & Coffin, 1992; Smith *et al.*, 1994; Scotese, 2001; Gaina *et al.*, 2007). However, the exact age of the onset of the seafloor spreading between the two blocks is not determined precisely, so far, because of the paucity of identifiable Mesozoic magnetic anomalies (Lawver *et al.*, 1992; Storey, 1995; Jokat & König, 2007; Eagles & König, 2008). At this point in time, Madagascar/India was separated from the remaining Gondwanan blocks (Smith *et al.*, 1994; Scotese, 2001). Northern South America and Africa drifted away in the Late Albian, about 100 Mya (Smith *et al.*, 1994; Pletsch *et al.*, 2001; Scotese, 2001). At this time, Africa was separated from the remaining Gondwanan landmasses (Smith *et al.*, 1994; Scotese, 2001). The continental block incorporating New Zealand, New Caledonia, the Campbell Plateau, the Lord Howe Rise, and the Norfolk Ridge drifted away from West Antarctica between 85 and 80 Mya, following sea-floor spreading in the Tasman Sea and South-West Pacific Basin (Veevers, Powell & Roots, 1991; Lawver *et al.*, 1992; Yan & Kroenke, 1993; Hallam, 1994; Storey, 1995; McLoughlin, 2001). It is now widely accepted that Australia and South America remained in contact across Antarctica until the Early Tertiary (for a review see Woodburne & Case, 1996). Rifting between Australia and East Antarctica began in the Late Cretaceous (96 Mya), but

seafloor spreading was very slow, and the two plates stayed in contact along Tasmania and the South Tasman Rise (Veevers *et al.*, 1991). The immersion of the South Tasman Rise by the earliest Tertiary (64 Mya) severed the land corridor between East Antarctica and Australia (Veevers *et al.*, 1991; Lawver *et al.*, 1992). Sweepstake dispersal was still possible until the Early Eocene (52 Mya), when a shallow marine seaway formed between Australia and Antarctica (Veevers *et al.*, 1991; Lawver *et al.*, 1992). Southern South America and Antarctica still remained in contact via the Antarctic Peninsula until the opening of the Drake Passage, which is dated as Middle Eocene–Early Oligocene (Lawver *et al.*, 1992; Lawver & Gahagan, 2003; Livermore *et al.*, 2005; Scher & Martin, 2006).

Cladistic biogeography aims to find congruence among patterns of area relationships (Nelson & Platnick, 1981; Humphries & Parenti, 1999). The present topology yields the following area cladogram: New Zealand, Madagascar, and Africa are successive sister areas of a biota comprising South America and Australia–New Guinea. Regarding relationships of the New Zealand biota, our area cladogram is not congruent with geological evidence, which indicates that the final separation between Africa and South America on the one side, and between India/Madagascar and Antarctica on the other side, took place before the isolation of New Zealand. If one admits that the geological evidence and the present phylogeny are correct, this incongruence can be explained by the following ad hoc hypothesis: the initial split separating moas–kiwis from all other ratites occurred prior to the break-up of Gondwana, and representatives of both clades were widespread in Gondwanaland before fragmentation began. Differential extinction events occurred after New Zealand drifted away from Antarctica: representatives of the elephantbird/long-legged ratite lineage became extinct in New Zealand, whereas the moa–kiwi lineage became extinct in all Gondwanan landmasses, except for New Zealand.

The link between South American and Australian biotas proposed here is in accordance with numerous studies that have evidenced closely related taxa on opposite sides of the Southern Pacific (e.g. Brundin, 1966; Humphries & Parenti, 1999; Sequeira & Farrell, 2001; Cranston, 2005). These repeated patterns of area relationships fully agree with geological evidence. In sum, the split between rheas on the one side and emu–cassowaries on the other can be interpreted as the result of a vicariance event that probably occurred in the earliest Tertiary. This inference coincides with the fossil record of the Rheidae, which extends back into the Paleocene: the earliest rheid is *Diogenornis fragilis*

Alvarenga, 1983, known from the Middle Paleocene of Brazil (Alvarenga, 1983) and Argentina (Tambussi, 1995). In contrast, the oldest fossils referable to the emu–cassowary clade come from the Late Oligocene–Late Miocene of Australia (Patterson & Rich, 1987; Boles, 1992, 2001).

The manifest Patagonian affinities of the marsupial fauna from the Eocene La Meseta Formation of Seymour Island, Antarctic Peninsula (Woodburne & Case, 1996; Goin *et al.*, 1999; Reguero, Marensi & Santillana, 2002), seem to concur with plate tectonics, which place the vicariance event that marked the separation of Antarctica and South America posterior to the severance of the land connection between Australia and Antarctica (see above). The appraisal of the phylogenetic position of the fossil ratite from the Eocene La Meseta Formation of Seymour Island (Tambussi *et al.*, 1994) would be critical to assess whether the history of South American, Antarctic, and Australian biotas matches with the timing of the break-up of Gondwana.

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#### REFERENCES

- Agnolin FL, Novas FE, Lio G. 2006.** Neornithine bird coracoid from the Upper Cretaceous of Patagonia. *Ameghiniana* **43**: 245–248.
- Alvarenga HMF. 1983.** Uma ave Ratitae do Paleoceno brasileiro: Bacia Calcária de Itaboraí, estado do Rio de Janeiro, Brasil. *Boletim do Museu Nacional (Rio de Janeiro), Geologia. n. s.* **41**: 1–11.
- Andrews CW. 1896.** On the skull, sternum, and shoulder-girdle of *Aepyornis*. *The Ibis* **2**: 376–389.
- Andrews CW. 1897.** Note on a nearly complete skeleton of *Aepyornis* from Madagascar. *Geological Magazine* **4**: 241–250.
- Andrews CW. 1904.** On the pelvis and hind-limb of *Mullerornis betsilei* M.-Edw. & Grand.; with a note on the occurrence of a ratite bird in the Upper Eocene beds of the Fayum, Egypt. *Proceedings of the Zoological Society of London* **1**: 163–171.
- Archev G. 1941.** The moa. A study of the Dinornithiformes. *Bulletin of the Auckland Institute and Museum* **1**: 1–145.
- Baker AJ, Huynen LJ, Haddrath O, Millar CD, Lambert DM. 2005.** Reconstructing the tempo and mode of evolution in an extinct clade of birds with ancient DNA: the giant moas of New Zealand. *Proceedings of the National Academy of Science of the United States of America* **102**: 8257–8262.

- Balanoff AM, Rowe T. 2007.** Osteological description of an embryonic skeleton of the extinct elephant bird, *Aepyornis* (Palaeognathae: Ratitae). *Journal of Vertebrate Paleontology* **27**, Memoir 9 (suppl. 4): 1–53.
- Ballmann P. 1969.** Les oiseaux miocènes de la Grive-Saint-Alban (Isère). *Geobios* **2**: 157–204.
- Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC. 1993.** *Handbook of avian anatomy: Nomina Anatomica Avium*, 2nd edn. Cambridge: Nuttall Ornithological Club.
- Bledsoe AH. 1988.** A phylogenetic analysis of postcranial skeletal characters of the ratite birds. *Annals of the Carnegie Museum* **57**: 73–90.
- de Boer LEM. 1980.** Do the chromosomes of the kiwi provide evidence for a monophyletic origin of the ratites? *Nature* **287**: 84–85.
- Boles WE. 1992.** Revision of *Dromaius gidju* Patterson and Rich 1987 from Riversleigh, Northwestern Queensland, Australia, with a reassessment of its generic position. *Natural History Museum Los Angeles County, Science Series* **36**: 195–208.
- Boles WE. 2001.** A new emu (Dromaiinae) from the Late Oligocene Etadunna Formation. *The Emu* **101**: 317–321.
- Bremer K. 1994.** Branch support and tree stability. *Cladistics* **10**: 295–304.
- Briggs JC. 2003.** Fishes and birds: Gondwana life rafts reconsidered. *Systematic Biology* **52**: 548–553.
- Brundin L. 1966.** Transantarctic relationships and their significance, as evidenced by chironomid midges, with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagytiae. *Kungliga Svenska Vetenskapsakademiens Handlingar Fjärde Serien* **11**: 1–472.
- Bunce M, Worthy TH, Ford T, Hoppitt W, Willerslev E, Drummond A, Cooper A. 2003.** Extreme reversed sexual size dimorphism in the extinct New Zealand moa *Dinornis*. *Nature* **425**: 172–174.
- Bühler P, Martin LD, Witmer LM. 1988.** Cranial kinesis in the Late Cretaceous birds *Hesperornis* and *Parahesperornis*. *The Auk* **105**: 111–122.
- Caspers GJ, Wattle J, de Jong WW. 1994.** Alpha A-crystallin sequences group tinamou with ratites. *Molecular Biology and Evolution* **11**: 711–713.
- Chatterjee S. 2002.** The morphology and systematics of *Polarornis*, a Cretaceous loon (Aves: Gaviidae) from Antarctica. In: Zhou Z, Zhang F, eds. *Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution, Beijing, 1–4 June 2000*. Beijing: Science Press, 125–155.
- Chiappe LM. 2002.** Basal bird phylogeny: problems and solutions. In: Chiappe LM, Witmer LM, eds. *Mesozoic birds – above the heads of dinosaurs*. Berkeley, CA: University of California Press, 448–472.
- Clarke JA. 2004.** Morphology, phylogenetic taxonomy, and systematics of *Ichthyornis* and *Apatornis* (Avialae: Ornithurae). *Bulletin of the American Museum of Natural History* **286**: 1–179.
- Clarke JA, Norell MA. 2002.** The morphology and phylogenetic position of *Apsaravis ukhaana* from the Late Cretaceous of Mongolia. *American Museum Novitates* **3387**: 1–46.
- Clarke JA, Tambussi CP, Noriega JI, Erickson GM, Ketchum RA. 2005.** Definitive fossil evidence for the extant avian radiation in the Cretaceous. *Nature* **433**: 305–308.
- Coffin MF, Rabinowitz PD. 1987.** Reconstruction of Madagascar and Africa: evidence from the Davie Fracture Zone and Western Somali Basin. *Journal of Geophysical Research* **92**: 9385–9406.
- Cooper A. 1997.** Studies of avian ancient DNA: from Jurassic Park to modern islands extinctions. In: Mindell DP, ed. *Avian Molecular Systematics and Evolution*. New York: Academic Press, 345–373.
- Cooper A, Lalueza-Fox C, Anderson S, Rambaut A, Austin J, Ward R. 2001.** Complete mitochondrial genome sequences of two extinct moas clarify ratite evolution. *Nature* **409**: 704–707.
- Cooper A, Mourer-Chauviré C, Chambers GK, von Haeseler A, Wilson AC, Paabo S. 1992.** Independent origins of New Zealand moas and kiwis. *Proceedings of the National Academy of Science of the United States of America* **89**: 8741–8744.
- Cracraft J. 1973.** Continental drift, paleoclimatology, and the evolution and biogeography of birds. *Journal of Zoology* **169**: 455–545.
- Cracraft J. 2001.** Avian evolution, Gondwana biogeography and the Cretaceous-Tertiary mass extinction event. *Proceedings of the Royal Society of London series B* **268**: 459–469.
- Cracraft J. 1974.** Phylogeny and evolution of the ratite birds. *The Ibis* **116**: 494–521.
- Cracraft J, Barker FK, Braun M, Harshman J, Dyke GJ, Feinstein J, Stanley S, Cibois A, Schikler P, Beresford P, García-Moreno J, Sorenson MD, Yuri T, Mindell DP. 2004.** Phylogenetic relationships among modern birds (Neornithes): towards an avian tree of life. In: Cracraft J, Donoghue MJ, eds. *Assembling the tree of life*. New York: Oxford University Press, 468–489.
- Cranston PS. 2005.** Biogeographic patterns in the evolution of Diptera. In: Wiegmann BM, Yeates DK, eds. *Evolutionary biology of flies*. New York: Columbia University Press, 274–311.
- Davis SJJF. 2002.** *Ratites and Tinamous: Tinamidae, Rheidae, Dromaiidae, Casuariidae, Apterygidae, Struthionidae*. New York: Oxford University Press.
- Dyke GJ. 2003.** The fossil record and molecular clocks: basal radiations within the Neornithes. In: Smith P, Donoghue P, eds. *Telling the evolutionary time – molecular clocks and the fossil record*. London: Taylor and Francis, 263–278.
- Dyke GJ, Van Tuinen M. 2004.** The evolutionary radiation of modern birds (Neornithes): reconciling molecules, morphology and the fossil record. *Zoological Journal of the Linnean Society* **141**: 153–177.
- Eagles G, König M. 2008.** A model of plate kinematics in Gondwana breakup. *Geophysical Journal International* **173**: 703–717.
- Elzanowski A. 1991.** New observations on the skull of *Hesperornis*, with reconstructions of the bony palate and otic region. *Postilla* **207**: 1–20.
- Feduccia A. 1999.** *The origin and evolution of birds*, 2nd edn. New Haven, CT: Yale University Press.

- Gaina C, Müller RD, Brown B, Ishihara T, Ivanov S. 2007.** Breakup and early seafloor spreading between India and Antarctica. *Geophysical Journal International* **170**: 151–169.
- García-Moreno J, Sorenson MD, Mindell DP. 2003.** Congruent avian phylogenies inferred from mitochondrial and nuclear DNA sequences. *Journal of Molecular Evolution* **57**: 27–37.
- Goin FJ, Case JA, Woodburne MO, Vizcaíno SF, Reguero MA. 1999.** New discoveries of ‘opossum-like’ marsupials from Antarctica (Seymour Island, Medial Eocene). *Journal of Mammalian Evolution* **6**: 335–365.
- Grellet-Tinner G. 2006.** Phylogenetic interpretation of eggs and eggshells: implications for oology and Paleognathae phylogeny. *Alcheringa* **30**: 130–180.
- Haddrath O, Baker AJ. 2001.** Complete mitochondrial DNA genome sequences of extinct birds: ratite phylogenetics and the vicariance biogeography hypothesis. *Proceedings of the Royal Society of London, Series B* **268**: 939–945.
- Hallam A. 1994.** *An outline of phanerozoic biogeography*. New York: Oxford University Press.
- Harrison GL, McLenachan PA, Phillips MJ, Slack KE, Cooper A, Penny D. 2004.** Four new avian mitochondrial genomes help get to basic evolutionary questions in the late Cretaceous. *Molecular Biology and Evolution* **21**: 974–983.
- Harshman J. 2007.** Classification and phylogeny of birds. In: Jamieson BGM, ed. *Reproductive biology and phylogeny of birds*. Enfield, NH: Science Publishers, 1–35.
- Heather BD, Robertson HA. 2005.** *The field guide to the birds of New Zealand*. Auckland: Viking.
- Hope S. 2002.** The Mesozoic radiation of Neornithes. In: Chiappe LM, Witmer LM, eds. *Mesozoic birds – above the heads of dinosaurs*. Berkeley, CA: University of California Press, 339–388.
- Houde P. 1988.** Paleognathous birds from the Early Tertiary of the Northern Hemisphere. *Publications of the Nuttall Ornithological Club* **22**: 1–148.
- Houde P, Haubold H. 1987.** *Palaeotis weigelti* restudied: a small Middle Eocene ostrich (Aves: Struthioniformes). *Palaeovertebrata* **17**: 27–42.
- del Hoyo J, Elliott A, Sargatal J. 1992.** *Handbook of the birds of the world. Vol. 1. Ostrich to ducks*. Barcelona: Lynx Edicions.
- Humphries CJ, Parenti LR. 1999.** *Cladistic biogeography, 2nd edition: interpreting patterns of plant and animal distributions*. Oxford: Oxford University Press.
- Huynen L, Millar CD, Scofield RP, Lambert DM. 2003.** Nuclear DNA sequences detect species limits in ancient moa. *Nature* **425**: 175–178.
- Jokat W, Boebel T, König M, Meyer U. 2003.** Timing and geometry of the early Gondwana breakup. *Journal of Geophysical Research* **108**: 1–15.
- Jokat W, König M. 2007.** Gondwana Breakup: the South American, African and Indian plate movements and remaining problems (USGS Open-File Report 2007-1047, Extended Abstract 154). In: Cooper AK, Raymond CR, eds. *Antarctica: A Keystone in a Changing World – online proceedings for the 10th International Symposium on Antarctic Earth Sciences*.
- Lamberton C. 1930.** Contribution à l'étude anatomique des *Aepyornis*. *Bulletin de L'Académie Malgache, Nouvelle Série* **13**: 151–174.
- Lamberton C. 1934.** Ratites subfossiles de Madagascar. Les Mullerornithidae. *Mémoires de l'Académie Malgache* **17**: 123–168.
- Lamberton C. 1946a.** Axis et premières cervicales du *Mullerornis agilis*. *Bulletin de l'Académie Malgache, Nouvelle Série* **27**: 47–51.
- Lamberton C. 1946b.** Oreille osseuse interne des *Aepyornis*. *Bulletin de l'Académie Malgache, Nouvelle Série* **27**: 43–46.
- Lawver LA, Gahagan LM. 2003.** Evolution of Cenozoic seaways in the circum-Antarctic region. *Palaeogeography, Palaeoclimatology, Palaeoecology* **198**: 11–37.
- Lawver LA, Gahagan LM, Coffin MF. 1992.** The development of paleoseaways around Antarctica. *American Geophysical Union Antarctic Research Series* **56**: 7–30.
- Lee K, Feinstein J, Cracraft J. 1997.** The phylogeny of ratite birds: resolving conflicts between molecular and morphological data sets. In: Mindell DP, ed. *Avian molecular systematics and evolution*. New York: Academic Press, 173–211.
- Livermore R, Nankivell A, Eagles G, Morris P. 2005.** Paleogene opening of Drake Passage. *Earth and Planetary Science Letters* **236**: 459–470.
- Livezey BC, Zusi RL. 2006.** Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. I. Methods and characters. *Bulletin of the Carnegie Museum of Natural History* **37**: 1–556.
- Livezey BC, Zusi RL. 2007.** Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. II. Analysis and discussion. *Zoological Journal of the Linnean Society* **149**: 1–95.
- Lowe PR. 1930.** On the relationships of the *Aepyornithes* to other *Struthionidae* as revealed by a study of the pelvis of *Mullerornis*. *The Ibis* **6**: 470–490.
- McKittrick MC. 1992.** Phylogenetic analysis of avian parental care. *The Auk* **109**: 828–846.
- McLoughlin S. 2001.** The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Australian Journal of Botany* **49**: 271–300.
- Marsh OC. 1880.** *Odontornithes: a monograph on the extinct toothed birds of North America*. *Reports of the United States Geological Exploration of the Fortieth Parallel* **7**: 1–201.
- Mayr G, Clarke J. 2003.** The deep divergences of neornithine birds: a phylogenetic analysis of morphological characters. *Cladistics* **19**: 527–553.
- Meise W. 1963.** Verhalten der Straußartigen Vögel und Monophylie der Ratitae. *Proceedings of the International Ornithological Congress* **13**: 115–125.
- Milne-Edwards A, Grandidier A. 1894.** Observations sur les *Aepyornis* de Madagascar. *Comptes Rendus Hebdomadaires de l'Académie des Sciences* **118**: 122–127.
- Milne-Edwards A, Grandidier A. 1895.** Sur les ossements d'oiseaux provenant des terrains récents de Madagascar. *Bulletin du Muséum d'Histoire Naturelle* **1**: 9–11.
- Monnier L. 1913.** Paléontologie de Madagascar. VII. Les *Aepyornis*. *Annales de Paléontologie* **8**: 125–172.

- Nelson GJ, Platnick NI. 1981.** *Systematics and biogeography: cladistics and vicariance*. New York: Columbia University Press.
- Nixon KC. 1999.** *WinClada 0.9.9 (Beta)*. Ithaca, NY: Author.
- Oliver WRB. 1949.** The moas of New Zealand and Australia. *Dominion Museum Bulletin* **15**: 1–206.
- Olson SL. 1985.** The fossil record of birds. In: Farner DS, King JR, Parkes KC, eds. *Avian biology*, Vol. 8. New York: Academic Press, 79–256.
- Olson SL. 1989.** Aspects of global avifaunal dynamics during the Cenozoic. *Proceedings of the International Ornithological Congress* **19**: 2023–2029.
- Parris DC, Hope S. 2002.** New interpretations of the birds from the Navesink and Hornerstown Formations, New Jersey, USA (Aves: Neornithes). In: Zhou Z, Zhang F, eds. *Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution, Beijing, 1–4 June 2000*. Beijing: Science Press, 113–124.
- Paton TA, Haddrath O, Baker AJ. 2002.** Complete mitochondrial DNA genome sequences show that modern birds are not descended from transitional shorebirds. *Proceedings of the Royal Society of London series B* **269**: 839–846.
- Patterson C. 1988.** Homology in classical and molecular biology. *Molecular Biology and Evolution* **5**: 603–625.
- Patterson C, Rich PV. 1987.** The fossil history of the emus, *Dromaius* (Aves: Dromaiinae). *Records of the South Australian Museum* **21**: 85–117.
- Pereira SL, Baker AJ. 2006.** A mitogenomics timescale for birds detects variable phylogenetic rates of molecular evolution and refutes the standard molecular clock. *Molecular Biology and Evolution* **23**: 1731–1740.
- Pereira SL, Johnson KP, Clayton DH, Baker AJ. 2007.** Mitochondrial and nuclear DNA sequences support a Cretaceous origin of Columbiformes and a dispersal-driven radiation in the Paleogene. *Systematic Biology* **56**: 656–672.
- de Pinna MGG. 1991.** Concepts and tests of homology in the cladistic paradigm. *Cladistics* **7**: 367–394.
- Pletsch T, Erbacher J, Holbourn AEL, Kuhnt W, Moulade M, Oboh-Ikuenobede FE, Söding E, Wagner T. 2001.** Cretaceous separation of Africa and South America: the view from the West African margin (ODP Leg 159). *Journal of South American Earth Sciences* **14**: 147–174.
- Powell CM, Roots SR, Veevers JJ. 1988.** Pre-breakup continental extension in East Gondwanaland and the early opening of the Eastern Indian Ocean. *Tectonophysics* **155**: 261–283.
- Prager EM, Wilson AC, Osuga DT, Feeney RE. 1976.** Evolution of flightless land birds on Southern continents: transferrin comparison shows monophyletic origin of ratites. *Journal of Molecular Evolution* **8**: 283–294.
- Rabinowitz PD, Coffin MF, Falvey D. 1983.** The separation of Madagascar and Africa. *Science* **220**: 67–69.
- Reguero MA, Marensi SA, Santillana SN. 2002.** Antarctic Peninsula and South America (Patagonia) Paleogene terrestrial faunas and environments: biogeographic relationships. *Palaeogeography, Palaeoclimatology, Palaeoecology* **179**: 189–210.
- Scher HD, Martin EE. 2006.** Timing and climatic consequences of the opening of Drake Passage. *Science* **312**: 428–430.
- Scotese CR. 2001.** Atlas of Earth History, PALEOMAP Project: Arlington, Texas.
- Sequeira AS, Farrell BD. 2001.** Evolutionary origins of Gondwanan interactions: how old are Araucaria beetle herbivores? *Biological Journal of the Linnean Society* **74**: 459–474.
- Sibley CG, Ahlquist JE. 1981.** The phylogeny and relationships of the ratite birds as indicated by DNA-DNA hybridization. In: Scudder GGE, Reveal JL, eds. *Evolution today, proceedings of the second International Congress of Systematics and Evolutionary Biology*. Pittsburgh: Hunt Institute for Botanical Documentation, Carnegie-Mellon University, 301–335.
- Sibley CG, Ahlquist JE. 1990.** *Phylogeny and classification of birds: a study in molecular evolution*. New Haven, CT: Yale University Press.
- Slack KE, Jones CM, Ando T, Harrison GL, Fordyce RE, Arnason U, Penny D. 2006.** Early penguin fossils, plus mitochondrial genomes, calibrate avian evolution. *Molecular Biology and Evolution* **23**: 1144–1155.
- Smith AG, Smith DG, Funnell BM. 1994.** *Atlas of Mesozoic and Cenozoic coastlines*. Cambridge: Cambridge University Press.
- Stapel SO, Leunissen JAM, Versteeg M, Wattel J, de Jong WW. 1984.** Ratites as the oldest offshoot of avian stem – evidence from alpha-crystallin A sequences. *Nature* **311**: 257–259.
- Storey BC. 1995.** The role of mantle plumes in continental breakup: case histories from Gondwanaland. *Nature* **377**: 301–308.
- Swofford DL. 1998.** *PAUP\* 4.0*. Sunderland, MA: Sinauer Associates.
- Tambussi CP. 1995.** The fossil Rheiformes from Argentina. *Courier Forschungsinstitut Senckenberg* **181**: 121–129.
- Tambussi CP, Noriega JI, Gazdzicki A, Tatur A, Reguero MA, Vizcaíno SF. 1994.** Ratite bird from the Paleogene La Meseta Formation, Seymour Island, Antarctica. *Polish Polar Research* **15**: 15–20.
- Van Tuinen M, Sibley CG, Hedges SB. 1998.** Phylogeny and biogeography of ratite birds inferred from DNA sequences of the mitochondrial ribosomal genes. *Molecular Biology and Evolution* **15**: 370–376.
- Van Tuinen M, Sibley CG, Hedges SB. 2000.** The early history of modern birds inferred from DNA sequences of nuclear and mitochondrial ribosomal genes. *Molecular Biology and Evolution* **17**: 451–457.
- Veevers JJ, Powell CM, Roots SR. 1991.** Review of sea-floor spreading around Australia. 1. Synthesis of the patterns of spreading. *Australian Journal of Earth Sciences* **38**: 373–389.
- Wiman C. 1935.** Über Aepyornithes. *Nova Acta Regiae Societatis Scientiarum Upsaliensis, Series IV* **9**: 1–57.
- Wiman C. 1937a.** Etude sur le segment terminal de l'aile des *Aepyornis* et des *Mullerornis*. *Bulletin de l'Académie Malgache, Nouvelle Série* **20**: 101–105.



- Wiman C. 1937b.** On supernumerary metapodials in *Aepyornis*, the moas, and some other birds. *Proceedings of the Zoological Society of London Series B* **107**: 245–256.
- Wiman C, Edinger T. 1941.** Sur les crânes et les encéphales d'*Aepyornis* et de *Mullerornis*. *Bulletin de L'Académie Malgache, Nouvelle Série* **24**: 1–47.
- Witmer LM. 1990.** The craniofacial air sac system of Mesozoic birds (Aves). *Zoological Journal of the Linnean Society* **100**: 327–378.
- Witmer LM, Martin LD. 1987.** The primitive features of the avian palate, with special reference to Mesozoic birds. *Documents des Laboratoires de Géologie de Lyon* **99**: 21–40.
- Woodburne MO, Case JA. 1996.** Dispersal, vicariance, and the Late Cretaceous to early Tertiary land mammal biogeography from South America to Australia. *Journal of Mammalian Evolution* **3**: 121–161.
- Worthy TH, Holdaway RN. 2002.** *The lost world of the moa: prehistoric life of New Zealand*. Bloomington: Indiana University Press.
- Yan CY, Kroenke LW. 1993.** A plate tectonic reconstruction of the Southwest Pacific, 0–100 Ma. *Proceedings of the Ocean Drilling Program, Scientific Results* **130**: 697–709.
- Zelenitsky DK, Modesto SP. 2003.** New information on the eggshell of ratites (Aves) and its phylogenetic implications. *Canadian Journal of Zoology* **81**: 962–970.

## APPENDIX 1

Description of characters used in the phylogenetic analysis.

1. Cavum cranii, fossa tecti mesencephali: crista tentorialis very prominent and flange-like: no (0); yes (1).
2. Cavum cranii, fossa bulbi olfactorii deep, ovoid, and higher than wide, so that foramen nervi olfactorii (rostral opening of fossa) fairly close to its counterpart: no (0); yes (1).
3. Condylus occipitalis pedicellate and sharply constricted at base: no (0); yes (1).
4. Condylus occipitalis large, sessile, and rounded in shape, with no distinct incisura mediana condyli: no (0); yes (1).
5. Os exoccipitale, facies externa, foramen rami occipitalis ophthalmicae externae located in concavity not far medial to crista nuchalis lateralis, and just dorsal to processus paroccipitalis; the ramus occipitalis of arteria ophthalmica externa runs on occiput into well-defined grooves: no (0); yes (1).
6. Processus paroccipitalis: not as follows (0); flange-like with concave anterior surface (1); greatly developed with anterior surface facing fully rostrally, and bearing curved ridge for attachment of membrana tympanica (2) (the aspect of the processus paroccipitalis in ratites is mentioned in Livezey & Zusi, 2006: character 129).
7. Processus paroccipitalis: not as follows (0); caudal tip in extreme dorsal position, making smooth angle with elongated and straight ventral edge (1); ventral edge rostrally oriented (2) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
8. Rostrum parasphenoidale, processus basiptyergoidei short, lateromedially elongated, and dorsoventrally compressed: no (0); yes (1).
9. Rostrum parasphenoidale bearing elongated and slender processus basiptyergoidei: no (0); yes (1).
10. Rostrum parasphenoidale semi-cylindrical, ending well rostral to orbita, and incompletely fused to septum interorbitale plus septum nasi osseum (see Livezey & Zusi, 2006: character 107): no (0); yes (1).
11. Rostrum parasphenoidale short and strongly compressed lateromedially: no (0); yes (1).
12. Lamina parasphenoidalis triangular, concave, well-defined caudally, with caudolateral corner bearing prominent tuberculum basilare: no (0); yes (1) (see Lee *et al.*, 1997: character 56).
13. Lamina parasphenoidalis greatly abbreviated caudo-rostrally, and bounded by evenly curved rostral edge: no (0); yes (1).
14. Lamina parasphenoidalis: not as follows (0); caudo-rostrally elongated, pentagonal in shape, ventrally protruding, and well-defined caudally and laterally (1); with prominent, caudo-rostrally elongated processus mediales parasphenoidales (2).
15. Tuba auditiva a deep elongated furrow, with sharp rostral and caudal edges: no (0); yes (1) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
16. Fossa temporalis, origo musculi pseudotemporalis superficialis: not as follows (0); deep, facing fully laterally (no dorsal extension), and bounded by distinct crista temporalis (1); very deep, narrow, and bounded by very sharp crista temporalis (2).
17. Processus zygomaticus greatly elongated, projecting over two-thirds of corpus ossis quadrati (Lee *et al.*, 1997: character 53).
18. Processus zygomaticus: not as follows (0); ventral side flat with sharp lateral ridge (1); lateral ridge strongly curved and caudally continuous with blade-like process (2).
19. Processus zygomaticus, rostral part of base bearing smooth prominence: no (0); yes (1).
20. Pila otica: not as follows (0); slender, sharply defined medially, protruding ventrally to foramen pneumaticum caudale (1).

21. Os lacrimale with elongated caudolaterally projecting processus supraorbitalis: absent (0); present (1) (Lee *et al.*, 1997: character 52); present and slender, with a pointed tip (2).
22. Cavum nasi: deep triangular cavum nasi olfactorii (Livezey & Zusi, 2006) bounded caudally by swollen os ectethmoidale, which is synostosed with os mesethmoidale and base of processus orbitalis ossis lacrimale: absent (0); present (1). This peculiar structure is illustrated in Livezey & Zusi (2006: fig. 7A).
23. Concha nasalis caudalis of huge size, formed into an olfactory chamber: no (0); yes (1) (Lee *et al.*, 1997: character 58).
24. Mandibula, pars caudalis gradually widening and medially curving just rostral to fossa articularis quadratica: no (0); yes (1).
25. Mandibula, partes intermedia et symphy-sialis distinctly curved ventralwards: no (0); yes (1) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
26. Mandibula, lateral wall of fossa articularis quadratica caudorostrally elongated and strongly convex: no (0); yes (1) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
27. Mandibula, fossa articularis quadratica narrow, lateromedially compressed, bounded medially by rostral continuation of processus medialis mandibulae: no (0); yes (1) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
28. Mandibula: not as follows (0); processus medialis et retroarticularis close to each other, dorsally protruding, and separated by sharp crista transversa fossae (1); caudally protruding and defining concave fossa caudalis (2) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
29. Mandibula, fossa caudalis: mediorostrally sloping, straight, with pointed processus retroarticularis, and rostrally protruding processus medialis; crista transversa fossae sharp and straight: no (0); yes (1).
30. Os premaxillare with narrow processus frontalis: no (0); yes (1).
31. Os maxillare, processus maxillopalatinus forming pocket with tiny caudal aperture; this pocket completely encloses the maxillary diverticulum of the sinus antorbitalis (see Witmer, 1990): no (0); yes (1) (modified from Lee *et al.*, 1997: character 57). A caudal aperture is absent in some *Apteryx* specimens.
32. Os maxillare, processus maxillopalatinus forming very large, thin-walled pocket to accommodate the maxillary diverticulum of the sinus antorbitalis (Witmer, 1990): no (0); yes (1) (modified from Lee *et al.*, 1997: character 57).
33. Os palatinum, fossa choanalis very deep, ovoid in shape, and in a vertical plane: no (0); yes (1) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
34. Vomer: not as follows (0); extending far caudally, contacting os pterygoideum and wide shallow pars choanalis of os palatinum (1); ventrally flat, not embracing rostrum parasphenoidale (2).
35. Os pterygoideum bearing conspicuous medial fossa just rostral to facies articularis basipterygoidea: no (0); yes (1) (Lee *et al.*, 1997: character 54).
36. Atlas, arcus atlantis forming overhang rostrally: no (0); yes (1).
37. Third to caudalmost vertebrae cervicales greatly elongated proximodistally: no (0); yes (1).
38. Vertebrae thoracicae, eminentiae costolaterales forming rostrolaterally projecting peduncle, the rostral border of which is convex: no (0); yes (1).
39. Vertebrae synsacrales, sectio I (Livezey & Zusi, 2006): processus transversi short, caudocranially thick, in ventral position, and lying horizontally, so that margo ventralis of ala preacetabularis ilii is level with facies ventralis of corpus vertebrae: no (0); yes (1).
40. Vertebrae synsacrales lumbares, sacrales et caudales (Livezey & Zusi, 2006), processus transversi broadened, fused with each other and with ilium to form a ventral plate: no (0); yes (1) (Lee *et al.*, 1997: character 25).
41. Pygostylus smaller than caudalmost vertebra caudalis libera, and fused to two or three additional vertebrae caudales that remain distinguishable: no (0); yes (1).
42. Sternum smooth and compact, devoid of carina sterni: no (0); yes (1) (see Cracraft, 1974: 503, 506; Lee *et al.*, 1997: character 1).
43. Sternum: not as follows (0); longer than it is wide with smooth margo caudalis sterni (1) (modified from Cracraft, 1974: 503; Bledsoe, 1988: character 4; Lee *et al.*, 1997: character 2); widening caudal to margo costalis sterni (2) (a narrowing of the corpus just caudal to margo costalis is described in Livezey & Zusi, 2006: character 1167).
44. Sternum, corpus sterni: not as follows (0); flattened and wider than long to square in shape, with trabecula mediana a smoothly curved convexity not exceeding length of corpus sterni (1) (modified from Lee *et al.*, 1997: character 5); slightly longer than wide, with well-developed trabecula mediana (2) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).

45. Sternum, facies visceralis sterni, strongly concave pars cardiaca and deep sulcus medianus: no (0); yes (1) (see Bledsoe, 1988: character 5).
46. Sternum, margo costalis sterni bearing four wide, oblique, and dorsally facing processus articulares sternocostales: no (0), yes (1). The orientation of the processus articulares sternocostales is mentioned by Livezey & Zusi (2006: characters 1120–1121.)
47. Sternum, margo cranialis sterni a straight ridge strongly protruding dorsally: no (0); yes (1) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
48. Sternum, margo cranialis sterni dorsal to sulci articulares coracoidei, thick, curved, smooth, and distinct from depression of facies visceralis sterni: no (0); yes (1).
49. Sternum, margo cranialis sterni, sulcus articularis coracoideus lateromedially narrow, widely separated from its counterpart, and located just medial to processus craniolateralis: no (0); yes (1) (see Cracraft, 1974: 503; Bledsoe, 1988: character 6; Lee *et al.*, 1997: character 3).
50. Sternum, margo cranialis sterni, processus craniolateralis convex at base of facies cranialis, and dorsally oriented: no (0); yes (1).
51. Os scapulocoracoideum (synostosis of scapula and os coracoideum): absent (0); present (1) (Cracraft, 1974: 503, 506; Lee *et al.*, 1997: character 8). A vestigial cavitas glenoidalis (Livezey & Zusi, 2006: character 1341) is related to the presence of an os scapulocoracoideum. A scapulocoracoideum is regarded as absent in *Emeus* and *Euryapteryx* (Worthy & Holdaway, 2002: Appendix 3, character 41); however, the same authors mention this bone as present and greatly reduced in these genera (Worthy & Holdaway, 2002: 95), which are coded as state 1 in the present analysis.
52. Os scapulocoracoideum, extremitas cranialis scapulae strongly protruding medially: no (0); yes (1). In *Struthio*, the bony ridge linking extremitas proximalis scapulae with extremitas sternalis coracoidei is regarded as autapomorphic; thus, this taxon is coded state 1. Taxa devoid of scapulocoracoideum are coded as non-applicable for this character.
53. Os scapulocoracoideum, coracoidal process (Cracraft, 1974) pronounced, knob-like, and projecting toward cavitas glenoidalis: no (0); yes (1) (Cracraft, 1974: 505, 508; Bledsoe, 1988: character 9; Lee *et al.*, 1997: character 9). Taxa devoid of scapulocoracoideum are coded as non-applicable for this character.
54. Os scapulocoracoideum, corpus coracoidei elongated, slender, and triangular in shape, with ridge on facies ventralis extending from prominent blunt processus procoracoideus: no (0); yes (1). Taxa devoid of scapulocoracoideum are coded as non-applicable for this character.
55. Os scapulocoracoideum, cavitas glenoidalis oriented dorsolaterally (Bledsoe, 1988: character 7; Lee *et al.*, 1997: character 10): no (0); yes (1). Taxa devoid of scapulocoracoideum are coded as non-applicable for this character. Moas lack a cavitas glenoidalis, and are also coded as non-applicable for this character.
56. Os scapulocoracoideum: cavitas glenoidalis cup-shaped, laterally facing, and roughly parallel with long axis of corpus coracoidei: no (0); yes (1). Taxa devoid of scapulocoracoideum are coded as non-applicable for this character. Moas lack a cavitas glenoidalis, and are also coded as non-applicable for this character.
57. Humerus, caput humeri separated from tuberculum dorsale plus crista deltopectoralis: no (0); yes (1) (modified from Livezey & Zusi, 2006: character 1390).
58. Humerus, tuberculum ventrale knob-like, ventrally prominent, protruding far proximally to, and continuous with, caput humeri: no (0); yes (1) (see Bledsoe, 1988: character 14; Lee *et al.*, 1997: character 12).
59. Humerus, corpus humeri: elongated, slender, straight in distal part, ventrally sloping in proximal part and bearing sharp linea musculi latissimi dorsii: no (0); yes (1) (modified from Bledsoe, 1988: character 11).
60. Humerus, corpus humeri, margo ventralis: sharp crest extending from extremitas distalis to foramen nutritium (Ballmann, 1969): absent (0); present (1).
61. Skeleton antebrachii et manus fused to form a single terminal segment: no (0); yes (1).
62. Ulna at least one-third shorter than humerus: no (0); yes (1) (see Cracraft, 1974: 505–506; Bledsoe, 1988: characters 11, 29; Lee *et al.*, 1997: character 11).
63. Ulna, corpus ulnae straight with margo caudalis showing no curvature towards olecranon: no (0); yes (1).
64. Ulna, proximal end of margo caudalis very sharp: no (0); yes (1).
65. Carpometacarpus, trochlea carpalis: internal and external margins essentially level with each other, and well rounded (Bledsoe, 1988: character 30; Lee *et al.*, 1997: character 14): no (0); yes (1).
66. Carpometacarpus, number of ossa metacarpales with facies articularis: three (0); one (1) (Bledsoe, 1988: character 34; Lee *et al.*, 1997: character 16). The absence of a facies articularis alularis (Bledsoe, 1988: character 31; Lee *et al.*, 1997:

- character 15) is considered to be correlated with the present character.
67. Pelvis: vertebrae synsacrales with poorly developed processus transversi and greatly elongated processus spinosi; ilium high, strongly sloping on either side, with ala preacetabularis ilii forming carina iliaca dorsales (Livezey & Zusi, 2006): no (0); yes (1) (see Cracraft, 1974: 503; Bledsoe, 1988: character 35; Lee *et al.*, 1997: character 19; Livezey & Zusi, 2006: character 926).
  68. Pelvis, cup-shaped acetabulum with small foramen acetabuli: no (0); yes (1).
  69. Ilium, rostral part of ala preacetabularis ilii rounded in shape and ventrally protruding: no (0); yes (1).
  70. Ilium, prominence dorsal to acetabulum plus antitrochanter: absent (0); present, feebly developed (1); present, well developed (2).
  71. Ilium, ala postacetabularis ilii: not as follows (0); wide, ventrally flat, bluntly pointed at tip, and protruding caudal to synsacrum (1); strongly convex laterally and evenly tapering rostrally (2) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
  72. Ilium, ala postacetabularis ilii lateromedially compressed and longer than ala preacetabularis ilii: no (0); yes (1) (Cracraft, 1974: 503; Bledsoe, 1988: character 37; Lee *et al.*, 1997: character 20).
  73. Ilium, ala postacetabularis ilii narrowing dorsoventrally and mediolaterally, tapering to a conical shape: no (0); yes (1) (modified from Cracraft, 1974: 503, 508; Bledsoe, 1988: character 40; Lee *et al.*, 1997: character 21). In contrast to previous authors, we found state 1 to occur only in the Rheidae.
  74. Ischium, caudal edge of acetabulum elongated, vertical, column-shaped, and perpendicular to ala ischii. This is correlated with the presence of a large spatium ilioischadicum (Livezey & Zusi, 2006): no (0); yes (1).
  75. Ischium, ala ischii narrow, slender, laterally concave, parallel with ventral edge of ala postacetabularis ilii, and perpendicular to caudal edge of acetabulum: no (0); yes (1).
  76. Symphysis ischiadica: absent (0); present (1) (see Cracraft, 1974: 503; Livezey & Zusi, 2006: character 1961).
  77. Ischium, processus terminalis ischii ending in a hammer-like expansion: no (0); yes (1) (modified from Lee *et al.*, 1997: character 22).
  78. Pelvis, surface formed by fused rostral ends of ischium and pubis, at caudal border of vertebrae synsacrales, sectio I (Livezey & Zusi, 2006): wide, medially convex, in a vertical plane: no (0); yes (1).
  79. Pelvis, ischium and pubis markedly projecting laterally so that acetabulum is oblique with respect to synsacrum: no (0); yes (1) (Worthy & Holdaway, 2002: appendix 3, character 75).
  80. Sutura ischiopubica distalis (processus terminalis ischii synostosed to pubis): absent (0); present (1) (see Cracraft, 1974: 503–504, 508; Bledsoe, 1988: characters 38, 42; Lee *et al.*, 1997: characters 23, 26; Livezey & Zusi, 2006: character 1952). We think that a broad fenestra ischiopubica (Livezey & Zusi, 2006: character 1784) is correlated with the synostosis of ischium and pubis.
  81. Femur, collum femoris elongated, proximally protruding, and separated from oblique plane of facies articularis antitrochanterica by distinct depression: no (0); yes (1) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
  82. Femur, trochanter bearing feebly developed crista trochanteris and lying perpendicular to facies articularis antitrochanterica, which is slightly oblique (in *Casuaris*) to horizontal: no (0); yes (1) (modified from Bledsoe, 1988: characters 43, 44; Lee *et al.*, 1997: characters 42, 43).
  83. Femur, caudal end of trochanter femoris continuous with well-defined, proximodistally elongated protuberance on facies caudalis: no (0); yes (1).
  84. Femur, corpus femoris evenly widening towards extremitas distalis: no (0); yes (1) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
  85. Femur, linea intermuscularis caudalis irregular and thickened, bending inwards distally to join medial border of fossa poplitea: no (0); yes (1) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
  86. Femur, condylus lateralis greatly enlarged and projecting distally beyond the level of condylus medialis: no (0); yes (1) (see Cracraft, 1974: 498, 506; Bledsoe, 1988: character 46; Lee *et al.*, 1997: character 44).
  87. Femur, proximal part of trochlea fibularis: not as follows (0); strongly protruding laterally (1); markedly convex, forming distinct overhang (2) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
  88. Femur, trochlea fibularis: not as follows (0); laterally prominent, noticeably rostral and distal to crista tibiofibularis (1) (see Bledsoe, 1988: character 48); bulbous, sharply defined, and oval in shape (2) (see Cracraft, 1974: 498, 507; Lee *et al.*, 1997: character 47).
  89. Femur with wide, narrow, and oblique intercondylar ridge; the deep bottom of fossa poplitea and the marked impressio ligamenti cruciati

- cranialis make this ridge particularly prominent: no (0); yes (1) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
90. Femur, condylus medialis distally flattened and continuous with short, thick, and proximally blunt crista medialis sulci patellaris (see Cracraft, 1974: 498–499, 508; Bledsoe, 1988: character 50; Lee *et al.*, 1997: character 46): no (0); yes (1).
  91. Femur, fossa poplitea large and deep, rounded at the bottom, and extending to margo medialis: no (0); yes (1) (modified from Lee *et al.*, 1997: character 51). In contrast to Lee *et al.* (1997), we found a large and deep fossa in all ratites except the Apterygidae plus Dinornithiformes.
  92. Femur, impressio ansae musculi iliofibularis a deep, proximodistally oriented, almond-shaped depression: no (0); yes (1) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
  93. Tibiotarsus, cristae cnemiales: not as follows (0); base of cristae somewhat compressed lateromedially; crista cnemialis cranialis evenly curved, projecting far proximorostrally (1) (Cracraft, 1974: 506); base of cristae sharply compressed lateromedially, crista cnemialis lateralis very poorly developed and knob-like (2) (modified from Cracraft, 1974: 502, 506–508; Bledsoe, 1988: characters 51, 52, 54; Lee *et al.*, 1997: character 33). Concerning state 2, we regarded the peculiar aspect of the crista cnemialis lateralis to be associated with the lateromedial compression at the base of the cristae.
  94. Tibiotarsus, sharp oblique ridge extending from crista cnemialis cranialis to mediodistal border of sulcus extensorius: no (0); yes (1).
  95. Tibiotarsus, proximal half of corpus tibiotarsi somewhat compressed lateromedially, exhibiting markedly convex facies rostralis and flattened facies medialis: no (0); yes (1).
  96. Tibiotarsus, facies rostralis, distal third of corpus tibiotarsi being flat lateral to sulcus extensorius, and showing very sharp margo lateralis: no (0); yes (1).
  97. Tibiotarsus with raised flat surface just lateral to distal end of sulcus extensorius: no (0); yes (1) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
  98. Tibiotarsus, distal end of sulcus extensorius shallow, medially open, with low medial edge (this feature is related to the absence of pons supratendineus): no (0); yes (1) (modified from Cracraft, 1974: 500, 501).
  99. Tibiotarsus, condylus lateralis triangular in shape and separated from condylus medialis by shallow, proximodistally narrow incisura intercondylaris: no (0); yes (1) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
  100. Tibiotarsus, condylus lateralis sharply undercut rostrally: no (0); yes (1) (modified from Cracraft, 1974: 500–501, 507–508; Bledsoe, 1988: character 61; Lee *et al.*, 1997: character 36). State 1 was found to occur only in the Rheidae.
  101. Tibiotarsus, condylus medialis strongly projecting rostrally and separated from distal end of canalis extensorius by marked depression: no (0); yes (1) (see Lee *et al.*, 1997: character 38). In the Tinamidae, the medial condyle protrudes more or less strongly rostrally, but the depression is absent.
  102. Tibiotarsus, condylus medialis with very deep ligamental pit (Cracraft, 1974): no (0); yes (1) (modified from Cracraft, 1974: 501, 506; Lee *et al.*, 1997: character 39).
  103. Tibiotarsus, conspicuous scar proximocaudal to epicondylus medialis: absent (0); present (1); present and deep (2).
  104. Tibiotarsus, sharp convex ridge continuing proximally to the epicondylus medialis: no (0); yes (1).
  105. Tibiotarsus, epicondylus medialis enlarged and plate-like, bounded distally by deep depressio epicondylaris medialis: no (0); yes (1) (modified from Cracraft, 1974: 501, 506; Lee *et al.*, 1997: character 39).
  106. Tibiotarsus, conspicuous furrow undercutting condylae at their proximal margin: absent (0); present (1).
  107. Tibiotarsus: incisura intercondylaris wide and shallow, so that condylus medialis continuous with condylus lateralis, the rostral margin of which tapers proximally: no (0); yes (1) (see Cracraft, 1974: 498, 506; Lee *et al.*, 1997: character 40).
  108. Tibiotarsus, crista trochleae lateralis strongly protruding caudally: no (0); yes (1) (see Cracraft, 1974: 500–501, 508; Bledsoe, 1988: character 62; Lee *et al.*, 1997: character 41).
  109. Fibula, caput fibulae: not as follows (0); roundish and proximocaudally protruding (1); with marked caudal extension (2).
  110. Fibula, smooth prominence continuing distally to the rostral corner of caput fibulae: absent (0); present (1).
  111. Tarsometatarsus, cotyla medialis dorsoplantarly elongated, protruding far dorsal to cotyla lateralis: no (0); yes (1).
  112. Tarsometatarsus, distinct prominence on facies dorsalis, just distal to cotyla medialis, separated from eminentia intercotylaris by depression: no (0); yes (1). The presence of such a depression in *Dromaius* and *Casuarius* is mentioned by

- Livezey & Zusi (2006: character 2306). In contrast with these authors, we think that this depression is also found in the Rheidae.
113. Tarsometatarsus, distinct processus on plantar edge of cotyla medialis: no (0); yes (1).
  114. Tarsometatarsus, eminentia intercotylaris: not as follows (0); poorly developed, with elongated lateral edge and short medial edge (1); very poorly developed, in median position, and dorsally concave (2) (modified from Cracraft, 1974: 503, 507; Bledsoe, 1988: character 70; Lee *et al.*, 1997: character 28).
  115. Tarsometatarsus, hypotarsus composed of two thick proximodistally short cristae hypotarsi that are widely separated from each other; only the crista medialis projects proximally: no (0); yes (1) (see Cracraft, 1974: 502, 506–508; Bledsoe, 1988: characters 66–68, 73; Lee *et al.*, 1997: character 27).
  116. Tarsometatarsus, hypotarsus, very large crista lateralis hypotarsi and feebly developed crista medialis hypotarsi: no (0); yes (1) (see Cracraft, 1974: 502, 507; Bledsoe, 1988: characters 66–68, 73; Lee *et al.*, 1997: character 27).
  117. Tarsometatarsus, hypotarsus, crista lateralis hypotarsi: not as follows (0); proximally expanded (1); strongly protruding proximally in the form of a sharp edge (2).
  118. Tarsometatarsus, corpus tarsometatarsi smooth and ovoid in transverse section, with flat facies dorsalis and low cristae plantares: no (0); yes (1) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
  119. Tarsometatarsus with very sharp crest on proximal third of corpus tarsometatarsi, continuing distally to the cotyla lateralis: no (0); yes (1).
  120. Tarsometatarsus, proximal part of corpus tarsometatarsi widening on either side towards extremitas proximalis: no (0); yes (1).
  121. Tarsometatarsus, greatly elongated corpus tarsometatarsi with facies subcutanea lateralis strongly flared plantarly: no (0); yes (1) (see Cracraft, 1974: 503; Bledsoe, 1988; Lee *et al.*, 1997: character 31).
  122. Tarsometatarsus, corpus tarsometatarsi, sulcus extensorius: shallow and broad proximally, flattens out distally (0); well defined, extending in distal half (1) (see Cracraft, 1974: 502–503, 507; Bledsoe, 1988: character 74; Lee *et al.*, 1997: character 30); very deep, narrow, and bounded by thick edges (2).
  123. Tarsometatarsus, corpus tarsometatarsi very short and dorsoplantarly flattened; trochlea metatarsi II elongated and medially deflected: no (0); yes (1) (for illustrations see, e.g., Archey, 1941; Oliver, 1949; Worthy & Holdaway, 2002).
  124. Tarsometatarsus, facies dorsalis of trochlea metatarsi III with distinct depression just proximal to median groove: no (0); yes (1).
  125. Pes: composed of four digiti (0); with only three digiti, II, III and IV (1) (Cracraft, 1974: 506; Lee *et al.*, 1997: character 32). The vestigial digitus II in *Struthio* is regarded as autapomorphic; this taxon is thus coded as state 1.
  126. Ossa digiti IV, phalanges proximales et intermediae gradually shortening towards phalanx unguialis, so that phalanx intermedia just proximal to the latter is either wider than long or nearly square in shape: no (0); yes (1).
  127. Digitus IV pedis with four phalanges: no (0); yes (1) (Worthy & Holdaway, 2002: appendix 3, character 72).
  128. Chick covered in a coat of plumae bearing dark stripes at hatching: no (0); yes (1) (del Hoyo *et al.*, 1992; Davis, 2002).
  129. Pennae contornae with hypopenna almost as long as rhachis plus vexillum: no (0); yes (1).

