

New morphological evidence supports congruent phylogenies and Gondwana vicariance for palaeognathous birds

PETER JOHNSTON*

Department of Anatomy with Radiology, University of Auckland, Private Bag 92019, Auckland, New Zealand

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There has been little agreement on the phylogeny of palaeognathous birds, with major differences amongst and between results from morphological and molecular data. Two recently published phylogenies using nuclear and mitochondrial DNA have substantial agreement in overall topology, with the ostrich as sister group of all other extant palaeognaths and a kiwi-emu-cassowary clade. Here I report a morphological phylogeny based mainly on new characters from the tongue apparatus and cranial osteology, with a theoretical ancestor as outgroup. A new interpretation of the evolution of the avian palate is included. This phylogeny is very similar to these recent molecular results; this is the first report of such congruence, and offers a credible basis for understanding the evolution of this clade. This phylogeny is fully consistent with a Gondwana vicariance model of evolution. Dates attributed from known geological events place the first extant radiation (ostrich) in the mid-Cretaceous, and offer a means of calibration of future molecular clock investigations.

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INTRODUCTION

The term palaeognathous means ‘having an ancient palate’ and was first used by Pycraft (1900); it is now applied to the volant tinamous of South America and the flightless ratites – ostrich, rheas, kiwis, emu, and cassowaries, together with the recently extinct moas of New Zealand and elephant birds of Madagascar, and a number of older extinct forms. Previous to this, Huxley (1867) had recognized the features common to the palate of the ratites and tinamous, but had placed the latter in a separate group and designated the tinamou palate as ‘dromaeognathous’ on account of similarities to the emu, then known as *Dromaeus*. These birds – also known as Palaeognathae, as opposed to Neognathae, the rest of modern birds – are

now taken to be monophyletic, although this was debated for many years, at least in part because of difficulty interpreting the various forms of palate osteology. The phylogeny within the group has been contentious ever since monophyly was accepted; Mayr (2011) notes that ‘the interrelationships of palaeognathous birds are among the most controversial of avian systematics, with the only uncontested hypothesis being sister group relationship between . . . emus and cassowaries’. Many different evolutionary trees based on morphological features have been produced; molecular phylogenies individually have had better statistical support but as a group have also been far from uniform. Until recently, monophyly of the ratites was supported by most studies (e.g. Bock, 1963; Lee, Feinstein & Cracraft, 1997; Dyke & Van Tuinen, 2004), whereas Slack *et al.* (2006) obtained equivocal results, and some subsequent molecular evidence has placed tinamous within ratites

*E-mail: psjohnston@clear.net.nz

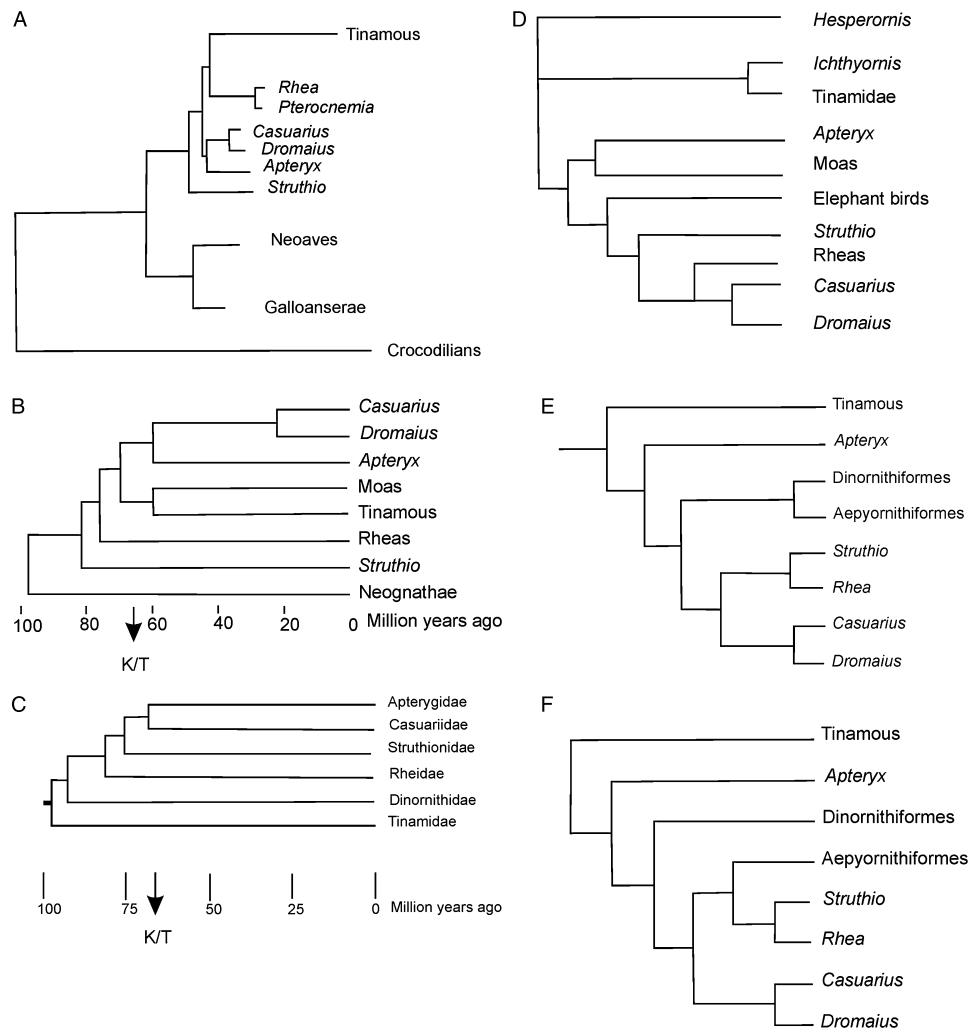


Figure 1. Palaeognathae phylogenies published 2007–2010. A, nuclear genomic (Harshman *et al.*, 2008); B, mitochondrial genomic (Phillips *et al.*, 2010); C, mitochondrial genomic (Baker & Pereira, 2009); D, morphological (Bourdon *et al.*, 2009); E, morphological, Livezey & Zusi (2007), original topology; F, morphological, Livezey & Zusi (2007) amended topology. K/T: Cretaceous-Tertiary boundary.

(Chojnowski, Kimball & Braun, 2008; Hackett *et al.*, 2008; Harshman *et al.*, 2008; Phillips *et al.*, 2010) Recent examples are given in Figure 1: the similar trees in the extensive analyses of Harshman *et al.* (2008) (Fig. 1A) and Phillips *et al.* (2010) (Fig. 1B) with the ostrich (*Struthio*) as the sister group of all other extant taxa offer a new hypothesis for palaeognath phylogeny. Within these topologies, however, some branchings are unclear. Harshman *et al.* (2008), using nuclear DNA, presented alternative topologies depending on selection of outgroups (crocodylians or neognathous birds) and method of analysis (parsimony, likelihood, or Bayesian). Figure 1A, with tinamous as sister group to rheas, is one of these results, and the alternative is with tinamous placed as sister group to the Australasian ratites. Phillips

et al. (2010), with mitochondrial DNA, found strongly supported sister groupings of tinamous and moas and of emu and cassowary, but the remaining taxa are poorly resolved. These recent similar results of Harshman *et al.* (2008) and Phillips *et al.* (2010) represent the first substantial agreement in overall topology of Palaeognathae, but the morphological implications of this have yet to be established: a model of 'plausible character distribution' (Janvier, 2007) is needed. Assis & Rieppel (2010) proposed that mapping of morphological characters in isolation onto a molecular phylogeny is 'epistemically (empirically) empty', as these characters cannot then be tested for congruence, which is a necessary condition for synapomorphy, in their argument: a morphological (or combined) phylogeny would be necessary for this

Table 1. Published data on palaeognath tongue muscles

	<i>Struthio</i>	<i>Rhea</i>	<i>Casuarius</i>	<i>Dromaius</i>	<i>Apteryx</i>	<i>Tinamous</i>
Owen (1879)					▲	
Gadow & Selenka (1891)		■				
Kautz (1931)	■	■	■		■	■
Lubosch (1933)	▼		■			
Kesteven (1942–1945)				■		
Webb (1957)	■					
Bock & Bühler (1988)	▲	▲		▲		▲
Müller & Weber (1998)	■	■	■		▲	■
Tomlinson (2000)	■	■		■		■
Current study	■	■	■	■	■	■

■ detailed description; ▲ incomplete description; ▼ specimen misidentified, see text.

inference. Thus far, the only morphological phylogeny which resembles the *Struthio* as sister group to other extant palaeognaths hypothesis (abbreviated hereafter as SSOP) is that of Elzanowski (1995), which is an informal rather than cladistic study. A limited number of characters are mapped for *Struthio*, non-struthious Palaeognathae and Neognathae. Bock & Bühler (1988), using some of the same anatomy as investigated here, also suggested SSOP, but again without a formal phylogeny. The features advanced by these authors in support of this could, however, also be used to suggest the *Struthio* branch leaving the Palaeognathae tree at positions other than the base. These authors take the differences between the tongue apparatus of *Struthio* and the rest of Palaeognathae to be significant enough to place *Struthio* as sister taxon to the rest of the group, and also place aepyornithids at a basal node on the basis of unpublished cranial anatomy.

The current study began with the observation that a preliminary phylogeny of characters identified in the tongue and hyobranchial apparatus of Palaeognathae was similar to the SSOP hypothesis of Harshman *et al.* (2008) and Phillips *et al.* (2010). These data were augmented with further new and published characters with the intention of exploring morphological and biogeographical implications of SSOP. The present study also includes, where possible, the extinct volant *Lithornis*, the moas (Dinornithiformes), and elephant birds (Aepyornithidae). It has been observed (Lee, Feinstein & Cracraft, 1997; Baker & Pereira, 2009) that many of the differences amongst published phylogenies could be a result of different positions of the root of the tree. An attempt is made to resolve this problem here by using characters with a priori designation of an ancestral state, and thus a theoretical ancestor as the outgroup.

The tongue muscles of palaeognaths have been described in various previous publications, as

summarized in Table 1. The kiwis *Apteryx* have not been documented in detail: the account of Owen (1879) accurately described and figured the superficial muscles only; Müller & Weber (1998) offered only a brief comment on similarity of the m. geniohyoideus to other palaeognaths from their examination of a serially sectioned kiwi head. The thesis of Kautz (1931) is not available in complete form as the illustrations are missing. The text is difficult to understand because of terminological issues, and contains anatomically incorrect statements. The hyobranchial skeleton of the moas has not to date been known in detail from the few remnants preserved, but is here reconstructed with components from two mummified heads.

The morphology of the bony palate has given its name to Palaeognathae but the sequence of its evolution from the palate of early avians and within the modern avian group is not understood, mainly because of the lack of a robust phylogeny. A new evolutionary sequence based on the overall shape of the palatal complex will be suggested here. *Archaeopteryx* is taken to have the ancestral palatal structure for the purposes of this analysis; the various Mesozoic birds less plesiomorphic than *Archaeopteryx* (summarized by Chiappe & Dyke, 2007) do not provide enough details of this region to be used here, with the exception of *Hesperornis*, which is included in this proposal. Other cranial anatomy analysed here includes the nasal hinge region and the disposition of jaw adductor muscles in the temporal fossa.

In terms of the current project's aim to use theoretical ancestral states prior to modern birds, there are difficulties using the character definitions and polarities in previous published work on palaeognath phylogeny. Bledsoe (1988) used tinamous as the outgroup, and in Bourdon, Ricqlès & Cubo (2009) tinamous have the same character assignment as the outgroup (*Hesperornis-Ichthyornis*) in almost every

character, making it impossible for tinamous not to branch from a basal node in both studies. Lee *et al.* (1997) used *Gallus* as an outgroup, with coding identical to tinamous in most characters, which again cannot be assumed to place the root in a correct ancestral position. Scoring of characters in these studies is not in question; the similarities between tinamous and neognathous birds would thus represent convergent evolution in terms of the phylogeny to be presented below. It was apparent when characters in these three publications were examined that a simple 're-rooting' or re-ordering of character states could not be applied, and detailed re-examination of material for individual characters would have been necessary.

The 2954-character set of Livezey & Zusi (2006) does not overtly assume a basal position for tinamous, and uses an 'archosauromorph', Crocodylia, and a variety of Mesozoic birds as ancestral groups. This work has been criticized, at least in its treatment of Neognathae, by Mayr (2008), who found paraphyletic designation of supraordinal taxa, incorrect character scoring, and failure to retrieve clades that are generally accepted by other researchers, together with strong support for proposed new unconventional groupings. Within Palaeognathae, some of these issues are also evident. Kiwis and moas are classified together as Apterygimorphae, which is clearly a paraphyletic grouping in Livezey & Zusi's (2006) phylogeny; this may be superficially misleading but is not of relevance to the present project and the use or non-use of characters. Coding differences for Palaeognathae are present between Livezey & Zusi (2006) and Mayr's own work (Mayr & Clarke, 2003), limiting the usefulness of both data sets without re-examination of material. Livezey & Zusi's (2007) original phylogeny recovers a Dinornithiformes-Aepyornithidae clade (Fig. 1E) with 100% bootstrap support (as re-analysed here); these authors declare this clade 'suspicious' without further elaboration, and re-analyse their data by omitting each of these taxa in turn and then combining the results (Fig. 1F). For these reasons, characters as defined and coded in this work could not have been adopted without substantial further investigation. Published data that have been adopted include morphology of eggshells (a surrogate for female reproductive tract physiology), manual digits, and hind limb muscles.

The idea of relating the evolution of these predominantly flightless birds to the break-up of the Gondwana southern super-continent has long been attractive and has been addressed for this and other avian groups particularly by Cracraft (2001), but again without a robust or widely corroborated phylogeny from which to work. Geographical separation of populations is accounted for by two

processes, vicariance and dispersal. Vicariance refers to separation by the establishment of a barrier between populations, usually by tectonic processes. Vicariant species are those resulting from the separation of a population by vicariance. Dispersal means movement over an existing barrier, such as an ocean or mountain range. The roles of vicariance and dispersal in any phylogeny can be difficult to determine, and many analytical methods have been proposed to address this (Kodandaramaiah, 2010). In a recent example, in a parrot phylogeny Wright *et al.* (2008) showed that vicariance is well supported at basal nodes in a parsimony-based reconstruction of ancestral areas, whereas dispersal has clearly occurred at crown-ward nodes. The attribution of dates to phylogenies has traditionally been carried out by correlation with fossils and strata (Benton & Donoghue, 2007), but is also possible from the dating of vicariance events. It has been hypothesized (Hedges, 2005) that this is a more accurate means of calibrating molecular clock calculations, as fossils are presumably nearly always terminal taxa, not nodes (ancestors), whereas dates of geographical separation can be applied to nodes. This method has been used occasionally (Ericson *et al.*, 2002; Baker *et al.*, 2005) and will be attempted here as it is particularly applicable to palaeognaths with their limited fossil record (Mayr, 2009) and their evolution of flightlessness.

The aims of the present study are to describe new cranial morphological features in palaeognaths, to use these to assess the phylogenetic relationships of these birds, and to place this phylogeny in the context of their evolution in Gondwana as the southern land-mass undergoes tectonic separation.

MATERIAL AND METHODS

COMPARATIVE MATERIAL

Material was examined from the following institutions: Natural History Museum (London); Natural History Museum (Tring, UK); Museum of New Zealand Te Papa Tongarewa (NMNZ), Wellington; Auckland Museum; Otago Museum; Department of Anatomy, University of Otago; Department of Anatomy with Radiology, University of Auckland.

COMPARATIVE MORPHOLOGY

Anatomical terminology follows *The Handbook of Avian Anatomy: Nomina Anatomica Avium* (Baumel *et al.*, 1993). Avian taxonomic nomenclature follows B. J. Gill *et al.* (2010) and F. Gill & Donsker (2010). Use of specimens of protected New Zealand species was in accordance with New Zealand legislation.

RECONSTRUCTION OF THE HYOBANCHIAL APPARATUS OF MOA

The complete hyobranchial skeleton of the moa *Megalapteryx didinus* was modelled from components present in two mummified heads, Natural History Museum (London) A16 and Museum of New Zealand Te Papa Tongarewa NMNZ S400. For the London specimen the curled-up remnant of the tongue with one attached ceratobranchiale was removed, fixed in formalin, and later unrolled to expose the elements of the tongue skeleton. In the Wellington specimen one ceratobranchiale with attached epibranchiale had been detached in the course of previous examination and was preserved in alcohol.

MYOLOGY OF THE TONGUE AND HYOBANCHIAL APPARATUS

Tongue muscles and hyobranchial skeleton were dissected in the following birds (numbers). Palaeognathous birds: *Apteryx australis* (4); *Apteryx mantelli* (3); *Struthio camelus* (4); *Dromaius novaehollandiae* (2); *Casuarius* sp. (2); *Rhea americana* (2); *Nothura maculosa* (2); *Nothoprocta pentlandii* (1); *Tinamus major* (1); *Crypturellus noctivagus* (1); *Crypturellus tataupa* (1); *Rhynchotus rufescens* (2); *Eudromia elegans* (1). Neognathous birds: *Pygoscelis adeliae* (1); *Diomedea exulans* (1); *Meliagris gallopavo* (2), *Gallus gallus* (2).

Findings were drawn freehand and photographed. Morphology of the larynx and its skeleton were observed in the course of this investigation, but a detailed study of laryngeal muscles was not carried out.

PALATE AND NASAL HINGE OSTEOLOGY

Skulls in complete, disarticulated, and computed tomography (CT) scan (University of Texas Digital Morphology Library <http://www.digimorph.org>) states were examined: *Ap. mantelli*, *Ap. australis*, *Struthio camelus*, *Dr. novaehollandiae*, *Casuarius casuarius*, *R. americana*, *Rhea (Pterocnemia) pennata*, *T. major*, *Eud. elegans*, *M. didinus*, *Anomalopteryx didiformis*, *Euryapteryx gravis*, *Pachyornis geranoides*, and *Dinornis novaezealandiae*. Morphology of the bony palate was examined in these birds. The palate osteology of *Hesperornis* was interpreted further from the findings of Elzanowski (1991) and Gingerich (1976) by adding the choana and vomer to Elzanowski's reconstruction. The nasal hinge region immediately rostral and caudal to the maxillary process of the nasal bone was examined in the same specimens. Data on elephant birds were taken from Simonetta (1960).

POSTCRANIAL OSTEOLOGY

Characters adopted from Mayr & Clarke (2003: characters 48–62, see Appendices 2, 3) were augmented by scoring for Dinornithiformes. The following moas were examined: *An. didiformis*, *Euryapteryx curtus*, *Pachyornis geranoides*, and *Dinornis novaezealandiae*.

MANDIBULAR ADDUCTOR MYOLOGY

Following the comment by Livezey & Zusi (2006: 381, character 2469) that the two muscles observed in the temporal fossa in the mummified moa *M. didinus* by Vickers-Rich *et al.* (1995) would in palaeognaths be better interpreted as m. pseudotemporalis superficialis and a belly of m. adductor mandibulae externus rather than two bellies of m. adductor mandibulae, the same specimen (NMNZ S400) was investigated by magnetic resonance imaging (MRI) with a Siemens Magnetom Avanto 1.5 Tesla scanner with a Siemens 12 channel head matrix coil and B17 software. Performance per axis details were: maximum amplitude 33 mT/m, minimum rise time 264 µs from 0–33 milliTesla/m, maximum slew rate 125 Tesla/m/s. T1 and T2 weighted turbo spin echo sequences were obtained. Soft tissue remnants were labelled on the image slices and reconstructed in 3D using Amira 5.2.1 (Visage Imaging), following the methods of Corfield *et al.* (2008). Interpretation of the MR images was aided by reference to a high-resolution CT scan of an *An. didiformis* skull. The mandibular adductors were dissected in *Ap. australis*, *Struthio camelus*, *Casuarius* sp., and *Dr. novaehollandiae*. MRI images of *Ap. australis* and *Ap. mantelli* were also examined.

PHYLOGENETIC ANALYSES

Character definition

Character definition has attempted to follow the approach advocated by Kearney & Rieppel (2006), which has been interpreted as follows: no character can be observed in the absence of some homology assumption, and characters used should be evaluated within a 'causality' such as a comparative anatomical framework with evolutionary, developmental, or functional significance. Homology is used here in the sense of 'transformation stages of the same character present in the ancestor of the taxa which display the characters' (Wiley, 1975). Some circularity (between homologies adopted and the product of phylogenetic analysis) cannot be avoided, but can be addressed by making character assignments testable and assumptions explicit. A list of assumptions is given here with the character list. An ancestral state is designated a priori for each character; this choice is directed at the issue of accurately rooting the tree and is also made necessary by the nature of the characters used: there

is no suitable archosaur outgroup for the tongue apparatus, as crocodilians are apomorphic in a different direction (Fürbringer, 1922), thus the conclusion of Rieppel (1978) that *Sphenodon* represents the generic lepidosaurian hyobranchial skeleton and musculature is extended to propose that this anatomy in all reptile groups can be interpreted as modifications of the *Sphenodon* pattern. The eggshell data described below have manoraptorian theropods as their ancestral state, and the palate osteology is based on *Archaeopteryx* as ancestor. No known taxon could represent an outgroup status for these features simultaneously, and use of multiple outgroups would lead to both multiple missing characters and less specific homology assumptions. The 'theoretical ancestor' used here is thus a composite outgroup, combining ancestral states of respective characters.

Further characters were sought from published studies (Bledsoe, 1988; Lee *et al.*, 1997; Mayr & Clarke, 2003; Livezey & Zusi, 2006; Bourdon *et al.*, 2009), aiming for a more inclusive morphological coverage and to strengthen the weaker nodes.

Character assemblage

Characters are organized as two groups: (1) a core group, comprising characters with an a priori ancestral state defined from original work as reported here (characters 1–24), characters designed to force basic avian phylogenetic assumptions (characters 40–42), eggshell (characters 25–39), and manual digit morphology (characters 45–47); and (2) an additional group comprising osteological characters (48–62) adopted from Mayr & Clarke (2003) where characters are informative for Palaeognathae and coding is not in conflict with other sources, and myological characters (63–85) from McKittrick (1991) with data for *Dromaius* added from Patak & Baldwin (1998), *Struthio* from Gangl *et al.* (2004), and for *Rhea* from Gadow (1880) and Picasso (2010), again where characters are informative and unambiguous. A priori designation of ancestral state is not possible for this hind-limb myology; the ancestral state for the characters from Mayr & Clarke (2003) is taken as that for the outgroups used in that study (*Apsaravis*, *Hesperornis*, *Ichthyornis*) where that state is unambiguous.

The eggshell data sourcing characters 25–39 (Grellet-Tinner & Dyke, 2005; Grellet-Tinner, 2006) are particularly suitable for the present project, as they represents an evolutionary series with a defined ancestral state, and also includes moas, elephant birds, and *Lithornis*. In defining my characters 45–47, I note that the identity (1-2-3 or 2-3-4) of the digits in the avian manus is a controversial topic, but from the embryological data presented by Maxwell & Larsson (2009) a transformation series can be identified, assuming the primitive reptilian formula 2-3-4-5-4/3

to be the ancestor rather than the debatable status of *Archaeopteryx*. Digit 3 of *Apteryx* is coded as ambiguous, as it comprises a variable number of phalanges in the adult (Parker, 1891). *Psittacus* (Homberger, 1986), *Gallus* (Homberger & Meyers, 1989), and *Columba* (Zweers, 1982) are included from literature descriptions as representative neognaths; this study is not designed to look at neognath phylogeny in itself, and the neognathous birds are designated as a single taxon in the trees described.

Phylogenetic inference

Phylogenetic analysis was carried out using PAUP* (Swofford, 2003) and TNT (Willi Hennig Society edition) (Goloboff, Farris & Nixon, 2008). All characters are treated as unordered. Analyses carried out were:

1. The core group of characters (1–47), with the branch-and-bound (PAUP*) and exact enumeration (TNT) algorithms.
2. The full character set (1–85), with the branch-and-bound (PAUP*) and exact enumeration (TNT) algorithms.
3. To look for additional characters that might strengthen the weaker nodes and in particular the rhea and tinamou groups, the data set of Livezey & Zusi (2006) was searched with the (*Struthio*, (*Rhea*, Tinamou (*Apteryx* (*Casuaris*, *Dromaius*)))) constraint tree with and without successive reweighting.
4. The alternative phylogenies of Livezey & Zusi (2007) (Fig. 1E, F) were compared with the Templeton test (Templeton, 1983) as implemented in PAUP* (heuristic search algorithm), using only the palaeognath taxa with *Archaeopteryx* and *Ichthyornis* as outgroups from the Livezey & Zusi (2006) matrix.
5. The phylogeny of Phillips *et al.* (2010) was compared with the 50% bootstrap majority tree obtained in the current study with a Templeton test implemented in PAUP*.

BIOGEOGRAPHICAL RECONSTRUCTION

The phylogeny recovered here was compared with and superimposed on the area cladogram of the separating southern super-continent Gondwana, with events and dates adopted from the Paleomap project (Scotese, 2001), Eagles & König (2008), Gaina *et al.* (2007), and secondary sources (McLoughlin, 2001), including the radiation of marsupials into Australia as collateral evidence (Woodburne & Case, 1996). The assumption was made that prior to any vicariance the ancestor is present throughout the relevant Gondwana-fragment, thus avoiding a 'centre-of origin' approach (Hedges, 2009b).

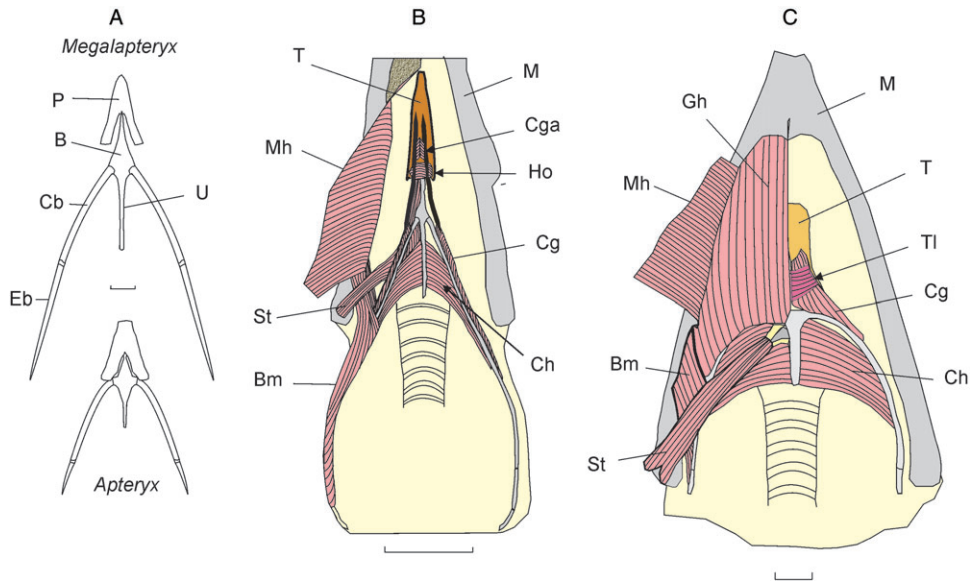


Figure 2. A, hyobranchial skeleton of *Megalapteryx* and *Apteryx*, ventral view. B, tongue muscles typical of a neognathous bird (*Tringa totanus*) after Burton (1974), ventral view. C, tongue muscles of *Apteryx australis*, ventral view. Abbreviations: B, basihyale; Bm, m. branchiomandibularis; Cb, ceratobranchiale; Cg, m. ceratoglossus; Cga, m. ceratoglossus anterior; Ch, m. ceratohyoideus; Eb, epibranchiale; Gh, m. geniohyoideus; Ho, m. hyoglossus obliquus; M, mandible; Mh, m. mylohyoideus (reflected back from the midline); P, paraglossale; St, m. stylohyoideus; T, tongue; Tl, m. transversus linguae; U, urohyale. Scale bars = 1 cm.

A Gondwana separation area cladogram and a fully resolved palaeognath phylogeny were mapped together and reconciled using TREEMAP (<http://taxonomy.zoology.gla.ac.uk/rod/treemap.html>) (Page, 1994).

RESULTS

COMPARATIVE MORPHOLOGY

Tongue muscles and hyobranchial apparatus

A full reconstruction of the hyobranchial skeleton of the moa *M. didinus* was made from observations of the structure present in two mummified heads (Fig. 2A). A plastic model of this reconstruction was examined with a skull of appropriate size. With the position of the larynx apposed to the choana, the relatively long (for Palaeognathae) epibranchial cartilages did not fit neatly in a curve around the occipital part of the skull, as in most Neognathae, and it was concluded that the hyobranchial skeleton lies entirely in a ventral location, as in *Struthio*. A muscle insertion ridge is visible on the lateral aspect of the ceratobranchiale, consistent with at least part of m. stylohyoideus inserting here.

The myology of this region in *Apteryx* is presented in Figure 2C, together with the typical anatomy of the same region in a neognathous bird (Fig. 2B). A new muscle was defined, or at least rediscovered, and is here named m. transversus linguae. This muscle is

situated as a sling between the ventral faces of the caudal ends of the paraglossalia, passing ventral to the m. ceratoglossus and the basibranchiale. This muscle is innervated by a branch of the hypoglossal nerve, which passes within the m. thyrohyoideus and dorsal to the rostral end of the ceratobranchiale. This muscle is a synapomorphy for *Apteryx*, *Dromaius*, and *Casuaris*, and has not been recognized as such in previous accounts of the latter two genera. A new feature for Palaeognathae is recognized as the form of the m. ceratoglossus, which is muscular throughout except for a variable tendinous intersection in *Apteryx*, as opposed to the long tendon within or at the rostral end of the muscle typically found in Neognathae (Fig. 2B). A newly recognized feature in the larynx was noted and used as a phylogenetic character: in the gross morphology of the larynx in *Struthio* and *Dromaius* (Crole & Soley, 2010) and in the arytenoid bones of the moas *Dinornis* and *Megalapteryx*, a raised medial rim is present, and in the former two birds the shape of this rim suggests that it may engage with the rim of the choana. Homology assumptions in defining characters from this and other regions for phylogenetic analysis are given in Appendix 1.

Palate osteology

Significant findings are: (1) posterior migration of the choana between *Archaeopteryx* and modern birds; (2)

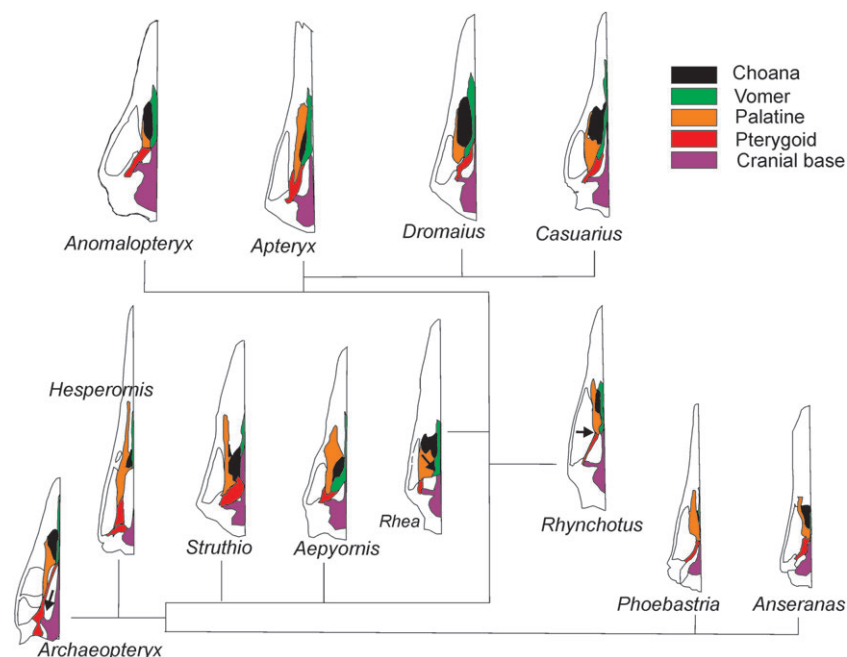


Figure 3. Evolution of the avian palate, ventral view, based on the phylogeny in Figure 4A. *Rhynchotus* is used as a representative of tinamous and *Anomalopteryx* of moas. *Phoebeastria* (Livezey & Zusi, 2006) (Neoaves), *Anseranas* (Murray & Vickers-Rich, 2004) (Galloanserae), *Archaeopteryx* (Elzanowski, 2001), and *Aepyornis* (Simonetta, 1960) are after published accounts. The reconstruction of *Hesperornis* has been extended from the accounts of Elzanowski (1991) and Gingerich (1976) by adding choana and vomer. The cranial base represents parasphenoid and basisphenoid, the caudal limit of the basisphenoid is approximate. The arrows indicate: in *Archaeopteryx*, the long axis of the palatine directed at the basal articulation (similar in *Hesperornis*, *Struthio*, and *Aepyornis*); in *Rhea*, the medial edge of the palatine is directed toward the midline (similar in *Anomalopteryx*, *Dromaius*, *Casuarius*, *Phoebeastria*, and *Anseranas*); in *Rhynchotus*, medial deviation of the lateral edge of the palatine toward the midline (similar in *Anomalopteryx*, *Dromaius*, *Phoebeastria*, and *Anseranas*).

the plesiomorphic position of the vomer at the caudo-medial edge of the choana is independently lost in *Struthio* and most Neognathae; (3) medial angulation or ‘waisting’ of the bony palate. The plesiomorphic condition is interpreted as that in *Archaeopteryx*, *Hesperornis*, *Struthio*, and Aepyornithidae, in which both medial and lateral borders of the palatine axis are directed at the basipterygoid articulation, whereas in all other taxa there is deviation of this axis or at least its medial border toward the midline. This is least developed in *Aptyryx*, in which the palate differs from other taxa in the addition of a maxillary buttress to form a broad palatal convergence on the basal articulation. This is presumably related to the probing function of the *Aptyryx* beak. Medial deviation of the palate is indicated by arrows in Figure 3, which is a schema for the evolution of the avian palate, patterned on the phylogeny set out below (Fig. 4A) and based on the assumptions that *Archaeopteryx* is close to the ancestral line of modern birds and that the most recently published reconstructions of its palate (Elzanowski, 2001; Mayr *et al.*, 2007) are accurate. The characters designed from the palate emphasize

the overall shape of the palatal complex, rather than details of individual bones.

Nasal hinge region

In *Struthio*, the cross-section at the nasal hinge region of the skull, immediately rostral to the maxillary process of the nasal bone, is flattened into a thin transverse strip, whereas in other Palaeognathae this region is reinforced in various ways: *Dromaius*, *Rhea*, and tinamous have a V-shaped cross section, *Casuarius* has a casque, and kiwis, moas, and elephant birds have a \cap shaped reinforcement. These forms are present in adult birds; in juvenile moa skulls the hinge region is flat and very similar to adult *Struthio*, and the same is evident for other juvenile palaeognaths in Pycraft (1900: plate LIII).

Mandibular adductors in the temporal fossa

In the moa *Megalapteryx didinus*, the MRI scan morphology of the muscle remnants in the temporal fossa reveals parts of two muscle bellies that are similar to the mm. adductor mandibulae externus and pseudotemporalis superficialis found in this location in the

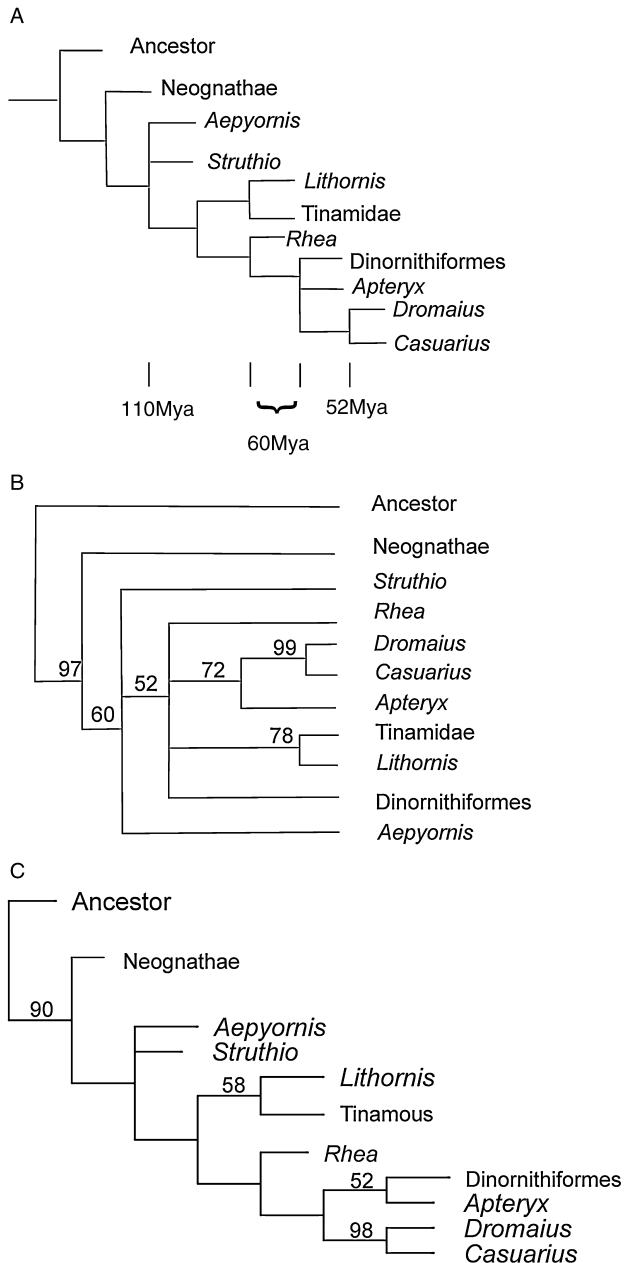


Figure 4. A, phylogeny inferred here from 47 morphological characters (core character group), consensus tree from TNT [four most parsimonious trees (MPTs) with explicit enumeration] and PAUP* (12 MPTs with branch-and-bound), with dates based on Gondwana separations (Scotese, 2001). Best tree length 96 steps, consistency index = 0.7624, retention index = 0.7798, rescaled consistency index = 0.5945. B, 50% bootstrap majority-rule tree from PAUP*. Maximum trees 10 000; replications 1000; tree bisection-reconnection algorithm. C, phylogeny from complete character set in TNT (two MPTs). Bootstrap support values > 50% are indicated.

kiwis as seen in Hofer (1950) and in original dissections and MRI scans; these muscles were designated as such in character 24. The muscle *M. adductor mandibulae externus* occupies the ventrolateral third of the fossa, and *m. pseudotemporalis* fills the remaining dorsomedial two-thirds. In *M. didinus* these muscles share an insertion via a short tendon to the coronoid eminence of the mandible. A full account of the reconstructed soft tissue anatomy of the moa head will be presented separately. The minor incursion of *m. adductor mandibulae* into the temporal fossa reported by Hofer (1950) in *Casuarius* and *Dromaius* could not be confirmed here: if present, this is a very subtle finding and was not accepted for scoring of character 24.

Characters used in phylogenetic analysis

A list of assumptions (Appendix 1), character list (Appendix 2), and matrix (Appendix 3) are attached.

PHYLOGENETIC ANALYSES

1. The consensus and 50% bootstrap majority trees produced by parsimony analysis of the core data set are given in Figure 4A and B. This phylogeny is similar to those in Figure 1A (Harshman *et al.*, 2008) and Figure 1C (Phillips *et al.*, 2010) in the position of *Struthio* as sister group to other extant palaeognaths, and the presence of an *Apteryx-Casuarius-Dromaius* clade. The bootstrap tree supports (52%) *Struthio* and aepyornithids as basal branches outside other palaeognath clades and supports (72%) the *Apteryx-Dromaius-Casuarius* clade, with a polytomy of other taxa between these.
2. Analysis of the complete data set (characters 1–85) yielded a phylogeny similar to the core characters alone, but with bootstrap support above 50% for only four clades (Fig. 4C).
3. Searching the Livezey & Zusi (2006) data set with the SSOP constraint tree produced a variety of unlikely groupings, notably placing Dromornithidae within Palaeognathae. In the unconstrained analysis of these data, Dromornithidae are placed with Gruidae, which is again in conflict with contemporary views on dromornithid phylogeny (Murray & Vickers-Rich, 2004). Searching the 543 cranial osteology characters of these data with the SSOP constraint gave 16 fully consistent characters; only one of these could be interpreted as an evolutionary series with an ancestral state.
4. Comparison of the two palaeognath phylogenies presented by Livezey & Zusi (2007), with the Templeton test applied to analysis of their matrix reduced to palaeognath taxa and outgroups, reveals that the modified phylogeny (Fig. 1F) is a longer tree than the consensus tree (Fig. 1E) but is

Table 2. Results from Templeton tests comparing topologies

	Tree	Length	P
a	Livezey & Zusi (2007)	1215	0.38
	Original topology (Fig. 1E)		
	Livezey & Zusi (2007)	1278	
b	Amended topology (Fig. 1F)		0.32
	Phillips <i>et al.</i> (2010) (Fig. 1B)	148	
	Johnston – current study, 50% bootstrap tree (Fig. 4B)	147	

not a significantly less likely topology for these data (Table 2A).

5. The position of moas differs significantly between the phylogeny recovered here (Fig. 4A) and that of Phillips *et al.* (2010) (Fig. 2B), although the bootstrap majority tree shown here (Fig. 4B) does not reject the Phillips *et al.* (2010) tree when the Templeton test is applied (Table 2B).

SYNAPOMORPHIES

The following synapomorphies were identified for palaeognath clades. Features that are common to palaeognaths but are identified as plesiomorphic reptilian states appear in the analysis as synapomorphies for Neognathae.

1. All palaeognaths except *Struthio* and aepyornithids: epibranchial length: long → short (reversed in Dinornithiformes); palatine, medial border: directed at basipterygoid articulation (BPA) → converge on midline rostral to BPA; eggshell layer 2: absent → present; nasal hinge region: flat → reinforced.
2. *Lithornis*-tinamous: palatine lateral border: directed at BPA → directed at midline rostral to BPA.
3. *Rhea* and Australasian ratites: epibranchial orientation: horizontal → dorsal (reversed in Dinornithiformes); egg shape: nearly spherical → elliptical broadest near centre; cristae iliacae dorsales and crista spinosa of synsacrum: unfused → fused; pedal digital flexors: type 4 of George & Berger (1966).
4. Australasian ratites: m. transversus linguae absent → present; eggshell layer 3 to layer 2 ratio: < 0.1 → > 0.1; third cervical vertebra osseous bridge absent → present; manual digit 2, phalanges 2 or more → 0.
5. *Apteryx*-Dinornithiformes: nasal chamber: simple → complex; nasal hinge region: flat → ∩-shape; m. adductor mandibulae in temporal fossa: absent → present.

6. *Casuarius-Dromaius*: eggshell characters 28, 29, 33, and 37, see matrix; notches on caudal margin of sternum: present → absent.

7. Neognathae: m. geniohyoideus: present → absent; m. ceratoglossus, reptilian form: present → absent; M. stylohyoideus (interhyoideus) insertion: ceratobranchiale and/or urohyale → paraglossalia.

BIOGEOGRAPHICAL RECONSTRUCTION

The phylogeny presented here is shown superimposed on a map of partly separated Gondwana in Figure 5. A possible phylogeny is shown mapped with the Gondwana area cladogram in Figure 6. The TREEMAP program used for this mapping only accepts fully resolved cladograms, thus a phylogeny is selected with aepyornithids as the first branch, which is plausible in both morphological and geographical contexts. Most nodes on the palaeognath tree coincide with continental separations; the nodes that occur prior to a separation are highlighted with circles in this figure. Based on dates of Gondwanan separation events, it is possible to apply dates to the nodes on the tree. These dates have been placed against nodes in Figure 4A, and are minimum dates, being the latest possible vicariations of sister groups. This places the aepyornithid line at 110 million years ago (Mya), being the final separation of the Madagascar–India block from the rest of Gondwana, the *Struthio* radiation at a similar date (the isolation of Africa), the South American lines (or more specifically the flightless *Rhea* radiation) at 60 Mya, a similar date for the Australasian ratites (separation of Australia–New Zealand from South America–Antarctica) and the *Casaurius-Dromaius* radiation at 52 Mya, the latest date postulated for the separation of the Australia and New Zealand blocks (Gaina *et al.*, 1998; Schellart, Lister & Toy, 2006). It should be noted that this date for the separation of the Australia and New Zealand land masses differs from the 82 Mya frequently quoted, e.g. Sanmartin & Ronquist (2004).

DISCUSSION

COMPARATIVE MORPHOLOGY

Tongue muscles and hyobranchial apparatus

The new data presented here include the first complete accounts of the tongue muscles in the kiwis *Apteryx* sp. and of the hyobranchial skeleton in the moa *M. didinus*. Specific palaeognath forms of the m. ceratoglossus are newly recognized, and reveal similarities with the m. hyoglossus of non-avian reptiles, leading to identification of these structures as homologues, as suggested originally by Edgeworth (1935). The avian terminology is misleading here: the avian m. hyoglossus is a completely different

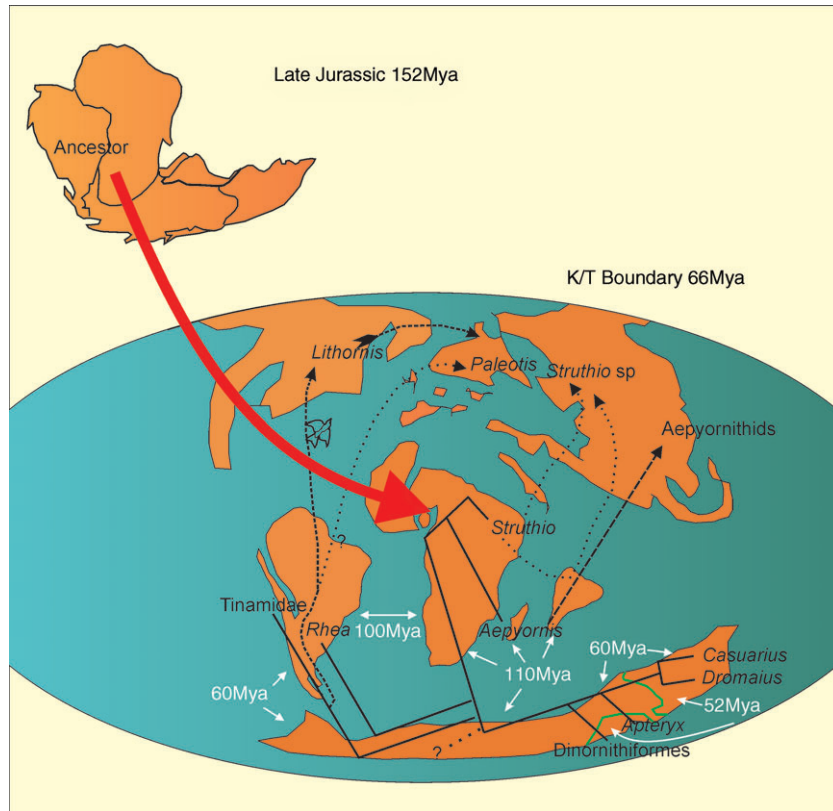


Figure 5. Schematic representation of the palaeognath ancestor in undivided Gondwana at 152 million years ago (Mya) and its distribution across divisions of the continent at 66 Mya according to the phylogeny presented here, with approximate dates of separation indicated in white type. It is assumed, based on the shape of the phylogeny, that ancestors of the South American taxa were present on the South America–Antarctica–Australasia fragment of Gondwana, rather than being the direct result of separation from Africa. Fossil palaeognath remains in Antarctica are not well enough characterized to fit into this phylogeny (Tambussi *et al.*, 1994) but are denoted with a question mark. Maps are modified from the Paleomap project (Scotese, 2001).

structure. The muscle newly designated here as *m. transversus linguae* does appear to have been identified previously: in one of his classic contributions to comparative anatomy Wilhelm Lubosch (1933) clearly figured and described this muscle in '*Struthio*' as *m. paraglossalis transversus*; however it is clear from other anatomical features (configuration of *mm. stylohyoideus* and *ceratohyoideus*) in his figure 13 that the bird in question was actually *Casuarius*. This would explain the inability of subsequent investigators (Hofer, 1950; Elzanowski, 1987) to confirm Lubosch's account of the mandibular adductors in '*Struthio*'. Transverse muscle fibres in this location have also been interpreted as the insertion of the *m. genioglossus* (Bock & Bühler, 1988), although this muscle was not recognized as separate from *m. geniohyoideus* in other members of Palaeognathae in the current study. Lubosch's term, *m. paraglossalis transversus*, has not been followed here as the Latin usage of *paraglossalis* refers to a singular paraglossale,

whereas in fact this muscle is spread across the base of the tongue between both paraglossalia. The other transverse muscle in the tongue identified by Lubosch (1933), *m. anularis paraglossi*, could not be identified in the specimens examined here, and it appears the structure referred to was the fibrous and elastic tissue sling that binds the basihyale to the paraglossalia as described by Tomlinson (2000). The *m. transversus linguae* as recognized here is a synapomorphy for kiwis, cassowaries, and emu.

The hyobranchial skeleton on the moa *M. didinus* is reconstructed from two of the three known mummified heads (Worthy & Holdaway, 2002), and is notable for relatively long epibranchial cartilages, which amongst other palaeognaths are seen only in *Struthio*. Tomlinson (2000) has pointed out important differences in hyolingual function between neognaths and palaeognaths, but there do not appear to be functional differences amongst individual palaeognath taxa (*Struthio*, *Rhea*, *Dromaius*) which correlate

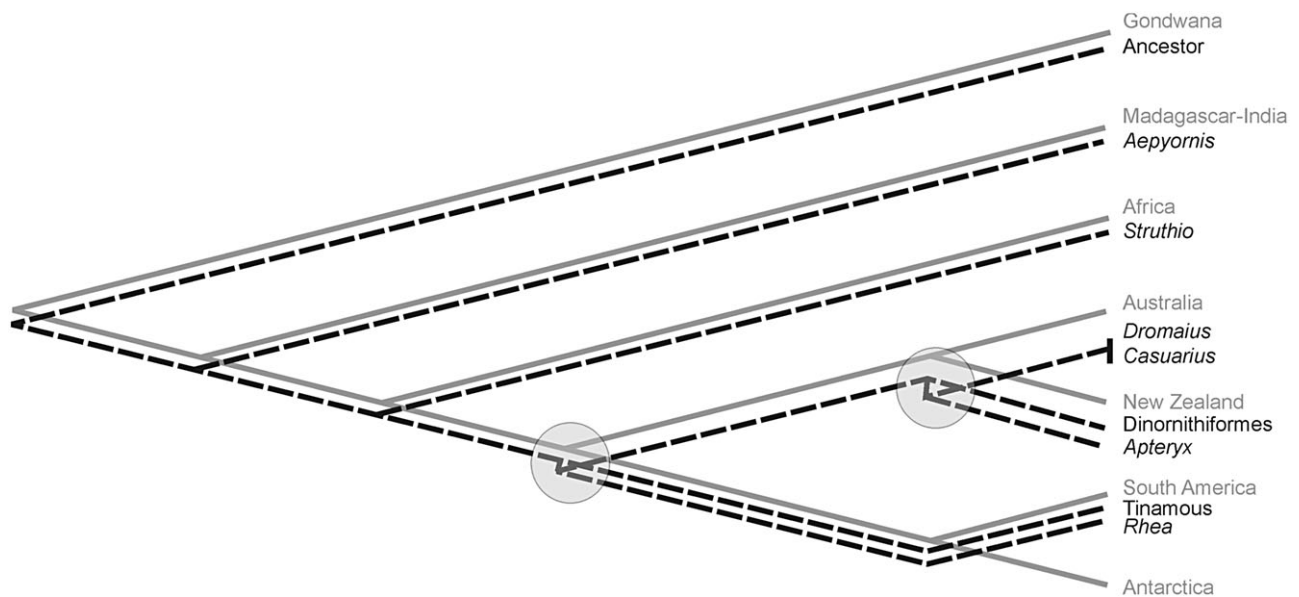


Figure 6. Gondwana area cladogram and a fully resolved palaeognath phylogeny (based on Fig. 4A) mapped together and reconciled with TREEMAP (<http://taxonomy.zoology.gla.ac.uk/rod/treemap.html>). Circles indicate nodes on the palaeognath tree that occur prior to geographical separations.

with the morphological variety within the group. The tongue muscle characters designated here are useful for members of Palaeognathae, but it can be noted that they may well not be discriminatory amongst members of Neognathae, as different morphologies are recorded in relatively closely related taxa (Burton, 1974, 1984). In the larynx, the possibility that the raised medial rim of the arytenoid in *Struthio*, *Dromaius*, and moas may engage within the choana does not appear to have been suggested previously and the function of this rim in respiration or vocalization is unknown; limited comparative anatomical data on the avian larynx have been assembled (McLelland, 1989) but the functional context of glottic closure or apposition to the choana seems to be little documented beyond basic details noted by Zweers (1982).

Palate osteology

The evolutionary sequence of palatal morphology (Fig. 3) is an original proposal consistent with the SSOP phylogeny, and offers a solution to the enigma of palatal evolution in Palaeognathae and in modern birds in general. The rostrocaudal trajectory of the palatine–pterygoid axis (similar to the ‘arcus pterygopalatinus’ of Zusi & Livezey, 2006) toward the basipterygoid articulation as found in *Archaeopteryx* and *Hesperornis* is taken to be the plesiomorphic avian condition, which persists in *Struthio* and aepyornithids. In other Palaeognathae and in all Neognathae, deviation of this axis toward the midline is seen. The possible derivation of the palatal

morphology of other palaeognaths from the *Struthio* state has been suggested previously by Webb (1957) in his developmental study. According to the morphological phylogeny proposed here, medial angulation has occurred independently in at least four avian lines: tinamous (with *Lithornis* and *Paleotis* as either the same or separate radiations), moas, the galloanserine radiation of Neognathae, and Neoaves (the rest of Neognathae). *Paleotis* has not been included in my phylogenetic analysis but is here considered as closest to the tinamou–*Lithornis* clade. Houde & Haubold (1986) considered it to be an ‘ostrich’ and this conclusion has been followed by others, although these authors admitted that this designation rests on ‘trivial’ features. *Paleotis* has a tinamou–*Lithornis* palate configuration, and is provisionally placed close to this line for the biogeographical discussion below.

Mayr (2011) raised a concern regarding the new molecular phylogenies (Harshman *et al.*, 2008; Phillips *et al.*, 2010), which place tinamous within ratites, in that no morphological correlates of such a grouping had been discovered. The palatal morphology discussed here now provides clear evidence for a derived position for tinamous within Palaeognathae.

The functional context of this palate morphology remains to be elucidated. Most discussion on the function of the avian palate has tried to relate the various configurations to cranial kinesis, but it has been shown that there is no significant difference in palatal function in kinesis between members of Palaeognathae and Neognathae (Gusseklou & Bout,

2005). The large eye and brain of modern birds have forced the jaw adductors into positions of relative mechanical disadvantage in many taxa (Goodman & Fisher, 1962); it may be that analysis of palatal structure in relation to the spatial and mechanical needs of these muscles will yield further insights.

Nasal hinge region

Prokinesis at the hinge region is assumed to have been present in the ancestor of modern birds (Zusi, 1984), as suggested for *Hesperornis* and *Ichthyornis*. The prokinetic hinge region of the ancestor appears to have migrated rostrally in palaeognaths and various neognaths to form a proximal potentially rhynchokinetic region, or alternatively the lacrimal and maxillary process of the nasal may have migrated towards the occiput. The functional value of the reinforcement noted in palaeognaths other than *Struthio* is not clear, given the rostral extent of the ossification of the interorbital septum in palaeognaths and the limitations this may impose on flexion at the nasal hinge region.

Mandibular adductors in the temporal fossa

The similarity of this morphology in kiwis and *Megapteryx* is a strong synapomorphy for a kiwi-moa clade within Palaeognathae. There is no obvious functional reason for convergent evolution to this morphology: kiwis probe in the ground with their long bills for small animals and seeds, and moas grazed on shrubs of appropriate height (Worthy & Holdaway, 2002). Mandibular adduction in all members of Palaeognathae is a simple movement in one plane and both muscles insert on the mandible at similar sites, with no obvious difference in mechanical advantage.

PHYLOGENETIC ANALYSIS

The phylogenetic approach used here, a priori definition of ancestral states where possible, is somewhat unconventional in current phylogenetic research, and is a return toward Hennig's original concepts of phylogenetics (Hennig, 1965; Wägele, 2004). The usual contemporary approach to morphological character definition is to attempt to minimize a priori assumption, and define homologies from the resulting phylogeny (Rieppel & Kearney, 2007). Recent use of the a priori approach has been directed at defining sister groups at basal nodes in cladistic (Stach, 2008) and noncladistic approaches (Carr, Johanson & Ritchie, 2009; Friedman & Brazeau, 2010) where the identity of an outgroup is not clear. The alternative in the current project would have been the use of multiple outgroups that could not have been coded for many characters. The a priori statement of homology

hypotheses may be seen as controversial (Sereni, 2009) but has a body of theoretical support (Neff, 1986; Bryant, 1989; Wägele, 2004; Kearney & Rieppel, 2006).

The alternative plan of overtly minimal homology definition expects the cladistic algorithm to discover both the phylogeny and the possible homologies; potential problems related to the circularity inherent in this method are pointed out by Wägele (2004). Furthermore, the dictum that homology is equivalent to synapomorphy (Patterson, 1982) has recently been challenged (Wägele, 2004; Assis & Rieppel, 2010; Mooi & Gill, 2010). An advantage of the a priori approach is that the algorithm searches for parsimony amongst homology hypotheses, not just similarities, thus with greater potential for results with biological significance. This approach depends on assumptions based on existing knowledge regarding evolutionary sequences, and may not be possible where such assumptions cannot be made, notably in palaeontology. The hypothetical ancestor used in this study is a composite of features from real taxa, and not inferred from ontogenetic or stratigraphical information, and is thus suitable for inclusion as a terminal taxon (outgroup) in parsimony analysis according to the theoretical approach of Bryant (1997).

As additional justification for the approach used here, it may be observed that although previous work has established a large amount of anatomical information as characters for morphological phylogeny, no convincing new understanding of morphological or geographical evolution of Palaeognathae has resulted (Mayr, 2011). Synapomorphy lists for palaeognath groupings tend to be series of rather disparate anatomical similarities, and biological relevance of these features is neither evident nor discussed. Bourdon *et al.* (2009) did, however, review biogeographical implications at length.

Further potential areas of controversy touched on by the present data are those of 'total evidence' (Kluge, 1989) and partitioning of data for separate analyses. The commonly held principle of total evidence requires inclusion of all relevant previously published characters unless excluded with specific explanation (Jenner, 2004). However, in practice there are problems with this approach: homoplasy is common (Scotland, Olmstead & Bennett, 2003), therefore morphological characters and character sets are not equal in phylogenetic utility. Additionally, morphological character definition is a conceptual process (Kearney & Rieppel, 2006); unless there is explicit documentation of characters (e.g. Asher, 2007) it is not clear how we are to equate and add together the conceptual processes of different investigators, and be sure we are not adding 'apples and oranges'. Some recent theoretical discussion (Richards, 2003; Nelson,

2004; Wägele, 2004; Rieppel, 2009) has considered that 'total evidence' is an ideal position but difficult in practice because of variable quality of characters and a tendency toward a phenetic approach; however, a solution to the issue of selection has not been developed by these authors. Selective use of data can be criticized as being subjective or *ad hoc*; however, as pointed out by Rieppel (2009), it follows from Popper's (1959) designation of character definition as 'low level hypothesis' (Popper, 1959: 75) and from the conceptual nature of character recognition that all character definition must be subjective. Popper's point is that all scientific observation is conditioned by the preconceptions of the observer, and hence cannot be 'theory-free'. Rieppel (2009) does not go as far as to state that 'total evidence' is an invalid concept, but parts of his argument point in that direction. It has also been noted that selection of characters can make a critical difference to the resulting phylogeny (Schultze, 1994). An alternative view (Scotland *et al.*, 2003; Nelson, 2004; Mayr, 2007) is that too many morphological characters bring too great a possibility of homoplasy, and tend to cloud the phylogenetic signal. The approach adopted in the present study is aligned with these latter authors, for a reason not emphasized by them: requiring total evidence would be logical if characters are independent, but this is presumably not the case. Division of an organism into morphological characters is an artificial process, and characters must be linked in functional and ecological ways that may not be apparent. As a very simple example, birds that do not fly depend more on their hind limbs, and the range of efficient modifications of a basic hind-limb pattern may be limited, with the resulting possibility that neither the vestigial wing or hind-limb morphology may be reliable for phylogeny in Palaeognathae. Cranial characters may thus be more informative, as suggested by Harshman *et al.* (2008). Reasons have been given above for the exclusion of published characters from the current study; a central issue in such exclusions has been the difficulty in defining an ancestral state without re-examination of anatomical features and homology assumptions across a range of taxa. As for inclusion of characters, it can be noted that the characters for palatal osteology could not have been identified without acknowledging the possibility of SSOP phylogeny.

It might be thought easy to search existing data sets for characters that conform with a phylogeny we consciously or unconsciously believe to be correct (Schultze, 1994); the Livezey & Zusi (2006) data were searched with an SSOP topological constraint, not to confirm this topology but to seek characters to strengthen the *Rhea* and tinamou lineages, which are weakly supported in this study and the two molecular phylogenies. This was largely unrewarding in terms

of the requirements of the current project, as described above. In the end result, whatever part subjectivity has played in character selection, the phylogeny generated is no more than a hypothesis, and is to be tested for biological plausibility and corroboration with other information. If the result is positive and we accept that parsimony (in this case) is an appropriate surrogate for the evolutionary process, the congruent hypotheses involved in character definition and selection are supported.

In the current study, this form of support comes from corroboration with the results of Harshman *et al.* (2008) and Phillips *et al.* (2010) and from the geographical correlation. The more important character hypotheses that are supported by this concordance are the homologies of tongue muscles in avians and non-avian reptiles, and the scheme proposed for evolution of the palate. The core data set used here are admittedly small and reflect mainly original morphological research. In this sense the data are preliminary as they cover only limited anatomical or physiological territories.

The interpretation of fossil material relies heavily on postcranial material, so the need to establish diagnostic criteria is great. The likelihood of homoplasy in postcranial osteology represents a particular challenge: many published characters are based on those of Bledsoe (1988), who in turn adopted the character set of Rich (1979) from her study of Dromornithidae. This study, however, placed Dromornithidae within Palaeognathae, a position which had to be rectified on the discovery of dromornithid skulls (Murray & Vickers-Rich, 2004), which are clearly gallo-anserine. Superiority of soft tissue anatomy over osteology for phylogenetic inference has been claimed in bony fish (Diogo, 2004) and primates (Gibbs, Collard & Wood, 2000), and could be a further factor in the differences amongst morphological phylogenies of Palaeognathae. The position of Aepyornithidae is of particular interest, and requires further data to confirm or refute the phylogenetic position recovered here.

BIOGEOGRAPHICAL RECONSTRUCTION

The reconstruction of palaeognath phylogeny presented here fits well with known geological facts: Madagascar–India (aepyornithids, possibly struthionids) and Africa (*Struthio*) separate first and second, followed by the separations of Australia–New Zealand from Antarctica–South America, later followed by parting of Australia–New Guinea (cassowaries, emu) from New Zealand (moas, kiwis), and South America (rheas, tinamous) from Antarctica [uncharacterized palaeognath (Tambussi *et al.*, 1994)]. The corroboration provided by the good fit to Gondwana separation is strongly supportive of this phylogeny if we accept

vicariant distribution: morphological and molecular evolution are not constrained to be parsimonious or avoid convergence (Sperling & Peterson, 2009), but continental drift must be much more a one-way process.

The relative importance of vicariance and dispersal are much debated, with vigorous argument for both modes, not least in relation to New Zealand taxa (Waters & Craw, 2006). Vicariance is obviously to the point in considering flightless birds, but it can be noted that dispersal is currently considered the most likely mode of distribution for animals as large as sauropodomorph dinosaurs (Rowe, Sues & Reisz, 2010). Harshman *et al.* (2008) (Fig. 1A) pointed out the general fit of their phylogeny with Gondwana vicariance but noted that their main conclusion of multiple losses of flight makes vicariance not an essential part of palaeognath biogeography. In fact, as summarized by Ericson (2008), a number of clades of volant modern birds have a distribution that conforms to Gondwana separation, despite capacity for flight including long migrations. The findings reported here with the inclusion of moas and elephant birds can be fitted exactly with known geological facts regarding the break-up of Gondwana (McLoughlin, 2001; Scotese, 2001; Eagles & König, 2008). Figure 5 shows the phylogeny branching from an ancestor in the undivided continent to taxa distributed across its division; this scheme assumes that the South American palaeognaths evolved there after its separation from the Antarctica–Australasia block, rather than after separation from Africa, although the latter is possible. The distribution of all fossil palaeognaths can be accounted for in this scheme if it is accepted that *Lithornis* and *Paleotis* arrived in North America and Europe by flying, although it is also possible that the ancestor of *Paleotis* was distributed overland from northern Africa in the Eocene.

The phylogeny proposed here fits rather better with geological events than other hypotheses, and much better than some: most have *Struthio* as part of a crown group with non-African genera. Some results have more than one lineage evolving flightlessness and large size having to cross large ocean barriers: Bourdon *et al.* (2009) acknowledged considerable problems in relating their phylogeny (Fig. 1D) to a plausible biogeography. The phylogeny of Phillips *et al.* (2010) in Figure 1B appears to be compatible with Gondwana vicariance, but the authors discounted this possibility based on their molecular clock calculation, which requires *Struthio* to originate after the separation of Africa from Gondwana; the geographical interpretation of this result is difficult and their explanation of *Struthio* in Africa is not conclusive. The ostrich fossil record has been interpreted as most consistent with origin in Africa

and distribution into Europe and Asia in the Neogene period (Mourer-Chauviré *et al.*, 1996).

ATTRIBUTION OF DATES

The dates attributed here are consistent with the SSOP hypothesis, although they are somewhat more speculative. The interpretation of Gondwana vicariance in relation to New Zealand ratites has been complicated by the theory the land mass was completely submerged by an Oligocene marine incursion (the ‘Oligocene drowning’ hypothesis; Waters & Craw, 2006) and consequent interest in dispersal possibilities. However, the presence of unique faunal elements, notably the *Leiopelma* frogs, has not been accounted for by dispersal theory. Recent new fossil evidence from all vertebrate groups (Worthy *et al.*, 2010) and new geological evidence (Bunce *et al.*, 2009) correlate well with retention of a large area of land during this period.

Heads (2009a) has analysed primate evolution against the known separation dates of Gondwana, and applied maximum dates to nodes, these being the first possible separation of populations by vicariance; this produces dates radically different to molecular clock estimations, possibly older than the projected origin of eutherian mammals. Minimum dates have been used in the present study as there appears to be better geological evidence at least for some separations, giving a greater number of nodes to which dates can be assigned, and more importantly the use of minimum dates accords better with the ‘hard minimum’ concept applied in molecular clock methodology (Benton & Donoghue, 2007).

The dates derived here are of the same order as those assigned in Figure 1C (Baker & Pereira, 2009), which is calibrated against distant dates from the fossil record such as the amphibian–amniote and archosaur–lizard divergences and recent fossils. Figure 1B (Phillips *et al.*, 2010), however, is calibrated in a similar fashion and the later result is used to argue against Gondwana vicariance. The dates given here offer another and possibly better system for calibration of palaeognath and avian molecular clocks: the use of multiple calibrations within a phylogeny has been emphasized (Benton & Donoghue, 2007). These dates place the earliest divergence of modern Palaeognathae in the mid-Cretaceous, contributing to the debate on whether modern avian radiations commenced before or after the Cretaceous–Tertiary (K–T) extinction event (Chiappe & Dyke, 2007; Brown *et al.*, 2008). The dates inferred are in accord with fossil evidence that modern birds existed before the K–T extinction event (Clarke *et al.*, 2005).

The ‘latest possible vicariance of sister groups’ approach used here to postulate dates for multiple nodes on a phylogeny does not appear to have been

attempted previously, although similar logic is implied by studies that apply a date based on a single geological event such as Baker *et al.* (2005). The similarity with the dates summarized by Baker & Pereira (2009) offers some support to this method, but corroboration is required from other phylogenies. Returning to the primate example given above, if we re-examine Heads' (2009a) hypothesis using latest vicariance, being careful to use an 'out-of-Gondwana' rather than 'out-of-Africa' sequence, and following Heads' own tenet that sister groups need not arise in the same place, we can derive dates such as 65 Mya for the lemur radiation (final separation of Madagascar), 60 Mya for New World monkeys (last separation of South America) and 45 Mya for lorises (collision of India with Asia), all of which are much closer to the molecular clock consensus (Steiper & Young, 2009) than Heads' dates of earliest vicariance. This 'latest-vicariance' primate reconstruction is a brief and speculative analysis that makes many more assumptions than the simpler palaeognath example; nevertheless, the results suggest at least some validity in the approach.

The congruent phylogenies discussed here represent a new approach to the long-standing puzzle of palaeognath evolution, and their morphological and biogeographical implications build towards a more complete picture than has been possible with previous hypotheses.

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APPENDIX 1

ASSUMPTIONS MADE IN CHARACTER DESIGN

(character number) (reference)

- a. The *Sphenodon* hyobranchial apparatus represents the plesiomorphic reptilian pattern. (1) (Rieppel, 1978)
- b. The paraglossale is a neomorph and is not part of the plesiomorphic reptilian pattern. (3) (Kallius, 1906)
- c. Ventral position of epibranchiale is the plesiomorphic reptilian state. (5) (Rieppel, 1978; Dal Sasso & Signore, 1998)
- d. The avian m. ceratoglossus is homologous to the reptilian (non-avian) m. hyoglossus. (6) (Edgeworth, 1935)
- e. The palaeognath m. geniohyoideus (genioceratoideus of Tomlinson, 2000) is homologous to the m. geniohyoideus of the plesiomorphic reptilian pattern. (7) (Müller & Weber, 1998)
- f. The avian m. hyoglossus (hyoglossus obliquus ± hyoglossus anterior) is a neomorph. (8)
- g. The avian m. stylohyoideus is homologous to the m. interhyoideus of the basic gnathostome pattern. (9) (Kesteven, 1942–1945)
- h. The avian m. branchiomandibularis is homologous to the reptilian (non-avian) m. hyomandibularis ± m. ceratohyoideus and both are homologues of the interarcualis ventralis 1 of the basic gnathostome pattern (Wiley, 1979) rather than the 'subarcualis rectus 1' of Edgeworth (1935) and Diogo *et al.* (2008). (11)
- i. The palaeognathous basipterygoid articulation is homologous with the basipterygoid articulation of non-avian reptiles. (17–19) (Weber, 1993)
- j. The palaeognath pterygoid is undivided, unlike the neognath situation in which the rostral part of pterygoid becomes incorporated into the 'palatine' with a resulting intrapterygoid articulation. (20) (Elzanowski, 1995)
- k. Titanosaur and troodontid eggshells are suitable ancestral types for avian eggshell morphology. (25–39) (Grellet-Tinner, 2006)
 1. Ancestors of modern birds had prokinetic skulls. (23) (Zusi, 1984)
- m. Palaeognathae and Neognathae are monophyletic radiations. (37–39)

APPENDIX 2

CHARACTER LIST

Characters taken from published sources are retained in their original format, although all character states may not appear in the taxa listed here.

1. Hyobranchial skeleton: basihyale+ceratobranchialia 1 + 2 (0); basihyale \pm urohyale+ceratobranchiale 1 (1).
2. Ossification of basihyale: no (0); partly (1); fully (2). Similar to Tomlinson (2003), character 2.
3. Presence of paraglossalia: absent (0); present, single structure (1); present, paired (2). Similar to Tomlinson (2003) characters 4, 5, 7.
4. Epibranchiale length: epibranchiale absent (0); short – less than 50% of ceratobranchiale length (1); long (2). Similar to Tomlinson (2003) character 6.
5. Epibranchiale orientation: epibranchiale absent (0); horizontal (1); ventral curve (2); dorsal curve (3). Similar to Tomlinson (2003) character 1.
6. M. ceratoglossus (reptilian m. hyoglossus): muscular throughout (0); tendinous intersection at crossing of m. transversus (1); longitudinal tendon or aponeurosis (2); multiple parallel muscle bodies (3).
7. M. geniohyoideus (genioceratoideus of Tomlinson, 2003): present (0); absent (1).
8. Avian m. hyoglossus: absent (0); single (1); paired (2).
9. Insertion of m. interhyoideus (avian m. styohyoideus): midline (0); midline + mid ceratobranchiale (1); mid ceratobranchiale (2); anterior ceratobranchiale \pm anterior urohyale (3); basihyale + other (4); basihyale (5).
10. M. transversus linguae: absent (0); present (1).
11. Avian m. branchiomandibularis/reptilian m. hyomandibularis: single – IX innervated (0); paired IX + XII innervated (1); paired IX innervated (2).
12. Intrinsic tongue muscle: present (0); absent (1).
13. Avian m. branchiomandibularis insertion within caudal 50% of m. mylohyoideus: yes (0); no (1).
14. M. serpihyoideus insertion: midline (0); cricoid (1).
15. Vomer: extends < 10% of skull length caudal to lacrimal (0); extends caudal to state 0 (1).
16. M. ceratoglossus anterior: lacking terminal m. ceratoglossus/reptilian hyoglossus tendon (0); absent (1); present (2).
17. Palatine, lateral border: directed at basipterygoid articulation (BPA) (0); directed at midline rostral to BPA (1); palaeognathous BPA absent (2).
18. Palatine, lateral borders: parallel or diverge rostrocaudal (0); converge rostrocaudal (1).
19. Palatine, medial border: directed at BPA (0); directed at midline rostral to BPA (1); palaeognathous BPA absent (2).
20. Pterygoid: reaches vomer near rostral limit of orbit (0); foreshortened, limited lateral junction with palatine (1); foreshortened, wide lateral junction with palatine (2); rostral terminal junction with palatine (3); intrapterygoid joint (4).
21. Dorsal surface of arytenoid bone or cartilage: flat (0); raised medial rim (1). (*Struthio*, *Megaplateryx*, and *Dinornis* have a raised medial rim, apparently able to engage in the choana).
22. Bony choana: vomer at caudal medial border (0); absence of state 0 (1).
23. Flattest cross-section at nasal hinge region: flat (0); V-shaped (1); \cap -shaped (2); casque (3).
24. Jaw adductor muscle in temporal fossa: m. adductor mandibulae alone (0); m. pseudotemporalis alone (1); both mm. adductor mandibulae and pseudotemporalis (2).
25. General egg symmetry: symmetrical all axes (0); asymmetrical (2). Grellet-Tinner (2006) character 1.
26. Egg shape variation: long elliptical, rounded poles, broader one pole (0); elliptical, broadest near one pole, other pole pointed (1); elliptical, broadest nearer centre (2); short elliptical, nearly spherical (3). Grellet-Tinner (2006) character 2.
27. Superficial eggshell ornamentation: ornamentation (0); no ornamentation (1). Grellet-Tinner (2006) character 3.
28. Superficial ornamentation morphologies: nodular (0); linear tuberculate (1); smooth (2); rugose (3); granulated (4). Grellet-Tinner (2006) character 4.
29. Pore canal shape: straight, bifurcate before reaching surface (0); oblique, round aperture (1); straight (2); diverticulate-arborescent (3); inner and outer pore canal tracks not aligned (4). Grellet-Tinner (2006) character 5.
30. Pore aperture: slit-like (0); round (1). Grellet-Tinner (2006) character 6.
31. Spherulite: acicular rhombohedral calcite crystals (0); short-bladed calcite crystals (1); long-bladed calcite crystals (2). Grellet-Tinner (2006) character 7.
32. Eggshell layer 3: absent (0); present (1). Grellet-Tinner (2006) character 8.
33. Eggshell layer 4: absent (0); present (1). Grellet-Tinner (2006) character 9.
34. Morphology of layer 3: absent (0); amorphous (1); blocky crystals (2); porous (3). Grellet-Tinner (2006) character 10.
35. Delimitation between eggshell layers 1 and 2: absent (0); prismatic (1); aprismatic (2). Grellet-Tinner (2006) character 11.

36. Delimitation between eggshell layers 2 and 3: layer 3 absent (0); prismatic (1); aprismatic (2). Grellet-Tinner (2006) character 12.
37. Delimitation between eggshell layers 3 and 4: layer 4 absent (0); prismatic (1); aprismatic (2). Grellet-Tinner (2006) character 13.
38. Ratio of layer 1 to layer 2: layer 2 absent (0); > 0.9 (1); $0.5 << 0.8$ (2); < 0.49 (3). Grellet-Tinner (2006) character 14.
39. Ratio of layer 3 to layer 2: layer 3 absent (0); > 0.1 (1); < 0.1 (2). Grellet-Tinner (2006) character 15.
40. Pygostyle: large (0); reduced (1). Elzanowski (1995) character PG1.
41. Paratympanic organ: present (0); absent (1). Starck (1995)
42. Chorda tympani: present (0); absent (1). Starck (1995)
43. Cranioquadrate articulation: quadrate-squamosal, not quadrate-prootic (0); separate quadrate-squamosal and quadrate-prootic (1); quadrate-squamosal-prootic-exoccipital (2); quadrate-squamosal-prootic-exoccipital-laterosphenoid (3). Modified from Livezey & Zusi (2006) character 598.
44. Expanded nasal chamber – large concha nasalis caudalis: absent (0); present (1). Bourdon *et al.* (2009) character 23.
45. Manual digit 2: two or more phalanges (0); one phalanx (1); zero phalanges (2).
46. Manual digit 3: three or more phalanges (0); fewer than three phalanges (1).
47. Manual digit 4: two or more phalanges (0); fewer than two phalanges (1).
48. Os lacrimale, caudally projecting processus supraorbitalis: absent (0); present (1). Mayr & Clarke (2003): character 13
49. Marked processus parasphenoidales mediales: absent (0); present (1). Mayr & Clarke (2003): character 30
50. Axis, corpus with pneumatic foramina on lateral sides: no (0); yes (1). Mayr & Clarke (2003): character 48
51. Axis, foramina transversaria: present (0); absent (1). Mayr & Clarke (2003): character 49
52. Third cervical vertebra, osseous bridge from processus transversus to processus articularis caudalis: absent (0); present (1). Mayr & Clarke (2003): character 52
53. Coracoid fused with scapula: no (0); yes (1). Mayr & Clarke (2003): character 68
54. Sternum, caudal margin: with four notches/fenestrae (0); two notches/fenestrae (1); without notches/fenestrae (2). Mayr & Clarke (2003): character 73
55. Ribs, processu uncinati: present, not fused to ribs (0); present, fused to ribs (1); absent (2). Mayr & Clarke (2003): character 74
56. Humerus, foramina pneumatica at bottom of fossa pneumotricipitalis or corresponding area in taxa without such fossa: absent (0); present (1). Mayr & Clarke (2003): character 77
57. Pelvis, number of vertebrae ankylosed in synsacrum: 9–10 (0); 11–12 (1); 13–14 (2); 15–16 (3); 17–18 (4). Mayr & Clarke (2003): character 91
58. Pelvis, cristae iliacae dorsales largely or completely fused cranially with crista spinosa of synsacrum: no (0); yes (1). Mayr & Clarke (2003): character 92
59. Pelvis, foramen ilioischiadicum caudally closed: no (0); yes (except Rheidae) (1); condition in Rheidae (considered nonhomologous to the closure in neognathous birds) (2). Mayr & Clarke (2003): character 94
60. Femur, crista trochantericus marked projected cranially: no (0); yes (1). Mayr & Clarke (2003): character 97
61. Tibiotarsus, distal end, ossified pons supratendineus: absent (0); present (1). Mayr & Clarke (2003): character 100
62. Tarsometatarsus, canalis interosseus distalis: present (0); absent (1). Mayr & Clarke (2003): character 107
63. M. iliotrochantericus cranialis, strongly fused with m. iliotrochantericus caudalis: unfused (0); fused (1). McKittrick (1991): character 6
64. M. femorotibialis externus, distal head: present (0); absent (1). McKittrick (1991): character 8
65. M. femorotibialis internus, longitudinal division: absent (0); present (1). McKittrick (1991): character 9
66. M. iliofibularis, ansa iliofibularis forms a single ligament: absent (0); present (1). McKittrick (1991): character 10
67. M. caudofemoralis: present (0); absent (1); poorly developed (2). McKittrick (1991): character 15
68. M. obturatorius lateralis, pars dorsalis: present (0); absent (1). McKittrick (1991): character 22
69. M. obturatorius medialis, two heads of origin: absent (0); present (1). McKittrick (1991): character 23
70. M. obturatorius medialis, number of tendons of insertion: one tendon (0); two tendons (1); three tendons (2). McKittrick (1991): character 24
71. Mm. obturatorius medialis and lateralis, distal fusion: fusion (0); independence (1). McKittrick (1991): character 26
72. M. ambiens, extent of origin: limited to pectineal process (0); extending from pectineal process to pubis (1); one origin from pectineal process

- and one origin from pubis (2). McKittrick (1991): character 30
73. *M. gastrocnemius pars medialis*, patellar band: present (0); absent (1). McKittrick (1991): character 33
74. *M. gastrocnemius pars medialis*, number of heads: one (0); two (1). McKittrick (1991): character 34
75. *M. tibialis cranialis*, number of tendons of insertion: bifurcated tendon (0); one tendon (1). McKittrick (1991): character 37
76. *M. fibularis brevis*: present (0); weak (1); absent (2). McKittrick (1991): character 43
77. *M. flexor perforans et perforatus digit III*, vinculum: present (0); absent (1). McKittrick (1991): character 44
78. *Mm. flexor hallucis longus* and *flexor digitorum longus*, type of flexor arrangement according to types 1–8 of George & Berger (1966: 447). McKittrick (1991): character 52
79. *M. flexor hallucis longus*, number of heads: one (0); two (1); three (2). McKittrick (1991): character 53
80. *M. popliteus*: present (0); absent (1). McKittrick (1991): character 57
81. *M. extensor hallucis longus*, number of heads: two (0); one (1). McKittrick (1991): character 61
82. *M. abductor digiti II*: present (0); absent (1); vestigial (2). McKittrick (1991): character 63
83. *M. adductor digiti II*: present (0); weak (1); absent (2). McKittrick (1991): character 64
84. *M. extensor brevis digiti IV*: present (0); vestigial (1); absent (2). McKittrick (1991): character 65
85. *M. lumbricalis*: absent (0); present (1); weak or vestigial (2). McKittrick (1991): character 66

APPENDIX 3
MATRIX

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Struthio</i>	1	0	2	2	2	0	0	0	2	0	0	0	1	0	0	0	0	0	0
<i>Rhea</i>	1	0	1	1	1	0	0	0	0	0	0	1	1	0	1	0	0	1	1
<i>Casurarius</i>	1	0	1	1	1	0	0	0	0	1	0	0	1	1	1	0	0	1	1
<i>Dromaius</i>	1	0	1	1	1	0	0	0	1	1	0	0	1	0	1	0	0	1	1
<i>Apteryx</i>	1	0	1	1	1	1	0	0	0	1	0	0	1	0	1	0	0	1	1
Tinamidae	1	1	1	1	3	0	0	0	0	0	0	0	1	0	1	0	1	1	1
<i>Psittacus</i>	1	2	2	2	3	3	1	2	5	0	2	0	0	0	1	2	2	1	2
<i>Gallus</i>	1	2	1	2	3	2	1	2	5	0	2	0	1	0	1	1	2	1	2
<i>Columba</i>	1	2	1	2	3	2	1	2	5	0	2	0	1	0	1	1	2	1	2
<i>Aepyornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	0	0
<i>Lithornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	1	1
Dinornithiformes	1	0	1	2	2	?	?	?	?	?	?	?	?	?	1	?	1	1	1
	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Struthio</i>	2	1	1	0	1	1	3	1	2	3	0	2	1	0	1	2	2	0	3
<i>Rhea</i>	2	0	0	1	1	1	2	1	2	?	0	2	1	0	1	2	2	0	2
<i>Casurarius</i>	2	0	0	3	1	1	2	0	4	4	0	1	1	1	3	2	2	1	2
<i>Dromaius</i>	2	0	0	1	1	1	2	0	4	4	0	1	1	1	3	2	2	1	2
<i>Apteryx</i>	2	0	0	2	2	1	2	0	?	2	0	1	1	0	2	2	2	0	2
Tinamidae	3	0	0	1	1	1	3	1	2	2	0	0	1	0	1	2	2	0	2
<i>Psittacus</i>	4	0	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Gallus</i>	4	0	1	0	0	1	1	0	2	2	0	1	1	0	1	1	1	0	3
<i>Columba</i>	4	0	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Aepyornis</i>	2	?	0	2	?	1	3	0	3	3	1	2	1	0	1	2	2	0	3
<i>Lithornis</i>	2	?	0	?	?	?	?	1	2	2	0	0	1	0	1	2	2	0	2
Dinornithiformes	2	1	0	2	2	1	2	1	2	2	1	2	1	0	2	2	2	0	2
	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Struthio</i>	2	1	1	1	2	0	0	0	0	1	0	1	?	0	1	1		0	2
<i>Rhea</i>	2	1	1	1	2	0	0	1	1	1	0	0	0	0	1	1	0	0	2
<i>Casurarius</i>	1	1	1	1	2	0	2	0	1	1	0	0	?	1	?	0	?	0	2
<i>Dromaius</i>	1	1	1	1	2	0	2	0	1	1	0	0	?	1	?	0	?	0	2
<i>Apteryx</i>	1	1	1	1	3	1	2	?	?	1	0	1	1	1	1	1	0	0	1
Tinamidae	2	1	1	1	2	0	1	0	1	0	1	?	0	0	0	1	1	1	1
<i>Psittacus</i>	?	0	0	0	1	0	1	0	0	?	0	0	1	?	0	0	1	1	2
<i>Gallus</i>	1	0	0	0	1	0	1	0	0	0	0	0	?	1	0	0	1	1	3
<i>Columba</i>	?	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	?	1	2
<i>Aepyornis</i>	2	1	?	?	2	0	?	?	?	0	?	1	?	?	?	1	?	?	?
<i>Lithornis</i>	1	1	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Dinornithiformes	1	1	?	?	1	1	2	1	1	0	1	1	0	1	1	1	?	?	4