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A species-level phylogeny of the Cretaceous Hesperornithiformes (Aves: Ornithuromorpha): implications for body size evolution amongst the earliest diving birds

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Despite extensive discoveries across the globe over the past two centuries, little phylogenetic work has been done on the Hesperornithiformes. Spanning the late Early to Late Cretaceous, hesperornithiforms are one of the most diverse groups of Mesozoic birds in terms of both their geographical distribution and the wide differences in body size and diving specializations. This study presents the first phylogenetic analysis of the Hesperornithiformes that includes a majority of the described taxa, enabling the first detailed look at evolutionary relationships within the clade. The results of this study support the monophyly of the Hesperornithiformes, which is recovered as the sister clade to the avian crown group, Neornithes. Within the Hesperornithiformes, the Brodavidae and Hesperornithidae are monophyletic while the Baptornithidae are polyphyletic. Little evidence of species-level taxonomic differentiation is found within *Hesperornis*, with many species indistinguishable from *Hesperornis regalis*. Evolution within the Hesperornithiformes provides a fascinating example of progressive development of specialized diving adaptations in birds. The acquisition of these diving specializations appears to be uncorrelated to the independent evolution of multiple large increases in body size.

Keywords: Aves; evolution; palaeontology; diving birds; body size

Introduction

The Hesperornithiformes are an extinct lineage of Cretaceous, toothed, foot-propelled diving birds with a wide geographical and stratigraphical range and a broad body size spectrum, known predominately from marine strata. Initially recognized by O. C. Marsh in the late 1800s from a wealth of fossils from the USA, these birds were amongst the first Mesozoic avians known to science after the famous *Archaeopteryx lithographica* (see Chiappe 2007). Numerous other specimens have since been documented around the Northern Hemisphere from sites dated at 113 to 66 million years old (Fig. 1). An isolated tarsometatarsus, *Neogaeornis wetzeli*, from Chile was initially grouped with hesperornithiforms and modern loons and grebes (Lambrecht 1929, 1933) and subsequently with the Baptornithidae (Martin & Tate 1976). However, Olson (1992) later determined *Neogaeornis* to be more closely related to modern loons, thus relegating hesperornithiform distribution to the Northern Hemisphere. Within this range, thousands of specimens are known from the USA and Canada, with far fewer numbers recovered from Eurasia. Despite this abundance of fossil material, little rigorous research has been undertaken to

investigate macroevolutionary patterns and interrelationships of hesperornithiforms – the bulk of previous investigations has focused on their taxonomy. While several researchers have worked on either North American (Marsh 1880; Martin & Tate 1976; Tokaryk *et al.* 1997; Martin & Lim 2002) or Eurasian (Seeley 1876; Nessov & Yarkov 1993; Rees & Lindgren 2005; Dyke *et al.* 2006) hesperornithiform fossils, a combined analysis of known fossil material from across the globe has not been published to date.

From the late 1800s to the late 1900s, research on hesperornithiforms consisted predominantly of describing new taxa. This focus on descriptive work without synthesizing research resulted in a plethora of little-understood species, many based on a single skeletal element (e.g. *H. bairdi*, *H. macdonaldi*, *H. mengeli* and many others). Studies looking at the evolutionary context of hesperornithiforms as a whole were rare, and most saw these birds as a primitive group of modern birds (e.g. Marsh 1880; Lucas 1903; Heilman 1926). It was not until the 1980s that a few authors began to evaluate phylogenetic relationships within the Hesperornithiformes (Fig. 2; Cracraft 1982; Martin 1984; Elzanowski & Galton 1991). These studies were limited in the number of hesperornithiforms

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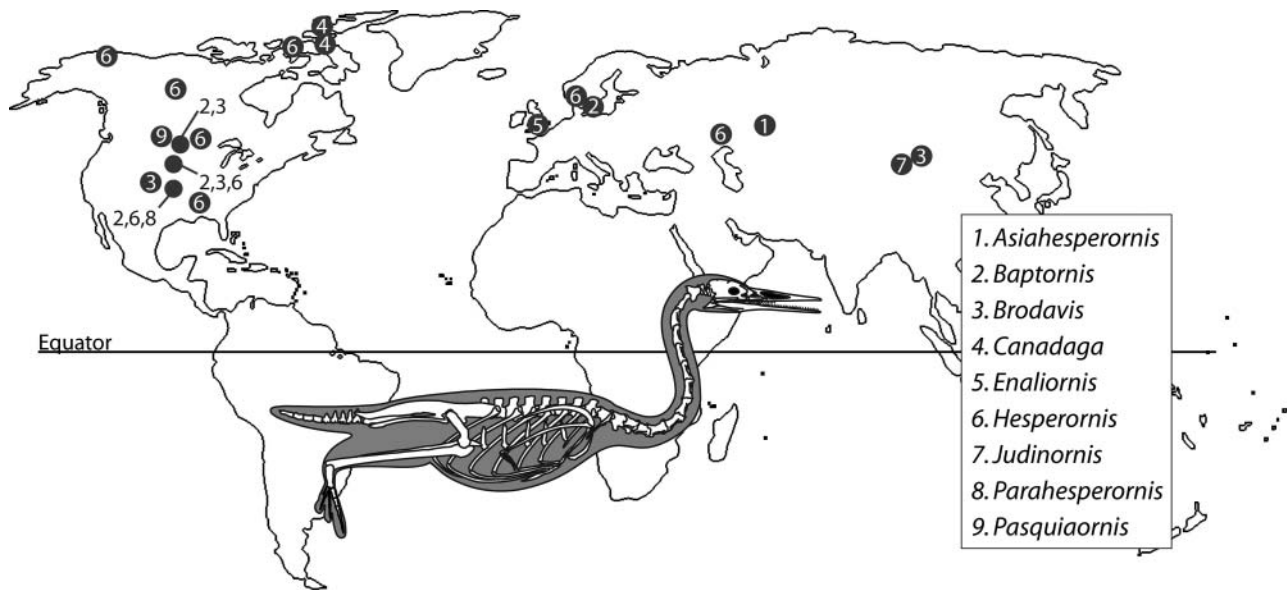


Figure 1. Geographical distribution of hesperornithiform specimens. The map reflects all reported hesperornithiform discoveries, with the genera known from each area identified. Skeleton shown is an artist's reconstruction of *Hesperornis regalis*.

included, and methods of phylogenetic inference have been refined since the original studies were conducted.

The discovery of abundant avian fossils in the Early Cretaceous of China, starting in the 1990s and continuing to this day, has prompted a dramatic increase in the amount of scientific research into the evolution of early birds (Zhou 2004; O'Connor *et al.* 2011). Whereas the systematic positions of some groups of fossil birds remain poorly resolved, hesperornithiforms have been consistently placed as one of the nearest sister groups to modern birds, in a larger clade referred to as the Ornithurae (e.g. Chiappe 2002; Clarke 2004; Bell *et al.* 2010; Wang *et al.* 2014). These birds are united by a number of synapomorphies, such as a reduced acetabulum relative to the length of the ilium, a prominent patellar groove on the femur, and a cranial cnemial crest on the tibiotarsus (Chiappe 1996, 2002; O'Connor *et al.* 2011). While phylogenetic studies such as these have firmly established the placement of hesperornithiforms within the evolutionary tree of Mesozoic birds, the relationships amongst the more than nine genera and 22 species of hesperornithiform birds remain poorly understood (Supplemental Table 1).

In his initial work with the hesperornithiforms *Hesperornis* and *Baptornis*, Marsh (1880) suggested that these birds were essentially modern, despite the presence of ancestral characters such as teeth, and most likely related to the ratites. Marsh (1872, 1880) based this determination on apparent similarities of the palate of *Hesperornis* with that of the ostrich. Despite Marsh's initial assessment, later researchers questioned the placement of hesperornithiforms within the modern ratite clade. Instead, they thought them to be either closely related to, but outside of, modern birds (i.e. Neornithes; Lucas 1903; Heilmann 1926), or basal ancestors of modern lineages, such as the

loons or grebes (Brodkorb 1963, 1971), or a combination of the two (Cracraft 1982). Despite utilizing morphological similarities to determine relationships between hesperornithiforms and modern birds, the relationships of various hesperornithiform species to each other have never been comprehensively investigated.

Homology, homoplasy and phylogenetic relationships within the Hesperornithiformes

Lucas (1903) was one of the first authors to note that amongst aquatic birds convergence of morphological features is prevalent and can complicate the interpretation of evolutionary relationships. Stolpe (1935) later undertook an in-depth study of morphological convergence as it relates to loons and grebes, and found that all of the features later used to unite *Hesperornis* with modern loons and grebes in a single group were most likely the result of convergence influenced by the similar diving specializations of these birds (Storer 1960).

A close look at the details of the apparently similar morphology shared by these three groups of foot-propelled divers — loons, grebes and hesperornithiforms — reveals key differences that point to homoplasy rather than homology. For example, all three birds have skeletal expansions in the knee joint for the attachment of the *m. gastrocnemius* and the *m. flexor perforates digiti IV*, muscles important for moving the foot during swimming (Wilcox 1952). However, the structure of this expansion is different in each of these birds. In loons, the muscles attach to a greatly expanded cnemial crest on the proximal tibia with no role for the patella; grebes possess a somewhat reduced cnemial crest (as compared to loons), in

Table 1. Estimates of body mass for genera of the Hesperornithiformes. Mean estimates (in kilograms) are given for each method and genus, with the number of specimens included listed (*n*).

	Maloiy <i>et al.</i> 1979	Alexander 1983	Peters & Peters 2009*	<i>n</i>
<i>Asiahesperornis</i>	2.30	2.69	3.43	2
<i>Baptornis</i>	1.06	1.50	1.91	2
<i>Hesperornis</i>	2.27	2.58	3.30	7
<i>Parahesperornis</i>	1.20	1.64	2.09	2
<i>Pasquiaornis</i>	0.52	0.86	1.09	4

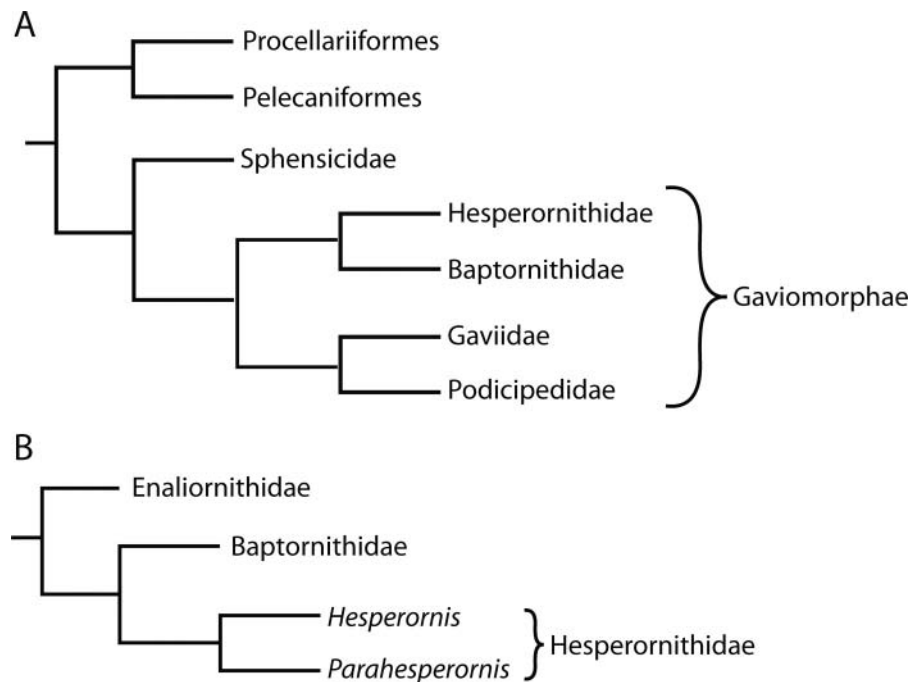
*Peters & Peters (2009) is developed from the equation derived by Prange *et al.* (1979).

conjunction with a robust patella that is incorporated into the muscular attachments (Storer 1960); and *Hesperornis* has a comparatively smaller cnemial expansion than that of either loons or grebes, along with a massive and highly elongate patella that bears numerous muscle scars. Thus each of these lineages has accomplished a superficially similar morphology in different ways. In regard to the modern loons and grebes, molecular analysis has since confirmed that, superficial similarities notwithstanding, the two groups are only distantly related (Hackett *et al.* 2008; McCormack *et al.* 2013; Jarvis *et al.* 2014).

A final trait found in both grebes and hesperornithiforms is a wide diversity of body sizes. Grebes range in size from *Tachybaptus dominicus*, weighing around 120 g, to *Podiceps major*, weighing around 1.7 kg, more than 14 times larger. While reconstructing body mass can be problematic in fossil organisms (see Anderson *et al.* 1985; Anyonge 1993; Smith 2002; Christiansen & Farina 2004),

a number of methods of mass estimation have been developed based on the length of the femur. Table 1 shows three different estimated body masses for each of the genera of hesperornithiforms for which femora are preserved. While not as variable as grebes, one of the largest hesperornithiforms, *Asiahesperornis bazhanovi*, was anywhere from just over 3 to 4.5 times larger than one of the smallest, *Pasquiaornis hardiei*. The evolution of this range in body sizes has not been addressed by previous research.

The first attempt to describe evolutionary relationships within the hesperornithiforms was an analysis that included *Hesperornis*, *Baptornis* and *Enaliornis*, as well as modern *Gavia* (loons), *Podicipedidae* (grebes), *Spheniscidae* (penguins) and *Pelecanus* (pelicans) made by Cracraft (1982). This paper presented a phylogenetic hypothesis (Cracraft 1982, p. 37) placing *Hesperornis* and *Baptornis* as sister taxa to *Gavia* and *Podicipedidae* in the clade *Gaviomorphae* (Fig. 2A). However, because hesperornithiforms were

**Figure 2.** A, hypothesis of the evolutionary relationships of the 'Gaviomorphae' by Cracraft (1982). B, evolutionary scheme of the Hesperornithiformes presented by Martin (1984).

assumed to be a modern lineage, the choice of *Pelecanus* as the outgroup taxon resulted in character states being interpreted as ancestral, when, in fact, they are derived within modern birds. The use of *Archaeopteryx* as the outgroup would have resulted in a much different understanding of character optimization in the analysis and helped differentiate homoplasy from homology.

A subsequent study by Martin (1984) identified 36 characters that united the Hesperornithiformes as a monophyletic group and placed *Paraesperornis* and *Hesperornis* as most closely related within the hesperornithiforms, with *Enaliornis* as the most primitive member of the group (Fig. 2B). This study was also one of the first modern studies to identify hesperornithiforms as more primitive birds, outside the crown group of modern birds (Martin 1984). However, this analysis was not a cladistic analysis in the sense that a group of characters was developed, coded for all taxa, and analysed using accepted phylogenetic algorithms. Rather, features that grouped taxa together were identified arbitrarily and then presented as a phylogenetic tree, which was more a visualization of an a priori hypothesis than a phylogeny derived from character optimization.

The most recent attempt to categorize hesperornithiform relationships was made by Elzanowski & Galton (1991) based on their highly detailed study of the braincase of *Enaliornis* and *Hesperornis* as well as *Archaeopteryx* and several modern birds. Elzanowski & Galton (1991) identified 17 morphological characters of the braincase that were considered to be of evolutionary significance, and then proceeded to discuss them in an evolutionary context; however, no phylogenetic analysis was conducted. While such a discussion is useful in determining potentially ancestral conditions, it has minimal relevance in differentiating homoplasy from homology and thus determining the interrelationships amongst these taxa.

The studies presented above highlight the need for a comprehensive numerical analysis of hesperornithiform relationships. In order to fill these gaps in hesperornithiform research, this study presents a large morphological dataset for a cladistic analysis investigating the species-level interrelationships of hesperornithiform birds. The results of this analysis support a monophyletic Hesperornithiformes, Brodavidae and Hesperornithidae, but not Baptornithidae, which is polyphyletic.

Methods

Institutional abbreviations

AMNH: American Museum of Natural History, New York, USA; **BGS:** British Geological Survey, Keyworth, UK; **NHUK:** Natural History Museum, London, UK; **CAGS:** Chinese Academy of Geological Science, Beijing,

China; **CFDC:** Canadian Fossil Discovery Center, Morden, Manitoba, Canada; **FMNH:** Field Museum of Natural History, Chicago, USA; **IZASK:** Institute of Zoology, Ministry of Science and Education, Almaty, Kazakhstan; **KUVP:** University of Kansas Museum of Palaeontology, Lawrence, USA; **LACM:** Natural History Museum of Los Angeles County, Los Angeles, USA; **RSM:** Royal Saskatchewan Museum, Regina, Canada; **SDSM:** South Dakota School of Mines Museum of Geology, Rapid City, USA; **SMC:** Sedgwick Museum of Geology, Cambridge, UK; **SMNH:** Sternberg Museum of Natural History, Hays, USA; **UNSM:** University of Nebraska State Museum, Lincoln, USA; **USNM:** United States National Museum of Natural History, Washington, DC, USA; **YORYMG:** Yorkshire Museum, Geology Collection, York, UK; **YPM:** Yale Peabody Museum of Natural History, New Haven, USA; **ZIN:** Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia.

Morphological characters

Evaluation of 272 hesperornithiform specimens as well as other basal and modern birds resulted in the development of a comprehensive database of 105 new cranial and postcranial characters. Additionally, 102 characters were adapted from other large cladistic analyses (Chiappe 2002; Clarke 2004; O'Connor *et al.* 2011), for a total of 207 characters, of which 147 were phylogenetically informative. While all portions of the skeleton are represented in the matrix, the majority of characters relate to the pelvic limb, as there is considerable bias in the hesperornithiform fossil record for these elements (Table 1). The complete list of characters can be found in Supplemental Appendix 1, and the coded matrix for the specimens in this analysis can be found in Supplemental Appendix 2. Of the 207 characters, 41 were multistate and of these 19 were ordered (see Supplemental Appendix 1). Ordering was imposed when a morphocline was present (Slowinski 1993; Thiele 1993), such as femoral head and neck: neck absent (0); neck merges into head without sharp margin (1); head is a distinct knob separated from neck (2) (character 123). Character polarity for binary and multistate characters was determined by comparison to the basal bird *Archaeopteryx*. Polymorphic characters were scored sequentially (e.g. [12]) in the matrix. Whenever possible, characters were erected to reflect diagnostic features that have been reported in the literature to define taxonomic groupings. For example, the degree of rounding of the intercortylar eminence of the tarsometatarsus (Martin & Lim 2002), as well as the relative breadths of the distal metatarsals (Martin *et al.* 2012), have been suggested as features that vary amongst species assigned to *Hesperornis* and have thus been cited as diagnostic features of these taxa. Therefore, character 183 [intercortylar eminence: absent (0); low relief (1); high relief (2)] and character

199 [distal end of tarsometatarsal shaft (just above trochlea), relative widths of metatarsals: II similar width to III and IV (0); III slightly wider than IV, II narrowest (1); II narrower than III and IV, which are of similar widths (2); II, III, and IV progressively wider, with IV twice as wide as III (3)] were erected to incorporate these diagnostic features into the cladistic analysis. It should be noted that during the development of the matrix, this approach highlighted a number of problems with existing hesperornithiform taxonomy. Firstly, a large number of taxa have been erected using entirely or partially plesiomorphic characters. Some examples of this include: lack of a supratendinal bridge on the distal tibiotarsus (Marsh 1880) and absence of hypotarsal grooves on the tarsometatarsus (Martin & Tate 1976) as diagnostic of the Hesperornithiformes; shortened sacrum as diagnostic of *Baptornis* (Lucas 1903); and the coracoid more slender than in *Hesperornis* as diagnostic of the Baptornithidae (Martin & Tate 1976). Secondly, some features have been cited as diagnostic of a particular species when, in fact, they are present in a much broader taxonomic spectrum. For example, a twisted tarsometatarsal shaft has been identified as diagnostic of *Asiahesperornis bazhanovi* (Dyke *et al.* 2006), when it is actually twisted in all hesperornithids. Finally, a number of characters that have been proposed as diagnostic features of various taxa are inaccurate. An example of this is the diagnosis of the Hesperornithiformes as lacking proximal foramina on the tarsometatarsus (Martin & Tate 1976), when all well-preserved specimens of hesperornithiforms preserve two proximal foramina on the plantar surface of the bone, one on either side of metatarsal II. These and other discrepancies highlight the need for a careful taxonomic revision of the Hesperornithiformes (Bell 2013). For development of the current character matrix, features that were either plesiomorphic at certain levels or used at an inappropriate phylogenetic level were still able to be included, as such features may provide phylogenetic information even if they do not help taxonomically.

Taxonomic sampling and operational taxonomic units (OTUs)

To date, 29 species in 13 genera and four families of Hesperornithiformes have been described (Supplemental Table 1); however, the validity of a number of these species and genera has been debated. Of these taxa, six have been invalidated by previous authors and will not be further considered here: *Baptornis varneri*, *Coniornis altus*, *Hargeria gracilis*, *Hesperornis montana*, *Lestornis crassipes* and *Parascaniornis stensoei*. Of the remaining 23 taxa, two were not included because of their extremely fragmentary nature (*Canadaga arctica*, known only from thoracic vertebrae, and *Potamornis skutchi*, an isolated quadrate). An additional three taxa were not available for direct study

and have been insufficiently reported in the literature for inclusion in the analysis (*Brodavis americanus*, *B. mongoliensis* and *Judinornis nogontsavensis*).

In total, 18 hesperornithiform taxa were evaluated during the course of this analysis (Table 1). Eight holotype specimens were available for direct study: *Baptornis advenus* (YPM 1465); *Brodavis baileyi* (UNSM 50665); *Brodavis varneri* (SDSM 68430); *Hesperornis regalis* (YPM 1200); *H. bairdi* (YPM 17208A); *H. chowi* (YPM 17208); *H. gracilis* (YPM 1473); *H. macdonaldi* (LACM 9728); *Parahesperornis alexi* (KUVP 2287); *Pasquiaornis hardiei* (RSM 2077.117, cast as YPM 57191); and *Pasquiaornis tankei* (RSM 2077.63, cast as YPM 57194), as well as the lectotype of *Enaliornis barretti* (NHMUK A477) and *E. seeleyi* (BGS 87935, cast as NHMUK A5304). The holotype of *Hesperornis mengeli* (CFDC B780108, mistakenly reported as BO 780106 by Martin & Lim 2002) and the lectotype of *Enaliornis sedgwicki* (SMC B55314) were coded for the matrix using publications (Galton & Martin 2002; Martin & Lim 2002) and photographs.

In addition to the holotypes, all available specimens with a species-level assignment to one of the hesperornithiform taxa, and that could be evaluated, were included. Despite the large number of specimens in museum collections, relatively few have actually been described and assigned to a species. Table 1 details these specimens, which were coded as separate OTUs in the matrix. In the case of *Baptornis advenus*, these specimens were particularly important, as the holotype is today represented by an isolated distal tarsometatarsus. Marsh (1877) initially described the holotype of *Baptornis advenus* as a complete tarsometatarsus; however, at some point the proximal half of the element was lost. Three hesperornithiform taxa, *Asiahesperornis*, *Enaliornis* and *Pasquiaornis*, are known entirely from isolated elements grouped into taxa on the basis of size (Galton & Martin 2002; Dyke *et al.* 2006; Sanchez 2010). *Asiahesperornis bazhanovi* is known from a small number of unassociated and highly fragmentary specimens that were not directly available for this study, and so was treated as a single OTU in this analysis and coded from the published material (Dyke *et al.* 2006) and photographs provided by that study's author (G. Dyke pers. comm.). The inclusion of the unassociated remains into a single taxon is justified by the proximity of the elements, which were all found at the same level within a single quarry, and the lack of any other similarly sized but morphologically different hesperornithiform remains (Dyke *et al.* 2006). Likewise, both *Enaliornis* and *Pasquiaornis* are multi-specific taxa known entirely from isolated, fragmentary specimens. While *Enaliornis* has been reported to consist of three separate species (*E. barretti*, *E. sedgwicki* and *E. seeleyi*; Galton & Martin 2002), these distinctions are based entirely on size without any differences in morphological

characters that might be used for cladistic analysis. Material belonging to *Pasquiaornis*, known by two separate species, was mostly unavailable for study and is currently highly under-reported in the literature. Furthermore, the bone bed assemblage from which *Pasquiaornis* was identified was reported to contain numerous other avian remains that have been identified as *Hesperornis*, enantiornithine and unidentified Aves (Sanchez 2010). Therefore, for the purposes of this analysis each of these taxa (*Enaliornis barretti*, *E. seeleyi*, *E. sedgwicki*, *Pasquiaornis hardiei* and *P. tankei*) is considered at the generic level as two OTUs (*Enaliornis* and *Pasquiaornis*) and coded from the collected elements assigned to each species. It should be noted that because none of the elements of these taxa are associated, there is some ambiguity in the assignment of all non-holotype elements to the same taxon.

The Late Jurassic *Archaeopteryx lithographica* (see Wellnhofer 2009), the Early Cretaceous *Gansus yumenensis* (see You *et al.* 2005), and the Late Cretaceous *Ichthyornis dispar* (Marsh 1872; Clarke 2004) and *Apsaravis ukhanna* (Norell & Clarke 2001; Clarke 2004) were used as outgroup taxa in the analysis. Unlike the majority of hesperornithiform OTUs, which were coded from individual specimens, most of these were coded from multiple specimens assigned to the respective taxa (see Supplemental Appendix 3). The crown clade Aves is represented by three modern birds, *Anas clypeata*, *Gallus gallus* and *Struthio camelus*. A total of 40 OTUs were coded for the character matrix, from which 24 OTUs were selected for the present analysis (Table 1, see below for discussion).

Analytical methods

The cladistic analysis was run in the parsimony program Tree Analysis using New Technology (TNT 1.1; Goloboff *et al.* 2008) using the Implicit Enumeration algorithm (an exact, or ‘branch and bound’ solution) rooted at *Archaeopteryx*. The program default of collapsing all branches with a minimum length of 0 was maintained. When multiple most-parsimonious trees were returned, strict consensus and Adams consensus trees were calculated. Bootstrap supports, branch lengths, and consistency and retention indices were calculated for all most-parsimonious trees. In order to assess the effect of uninformative characters on tree statistics, for each analysis uninformative characters were identified and removed from consideration and the analysis rerun, with the consensus, retention and re-scaled retention index recalculated.

Phylogenetic results

Coding of OTUs

After the 40 OTUs discussed previously were coded, the character matrix was evaluated to identify any

redundancies or discrepancies within specimens assigned to a single taxon or genus. OTUs that were found to be in agreement with other OTUs assigned to the same species or genus were then combined into a single OTU for the phylogenetic analysis in order to remove redundancy from the final character matrix. The following OTUs were found to be synonymous and combined: *Pasquiaornis hardiei* and *P. tankei* into *Pasquiaornis*; *Enaliornis barretti*, *E. seeleyi* and *E. sedgwicki* into *Enaliornis*; *Baptornis advenus* specimens YPM 1465, KUV 2290, KUV 16112 and *Baptornis* specimen SMNH 6318 into *Baptornis advenus*; *Hesperornis gracilis* specimens YPM 1473, YPM 1478 and YPM 1679 into *H. gracilis*; *Hesperornis regalis* specimens YPM 1200, YPM 1207, FMNH 218, KUV 71012, as well as *Asiahesperornis bazhanovi*, *H. chowi* YPM 17208, *H. crassipes* YPM 1474, *H. mengeli* CFDC 78.01.06, *H. macdonaldi* LACM 9728 and *H. rossicus* ZIN 5463 into *Hesperornis regalis*; and *Paraesperornis* specimens KUV 2287, KUV 24090 and SMNH 17312 into *Paraesperornis alexi*. This reduced the coded matrix to 24 OTUs used in the phylogenetic analysis. It should be noted that during the course of this reduction of non-conflicting OTUs, specimens assigned to both *Baptornis advenus* (AMNH 5101, FMNH 395, UNSM 20030) and *Hesperornis regalis* (YPM 1476, YPM 1477, UNSM 13580) were identified as conflicting with the holotype specimens for their respective species. In these cases, the specimens were retained as separate OTUs for the phylogenetic analysis.

Phylogenetic analysis

Analysis of the coded matrix resulted in 69 most parsimonious trees of 372 steps. The strict and Adams consensus trees were identical (Fig. 3). The strict consensus tree has a well-resolved topology, with a polytomy amongst the *Hesperornis* OTUs and another amongst two of the conflicting specimens of *Baptornis* (AMNH 5101 and FMNH 395) and *Baptornis advenus*. In both trees the Hesperornithiformes are identified as monophyletic. Following *Archaeopteryx*, *Apsaravis* is recovered as the most basal bird included in the analysis, followed by *Gansus* and *Ichthyornis*, respectively. The Hesperornithiformes are united with modern birds in a clade. Within the hesperornithiform clade, *Pasquiaornis* is the most basal taxon, followed by *Enaliornis* and the *Baptornis* clade. The two species of brodiaeids (*B. baileyi* and *B. varneri*) are returned as monophyletic and placed as the sister-taxa to UNSM 20030, a specimen identified as *Baptornis advenus* (see Martin & Tate 1976) but which conflicted with other specimens in many characters, followed by *Paraesperornis*, which is the sister taxon to the *Hesperornis* polytomy.

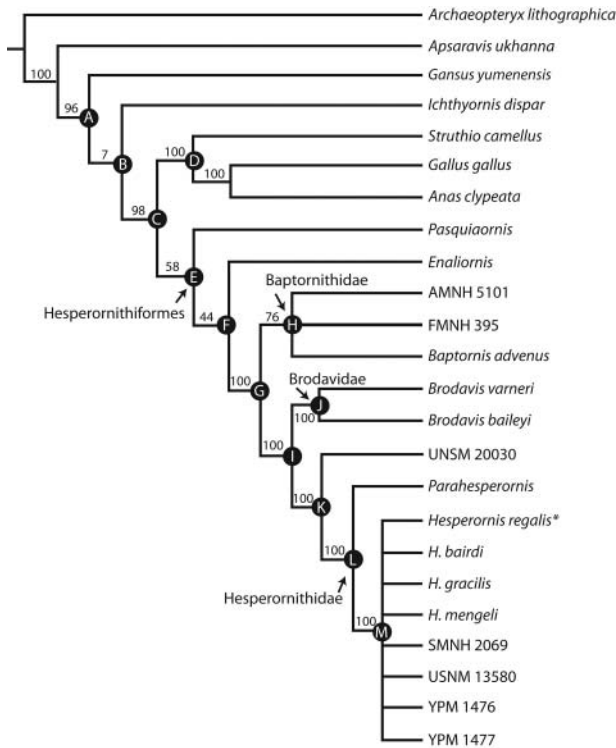


Figure 3. Strict consensus of the 69 most parsimonious trees returned from analysis of the data matrix. Labels at the nodes correspond to the following groups of unambiguous synapomorphies (character followed by character state): A: 31(1), 46(1), 48(1), 50(0), 71(1), 72(1), 82(1), 84(1), 166(1), 167(1), 192(1), 199(1), 200(1), 204(1); B: 30(1), 67(0), 103(1); C: 37(1), 57(0), 58(0), 113(2), 124(1), 127(1), 137(1), 138(1), 139(1), 143(1), 186(1); D: 2(1), 3(1), 4(1), 7(1), 8(1), 9(1), 15(1), 18(1), 31(2), 32(2), 37(2), 45(2), 70(1), 104(1), 110(1), 136(1), 182(1), 204(2); E: 29(1), 157(1), 188(1), 203(1); F: 117(1), 118(0), 119(1), 178(1); G: 158(1), 168(1), 199(2); H: 121(1), 198(0); I: 178(2), J: 188(2), 191(2); K: 189(1), 192(2), 195(2), 197(1), 201(2); L: 103(2), 115(2), 117(2), 120(1), 126(1), 127(2), 130(2), 131(1), 133(2), 134(2), 138(2), 141(1), 145(1), 148(1), 149(1), 152(1), 154(1), 155(0), 159(1), 162(1), 163(1), 172(2), 173(1), 182(1), 199(3), 200(2), 206(1), 207(1); M: 118(3), 121(1), 137(0), 156(1), 171(2), 175(1), 183(2), 202(3). Bootstrap values are labelled on the tree. Consistency index = 0.694, retention index = 0.836.

Derived placement of the Hesperornithiformes

The derived placement of the Hesperornithiformes as sister taxon to modern birds, as found in this analysis, is a source of disagreement amongst phylogenetic studies of modern birds. While some studies are in agreement with these results and find a derived Hesperornithiformes (e.g. O'Connor *et al.* 2013; O'Connor & Zhou 2013), others find *Ichthyornis* to be the sister taxon to modern birds (e.g. Chiappe 2002; Clarke 2004; Wang *et al.* 2014). While in general it is difficult to compare different phylogenetic studies, an attempt to do so in this case is warranted. While some studies do not provide the necessary character information in the form of the complete matrix to analyse specific nodes within a cladogram (e.g.

O'Connor *et al.* 2013; O'Connor & Zhou 2013; Wang *et al.* 2014), those that do can help to illuminate the disagreement. In the early study of Chiappe (2002), *Ichthyornis* was united with the crown clade Aves on the basis of two synapomorphies of the alular metacarpal and ungual phalanx of digit I, both of which were used and coded similarly in the present analysis. *Ichthyornis* was resolved as more closely related to modern birds than *Hesperornis* on the basis of five synapomorphies by Clarke (2004) (the presence of pneumatic foramina on the dorsal surface of the sternum; ossified connective tissue present on the dorsal processes of the thoracic vertebrae; the number of sacral vertebrae anterior to the acetabulum; lateral process of the coracoid present; and a depressed medial surface of the coracoid in the region of the *foramen n. supracoracoideus*), all of which were used and coded similarly. In the present analysis, the clade containing modern birds and hesperornithiforms is united by 11 unambiguous synapomorphies (Fig. 3, node C). As the only other differences between this and the study of Chiappe (2002) are the OTUs included in the analyses, it appears that the fine-scale resolution of *Ichthyornis*, hesperornithiforms and modern birds is highly contingent on the specific choice of OTUs in the analysis.

Monophyly of the Baptornithidae

Under the current taxonomic framework, *Pasquiaornis* is united with *Baptornis advenus* in the Baptornithidae (Tokaryk *et al.* 1997; see also Martin & Lim 2002; Cumber *et al.* 2006). The results of the present analysis call this placement into question. *Pasquiaornis* was originally placed in the Baptornithidae on the basis of not sharing three similarities with *Paraheperornis* and *Hesperornis*: a robust femur, prominent intramuscular lines on the femur, and an enlarged trochlea IV on the distal tarso-metatarsus (Tokaryk *et al.* 1997). However, the lack of all three of those features represents the plesiomorphic condition, as *Hesperornis* and *Paraheperornis* are both highly derived, and does not provide support for the placement of *Pasquiaornis* within the Baptornithidae. In the present analysis, *Pasquiaornis* resolves as the basal-most hesperornithiform, separated from *Enaliornis* + other hesperornithiforms by four unambiguous synapomorphies (Fig. 3, node E). Therefore, the present analysis supports removal of *Pasquiaornis* from the Baptornithidae.

Placement of conflicting *Baptornis* specimens

Three specimens previously assigned to *Baptornis* (AMNH 5101, FMNH 395, UNSM 20030) displayed conflicting codings with the holotype of *Baptornis advenus*, YPM 1465, and other *Baptornis* specimens. Of these, AMNH 5101 and FMNH 395 both conflicted in a single character. In AMNH 5101, the intertrochlear space

between trochlea of metatarsals III and IV was coded as widely spaced instead of reduced and narrow, as in YPM 1465 (character 178). In FMNH 395, the distal tibiotarsal shaft was coded as symmetrical, with medial and lateral condyles evenly expanded on either side of the shaft, while in other *Baptornis* specimens the medial condyle is more expanded than the lateral (character 165). These specimens formed a polytomy with *Baptornis advenus*, coded from the holotype and the non-conflicting *Baptornis* specimens. Because of the unification of AMNH 5101 and FMNH 395 with *Baptornis* in the consensus tree as well as the small amount of variation in codings, maintaining the assignment of these specimens to *Baptornis* is reasonable at this time.

The third conflicting specimen, UNSM 20030, conflicted with all other *Baptornis* specimens in the coding of 23 characters. UNSM 20030, a partial post-cranial skeleton from the Niobrara Chalk of Kansas, USA, was originally assigned to *Baptornis advenus* by Martin & Tate (1976), however no justification for such assignment was provided. The phylogenetic analysis presented here placed UNSM 20030 as more derived than *Baptornis advenus* or the brodavids and united it in a clade with *Paraesperornis* + *Hesperornis* on the basis of five unambiguous synapomorphies (Fig. 3, node K). This supports the removal of UNSM 20030 from *Baptornis advenus* and suggests it has unique taxonomic standing. A full description of this specimen is currently in progress (Bell & Chiappe in prep). This result has significant ramifications for the use of *Baptornis* as an OTU in earlier cladistic analyses, in which, following Martin & Tate (1976), '*Baptornis*' was scored using multiple specimens, usually AMNH 5101, UNSM 20030 and FMNH 395 in addition to the holotype (e.g. Chiappe 2002; Clarke 2004; O'Connor *et al.* 2011). While it is unclear to what extent the codings developed in these previous analyses were based specifically on UNSM 20030, it is likely that the removal of UNSM 20030 from *Baptornis advenus* would have resulted in changes to the scoring of *Baptornis* in these studies.

Monophyly of the Brodavidae

The current taxonomic framework of the Hesperornithiformes recognizes four species of *BroDavis*, three of which are represented by isolated, partial tarsometatarsi (*B. americanus*, *B. baileyi* and *B. mongoliensis*), and the fourth of which is represented by a poorly preserved partial skeleton, including the tarsometatarsus, originally described as a second species of *Baptornis* (*Baptornis varneri*, originally described by Martin & Cordes-Person 2007, reassigned to *BroDavis* by Martin *et al.* 2012). *BroDavis varneri* and *B. baileyi* were recovered as a clade supported by two unambiguous synapomorphies, characters 188 (dramatically curved shaft of metatarsal II) and 191 (highly constricted midshaft of the tarsometatarsus).

These morphologies were not mentioned in the descriptive work of the group (Martin *et al.* 2012), however character 191 was identified as diagnostic of the species *B. varneri* in the original descriptive work of the species (Martin & Cordes-Person 2007). The results of the phylogenetic analysis support a clade composed of *B. varneri* and *B. baileyi*; however, what effect the inclusion of other broavid taxa would have remains uncertain, as *B. americanus* and *B. mongoliensis* could not be included in the analysis. Unfortunately the fragmentary nature and poor preservation of the specimens makes more definitive work on this group difficult. In the present analysis *B. varneri* could only be coded for 18% of the characters and *B. baileyi* for 8%. As an additional note, there is a very large difference in the sizes of the two holotypes, with the smaller (*B. baileyi*) appearing to be fully mature. Future work on this group is certainly warranted.

Monophyly of the Hesperornithidae

While a number of genera have been proposed within the Hesperornithidae over the course of hesperornithiform research, four genera are generally accepted as valid (see Supplemental Table 1). Three of these, *Hesperornis*, *Paraesperornis* and *Asiahesperornis*, were included in this study. As *Asiahesperornis* shared all character codings with the holotype of *H. regalis*, YPM 1200, it was not included in the phylogenetic analysis. This analysis found *Hesperornis* + *Paraesperornis* to form a clade supported by 28 unambiguous synapomorphies (Fig. 3, node L), making this one of the best-supported hesperornithiform clades.

Monophyly of *Hesperornis*

All OTUs assigned to *Hesperornis* were resolved into a clade united by eight unambiguous synapomorphies (Fig. 3, node M). The lack of resolution in this clade, even amongst different specimens assigned to *Hesperornis regalis*, implies that perhaps not all species are valid. In particular, the lack of conflict in character codings between *H. regalis* and *Asiahesperornis bazhanovi*, *H. chowi*, *H. crassipes*, *H. macdonaldi* and *H. rossicus*, despite the use of reported diagnostic features in the matrix, indicates that these taxa need additional work. Many of these species were erected in part due to large size or proportional differences with *H. regalis* (see Nesov & Yarkov 1993; Martin & Lim 2002; Dyke *et al.* 2006). In the case of *H. macdonaldi* and *H. mengeli*, the small size of the individuals may be due to the immature ages of the specimens, which is difficult to determine due to the poor preservation of the elements and in the absence of histological data. As the purpose of this study is the determination of evolutionary relationships within the

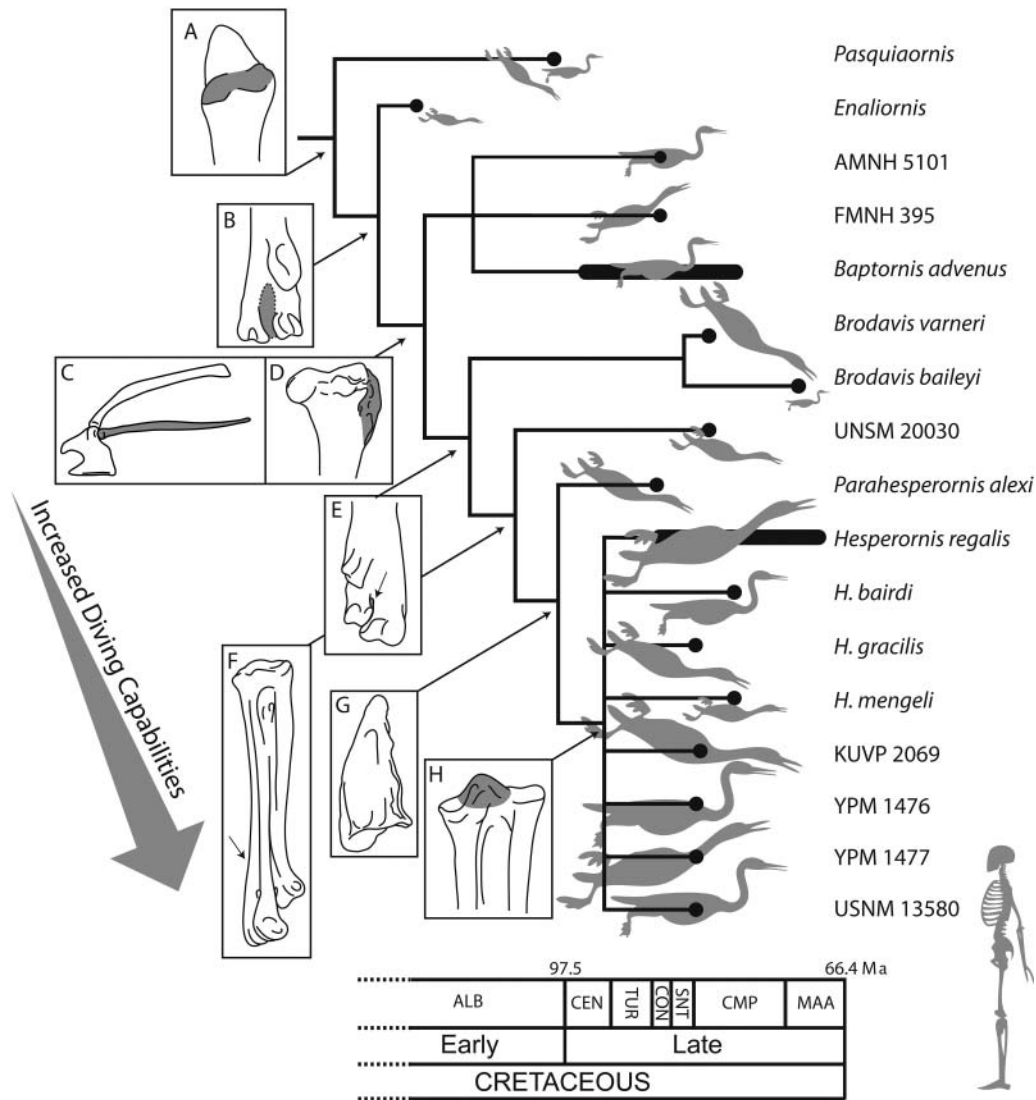


Figure 4. Evolution of diving specializations within the Hesperornithiformes. The hesperornithiform clade returned in the phylogenetic analysis (Fig. 3) is shown with the terminal OTUs calibrated to time using the stratigraphical range of fossil specimens and approximate body size silhouettes shown for size comparison with a human skeleton (body sizes are approximate and were determined by geometric scaling of the tarsometatarsus or femur, in comparison with YPM 1200, *Hesperornis regalis*). Skeletal adaptations interpreted as potentially enhancing diving capabilities are as follows (relevant region of the figure is shaded). A: inclined articular surface of the tibiotarsus (character 157); B: reduction of space between the trochlea of metatarsals III and IV in the distal tarsometatarsus (character 178); C: reduction of the humerus (character 63); D: expansion of the femoral trochanter (character 127); E: extreme reduction of space between the trochlea of metatarsals III and IV in the distal tarsometatarsus (character 178); F: shingled or stacked arrangement of the metatarsals in the tarsometatarsus (character 192); G: enlarged patella (character 148); H: exaggerated intercotylar eminence on the tarsometatarsus (character 183). Stratigraphical abbreviations: ALB, Albian; CEN, Cenomanian; TUR, Turonian; CON, Coniacian; SNT, Santonian; CMP, Campanian; MAA, Maastrichtian.

Hesperornithiformes, a taxonomic review of *Hesperornis* is beyond the scope of this study, but is clearly warranted.

Discussion

While the Hesperornithiformes are known predominantly from the Late Cretaceous, time calibration based upon stratigraphical ranges of the terminal nodes of the strict

consensus cladogram derived from the present analysis indicates that all lineages of hesperornithiforms had likely diversified by the Early Cretaceous. This timeline reveals a number of ghost lineages, the longest of which is that of the Brodavidae (Fig. 4). Additionally, the calibrated cladogram highlights that the acquisition of highly specialized diving adaptations evolved in a step-wise fashion over millions of years. This contrasts with the fossil record of some other Cretaceous clades (e.g. Enantiornithes), in

which the main trademarks of the group appear more abruptly in the fossil record (Chiappe & Dyke 2002).

The presence of birds highly adapted to an aquatic life-style amongst some of the oldest known fossil birds points to interesting questions regarding the evolution of derived locomotion in primitive birds. The cladistic analysis presented here highlights the development of individual skeletal morphologies hypothesized to enhance diving capabilities (Fig. 4). For example, one feature that becomes progressively more derived within the Hesperornithiformes is the spacing of the trochlea of the tarsometatarsus, which become close together in *Enaliornis* and are virtually touching each other in *Paraesperornis* and *Hesperornis* (Fig. 4B, E). In modern grebes, closely spaced trochlea (to a degree similar to that seen in *Enaliornis*) allow for the tight, overlapped folding of the toes during the recovery stroke while swimming, thus reducing drag and lowering the energy requirements for the bird to return its foot to the

propulsive position (Johansson & Lindhe Norberg 2001). The orientation of the hind limb is particularly important for maximizing diving efficiency by streamlining the body and reducing drag (Wilcox 1952; Johansson & Lindhe Norberg 2001). Within the Hesperornithiformes, even the most primitive taxa possess an inclined articular surface on the tibiotarsus, a feature that assists in the rearward orientation of the hind limb (Fig. 4A; Wilcox 1952). More derived hesperornithiforms also possess a greatly enhanced, bulbous femoral trochanter, which served as the attachment point for muscles such as the *mm. ilirotrochanterici*, crucial to holding the femur in a splayed position and allowing the femur to rotate inwards or outwards (Fig. 4D; Zinoviev 2011). The most derived hesperornithiforms, *Paraesperornis* and *Hesperornis*, also display a mediolaterally compressed tarsometatarsus with the individual metatarsals offset cranio-laterally (sometimes referred to as shingled metatarsals; see Martin & Tate 1976), another adaptation

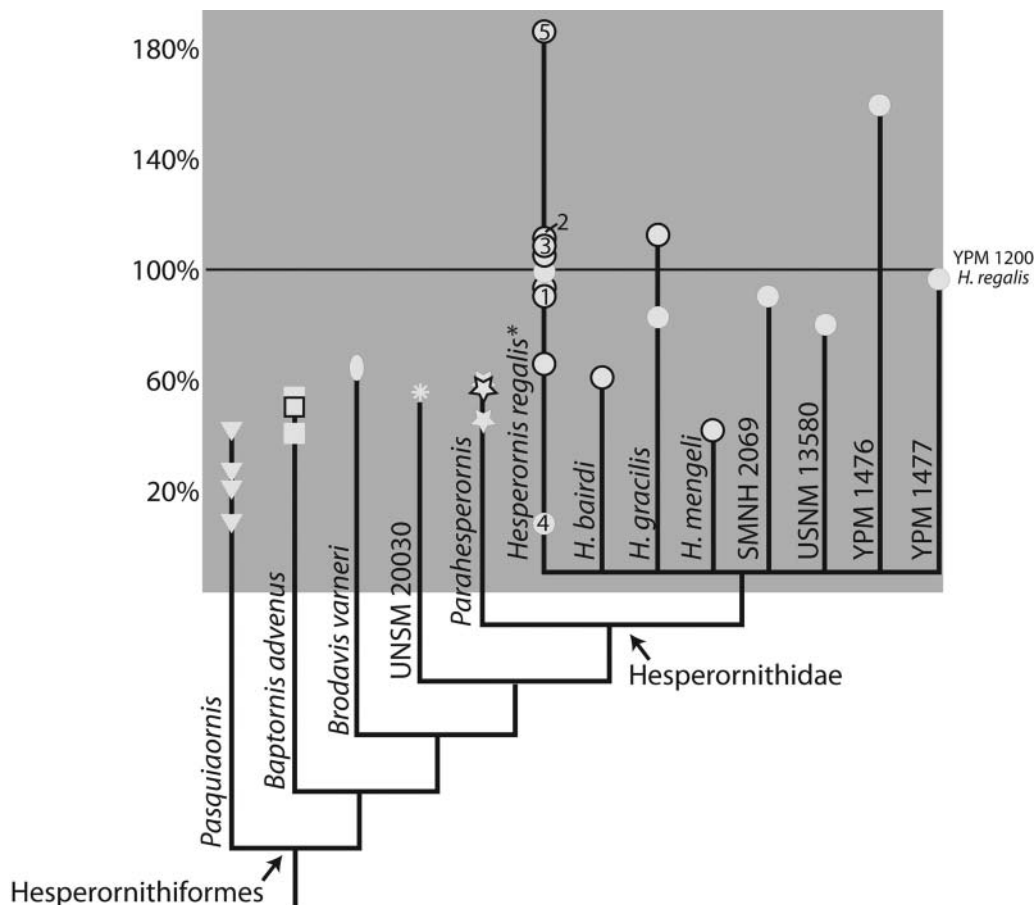


Figure 5. Estimates of body masses mapped onto the phylogeny. The mass of each specimen included in the phylogenetic analysis for which a femur or tarsometatarsus was preserved was estimated using the three equations shown in Table 1, of which an average mass is plotted here as a percentage of the estimated mass of YPM 1200, the holotype of *Hesperornis regalis*. Symbols correspond to genus. Specimens for which a femur was not available are outlined in black. For these specimens, the length of the tarsometatarsus was used to estimate a femur length from comparison with similarly-sized specimens preserving both a femur and tarsometatarsus. **Hesperornis regalis* includes all specimens and taxa found to be indistinguishable in the character database from specimens assigned to *Hesperornis regalis*: 1, *Asiahesperornis bazhanovi*; 2, *H. chowi*; 3, *H. crassipes*; 4, *H. macdonaldi*; 5, *H. rossicus*.

for reducing drag during the recovery stroke (Johansson & Lindhe Norberg 2001), and a robust, elongate patella that served as the attachment for muscles responsible for protraction of the femur during the recovery stroke (*m. iliotibialis cranialis*) and extension of the foot during the propulsive stroke (*m. gastrocnemius medialis*) (Zinoviev 2011). One of the more prominent features of derived hesperornithiforms such as *Baptornis* and *Hesperornis* is the extreme reduction of the forelimb (Marsh 1880), particularly as compared to the more primitive *Pasquiaornis* (Fig. 4C). The forelimb is so reduced that most hesperornithiforms were almost certainly flightless, with the possible exception of *Pasquiaornis* (unfortunately the forelimbs of *Brodavis* and *Enaliornis* are unknown).

Independent of the evolution of diving specializations of the skeleton is the evolution of increased body size in several hesperornithiform clades. The present study indicates that hesperornithids, *Brodavis* and *Pasquiaornis* all underwent independent events of substantial size increase. This is the most striking in *Brodavis*, where *B. varneri* is about twice as large as *B. baileyi*, yet displays similar diving adaptations in the morphology of the tarsometatarsus. Even within *Hesperornis* several species have been reported as approximately half (*H. macdonaldi* and *H. mengeli*) or two-thirds (*H. bairdi*) the size of *Hesperornis regalis*, yet none preserve any differences in skeletal diving specializations (Fig. 5). Despite the fact that these taxa are poorly represented and it is not possible to rule out ontogeny playing a role in the small size of the individual specimens, these findings suggest that these independent events of body size increase were decoupled from the development of diving specializations in skeletal anatomy. Numerous studies of modern diving birds and mammals have shown that an increase in body size is coupled with larger lung capacity and the capability of greater oxygen enrichment of the bloodstream, thus maximizing diving potential (Zavalga & Jahncke 1997; Noren & Williams 2000; Zavalga *et al.* 2007). In this sense, acquisition of a large body size can itself be seen as a diving specialization. This indicates that within some hesperornithiforms, such as the brodavidids and hesperornithids, different species may have varied greatly in diving capabilities despite similar skeletal morphologies usually interpreted as adaptations for enhancing diving capabilities, thus decoupling the evolution of body size with that of diving-related skeletal specializations in the Hesperornithiformes.

Conclusions

The cladistic analysis conducted here supports a monophyletic Hesperornithiformes. Within the Hesperornithiformes, the Baptornithidae is not supported as monophyletic, with *Pasquiaornis* being more closely related to *Enaliornis*.

UNSM 20030 differs from other specimens assigned to *Baptornis advenus* in numerous morphological features and should be removed from the Baptornithidae. Within the remaining specimens of *Baptornis advenus*, some slight variations in morphology do exist; however, at this time taxonomic distinction for these specimens does not seem warranted. While the monophyly of the Hesperornithidae has strong support, the recognition of multiple species within *Hesperornis* is not supported by the present analysis, particularly in regards to *Asiahesperornis bazhanovi*, *H. chowi*, *H. crassipes*, *H. macdonaldi* and *H. rossicus*, none of which differ morphologically from *H. regalis*, as identified through the character matrix of this study. Other taxa, such as *H. bairdi* and *H. mengeli*, differ in a single character coding, indicating further work is warranted on these taxa as well. Given the paucity of material in most of these species, the role of untested size-related diagnostic features, and the inability to confirm the ontogeny of many specimens, the recognition of these species should be considered tentative at best.

Clade divergence within the Hesperornithiformes predated their most abundant occurrences during the Late Cretaceous by many millions of years. The identification of multiple independent events in which body size increased substantially within a lineage suggests that such evolutionary events were decoupled from the step-wise origination of diving-correlated traits throughout the evolutionary history of the Hesperornithiformes. The results of this study document the evolution and divergence of a clade of ancient diving birds, from basal, possibly flighted birds with limited diving capabilities to derived, flightless birds with highly advanced diving specializations similar to those seen in modern avian divers. The evolution of hesperornithiforms is made more complex by the numerous, independent increases in body size that occurred in at least three different hesperornithiform lineages and likely contributed to the birds' capabilities as divers.

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Supplemental data

Supplemental material for this article can be accessed here: <http://dx.doi.org/10.1080/14772019.2015.1036141>

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