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Evolution in the Mesozoic Diving Birds

(中生代における潜水鳥類の進化)

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Evolution in the Mesozoic Diving Birds

By

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Evolution in the Mesozoic Diving Birds

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ABSTRACT

Secondary aquatic adaptation from land to water is a key evolutionary event in the history of life, and the fossil record provides crucial insights into macroevolution on a geological time scale. Secondary aquatic adaptation has occurred multiple times in the evolutionary history of tetrapods. The morphological transformations that have occurred during terrestrial–marine transitions are well-studied, predominantly in fossils of marine mammals. However, little is known about these transformations in other tetrapod lineages.

The fossil records of Mesozoic birds are ideal resources for revealing the macroevolutionary morphological transition associated with secondary aquatic adaptation in tetrapods because they preserve the gradual evolutionary process toward a remarkable specialization for foot-propelled diving. Ornithuromorpha includes the avian group which first became highly adapted to an aquatic lifestyle during the early Cretaceous. This study aims to reveal the patterns and processes of secondary aquatic adaptation in early avian evolutionary history using phylogenetic, morphological, and biostatistical approaches.

In Chapter 1, a new morphological dataset, including comprehensive characters related to aquatic adaptation (43 taxa and 349 characters

including 39 novel characters), was constructed to reassess the phylogenetic relationships of Mesozoic ornithuromorphs. A new bird specimen (MM V-2487, described in Chapter 4) was also described in detail. Phylogenetic analysis using this new dataset revealed that terrestrial ornithuromorphs were positioned basally and freshwater taxa (e.g., hongshanornithids and songlingornithids) were a more derived group. Hesperornithiformes, the preeminent seabird taxon during the Cretaceous, was positioned as a sister group to the clade of *Ichthyornis* and Neornithes (modern birds). MM V-2487 was deeply nested within Hesperornithidae.

Chapter 2 describes two undescribed hesperornithiform remains from Mongolia and Japan and reviews hesperornithiform fossil records and paleoecology. The morphological features of the newly described Hesperornithiformes revealed that the habitat of this group during the Maastrichtian included both terrestrial and marine environments in Asia and North America.

Chapter 3 discusses the evolution of functional aquatic locomotion in Mesozoic ornithuromorphs based on their morphologies. This chapter also explores the potentially functional trade-off between their fore and hind limbs using phylogenetic logistic regression analysis. This analysis indicated that morphological transformations of fore- and hind limbs through flightlessness and diving adaptation are correlated. The present results implied that the stabilizing function during underwater locomotion shifted from humeri to IVth toes.

Chapter 4 describes a new small hesperornithiform from Canada and provides a new method of body mass estimation for foot-propelled diving birds. This chapter also explores macroevolutionary body mass changes of Hesperornithiformes using a phylogenetic framework. Ancestral state reconstruction demonstrates gradual body mass increase in non-hesperornithid Hesperornithiformes and rapid body mass increase in Hesperornithidae in the late Santonian to earliest Campanian. The timing is not associated with the beginning of the late Cretaceous global cooling.

Instead, the Cretaceous marine high productivities may have been one of the major driving forces of body mass diversity in Hesperornithiformes.

In Chapter 5, morphological rate and disparity analyses were conducted to reveal the tempo and mode of evolution of Mesozoic aquatic birds. These analyses showed no significant accelerated morphological change in any freshwater bird clades, whereas high morphological rates were identified at the origin of Hesperornithiformes and in their derived groups. No distinct morphological differences between the terrestrial and freshwater forms were identified, whereas marine Hesperornithiformes were significantly morphologically different from the terrestrial and freshwater forms. These results suggest that the earliest seabirds experienced rapid morphological evolution when they first invaded the marine realm in the early Cretaceous.

EVOLUTION IN THE MESOZOIC DIVING BIRDS

Tomonori Tanaka

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GENERAL INTRODUCTION

Invasion of, and adaptation to, a novel environment is the most innovative event in the macroevolution of life. In their 500 million year history, tetrapods have adapted to specific environments and radiated onto land, into the air, and into the water (Carroll 1997; Dial *et al.* 2015). Such changes in lifestyle involve great transformations in body structure and physiology to adapt to the novel environments. Paleontological studies can provide insight into the major transformations of life on a geological time scale, and fossil records play a central role in understanding macroevolution. Therefore, many studies have attempted to clarify the sequence of morphological and physiological changes that have enabled tetrapods to overcome the challenges associated with their transitions to novel habitats (e.g., Ashley-Ross *et al.* 2013; Houssaye & Fish 2016).

Birds are the most successful group of terrestrial tetrapods (Chiappe & Dyke 2002). They represent a continuum of millions of years of theropod evolution and are the only dinosaurs that survived until today (Gauthier 1986; Brusatte *et al.* 2014; Field *et al.* 2018). Two drastic transitions of

lifestyle have occurred in the evolutionary history of theropods since the late Triassic. One is the transition from land into the air, with the evolution of miniaturization, specialized forelimbs, and feathers. The other is the secondary radiation into the water, with associated changes in physiology and specialized fore and hind limbs. Although the former evolutionary event has been well studied (e.g., Ostrom 1974), little is known about the latter (e.g., Fish 2016). Ornithuromorpha is the largest clade in Avialae and includes all extant birds and all aquatic birds. Although the most diversified Mesozoic terrestrial tetrapod non-avian dinosaurs have never adapted to inhabit the ocean, several avian lineages have become highly adapted to marine ecosystems since the early Cretaceous. Therefore, an understanding of ornithuromorph evolution may shed new light on the mechanism of the first secondary aquatic adaptation in dinosaurs, the preeminent terrestrial vertebrates.

Unlike mammals, which have an expanding fossil record for intermediate aquatic forms, fossils of birds are relatively rare (Fish 2016) and the mechanisms of diving adaptation in birds are poorly understood. However, the growth of avian paleontology within the past 30 years is striking.

Numerous excellent fossils, including several aquatic birds (e.g., Hongshanornithidae, gansuids), have been reported from Lagerstätten, particularly in northeast China (Mayr 2016; Chiappe & Qingjin 2017). Hesperornithiformes, the oldest group of marine diving birds (Marsh 1880), have been reported from North America, the Arctic region, Europe, and Asia (Galton & Martin 2002; Bell & Chiappe 2016). *Hesperornis* is a flightless foot-propelled diving bird with rudimentary forelimbs, extremely developed hind limbs, and large body size comparable to that of humans. Although these iconic Mesozoic marine birds have been studied for over 140 years, their phylogenetic and biological aspects have received little attention (Wilson *et al.* 2011; Bell & Chiappe 2015a; Wilson & Chin 2016; Tanaka *et al.* 2017; Bell *et al.* 2019; Wilson 2019). The rich fossil record of Mesozoic birds can provide critical insights into how they invaded freshwater and finally the marine realm. This dissertation aims to understand the patterns and processes of the first secondary aquatic adaptation in Mesozoic avian evolution using phylogenetic, morphological, and biostatistical approaches.

Chapter 1 establishes a novel morphological dataset for ornithuromorphs and proposes a phylogenetic hypothesis of their

relationships. Morphological character descriptions of Mesozoic Ornithuromorpha are also provided. This morphological dataset is fundamental information for the following chapters.

In Chapter 2, three previously undescribed Mesozoic bird specimens from Mongolia and Japan are described. The fossil records of the preeminent seabird Hesperornithiformes are reviewed to identify the distribution and taxonomic diversification of Mesozoic seabirds. In addition, their paleoecological shifts during the Cretaceous are discussed.

Chapter 3 discusses the functional aquatic locomotion of Mesozoic ornithuromorphs based on morphological characters related to aquatic locomotion. This chapter also explores potentially functional trade-offs of their fore and hind limbs through flightlessness and diving adaptation using phylogenetic logistic regression analysis.

Chapter 4 describes the remains of a new small hesperornithiform from Manitoba, Canada. In addition, a new method for body mass estimation of foot-propelled diving birds is established based on linear measurements of extant birds. This chapter also investigates the evolutionary history of hesperornithiform body mass using a phylogenetic framework and speculates

on the driving force of their body mass evolution.

Chapter 5 aims to understand the association of a major ecological transition with morphological evolutionary rates and disparity in Ornithuromorpha. Morphological Rate and disparity analyses are conducted to reveal tempo and mode in the morphological evolution of Mesozoic birds, focusing on the terrestrial–marine transition via the freshwater environment.

CHAPTER 1

Phylogenetic Reassessment of Mesozoic Ornithuromorpha

Abstract

Ornithuromorpha is the largest avian clade and includes all modern birds (Neornithes). Ornithuromorpha also includes all aquatic birds, thus understanding their phylogenetic interrelationships and evolutionary history is essential for revealing the evolutionary processes and patterns of avian secondary aquatic adaptation. To date, there is no consensus on the phylogenetic interrelationships of ornithuromorphs. Terrestrial and aquatic birds from the Mesozoic have nested together in phylogenetic analyses; therefore, little is known about the paleoecological evolutionary process of the origin of aquatic birds. In this chapter, a new morphological dataset, including comprehensive characters related to aquatic adaptation (43 taxa and 349 characters), was constructed to reassess the phylogenetic relationships of Mesozoic ornithuromorphs. A phylogenetic analysis using the new dataset revealed that terrestrial ornithuromorphs (e.g., *Patagopteryx*) are positioned basally and freshwater taxa (e.g., hongshanornithids and songlingornithids)

are a more derived group. Hesperornithiformes, the preeminent seabird taxon during the Cretaceous, is positioned as a sister group to the clade of *Ichthyornis* and Neornithes. The results of the present phylogenetic analysis provide a basis for revealing the evolutionary processes and patterns of Mesozoic aquatic birds.

Introduction

Ornithuromorpha, the most inclusive clade of Avialae

With more than 10,000 species, birds are the most diversified terrestrial tetrapods today and exhibit a striking array of global ecologies (Gill 2006; Morrison *et al.* 2018). Recent discoveries of Cretaceous birds reveal that Enantiornithes and Ornithuromorpha were the two major avian groups in the Mesozoic (O'Connor *et al.* 2011). Ornithuromorpha, the most inclusive Avian clade, includes modern birds (Neornithes) that survived the K/Pg mass extinction at the end of the Mesozoic. While enantiornithines adapted to arboreal environments as reflected by their curved claw and perching feet (e.g., O'Connor *et al.* 2011), ornithuromorphs adapted to terrestrial or aquatic environments as reflected by their long hind limbs and weak claws (e.g., Zhou *et al.* 2005; Zhou *et al.* 2012; Chiappe *et al.* 2014).

Ornithuromorpha have been reported globally, except for Australia, from Cretaceous sedimentary rocks (Fig. 1.1). To date, from 68 species within 51 genera of Mesozoic ornithuromorphs are known (Table 1.1). The oldest ornithuromorph reported to date is *Archaeornithura* from the Lower Cretaceous Huajiyang Formation in northwest China (Hauterivian, 130.7 Ma)

(Wang *et al.* 2015).

Mesozoic Diving Birds

There are two types of highly specialized diving birds: wing-propelled diving birds (e.g., penguins, auks, and the Cenozoic *Plotopterum*) and foot-propelled diving birds (e.g., diving ducks, cormorants, loons, grebes, and the Cretaceous *Hesperornis*) (Gill 2006). All Mesozoic diving birds reported to date are estimated to have been foot-propelled divers, and no wing-propelled divers have been reported from the Cretaceous.

In the last 30 years, numerous bird remains from the Cretaceous have been discovered, mainly in China (Zhou 2014; O'Connor *et al.* 2015), including freshwater-adapted birds (e.g., hongshanornithids, songlingornithids, and ‘gansuid’ birds) (Zhou & Zhang 2005; You *et al.* 2006; O'Connor *et al.* 2010; Wang *et al.* 2014; Liu *et al.* 2014; Wang *et al.* 2015). Several seabirds have been reported: Hesperornithiformes from the early to late Cretaceous in North America, Europe, and Asia (Marsh 1872; Seeley 1876; Marsh 1880; Martin 1986; Galton and Martin 2002; Bell and Chiappe 2015; Tanaka *et al.* 2017); *Maaqwi cascadiensis* (McLachlan *et al.* 2017) from the upper

Campanian in British Columbia; *Neogaeornis wetzeli* (Lambrecht 1929; Olson 1992) from the Campanian to Maastrichtian in Chile; *Polarornis gregorii* (Chatterjee 2002; Agnolin *et al.* 2017) and *Vegavis iaai* (Clarke *et al.* 2005; Agnolin *et al.* 2017) from the Maastrichtian in Antarctica. These birds are considered as foot-propelled diving birds based on their coracoid or hind limb morphologies, and have osteosclerotic bones, which are characteristic of seabirds (Habib & Ruff 2008).

Several studies on Mesozoic birds have attempted to reconstruct the phylogenetic relationships of early birds known to date (Chiappe 1996; Clarke 2002; O'Connor *et al.* 2011; Wang *et al.* 2015); however, no consensus was reached (Fig. 2). Terrestrial and freshwater birds nested together (Fig. 2), thus little is known about their paleoecological evolutionary process or the origin of freshwater birds.

Phylogenetic Interrelationships of Hesperornithiformes

Hesperornithiformes is one of the largest clades of Mesozoic ornithuromorphs and is known as the group of the oldest marine diving bird (Marsh 1880). Although Hesperornithiformes is known as iconic Mesozoic diving birds since

O. C. Marsh's monograph was published in 1880, few studies focused on the phylogenetic relationships of the Hesperornithiformes. Earlier work by Martin (1984) investigated the interrelationships within the Hesperornithiformes and determined the group was monophyletic with three families; Enaliornithidae, Baptornithidae, and Hesperornithidae. Chiappe (2002) and Clarke (2004) conducted phylogenetic analyses of Mesozoic birds including two Hesperornithiformes taxa, *Hesperornis regalis* (Marsh 1872) and *Baptornis advenus* (Marsh 1877). Subsequent work by O'Connor *et al.* (2011) included *Enaliornis* (Seeley 1876), *Brodavis varneri* (*Baptornis varneri* in Martin & Cordes-Parson, 2007; see Martin *et al.* 2012) , and *Paraesperornis alexi* (Martin 1984) in their panoptic phylogenetic analysis of Mesozoic birds (Fig. 1.3A). Using 209 morphological characters, Bell & Chiappe (2015a) attempted the first phylogenetic analysis of the group, focusing on species-level interrelationships within the Hesperornithiformes (Fig. 1.3B). Subsequent study Tanaka *et al.* (2017) reassessed phylogenetic relationships of hesperornithiforms including a new hesperornithiform from Japan.

New Morphological Dataset for Phylogeny of Ornithuromorpha

The aim of this chapter is to build a new morphological dataset for of Mesozoic birds and reassessment of phylogenetic interrelationships of Mesozoic ornithuromorphs. In particular, phylogenetic inter-relationships and morphological comparisons of the Mesozoic swimming birds are discussed in detail. The present dataset includes an undescribed bird skeletal remains: Manitoba Specimen, MM V-2487, from the Gammon Ferruginous Member (early Campanian) of the Pierre Shale in Manitoba, Canada (described in Chapter 4).

Material and Methods

Three previous panoptic phylogenetic studies used large datasets for Mesozoic birds (Chiappe 2002: 169 characters and 24 taxa; Clarke *et al.* 2006: 205 characters and 25 taxa; Wang *et al.* 2015: 262 characters and 59 taxa). Bell & Chiappe (2015a) provided the first species-level phylogeny of Hesperornithiformes with a matrix of 24 taxa (17 hesperornithiforms) and 209 morphological characters, which is composed of 105 characters from previous studies (Chiappe 2002; Clarke 2004) and 104 new characters.

A phylogenetic analysis was conducted using 349 characters and 43 taxa. The morphological dataset is built upon four previous large data sets for Mesozoic birds: 135 characters from Clarke *et al.* (2006) , 104 characters from Wang *et al.* (2015) , 47 characters from Bell & Chiappe (2015a). In addition, we added 20 characters from Tanaka *et al.* (2017) and 14 characters as new characters. All new added characters are scored as unordered and are equally weighted. The cited 31 characters are ordered following the original data sets (Clarke *et al.* 2006, Wang *et al.* 2015, and Bell & Chiappe 2015a). The distribution of morphological characters by skeletal region is shown in Fig. 1.4. The character description provided in Appendix 1.1 is based on a direct observation of Ornithuromorph specimens by T.T.

Archaeopteryx (Meyer 1861) is assigned as the outgroup to root the tree. The data set is including two enantiornithine birds, *Protopteryx* (Zhang & Zhou 2000) and *Pengornis* (Zhou *et al.* 2008), and 41 Ornithuromorpha (10 hesperornithiforms), including *Archaeorhynchus* (Zhou & Zhang 2006), *Patagopteryx* (Alvarenga & Bonaparte 1992), *Vorona* (Forster *et al.* 1996), *Jianchangornis* (Zhou *et al.* 2009), *Dingavis* (O'Connor *et al.* 2016), *Xinghaiornis* (Xuri *et al.* 2013), *Belluornis* (Wang *et al.* 2016), *Schizoura*

(Zhou *et al.* 2012), *Zhongjianornis* (Zhou & Li 2010), *Apsaravis* (Norell & Clarke 2001), *Tianyornis* (Zheng *et al.* 2014), *Archaeornithura* (Wang *et al.* 2015), *Parahongshanornis* (Li *et al.* 2011), *Hongshanornis* (Zhou and Zhang 2005), *Longicrusavis* (Li *et al.* 2011), *Piscivoravis* (Zhou *et al.* 2014), *Yixianornis* (Zhou and Zhang 2001; Clarke *et al.* 2006), *Yanornis* (Zhou & Zhang 2001), *Changzuiornis* (Huang *et al.* 2016), *Iteravis* (Zhou *et al.* 2014), *Gansus zheni* (Liu *et al.* 2014), *Gansus yumenensis* (Hou & Liu 1984), *Enaliornis* (Seeley 1876), *Pasquiaornis* (Tokaryk *et al.* 1997), *Chupkaornis* (Tanaka *et al.* 2017), *Brodavis* (Martin & Cordes-Person 2007; Martin *et al.* 2012), *Baptornis* (Marsh 1877), *Fumicollis* (Bell & Chiappe 2015a), MM V-2487 (undescribed material), *Hesperornis regalis* (Marsh 1872), *H. gracilis* (Marsh 1876), *Ichthyornis dispar* (Marsh 1872), *Lithornis* (Houde 1988), *Vegavis* (Clarke *et al.* 2005), and five extant birds (*Eudromia elegans*, *Chauna torquata*, *Anas platyrhynchos*, *Gallus colchicus*, and *Gallus gallus*). Data matrix are provided in Appendix 1.2, respectively. The following terminal taxa were combined: *Enaliornis barretti*, *E. seeleyi*, and *E. segwicki* into *Enaliornis*; *Pasquiaornis hardiei* and *P. tankei* into *Pasquiaornis*; *Brodavis vaneri* and *B. americanus* into *Brodavis*; *Lithornis previous* and *L.*

promissucs into *Lithornis*.

A maximum parsimony analysis was conducted with the new data matrix by using the software TNT ver.1.5 (Goloboff & Catalano 2016). The tree search was performed using the traditional search, and the settings for the tree search were 1,000 replicates and the TBR (tree bisection reconnection) branch swapping algorithm, saving single tree per replication. Branches with a minimum length of zero were collapsed. Consistency (CI) and retention (RI) indices were calculated in TNT.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York, USA; **CAGS**, Chinese Academy of Geological Sciences, Beijing, China; **CAMSM** (SMC), Sedgwick Museum of Earth Sciences, The University of Cambridge, Cambridge, England; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **IGM**, Institute of Geology, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **KUVP**, The University of Kansas, Vertebrate Paleontology, Museum of Natural History, Lawrence, Kansas,

USA; **MACN**, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; **MCM**, Mikasa City Museum, Mikasa, Hokkaido, Japan; **MM**, the Manitoba Museum, Winnipeg, Manitoba, Canada; **NHMUK** (BMNH), British Museum of Natural History, London, England; **RSM** (SMNH), Royal Saskatchewan Museum, Saskatchewan, Canada; **SDSM**, Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota, USA; **SMNH**, Sternberg Museum of Natural History, Hays, Kansas, USA; **UCMP**, University of California Museum of Paleontology; **UNSM**, University of Nebraska state Museum, Lincoln, Nebraska, USA; **YPM**, Yale Peabody Museum, New Haven, Connecticut, USA.

Results

The present analysis based on the new data matrix produced two most parsimonious trees (Fig. 1.5), with 777 steps (CI = 0.58, RI = 0.79, RC = 0.46).

The strict consensus tree (Fig. 1.6) shows that Ornithothoraces consists of Enantiornithes (*Propteryx* and *Pengornis*) and Ornithuromorpha (remaining taxa except for *Archaeopteryx*). $[[Archaeorhynchus + Patagopteryx] + Vorona]$ and $[Belluornis + [Zhongjianornis + Schizooura +$

Xinghaiornis] form monophyletic clades. *Jianchangornis* was recovered as a basal ornithuromorph. *Apsaravis* was recovered as a basal ornithuromorph, contrary to several previous studies suggesting its close affinity with Ornithurae (Norell & Clark 2001; Clark & Norell 2002; Wang *et al.* 2016) . Hongshanornithidae is composed of *Hongshanornis*, *Archaeornithura*, *Tianyuornis*, *Longicrusavis*, and *Parahongshanornis*, supported by six characters. Songlingornithidae (*Yixianornis*, *Yanornis*, and *Piscivoravis*) is supported by two characters. Hesperornithiformes (*Enalioniornis*, *Pasquiaornis*, *Chupkaornis*, *Brodavis*, *Baptornis*, *Fumicollis*, and hesperornithids) is supported by 11 characters, and Hesperornithidae (MM-V 2487, *Paraesperornis*, *Hesperornis regalis*, and *H. gracilis*) is supported by 36 characters. In our analysis, *Ichthyornis* was united with the Neornithes in a monophyletic clade in the analysis, as in the studies by Chiappe (2002) and Clarke (2004), but unlike O'Connor *et al.* (2011) and Bell & Chiappe (2015a). *Vegavis iaai* is positioned as a sister taxon of *Anas*. The complete synapomorphy list of the most parsimonious tree can be found in Appendix 1.3.

Within the Hesperornithiformes clade, *Enaliornis* was recovered as the

basal-most taxon, and *Pasquiaornis*, *Chupkaornis*, *Brodavis*, *Baptornis*, and *Fumicollis* were successive sister groups of the Hesperornithidae. The present analysis recovered MM V-2487 as a member of Hesperornithidae, more derived than *Parahesperornis* and more basal than the clade of *Hesperornis regalis* + *H. gracilis*. The detailed morphological comparison of MM V-2487 is discussed in Chapter 4.

Discussion

Phylogenetic Reassessments of Apsaravis and Gansus

Norell & Clarke (2002) originally reported *Apsaravis ukhaana* from the Djadkhata Formation (Campanian) in the southern Gobi of Mongolia, and they concluded that *Apsaravis* is a member of Ornithurae and is more derived than Hesperornithiformes. Several subsequent phylogenetic studies also suggested that *Apsaravis* is a derived member of ornithuromorphs (e.g. O'Connor *et al.* 2011; Wang *et al.* 2015; Huang *et al.* 2017). The phylogenetic analysis of Huang *et al.* (2017) showed that *Apsaravis* is placed more closely to Neornithes than *Ichthyornis* (Fig. 1.1A) by the following six characters: dentary teeth absent; dentaries joined by a bony symphysis; cervical

vertebrae with heterocoelous anterior and posterior centra; metatarsal II shorter than metatarsal IV, but reaching distally farther than the base of the metatarsal IV trochlea; over half of the glenoid facet of coracoid lies omal to the cotyla in lateral view (Huang *et al.* 2017).

The present analysis supports that *Apsaravis* is placed in a clade with *Dingavis*, and the clade is more derived than *Patagopteryx*, *Zhonjianornis*, and *Jianchangornis* (Fig. 1.6). The analysis also suggest *Apsaravis* is more basal than Hongshanornithidae, *Yanornis*, *Yixianornis*, *Gansus yumenensis*, *G. zheni*, *Iteravis*, and Ornithurae (Fig. 1.6). The clade [[*Apsaravis* + *Dingavis*] + higher taxa] share following five characters: elongated thoracic vertebrae (71: 1); proximally displaced plantarly Metatarsal III, relative to metatarsals II and IV (304: 1); weakly expanded (305: 1) and symmetrically projected (306: 1) intercotylar eminence of tarsometatarsus; and weak pedal claws (346: 1). On the other hand, the synapomorphies of the clade of Hongshanornithidae + higher taxa are following seven characters: absent of maxillary teeth (6: 0); absent of dentary teeth (48: 1); laterally expanded lateral process of the coracoid (136: 1); approximately the same length of the ulna and humerus (149: 1); developed ventral condyle of the humerus (173:

1); and the J-shaped metatarsal I (314: 1).

Gansus yumenensis from the Xiagou Formation (Aptian) of China was originally reported by Hou *et al.* (1989) and was firstly discussed its phylogenetic position by You *et al.* (2006) based on the additional specimens. You *et al.* (2006) suggested that *G. yumenensis* is placed more closely to Neornithes than Hesperornithiformes by the following four characters: three sacral vertebrae with dorsally-directed costolateral eminences; lateral process of coracoid present; medial surface of coracoid in vicinity of supracoracoideus nerve foramen flat to convex; and ischium straight, with no dorsal process (You *et al.* 2006). Subsequent study Wang *et al.* (2015) described additional specimens of *G. yumenensis* and hypothesized that *G. yumenensis* is placed in a polytomy with *Jiuquanornis*, *Yumenornis*, *Changmaornis*, *Enaliornis*, Hesperornithiformes, the clade [*Ichthyornis* + Neornithes], supporting by seven synapomorphies: the synsacrum formed by ten ankylosed sacral vertebrae; costal facets on the sternum present; pisiform process of the carpometacarpus present; alular digit short; intercotylar eminence of the tarsometatarsus present; and metatarsal II trochlea strongly displaced plantarly relative to III and IV.

Liu *et al.* (2014) described a new species *Gansus zheni* from the Jiufotang Formation (Aptian) and suggested that *G. zheni* is a sister taxon of *G. yumenensis* based on the following six synapomorphies: lateral trabecula mainly parallel to the long axis of the sternum; supracoracoid nerve foramen of the coracoid absent; hooked lateral process of the coracoid; intermetacarpal space terminates distal to end of metacarpal I; intermembral index = (length of humerus + ulna)/(length of femur + tibiotarsus) between 0.9 and 1.1; distal extent of metatarsal II relative to metatarsal IV; and metatarsal II shorter than metatarsal IV, reaching distally only as far as base of metatarsal IV trochlea (Liu *et al.* 2014). Subsequent phylogenetic analysis of Huang *et al.* (2017) suggested *G. zheni* compose a clade with *Iteravis* (Wang *et al.* 2014) from the Jiufotang Formation, supporting by one synapomorphy, distal end of pubes expanded or flared. Their phylogenetic analysis suggested that *G. yumenensis* is more derived taxon than the clade of *G. zheni* + *Iteravis* (Fig. 1.2A). The later phylogenetic analysis of Wang *et al.* (2018) suggested that the clade of *G. zheni* + AGB5841 + *Iteravis* is supported by the following three synapomorphies: distal end of pubis expanded or flared; the length of pedal digit III almost equal to digit IV and digit II shortest; and presence of

shallow salt grand fossa. Wang *et al.* (2018) also mentioned that the holotype of *G. zheni* is referable to the holotype *Iteravis*.

In the present analysis, *G. zheni* composes a clade with *Iteravis* by supporting one synapomorphy; dentary strongly forked with the dorsal and ventral rami (52: 1). *G. yumenensis* was not recovered as part of the clade [*G. zheni* + *Iteravis*], but more derived than the clade [*G. zheni* + *Iteravis*] (Fig. 1.5). *G. yumenensis* was positioned as a sister taxon of Ornithurae ([[Hesperornithiformes] + *Ichthyornis* + Neornithes]), supporting by the following synapomorphies: V-shaped ulnare (188:1); intermetacarpal space of the carpometacarpus terminates distal to end of the metacarpal I (199:1); and intermetacarpal process of tubercle of the carpometacarpus present as scar (202:1).

Reassessment of phylogenetic relationships of basal Hesperornithiformes

The present analysis suggests the most basal status within this group is occupied by *Enaliornis* followed by *Pasquiaornis* (Fig. 1.7), in contrast to the recent phylogenetic study by Bell & Chiappe (2015a) that identified *Pasquiaornis* as the most basal Hesperornithiformes. Both genera *Enaliornis*

and *Pasquiaornis* have long been recognized as primitive taxa within the Hesperornithiformes (Martin 1987; Tokaryk *et al.* 1997; Galton & Martin 2002a, b; Sanchez 2010). Galton & Martin (2002a) mentioned some osteological similarity between *Enaliornis* and *Pasquiaornis*, although detailed osteological comparison has yet to be conducted. Thus, the phylogenetic relationship between these taxa remains obscure. Tanaka *et al.* (2017) reassessed the phylogenetic relationships of basal hesperornithiform taxa including *Enaliornis* and *Pasquiaornis*.

The clade of *Pasquiaornis* and higher taxa (Fig. 1.7, node 2) is supported by three unambiguous synapomorphies of the hindlimbs. One of these unambiguous synapomorphies is related to the degree of anterior development of the trochanteric crest of the femur. In *Enaliornis*, the trochanteric crest of the femur is significantly expanded anteriorly compared to the femoral head in proximal view (247:0, see Fig. A1.13A of Appendix 1.1), sharing a plesiomorphic state with *Archaeopteryx lithographica* and *Gansus yumenensis*. The trochanteric crest of *Pasquiaornis*, *Baptornis*, and *Fumicollis* is positioned at the same level as the anterior surface of femoral head (247:1, Fig. A1.13E, H, K). Another synapomorphy is the condition

between the femoral trochanter and head. In *Enaliornis*, the femoral trochanter and head are nearly continuous or separated by a shallow notch (242:0, Fig. A1.13B), a condition that is different from *Pasquiaornis* and higher taxa (242:1, Fig. A1.13F, I, J). The third synapomorphy is the absence of a plantarly projected hypotarsus of the tarsometatarsus. In *Enaliornis* (Fig. A1.20G, K), as well as in *Gansus yumenensis* (Fig. A1.20A, E) and *Ichthyornis dispar* (Fig. A1.19J, N), a well-defined hypotarsus without a distinct groove and crest is well developed on the plantar surface of the proximal end of the tarsometatarsus (310:1). In contrast, *Pasquiaornis* and the more derived hesperornithiform birds share a flat surface of the hypotarsus area (310:0, Fig. A1.20M, P, Q, T, U, X).

The present analysis recovered *Chupkaornis* (MCM.A 773) as one of the basal hesperornithiforms, but more derived than *Enaliornis* and *Pasquiaornis* (Fig. 1.7; Tanaka *et al.* 2017). The clade of *Chupkaornis* and the more derived taxa (Fig. 1.7, node 3) is supported by two unambiguous synapomorphies. One of the unambiguous synapomorphies is the presence of a heterocoelous articular surface of thoracic vertebrae, characterized by articular surfaces which are strongly saddle-shaped (69:2, Fig. A1.2G). The

heterocoelous articular surface is compressed dorsoventrally, which differs from the subrounded outline of the articular surfaces (e.g. amphicoelous or ophisthocoelous) as seen in *Gansus yumenensis* and *Ichthyornis* (Fig. A1.2A). Previously, Galton & Martin (2002) suggested that the thoracic vertebral articular surface of *Enaliornis* is strongly heterocoelous. However, although the dorsoventrally compressed articular surface of the sixth thoracic vertebra of *Enaliornis* (CAMS B55277) possesses a general heterocoelous outline, the articular surface is only weakly concave and almost flat, lacking saddle-shaped articular surface, concave on one axis and convex on the other (Fig. A1.2C). As in *Enaliornis*, the articular surfaces of the thoracic vertebrae of *Pasquiaornis* are also compressed dorsoventrally (Fig. A1.2E) and have a more pronounced concavity. These features in *Enaliornis* and *Pasquiaornis* (69:1) are different from those in *Chupkaornis* and the more derived hesperornithiforms, which have true heterocoelous articular surfaces (69:2). The other unambiguous synapomorphy is a depressed medial margin of the medial condyle of the femur (261:1; Fig. A1.13J, M).

The clade of *BroDavis* and more derived taxa (Fig. 1.7, node 4) is supported by one unambiguous synapomorphy: the lateral excavations are

depressed without the well-defined edge of the ventral margin (73:1, Fig. A1.2H). The lateral excavations are deep with a pronounced and sharply defined edge of the ventral margin in *Chupkaornis*, *Ichthyornis* (Fig.A1.2B), *Pasquiarornis* (Fig.A1.2F), and most other Mesozoic birds. The edge of the ventral margin of the lateral excavation is not seen in *BroDavis*, *Baptornis*, *Fumicollis*, and hesperornithids (Fig. A1.2H).

Reassessment of phylogenetic relationship of BroDavis and Baptornis advenus

O'Connor *et al.* (2011) and Bell & Chiappe (2015a) suggested *BroDavis* is more derived than *Baptornis advenus*. In contrast, the present analysis supports a more derived position of *Baptornis* than *BroDavis* based on one unambiguous synapomorphy of the tarsometatarsus. While the tarsometatarsus of *Baptornis* and higher taxa has the dorsal edge of the metatarsal trochlear IV positioned more dorsal to that of trochlear III (333:2, Fig. A1.20S, W), the dorsal edge of metatarsal trochlear IV of *BroDavis* and more basal hesperornithiforms, *Enaliornis* and *Pasquiaornis*, are positioned at about the same level with that of metatarsal trochlear III (333:1, Fig. A1.20J, O). This

arrangement of the metatarsal trochleae seen in *Baptornis* and higher taxa is unique among all birds.

Morphology of Fumicollis hoffmani and the Hesperornithidae

UNSM 20030 was originally described by Martin & Tate (1976) as *Baptornis advenus* and later reassigned to *Fumicollis hoffmani* by Bell & Chiappe (2015b). The present analysis shows that *Fumicollis* is positioned as a sister taxon to the Hesperornithidae, corroborating the results of Bell & Chiappe (2015b). The clade of [*Fumicollis* + Hesperornithidae] (Fig. 1.7, node 6) is supported by five unambiguous synapomorphies: present of the prominent patellar groove of the femur (255: 1); the lateral condyle of the femur constricts into neck before widening at shaft (262:1); projected distal surface of lateral condyle of the femur (265:2); distal extent of trochlea IV slightly further than trochlea III (317:2); and the intertrochlear incision between metatarsal trochlea III and IV is tear-drop shaped in plantar view (328:2; Fig. A1.20X).

The monophyly of the Hesperornithidae (Fig. 1.7, node 7) is supported by 36 unambiguous synapomorphies related to the pectoral girdle and

hindlimbs. In hesperornithid birds, the acetabular foramen of the pelvis is extremely reduced by ossification (224:1, Fig. A1.11E). The antitrochanter of hesperornithids is oriented dorsally (230:2, Fig. A1.11E) in contrast to that of other Mesozoic birds where it is oriented dorsoposteriorly (230:1, Fig. A1.11A, B). The trochanteric crest and the fibular condyle of the femur are greatly expanded laterally (Fig. A1.13I, L), giving them a short and robust appearance (248:2, 266:2). The tubercle for *muscular iliofemoralis* and *m. caudofemoralis* in the medial margin of the femoral shaft is well developed (251:1, Fig. A1.13I, L). The patella is compressed laterally and is highly elongated (269:1, Fig. A1.15B). These osteological changes indicate that the area of muscle attachment on the hindlimb bone elements increased in hesperornithids and likely served for powerful foot-propelled diving behavior. In the tibiotarsus, both medial and lateral cotylae of the proximal articular surface are strongly tilted laterally (274:2, Fig. A1.18K, L). The tibial incision of the proximal end of the tibiotarsus, a groove for the tendon of the femoral caput of *m. tibialis cranialis*, is remarkably deep (277:1, Fig. A1.18I, M), differing from non-hesperornithid hesperornithiforms. The groove likely reflects the development of the *m. tibialis cranialis* for powerful dorsal flexion

of intertarsal joint during the recovery stroke. The lateral margin of the lateral cnemial crest of the tibiotarsus is only slightly flared laterally in hesperornithids (279:1, Fig. A1.18J, N) such that the lateral cotyla of the tibiotarsus is positioned lateral to the lateral cnemial crest. In contrast, the lateral cnemial crest is well-flared laterally and overlaps the lateral cotyla completely in non-hesperornithid birds (279:0, Fig. A1.18B, F).

The clade of [MM V-2487 + [*Hesperornis regalis* + *H. gracilis*]] is supported by three unambiguous synapomorphies: the fibular condyle of the femur oriented entirely laterally (259:1); remarkably flat femur (267:0); and the highly expanded intercotylar eminence of the tarsometatarsus (305:2).

The clade of [*Hesperornis regalis* + *H. gracilis*] (Fig. 1.7. Node 9) is supported by two unambiguous synapomorphies: the lateral condyle of the femur similar extent as medial condyle (257:0); a strongly concave lateral surface of the fibular condyle of the femur (260:1, Fig. A1.13M) unlike the smooth lateral surface of the fibular condyle in other taxa (260:0, Fig. A1.13D, G, J) in distal views, the foramen for *m. ambiens* of the patella is located at around the center in medial view (270:1, Fig. A1.15C), and remarkable distal extent of metatarsal trochlea IV (317:3; Fig. A1.20V).

Conclusion

The phylogenetic analysis conducted herein using a new morphological dataset show a new hypothetical phylogenetic inter-relationship of Ornithuromorpha. *Apsaravis ukhaana* is more basal than Gansuid birds (*Gansus yumenensis*, *G. zheni*, and *Iteravis*). As several previous studies mentioned, *Gansus zheni* is likely to be a synonym of *Iteravis*. *Gansus yumenensis* is the sister taxa of the clade Ornithurae, which consists of *Ichthyornis*, Neornithes, and Hesperornithiformes. The present analysis also suggests new phylogenetic relationships within the Hesperornithiformes; *Enaliornis* is the most basal hesperornithiform, and *Baptornis advenus* is more derived taxon than *BroDavis*. A new skeletal specimen, MM V-2487 (described in Chapter 4), is assigned as the members of Hesperornithidae. The new hypothetical phylogenetic tree sheds new light on the phylogenetic comparative studies on these Mesozoic birds. In the following chapter 2 and 3, the secondary aquatic adaptation of Mesozoic birds and the body mass evolution of Hesperornithiformes are discussed based on the phylogenetic tree provided in this chapter.

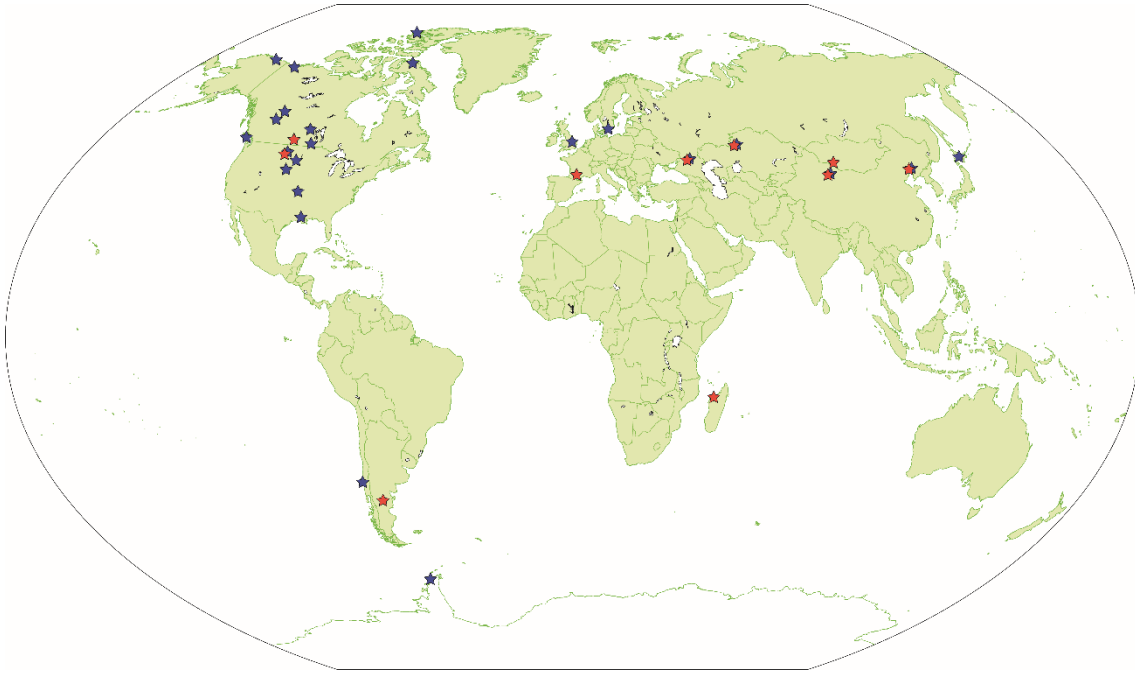


Fig. 1.1 Geographic distribution of the Mesozoic ornithuromorph fossil records. Red stars, terrestrial birds; Blue stars, aquatic birds.

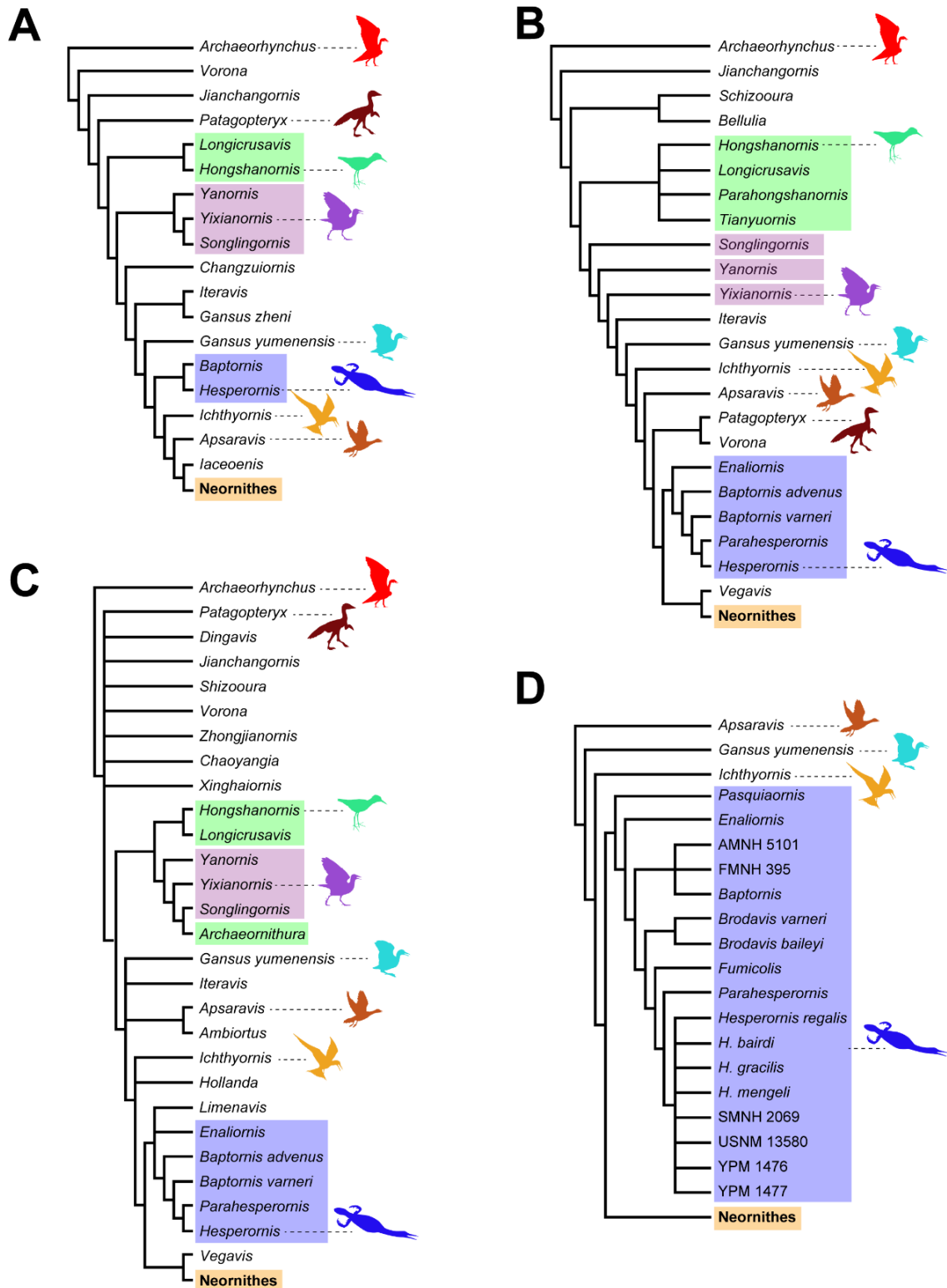


Fig. 1.2 Strict consensus trees of Mesozoic Ornithuromorpha presented by: **A**, Huang *et al.* (2017); **B**, O'Connor *et al.* (2016); **C**, Wang *et al.* 2015; and **D**, Bell & Chiappe (2015). Green, Hongshanornithidae; purple, Songlingornis; blue, Hesperornithiformes; and Orange, Neornithes (modern birds).

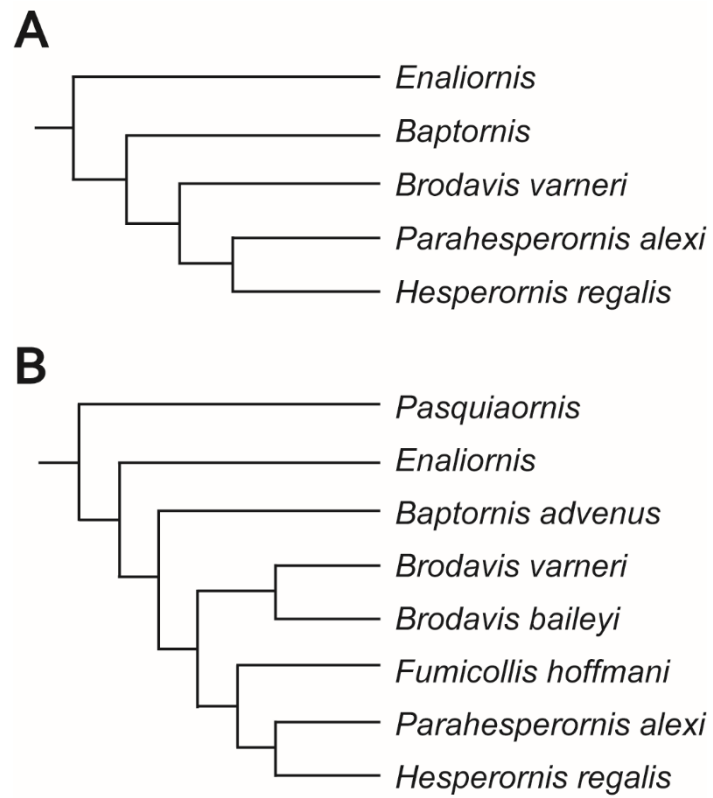


Fig. 1.3 **A**, phylogenetic relationship of the Hesperornithiformes presented by O'Connor et al. (2011) and **B**, by Bell & Chiappe (2015a).

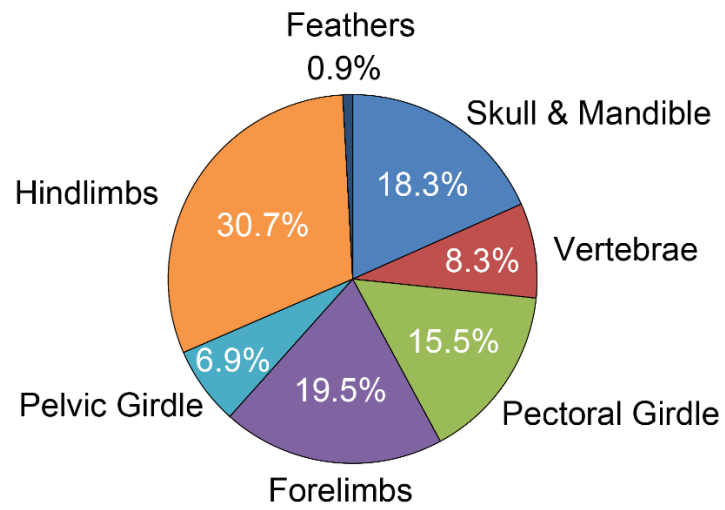


Fig. 1.4 The distribution of the 349 character from the present morphological data set, showing cranial, vertebrae, pectoral girdle, forelimbs, pelvic girdle, hindlimbs, and feathers.

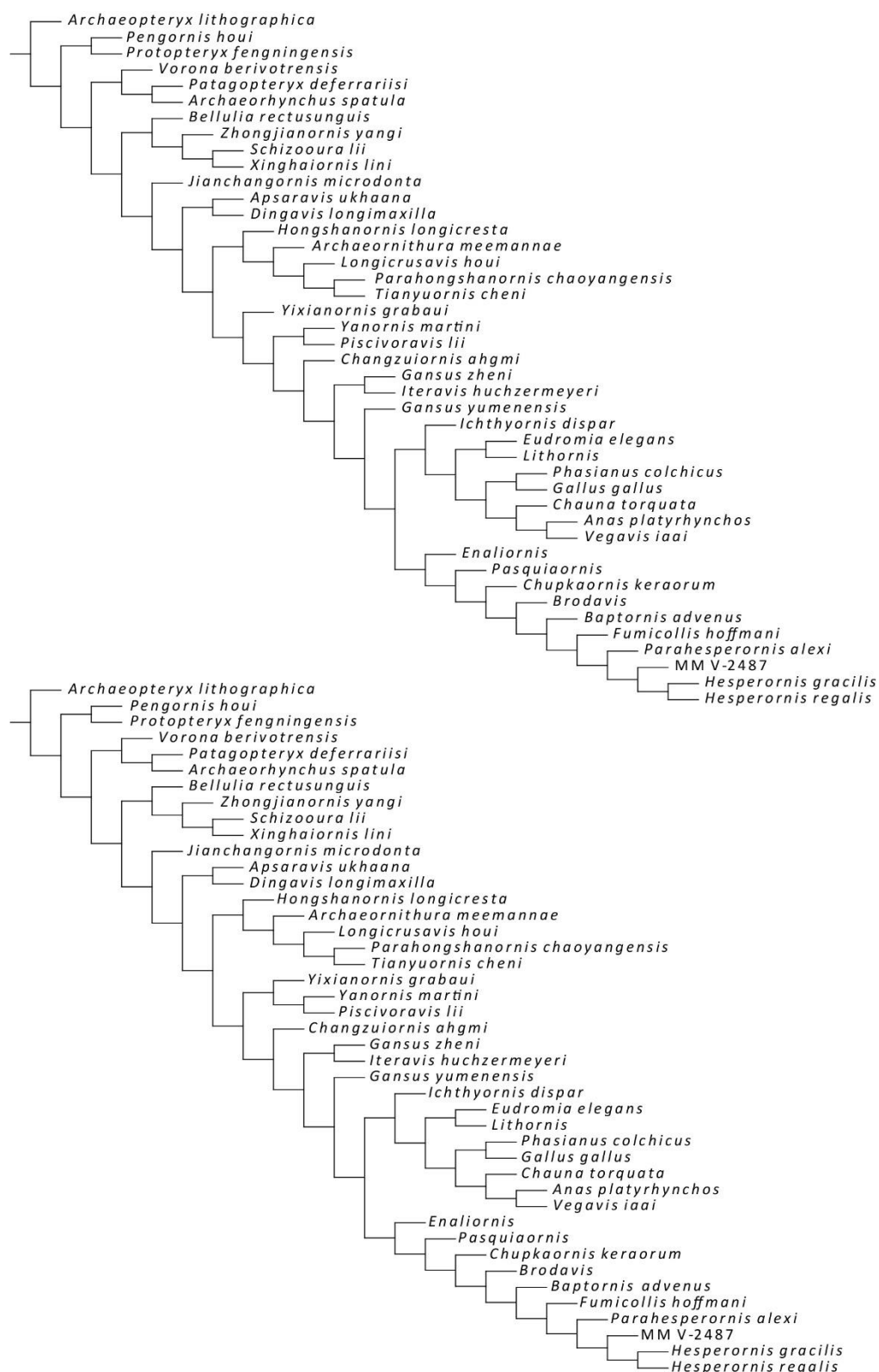


Fig. 1.5 Two most parsimonious trees returned by the present phylogenetic analysis.

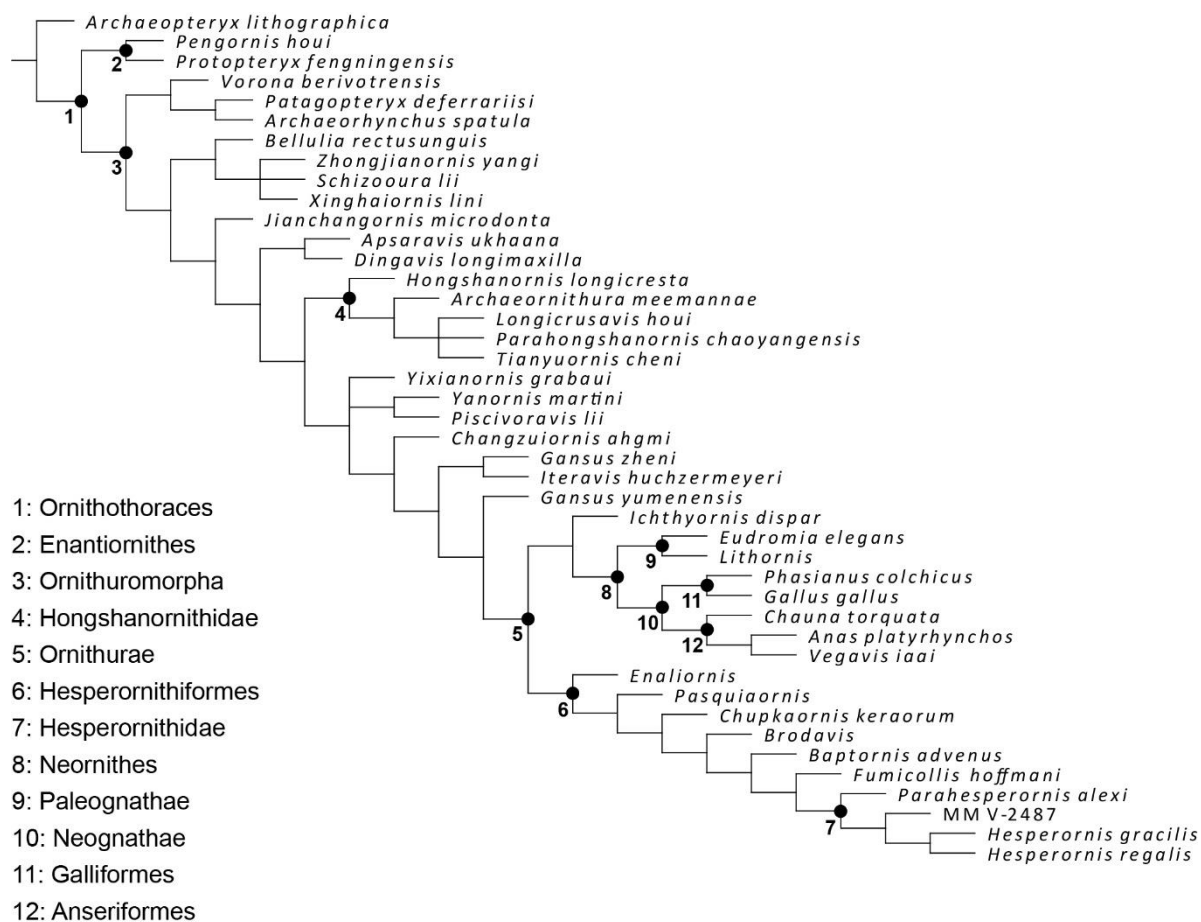


Fig. 1.6 Cladogram of the most parsimonious tree (tree length: 777 steps, consistency index = 0.58, rendition index = 0.79) showing the hypothetical phylogenetic relationships of Mesozoic birds. Note that MM V-2487 (described in Chapter 4) are resolved as members of the Hesperornithidae.

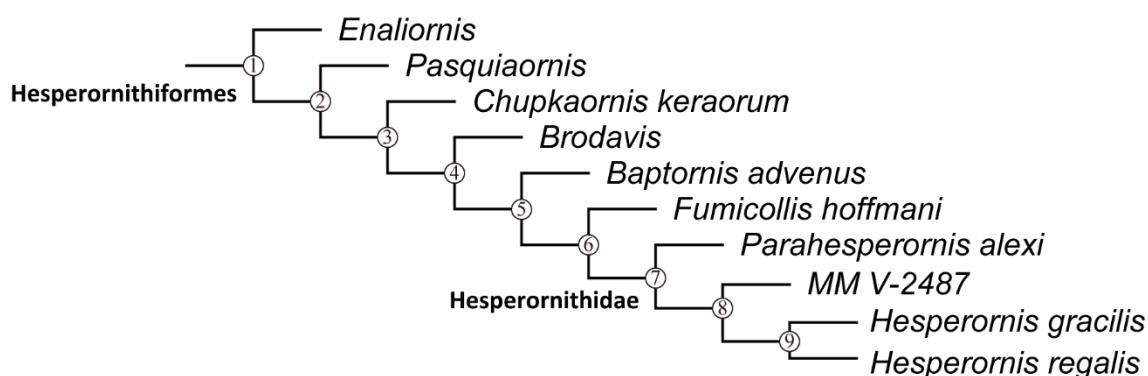


Fig. 1.7 The hypothetical phylogenetic relationships of Hesperornithiformes. Note that MM V-2487 is resolved as a basal member of the Hesperornithiformes. Synapomorphies for each node: Node 1 (69: 0>1, 248: 0>1, 249: 0>1, 251: 0>1, 252: 0>1, 257: 0>1, 265: 0>1, 266: 0>1, 267: 0>1, 268: 0>1; 298: 0>1, 317: 0>1, 319: 0>1, 324: 0>1, 333: 0>1); Node 2 (242: 0>1, 247: 0>1, 310: 1>0); Node 3 (69: 1>2, 261: 0>1); Node 4 (73: 0>1); Node 5 (333: 1>2); Node 6 (255: 1>2, 262: 0>1, 265: 1>2, 317: 1>2, 328: 1>2); Node 7 (224: 0>1, 230: 1>2, 244: 1>2, 246: 1>2, 247: 1>2, 248: 1>2, 249: 1>2, 253: 0>1, 256: 0>1, 266: 1>2, 269: 0>1, 274: 1>2, 276: 0>1, 277: 0>1, 279: 0>1, 281: 0>1, 282: 1>0, 283: 0>1, 293: 1>2, 294: 0>1, 301: 3>2, 302: 0>1, 307: 0>1, 308: 0>1, 316: 1>2, 318: 0>2, 319: 1>2, 320: 0>1, 321: 0>1, 324: 1>2, 334: 0>1, 336: 0>1, 337: 0>1, 338: 0>1, 339: 0>1); Node 8 (259: 0>1, 267: 1>0, 305: 1>2); Node 9 (257: 1>0, 260: 0>1, 270: 0>1, 317: 2>3). See Appendix 1.3 for list of synapomorphies.

Table 1.1 List of Mesozoic Ornithuromorpha.

Genus	Species	clade	Region	Group	Formation	Member	Age
<i>Candaga</i>	<i>arctica</i>	Hesperornithidae	Canada	-	-	-	Maast.
<i>Maaqwi</i>	<i>cascadensis</i>	Vegaviidae	Canada	-	Northumberland Fm.	-	L.Camp.
<i>Brodavis</i>	<i>americanus</i>	Brodavidae	Canada	-	Frenchman Fm.	-	L.Maast.
<i>Pasquiaornis</i>	<i>tankei</i>	Hesperornithiformes	Canada	-	Ashville Fm.	Belle Fourch Mb.	Cen.
<i>Pasquiaornis</i>	<i>hardiei</i>	Hesperornithiformes	Canada	-	Ashville Fm.	Belle Fourch Mb.	Cen.
<i>Hesperornis</i>	<i>chowi</i>	Hesperornithidae	Canada	-	Pierre Shale	Sharon Springs Mb.	E.Cam.
<i>Hesperornis</i>	<i>macdonaldi</i>	Hesperornithidae	Canada	-	Pierre Shale	Sharon Springs Mb.	E.Cam.
<i>Hesperornis</i>	<i>bairdi</i>	Hesperornithidae	Canada	-	Pierre Shale	Sharon Springs Mb.	E.Cam.
<i>Hesperornis</i>	<i>mengeli</i>	Hesperornithidae	Canada	-	Pierre Shale	Pembina Mb.	E.Cam.
<i>Hesperornis</i>	<i>lumgairi</i>	Hesperornithidae	Canada	-	Pierre Shale	Pembina Mb.	E.Cam.
<i>Brodavis</i>	<i>varneri</i>	Brodavidae	Canada	-	Pierre Shale	Sharon Springs Mb.	Cam.
<i>Brodavis</i>	<i>baileyi</i>	Brodavidae	U.S.A	-	Hell Creek Fm.	-	L.Maast.
<i>Potamornis</i>	<i>skutchi</i>	Hesperornithiformes	U.S.A	-	Lance Fm.	-	L.Maast,
<i>Hesperornis</i>	<i>altus</i>	Hesperornithidae	U.S.A	-	Claggett Fm.	Claggett Fm.	E.Cam.
<i>Baptornis</i>	<i>advenus</i>	Baptornithidae	U.S.A	-	Niobrara Fm.	Smoky Hill Mb.	L.San.-E.Cam.
<i>Fumicollis</i>	<i>hoffmani</i>	Hesperornithiformes	U.S.A	-	Niobrara Fm.	Smoky Hill Mb.	L.San.-E.Cam.
<i>Parahesperornis</i>	<i>alexi</i>	Hesperornithidae	U.S.A	-	Niobrara Fm.	Smoky Hill Mb.	L.San.-E.Cam.
<i>Hesperornis</i>	<i>regalis</i>	Hesperornithidae	U.S.A	-	Niobrara Fm.	Smoky Hill Mb.	L.San.-E.Cam.
<i>Hesperornis</i>	<i>crassipes</i>	Hesperornithidae	U.S.A	-	Niobrara Fm.	Smoky Hill Mb.	L.San.-E.Cam.
<i>Hesperornis</i>	<i>gracilis</i>	Hesperornithidae	U.S.A	-	Niobrara Fm.	Smoky Hill Mb.	L.San.-E.Cam.

Genus	Species	clade	Region	Group	Formation	Member	Age
<i>Apatornis</i>	<i>celer</i>	Ornithurae	U.S.A	-	Niobrara Fm.	Smoky Hill Mb.	L.San.-E.Cam.
<i>laceornis</i>	<i>marshi</i>	Ornithurae	U.S.A	-	Niobrara Fm.	Smoky Hill Mb.	L.San.-E.Cam.
<i>Enaliornis</i>	<i>barretti</i>	Enaliornithidae	U.K	-	West Melbury Chalk Fm.	Cambridge Greensand Mb.	L.Apt
<i>Enaliornis</i>	<i>seeleyi</i>	Enaliornithidae	U.K	-	West Melbury Chalk Fm.	Cambridge Greensand Mb.	L.Apt
<i>Enaliornis</i>	<i>sedgwicki</i>	Enaliornithidae	U.K	-	West Melbury Chalk Fm.	Cambridge Greensand Mb.	L.Apt
<i>Garganturavis</i>	<i>philoinos</i>	Ornithurae	France	-	Marnes de la Marine Fm.	-	L.Cam.- E.Maast.
<i>Hesperornis</i>	<i>rossicus</i>	Hesperornithidae	Russia	-	Rybushka Fm.	-	E.Cam.
<i>Asiahesperornis</i>	<i>bazhanovi</i>	Hesperornithidae	Kazakhstan	-	-	-	Maast.
<i>Apsaravis</i>	<i>ukhaana</i>	Ornithuromorpha	Mongolia	-	Djadokhta Fm.	-	L.Cam.
<i>Brodavis</i>	<i>mongoliensis</i>	Brodavidae	Mongolia	-	Nemegt Fm.	-	E.Maast.
<i>Judinornis</i>	<i>nogontsavensis</i>	Hesperornithiformes	Mongolia	-	Nemegt Fm.	-	E.Maast.
<i>Ambiortus</i>	<i>dementjevi</i>	Ornithurae	Mongolia	-	Andaikhudag Fm.	-	Haut.-Bar.
<i>Archaeorhynchus</i>	<i>spatula</i>	Ornithuromorpha	China	Jehol Gp.	Yixian Fm.	-	Apt.
<i>Belluornis</i>	<i>rectusunguis</i>	Ornithuromorpha	China	Jehol Gp.	Jiufotang Fm.	-	Apt.
<i>Zhongjianornis</i>	<i>yangi</i>	Ornithuromorpha	China	Jehol Gp.	Jiufotang Fm.	-	Apt.
<i>Eogranivora</i>	<i>edentulata</i>	Ornithuromorpha	China	Jehol Gp.	Yixian Fm.	-	Apt.

Genus	Species	clade	Region	Group	Formation	Member	Age
<i>Chaoyangia</i>	<i>beishanensis</i>	Ornithuromorpha	China	Jehol Gp.	Jiufotang Fm.	-	Apt.
<i>Schezoooura</i>	<i>lii</i>	Ornithuromorpha	China	Jehol Gp.	Jiufotang Fm.	-	Apt.
<i>Mengciusornis</i>	<i>dentatus</i>	Ornithuromorpha	China	Jehol Gp.	Jiufotang Fm.	-	Apt.
<i>Jianchangornis</i>	<i>microdonta</i>	Ornithuromorpha	China	Jehol Gp.	Jiufotang Fm.	-	Apt.
<i>Juehuaornis</i>	<i>zhang</i>	Ornithuromorpha	China	Jehol Gp.	Jiufotang Fm.	-	Apt.
<i>Xinghaiornis</i>	<i>lini</i>	Ornithuromorpha	China	Jehol Gp.	Yixian Fm.	-	Apt.
<i>Dingavis</i>	<i>longimaxilla</i>	Ornithuromorpha	China	Jehol Gp.	Yixian Fm.	-	Apt.
<i>Hongshanornis</i>	<i>longicresta</i>	Hongshanornithida e	China	Jehol Gp.	Yixian Fm.	-	Apt.
<i>Archaeornithura</i>	<i>meemannae</i>	Hongshanornithida e	China	Jehol Gp.	Huajiyang Fm.	-	Haut.
<i>Parahongsnanornis</i>	<i>chaoyangensis</i>	Hongshanornithida e	China	Jehol Gp.	Jiufotang Fm.	-	Apt.
<i>Longicrusavis</i>	<i>houi</i>	Hongshanornithida e	China	Jehol Gp.	Yixian Fm.	-	Apt.
<i>Tianyuornis</i>	<i>cheni</i>	Hongshanornithida e	China	Jehol Gp.	Yixian formation	-	Apt.
<i>Songlingornis</i>	<i>linghensis</i>	Songlingornithidae	China	Jehol Gp.	Jiufotang Fm.	-	Apt.
<i>Yixianornis</i>	<i>grabau</i>	Songlingornithidae	China	Jehol Gp.	Jiufotang Fm.	-	Apt.
<i>Yanornis</i>	<i>martini</i>	Songlingornithidae	China	Jehol Gp.	Jiufotang Fm.	-	Apt.
<i>Yanornis</i>	<i>guozhang</i>	Songlingornithidae	China	Jehol Gp.	Yixian Fm.	-	Apt.

Genus	Species	clade	Region	Group	Formation	Member	Age
<i>Yanornis</i>	<i>guozhangii</i>	Songlingornithidae	China	Jehol Gp.	Yixian Fm.	-	Apt.
<i>Piscivoravis</i>	<i>lii</i>	Songlingornithidae	China	Jehol Gp.	Jiufotang Fm.	-	Apt.
<i>Changzuiornis</i>	<i>ahgmi</i>	Ornithuromorpha	China	Jehol Gp.	Jiufotang Fm.	-	Apt.
<i>Gansus</i>	<i>zheni</i>	Ornithuromorpha	China	Jehol Gp.	Jiufotang Fm.	-	Apt.
<i>Iteravis</i>	<i>huchzermeyeri</i>	Ornithuromorpha	China	Jehol Gp.	Jiufotang Fm.	-	Apt.
<i>Gansus</i>	<i>yumenensis</i>	Ornithuromorpha	China	Xinminpu Gp.	Xiagou Fm.	-	Apt.
<i>Changmaornis</i>	<i>houi</i>	Ornithuromorpha	China	Xinminpu Gp.	Xiagou Fm.	-	Apt.
<i>Yumenornis</i>	<i>huangi</i>	Ornithuromorpha	China	Xinminpu Gp.	Xiagou Fm.	-	Apt.
<i>Jiuquanornis</i>	<i>niui</i>	Ornithuromorpha	China	Xinminpu Gp.	Xiagou Fm.	-	Apt.
<i>Chupkaornis</i>	<i>keraorum</i>	Hesperornithiformes	Japan	Yezo Gp.	Kashima Fm.	-	Con.-San.
<i>Vorona</i>	<i>berivotrensis</i>	Ornithuromorpha	Madagascar	-	Maevvarano Fm.	-	Maast.
<i>Neogaeornis</i>	<i>wetzelii</i>	Gaviidae	Chile	Arauco Gp.	Quiriquina Fm.	-	Maast.
<i>Limenavis</i>	<i>patagonica</i>	Neornithes	Argentina	-	Allen Fm.	-	Cam.-Maast.
<i>Patagopteryx</i>	<i>deferrariis</i>	Ornithuromorpha	Argentina	-	Rio Colorado Fm.	Bajo de la Carpa Mb.	Cam.
<i>Polarornis</i>	<i>gregorii</i>	Vegaviidae	Antarctica	-	López de Bertodano Fm.	-	Maast.
<i>Vegavis</i>	<i>iaai</i>	Vegaviidae	Antarctica	-	López de Bertodano Fm.	Sandwich Bluff Mb.	Maast.

CHAPTER 2

Hesperornithiforms from the Maastrichtian: Implication for the Paleoeological Diversity in the End of Cretaceous

Abstract

Asian hesperornithiforms are extremely rare in contrast to North American records, and thus their diversity in Asia during the Cretaceous is unclear. Maastrichtian hesperornithiform materials have been reported from both fluvial and marine deposits in North America but only from fluvial deposits in Asia. Asian hesperornithiforms from Maastrichtian deposits have been considered as freshwater taxa because these occurrences from fluvial sediments and histological features. Here we report two undescribed hesperornithiform remains from Mongolia and Japan; the former has been unearthed from the inner continental fluvial deposit of the Nemegt Formation of southwest Mongolia, and the latter is from the inter-arc basin deposit of the Kita-ama Formation, Izumi Group of southwest Japan. They represented by an isolated tibiotarsus. The Japanese specimen is the first hesperornithiform record from marine deposits of Maastrichtian in Asia. Both

have a shallow tibial incision, fibular crest extending to the mid shaft, and laterally angled proximolateral articular surface, suggesting that they belong to non-hesperornithid hesperornithiforms. A remarkably thick cortical area of the Japanese hesperornithiform suggests that this bird was a sea-dwelling bird and that the habitat of this group during the Maastrichtian was extended to both terrestrial and marine environments in Asia and North America.

Introduction

Hesperornithiformes are the oldest flightless seabirds, including 27 species from four families (Enaliornithidae, Baptornithidae, Brodavidae, and Hesperornithidae; Galton & Martin, 2002; Martin 1984), and flourished in the Northern Hemisphere from the late Albian to the latest Maastrichtian (Bell & Chiappe, 2015; Galton & Martin, 2002; Martin *et al.* 2012). The fossil records of this group were predominantly reported from marine deposits such as the Western Interior Seaway deposits (Cenomanian to Campanian) of the North American continent (Aotsuka & Sato 2016; Everhart 2017; Marsh 1880; Martin & Tate 1976; Martin 1984; Tokaryk *et al.* 1997) and the Turgai Strait deposits (Campanian to Maastrichtian) of the Eurasian continent (Dyke *et al.* 2006; Rees & Lindgren 2005; Nesov & Prizemlin 1991; Nesov & Yakov 1993; Panteleyev *et al.* 2004; Zelenkov *et al.* 2017). Several Maastrichtian hesperornithiforms have been recovered from non-marine depositional environments of North America (Elzanowski *et al.* 2001; Martin *et al.* 2012; Pearson *et al.* 2002; Tokaryk *et al.* 1997) and Mongolia (Kurochkin 2000; Martin *et al.* 2012; Nesov & Borkin 1983).

In contrast to abundant fossil records in North America, Asian forms

are extremely rare (Tanaka *et al.* 2017), and thus the diversity of Asian hesperornithiforms is still unclear. Notably, all Asian hesperornithiforms from the Maastrichtian were known from the inner continental fluvial settings and are regarded as freshwater taxa (Kurochkin 2000; Martin *et al.* 2012; Nessel & Borkin 1983), including *Brodavis mongoliensis* from Mongolia, which has a thin cortical bone and possibly retained a flight capability (Martin *et al.* 2012).

Here we report on two tibiotarsi (KID 310 and MNHAH D1-048531) of freshwater and marine hesperornithiforms from the Nemegt Formation of southwest Mongolia and the Kita-ama Formation of southwest Japan, respectively (both are the lower Maastrichtian). These materials provide insights into the taxonomic and ecological diversities of this unique diving bird in the end of the Cretaceous.

Institutional abbreviations

AMNH: American Museum of Natural History, New York, USA; **CAMSM:** Sedgwick Museum of Earth Sciences, The University of Cambridge, Cambridge, England; **FMNH:** Field Museum of Natural History, Chicago,

Illinois, USA; **FHSM**: Fort Hays Sternberg Museum, Hays, Kansas; **KUVP**: The University of Kansas, Vertebrate Paleontology, Museum of Natural History, Lawrence, Kansas, USA; **MNHAH**: Museum of Nature and Human Activities, Hyogo, Sanda City, Hyogo, Japan; **NHMUK**: Natural History Museum, London, England; **RSM**: Royal Saskatchewan Museum, Saskatchewan, Canada; **SDSM**: Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota, USA; **UCMP**: University of California Museum of Paleontology, Berkeley, California, USA; **UNSM**: University of Nebraska State Museum, Lincoln, Nebraska, USA; **YPM**: Yale Peabody Museum, New Haven, Connecticut, USA.

Geological setting

KID 310

KID 310 described herein have been collected by Robin Sissons from the lowermost Nemegt Formation at the Hermin (Khermin) Tsav in the southern Gobi (Fig. 2.1) during the 2008 Korea-Mongolia International Dinosaur (KID) Expedition. In the locality, the transitional interval of Nemegt and underlying Baruungoyot formations and the lowermost Nemegt Formation, which is

composed of a stacked succession of light grey alluvial deposits (channel, crevasse splay, and floodplain), indicating dominantly fluvial environments (Gradziński *et al.* 1977; Eberth *et al.* 2009; Eberth 2017). The lowermost Nemegt Formation cropped out in the Hermin Tsav is composed of repeated relatively small fining-upward succession (less than 3m in depth) including caliches and calcretes (Eberth 2017). The discovery point of the new hesperornithiform remain is located slightly west of the Nemegt Cliff section in Eberth (2017), and the paleoenvironment is assumed purely alluvial plain setting with meandering rivers in a seasonally wet-dry climate setting (Eberth 2017).

In the southern Gobi, several Mesozoic avian remain have been reported: an enantiornithine *Elsornis* and an ornithuromorph *Apsaravis* from the Djadokhta Formation (Chiappe *et al.* 2007; Norell & Clarke 2001); a ornithuromorphs *Hollanda* from the Baruungoyot Formation (Bell *et al.* 2010); and a presbiornithid (Anseriformes) *Teviornis* (Kurochkin *et al.* 2002), , three Ornithurae (Clarke & Norell 2004), and four hesperornithiforms (Nesov & Borkin 1983; Kurochkin 2000; Kurochkin *et al.* 2002; Martin *et al.* 2012) from the Nemegt Formation. *Brodavis mongoliensis* (Martin *et al.* 2012) from

the middle to upper Nemegt Formation at Bugiin Tsav, which paleoenvironments are assumed mixed fluvial, lacustrine, and paludal and fluvial, respectively.

MNHAH D1-048531

The tibiotarsus (MNHAH D1-048531) was collected by a local amateur fossil collector, Teruhiro Kikyo, in August 2004 from a dark grey mudstone of the Kita-ama Formation, exposed at an ammonite-rich locality (Loc. Aw14) (Morozumi 1985) in Sumoto City of southeastern Awaji Island, Hyogo Prefecture, Japan (Fig. 2.2). The Kita-ama Formation is inter-arc basin deposits, composed of conglomerate, sandstone, mudstone, and the turbidite beds (fossiliferous dark grey mudstones) (Fig. 2.2C, D). This locality is rich in marine invertebrate fossils such as ammonoids, inoceramids, and decapods (e.g. Iwaki and Maeda, 1989; Karasawa et al., 2019; Morozumi, 1985) and has yielded several vertebrate fossils, including sharks, sea turtles, mosasaurs, plesiosaurs, pterosaurs, and a lambeosaurine dinosaur (Kobayashi *et al.* 2006; Sato *et al.* 2012; Suzuki *et al.* 2005; Tanimoto 2005). The stratigraphic section at the locality belongs to the *Nostoceras hetonaiense* ammonite zone,

which is correlated to the early Maastrichtian in age (Kodama 1990; Morozumi 1985; Toshimitsu *et al.* 1995).

Systematic Paleontology

KID 310

Avialae Gauthier, 1986

Ornithothoraces Chiappe, 1996

Ornithuromorpha Chiappe, 2002

Hesperornithiformes Fürbringer, 1888

Material. KID 310, an isolated right tibiotarsus. The specimen is housed in the Mongolia Paleontological Centre, Ulaanbaatar, Mongolia.

Locality and horizon. Hermin Tsav, omno gov, southwestern Mongolia; lowermost Nemegt Formation (lower Maastrichtian).

MNHAH D1-048531

Avialae Gauthier, 1986

Ornithothoraces Chiappe, 1996

Ornithuromorpha Chiappe, 2002

Hesperornithiformes Fürbringer, 1888

Material. MNHAH D1-048531, an isolated left tibiotarsus. The specimen is housed in the Museum of Nature and Human Activities, Hyogo, Sanda City, Hyogo Prefecture, Japan.

Locality and horizon. Loc. Aw14 (Morozumi 1985) of Yura Town, Sumoto City, Hyogo Prefecture, Japan; Kita-ama Formation (lower Maastrichtian), Izumi Group.

Description and Comparisons

KID 310

The rotular process on the proximal epiphysis of the tibiotarsas is well-projected proximally as in other foot-propelled diving birds including Cretaceous hesperornithiforms (Fig. 2.3). The fibular crest extends approximately half-way, which is a shared character for the clade of Hesperornithiformes (Fig. 2.8C-H). In anterior view, lateral margin of the lateral cnemial crest is well flared laterally, hiding the lateral cotyla (Figs 2.3, 2.5) as in non-hesperornithid hesperornithiforms (*Enaliornis*, *Pasquiaornis*, *Baptornis*, *Brodavis*, and *Fumicollis*). In the hesperornithids, the lateral margin of the lateral cnemial crest is slightly flared laterally, not hiding the lateral cotyla in anterior view (Figs 2.3, 2.5). The relatively flat medial cotyla and the shallow fibular incision is also similar with non-hesperornithid hesperornithiforms. In the distal end, the astragalus and the calcaneus completely fused. They also completely fused to the distal epiphysis and the surface of the diaphysis is smooth, suggesting the bird individual is an adult when it died. The extensor groove is deep and not covered distally by an ossified supratendinal bridge (Fig. 2.3).

MNHAH D1-048531

MNHAH D1-048531 is smaller than non-hesperornithid hesperornithiforms such as *BroDavis varneri* (SDSM 68431), *Baptornis advenus* (FMNH UC 395) and *Fumicollis hoffmani* (UNSM 20030) (Table 2.1). The proximal end of the tibiotarsus is rounded with a dimpled surface (Fig. 2.4) as in an immature individual of *Enaliornis barretti* (CAMSM B55312) (Fig. 2.6C, D), indicating it was covered with a cartilage during life (Galton & Martin 2002). The rotular process of tibiotarsus is not developed in MNHAH D1-048531 (Fig. 2.6A, B) as in an immature *Enaliornis barretti* (Fig. 2.6C, D) and the chicks of extant birds, different from an adult individual of *Enaliornis sedgwicki* (Fig. 2.6E, F). The undeveloped rotular process suggests the new material is ontogenetically immature. On the proximoanterior side of the proximal epiphysis, the cranial and lateral cnemial crests are only incipiently defined (Fig. 2.6E). The lateral articular surface of the proximal epiphysis is rounded and angled laterally. The flexor fossa is shallow on the proximal articular surface (Fig. 2.6B). The fibular crest extends halfway down the diaphysis (Fig. 2.6A), which is a shared character for the clade of Hesperornithiformes (Fig. 2.8C-H). On the posterolateral surface of the mid shaft, the nutrient foramen

(Fig. 2.4B) opens nearly at the same position as in *Baptornis* (AMNH 5101) and *Fumicollis* (UNSM 20010). The distal epiphysis of the tibial shaft is porous. The proximal tarsals are unfused with the tibial shaft, and the ascending process of the proximal tarsals is elongated proximally (Fig. 2.7A) as in a juvenile individual of *Baptornis* (FMNH UC 395; Fig. 2.7C, D). The ascending process of the proximal tarsals in MNHAH D1-048531 (Fig. 2.7A) is slenderer than that of *Baptornis* (Fig. 2.7C). In an adult *Baptornis* (AMNH 5101), the proximal tarsals are completely fused with the distal epiphysis (Fig. 2.7E, F). The open extensor groove is deep, and the distal epiphysis is angled medially in MNHAH D1-048531 (Fig. 2.7A), similar to *Fumicollis* (UNSM 20030) and *Hesperornis* (YPM 1200). The cortical bone is remarkably thick in the mid shaft in MNHAH D1-048531 (Fig. 2.4G: cortical area/total periosteal area = 83%) as in penguins (Ksepka *et al.* 2015) and *Hesperornis* (Wilson & Chin 2014), suggesting the adaptation for a diving behavior (Habib & Ruff 2008).

Discussion

Taxonomic Status of KID 310

The fibular crest of KID 310 extends halfway down the diaphysis, which is characteristic feature of Hesperornithiformes within Mesozoic birds (Fig. 2.8). The shallow tibial incision (Fig. 2.3E) and the relatively flat medial articular surface (Fig. 2.3B) as in *Pasquiaornis tankei* (RSM P.2957.22) and *Baptornis advenus* (KUVP 2290), suggesting KID 310 can be assigned in non-hesperornithid hesperornithiforms. In addition, KID 310 can be differentiated from all other hesperornithiforms based on the unique presence of remarkably flared and pointed the lateral margin of lateral cnemial crest (Fig. 2.5C), suggesting KID 310 is potential new taxon. Although the rotular process on the proximal end is well-projected proximally, the process shows low-relief compared with other marine hesperornithiforms (Fig. 2.5G, H). This morphology may infer that the foot-propelled diving ability of the freshwater hesperornithiform relatively low than that of marine relatives.

Taxonomic Status of MNHAH D1-048531

MNHAH D1-048531 belongs to Hesperornithiformes because the fibular crest of the tibiotarsus extends halfway (or more) down the diaphysis (Figs 2.4A-D), which is one of the unique characteristics of hesperornithiforms (Fig.

2.8C-H). In non-hesperornithiform ornithuromorphs, the fibular crest is restricted to upper one third of the shaft (Fig. 2.8A, B). The remarkably thick cortical bone of the tibiotarsus (Fig. 2.4G) is considered as a diving adaptation (Habib & Ruff 2008), and this feature is also suggested as a characteristic of hesperornithiforms (Chinsamy *et al.* 1998; Wilson & Chin 2014). Such a thick cortical bone is only seen in flightless sea-dwelling birds such as flightless diving sea ducks (De Mendoza & Tambussi, 2015), flightless Alcidae (Smith & Clarke 2014), and Sphenisciformes (Ksepka *et al.* 2015). Therefore, MNHAH D1-048531 can be considered as a sea-dwelling hesperornithiform.

Among hesperornithiforms, MNHAH D1-048531 belongs to the non-hesperornithid hesperornithiforms (*Enaliornis*, *Pasquiarnis*, and *Baptornis*) based on the combination of the following characters: shallow tibial incision (Fig. 2.4E); flat medial and laterally angled lateral articular surfaces (Fig. 2.4B); and fibular crest of tibiotarsus extended to the mid shaft (Fig. 2.8C). In contrast to non-hesperornithids, Hesperornithidae (e.g. *Parahesperornis alexi* and *Hesperornis regalis*) exhibit the remarkably deep tibial incision (Bell & Chiappe 2015a), laterally angled medial and lateral articular surfaces (Tanaka *et al.* 2017), and the fibular crest extended distally over the mid shaft,

which is interrupted by a transverse groove (Fig. 2.8G, H; Bell & Chiappe 2015a).

Distribution of Hesperornithiformes in Cretaceous

Numerous hesperornithiform specimens have been recovered from Cretaceous rocks of the Northern Hemisphere. From the Southern Hemisphere, several hesperornithiform remains have also been reported, however, those attributions remain controversial.

Neogaenornis wetzeli from the Maastrichtian of Chile was initially grouped with the hesperornithiforms (Lambrecht 1929, 1933; Martin & Tate 1976). However, Olson (1994) later re-defined the holotype as a Cretaceous loon (Gaviidae). Kurochkin (1995) and Feduccia (1999) mentioned hesperornithiform materials from the Maastrichtian of Antarctica. However, the existence of Hesperornithiformes in Antarctica must be viewed as tentative because these specimens have never been described.

Recently, the distal end of a tibiotarsus that possibly represents an immature hesperornithiform individual was reported from the Upper Cretaceous Los Alamos Formation, Argentina (Agnolin & Martinelli 2009).

Agnolin & Martinelli (2009) assigned this specimen, the distal end of a tibiotarsus, to cf. Hesperornithiformes based on characters such as a deep fibular sulcus, a transversely expanded articular surface for the ascending process of the astragalus, and a transversely expanded and craniocaudally compressed distal end. However, the finer-scale taxonomy of the specimen is still unclear (Agnolin & Martinelli 2009).

In this study, only definitive hesperornithiform remains were used for palaeobiogeographical analysis. Therefore, the well-recognized hesperornithiform remains known today are restricted to the Northern Hemisphere (Marsh 1893; Shufeldt 1915; Fox 1974; Martin & Bonner 1977; Bryant 1983; Nessel & Prizemlin 1991; Martin & Varner 1992; Tokaryk & Harington 1992; Tokaryk *et al.* 1997; Malakhov & Ustinov 1998; Hills *et al.* 1999; Hou 1999; Galton & Martin 2002a, b; Martin & Lim 2002; Panteleyev *et al.* 2004; Bell & Everhart 2009; Everhart 2011; Wilson *et al.* 2011; Martin *et al.* 2012; Bell *et al.* 2015; Aotsuka & Sato 2016; summarized in Fig. 2.7 and Appendix 2.1).

The oldest known hesperornithiform, *Enaliornis*, occurs only from the latest Albian Cambridge Greensand Member of the West Melbury Chalk

Formation in England (Fig. 2.10). From Cenomanian rocks, one of the basal hesperornithiforms, *Pasquiaornis*, is known from two localities; the Carrot River locality and the Bainbridge River locality, both in northeastern Saskatchewan of Canada (Tokaryk *et al.* 1997; Cumbaa *et al.* 2006; Sanchez 2010). Another Cenomanian hesperornithiform, a baptonithid, has been reported from the Greenhorn Formation of Kansas (Everhart & Bell, 2009). During the Coniacian to the latest Campanian, hesperornithiforms more widely inhabited the Western Interior Seaway of North America, including north of the Arctic Circle in Canada and Alaska (Fig. 2.10). *Hesperornis*, which was highly adapted for marine environments, appears to be limited to marine sediments. Unpublished museum records (e.g. UCMP 130124 and UCMP 131164), however, indicate its possible presence in the non-marine Hell Creek Formation of Montana (USA). The taxa which may have inhabited terrestrial freshwater environments, such as *Potamornis* (Elzanowsky *et al.* 2001), *Brodavis mongoliensis*, *B. americanus*, and *B. baileyi* (Martin *et al.* 2012), have been reported from the Maastrichtian of North America and Asia.

The fossil record of the hesperornithiforms suggests that they were widely dispersed in Europe and Asia during the Santonian through the

Maastrichtian (Fig 2.10). Most of the hesperornithiforms that have been reported from Western Interior Seaway deposits in North America occur from the Late Cretaceous. In contrast, Asian hesperornithiforms are extremely rare. In Asia, both previously known hesperornithiformes (*Judinornis* and *BroDavis mongoliensis*) are found within the non-marine deposits of the Maastrichtian Nemegt Formation.

Ecological diversity of Hesperornithiformes

The hesperornithiform species were diversified in North America, Europe (western landmass of Eurasia to the Cretaceous epicontinental seaway Turgai Strait), Asia (eastern landmass of Eurasia to the Turgai Strait), and their cumulative sum are shown in Fig. 2.9 (also see Appendix 2.1). The fossil occurrences and their depositional environments [marine, transitional (marine influenced fluvial, coastal plain or swamp, and estuary), and terrestrial (inner continental fluvial) settings: Bell *et al.* (2019)] are plotted on the paleogeographical map of the Cretaceous (Fig. 2.10).

The Hesperornithiformes first appeared in Europe during the Albian when the sea level abruptly rose (Haq 2014). In the mid-Cretaceous, two large

epicontinental seaways, the Western Interior Seaway of North America and the Turgai Strait of Eurasia, were joined via the Arctic Ocean, forming the Northern Hemisphere Megastrait (Baraboshkin *et al.* 2003; Jones 2011). From the late Santonian to the middle Campanian, the derived hesperornithids diversified in the Western Interior Seaway of North America (Figs 2.9, 2.10). Although the faunal exchange between these two epicontinental seaways is unclear, hesperornithids are also known from both the Western Interior Seaway and the Turgai Strait deposits of the Campanian and Maastrichtian (Figs 2.9, 2.10). In the early Maastrichtian of North America, closure of the Western Interior Seaway began by the regional uplift (Blakey & Ranney 2017), which had completed in the late Maastrichtian (Blakey & Ranney 2017; Scotese 2014b). Despite the disappearance of the Western Interior Seaway, North American hesperornithiforms maintained their high taxonomic diversity during the Maastrichtian (Fig. 2.9).

All hesperornithiforms from the late Albian-early Campanian deposits have been reported from marine settings (Fig. 2.9). On the other hand, several North American hesperornithiforms during the middle to late Campanian and most of the North American and all Asian hesperornithiforms during the

Maastrichtian are known from the transitional or terrestrial environments (Fig. 2.9). In Asia, two Maastrichtian hesperornithiform species have been previously reported from the fully inner continental fluvial deposits of southwest Mongolia (Martin *et al.* 2012; Nesov & Borkin 1984). *Brodavis mongoliensis* shows a thin cortical area of the tarsometatarsus and is considered as an inner continental freshwater taxon (Martin *et al.* 2012). The occurrence of KID 310 suggests that taxonomic diversity of inner continental freshwater hesperornithiforms, and MNHAH D1-048531 from a Maastrichtian marine deposit in Asia suggests that hesperornithiforms were diversified both marine and fluvial environments during the Maastrichtian in Asia as seen in North America.

Conclusion

A tibiotarsus from the terrestrial Nemegt Formation (lower Maastrichtian) in southwest Mongolia (KID 310) and the marine Kita-ama Formation (lower Maastrichtian) in southwest Japan (MNHAH D1-048531) are described herein. Both are referable to a non-hesperornithid hesperornithiform. KID 310 can be differentiated from all other hesperornithiforms based on the

unique presence of remarkably flared and pointed the lateral margin of lateral cnemial crest, suggesting KID 310 is potential new taxon of Hesperornithiformes. MNHAH D1-048531 is of an immature individual because the proximal and distal epiphyses are unfused. Our study suggests that hesperornithiforms successfully diversified towards the end of the Cretaceous despite the disappearance of the Western Interior Seaway of North America. Although hesperornithiforms are predominantly known from the marine deposits, several occurrences in the middle upper Campanian of North America, and the majority of the occurrences in the Maastrichtian of North America and Asia are from the non-marine deposits. KID 310 shows that taxonomic diversity of inner continental freshwater hesperornithiforms. MNHAH D1-048531 shows that hesperornithiforms were diversified both inland freshwater and marine realm in the Northern Hemisphere before their extinction in the end of the Cretaceous.

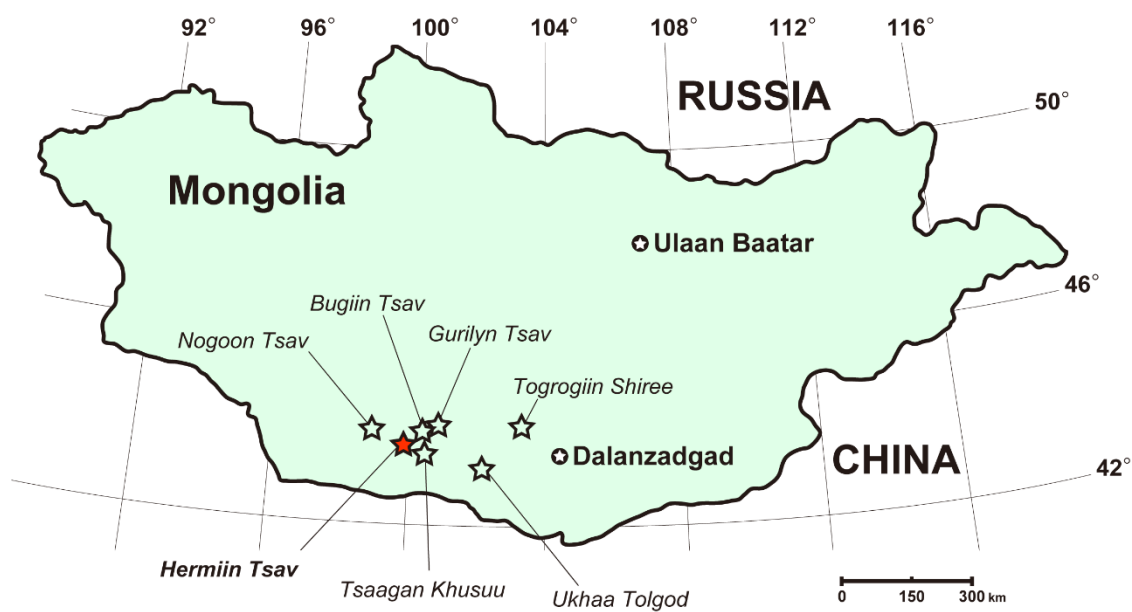


Fig. 2.1 The geographic position. Stars indicate localities of Mesozoic bird remains. Red star indicates the Hermin Tsav, the KID 310 locality.

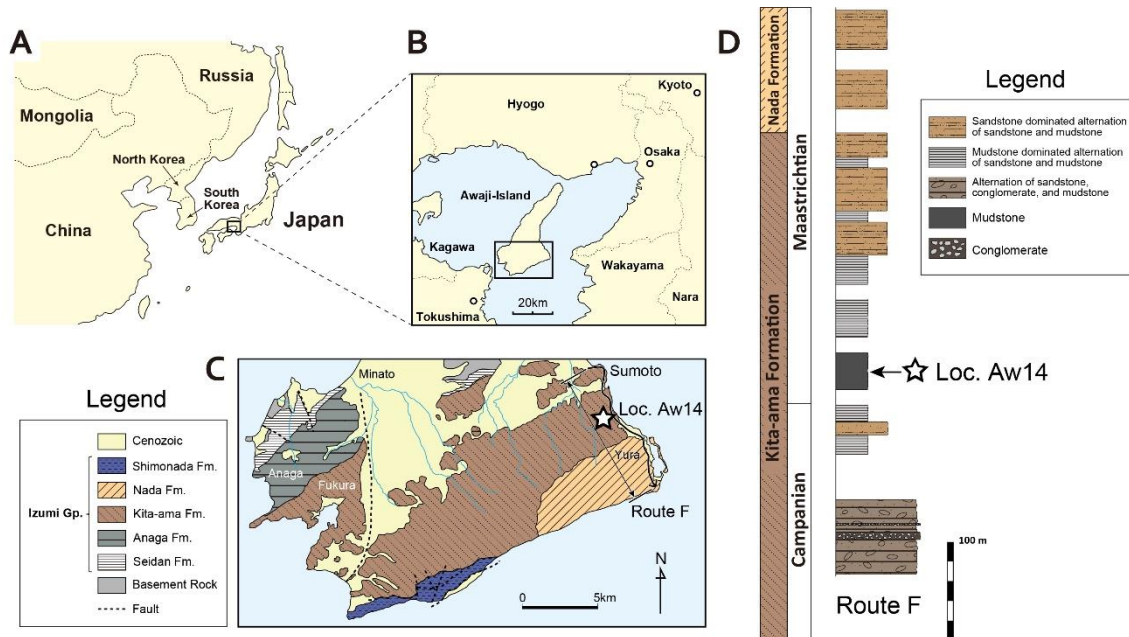


Fig. 2.2 Geographic and geologic settings. **A**, **B**, Geographic position of the Locality and **C**, geological map of the Izumi Group in Awaji Island. Star in **C** indicates Loc. Aw14 (an ammonite locality after Morozumi, 1985). Geological map (**C**) and stratigraphic section of the route F (**D**) are modified from Morozumi (1985).

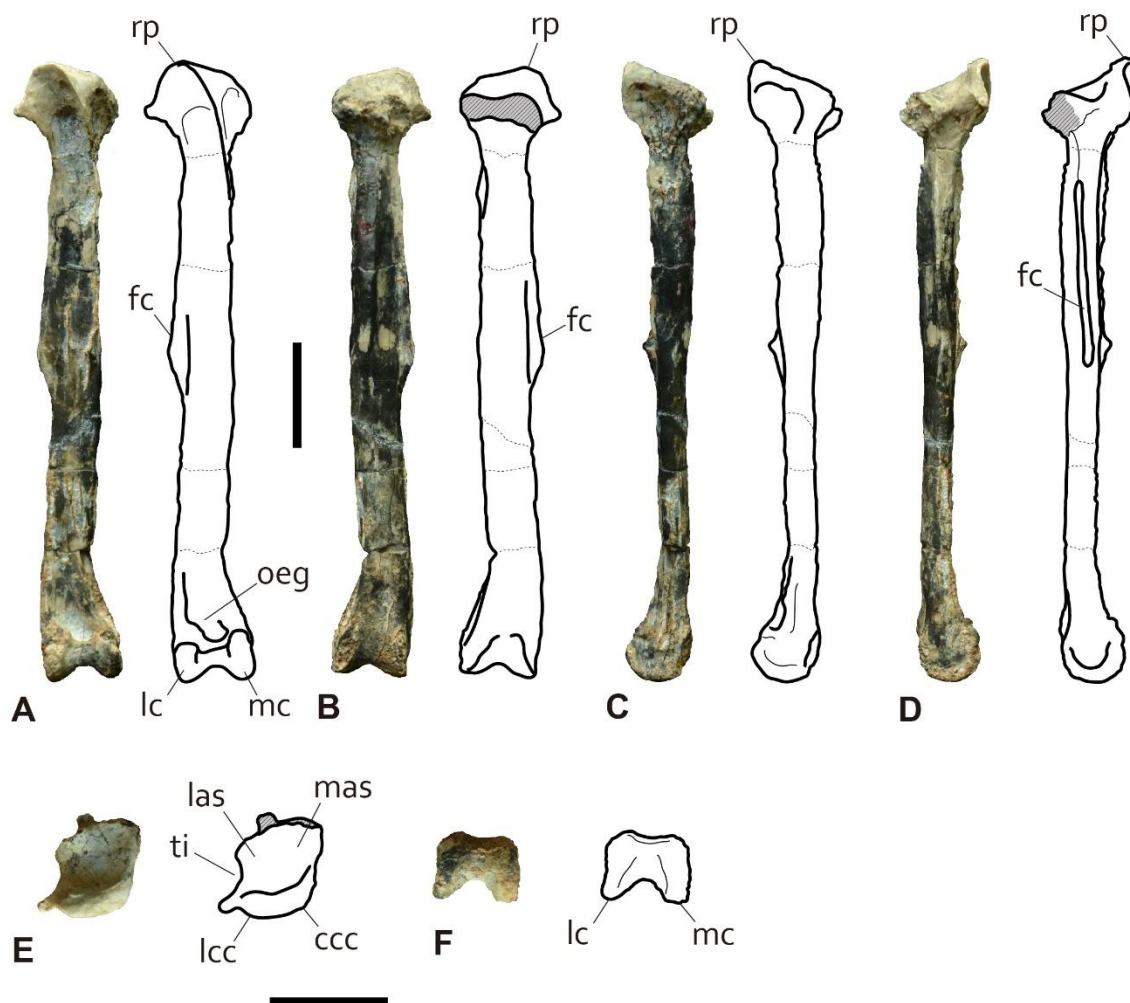


Fig. 2.3 The right tibiotarsus of KID 310 in **A**, anterior; **B**, posterior; **C**, medial; **D**, lateral; **E**, proximal; and **F**, and distal views. Abbreviations: ccc, cranial cnemial crest; fc, fibular crest; las, lateral articular surface; lcc, lateral cnemial crest; mas, medial articular surface; oeg, open extensor groove; ro, rotular process; and ti, tibial incision. Scale bar = 2cm.

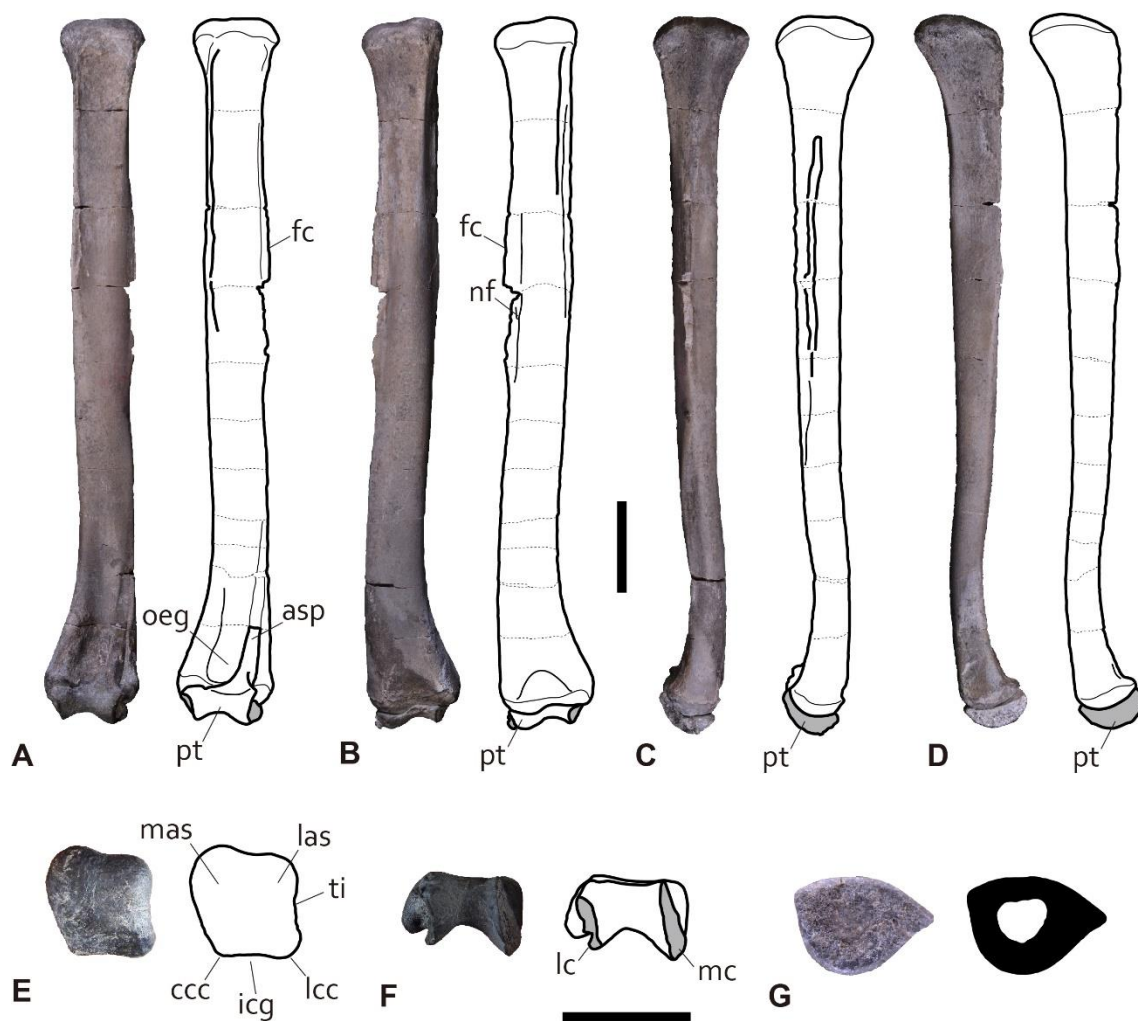


Fig. 2.4 The left tibiotarsus of MNHAH D1-048531 in **A**, anterior; **B**, posterior; **C**, lateral; **D**, medial; **E**, proximal; **F**, and distal views. The cross section of the tibiotarsus at the middle diaphysis (**G**) shows the thickness of the cortical bone. Abbreviations: asp, ascending process; ccc, cranial cnemial crest; fc, fibular crest; icg, intercnemial groove; las, lateral articular surface; lcc, lateral cnemial crest; mas, medial articular surface; nf, nutrient foramen; oeg, open extensor groove; pt, proximal tarsals; and ti, tibial incision. Scale bar = 2cm.

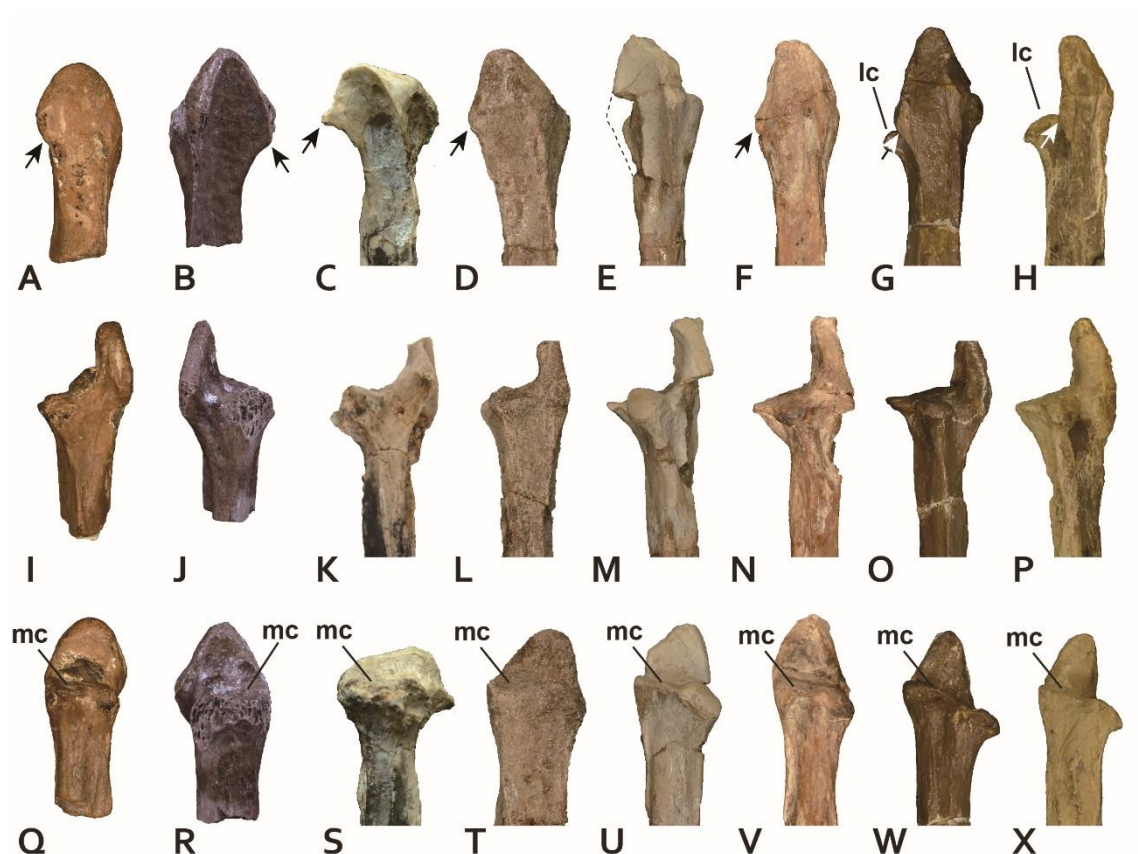


Fig. 2.5 Comparisons of the proximal end of tibiotarsus in anterior (A to H), lateral (I to P), and posterior (Q to X) aspects in: **A, I, Q**, *Enaliornis sedgwicki* (CAMSM B55314); **B, J, R**, *Pasquiaornis tankei* (RSM P2625); **C, K, S**, KID 310; **D, L, T**, *BroDavis varneri* (SDSM 68430); **E, M, U**, *Baptornis advenus* (KUVP 2290); **F, N, V**, *Fumicollis hoffmani* (UNSM 20030); **G, O, W**, *Paraesperornis alexi* (KUVP 2287); and **H, P, X**, *Hesperornis regalis* (YPM 1476). Arrows indicate the lateral margin of lateral cnemial crest. Figures are not to scale. Abbreviations: lc, lateral cotyla; and mc, medial cotyla.

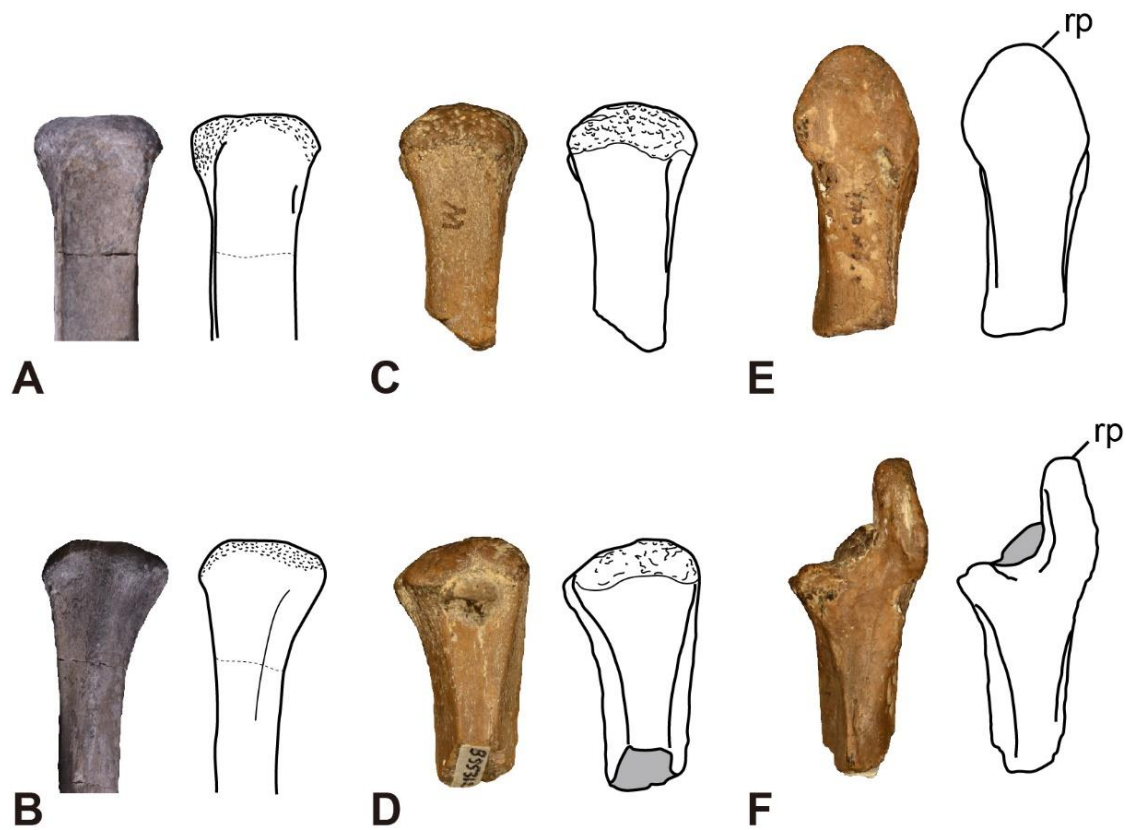


Fig. 2.6 Morphological comparisons of the proximal epiphyses of left tibiotarsus in anterior (**A, C, E**) and lateral aspects (**B, D, F**) in: MNHAH D1-048531 (**A, B**), chick *Enaliornis barretti* (SMC B55312) (**C, D**), and adult *Enaliornis sedgwicki* (SMC B55314) (**E, F**). Abbreviation: rp, rotular process.

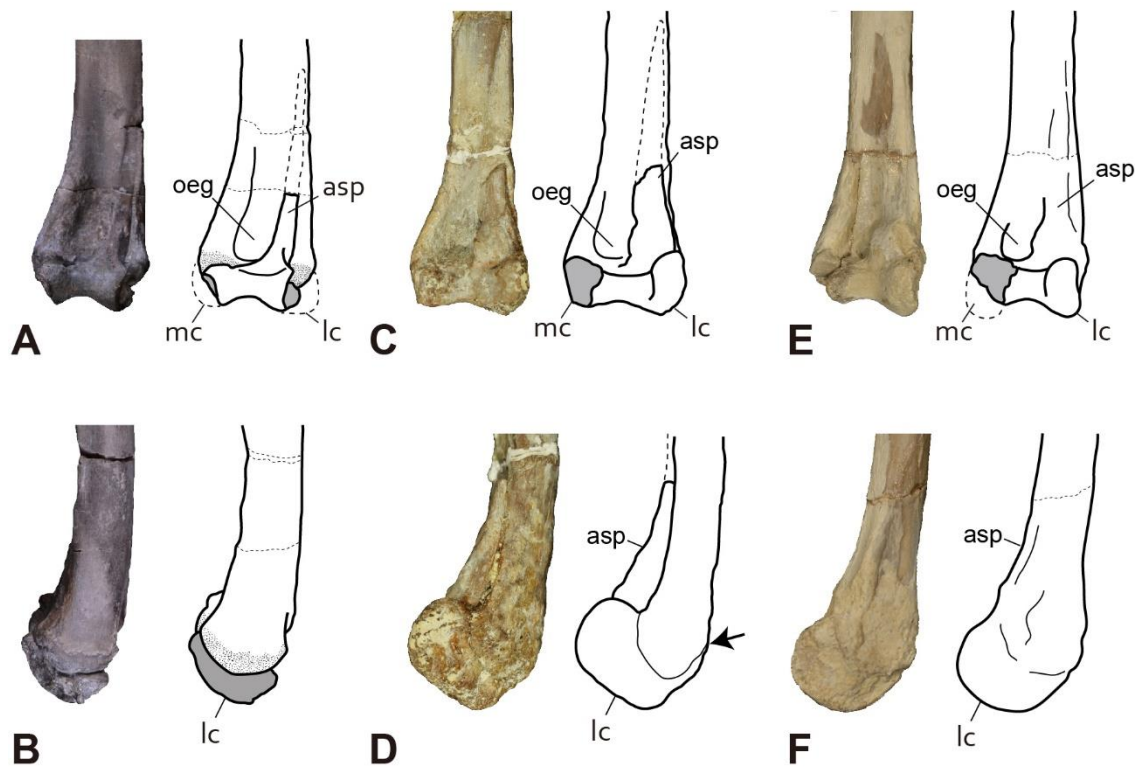


Fig. 2.7 Morphological comparisons of the distal epiphyses of left tibiotarsus in anterior (**A, C, E**) and medial (**B, D, F**) aspects in: MNHAH D1-048531 (**A, B**), juvenile *Baptornis advenus* (FMNH UC 395) (**C, D**), and adult *B. advenus* (AMNH 5101) (**E, F**). Arrow indicate that the suture line. Abbreviations: asp, ascending process; lc, lateral condyle; mc, medial condyle; and oeg, open extensor groove.



Fig. 2.8 Comparisons of the tibiotarsus in: **A**, *Patagopteryx deferrarisii* (MACN-N-03); **B**, *Gansus yumenensis* (CAGS 04-CM-018); **C**, MNHAH D1-048531; **D**, *Brodavis varneri* (SDSM 68430) ; **E**, *Baptornis advenus* (AMNH 5101); **F**, *Fumicollis hoffmani* (UNSM 20030); **G**, *Parahesperornis alexi* (KUVP 2287); and **H**, *Hesperornis regalis* (YPM 1476). Abbreviations: fc, fibular crest; and tg, transverse groove. Arrows indicate the distal end of the fibular crest. Scale bars = 2cm.

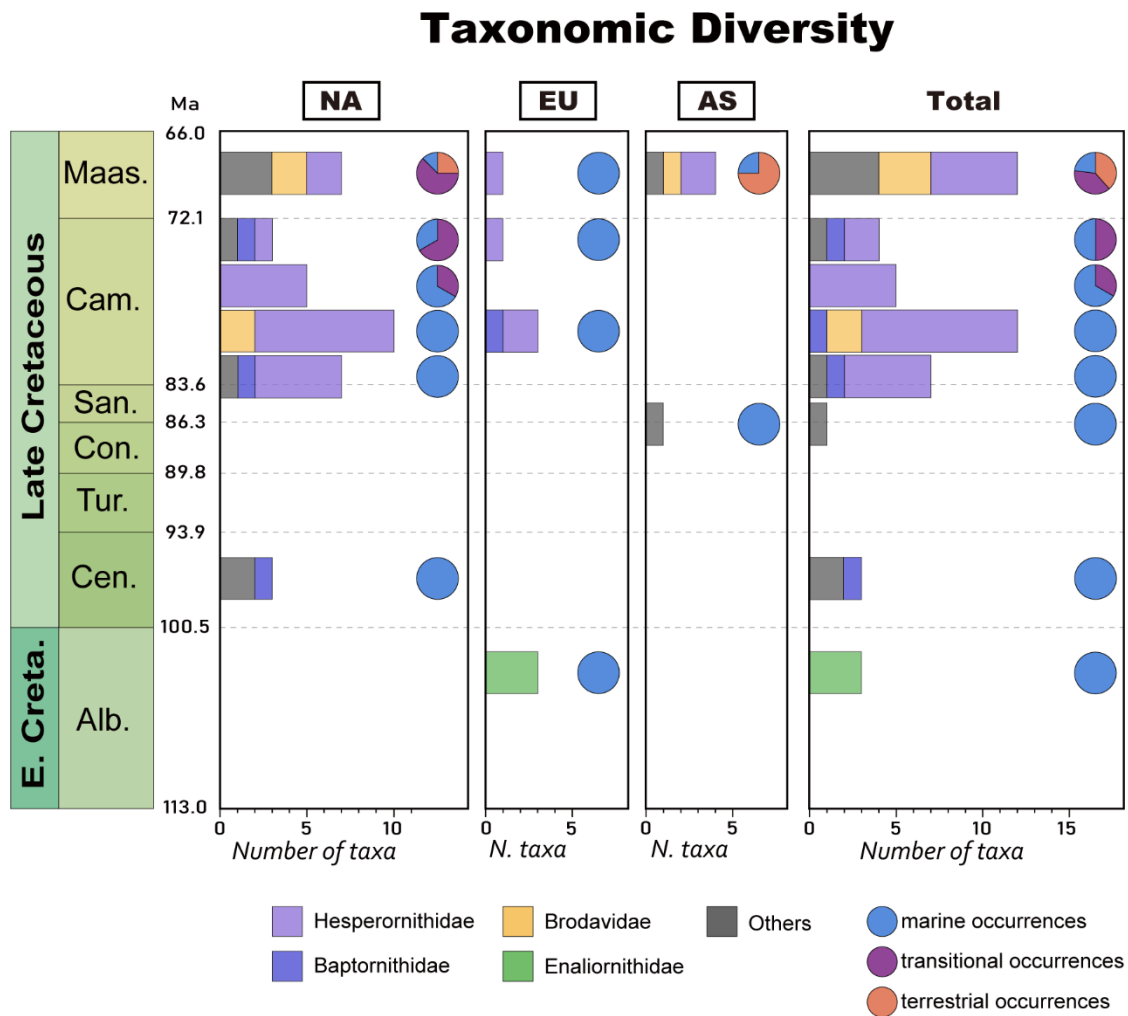


Fig. 2.9 Hesperornithiform taxonomic diversity during the Cretaceous (Albian to Maastrichtian). Abbreviations: NA, North America; EU, Europa; and AS, Asia.

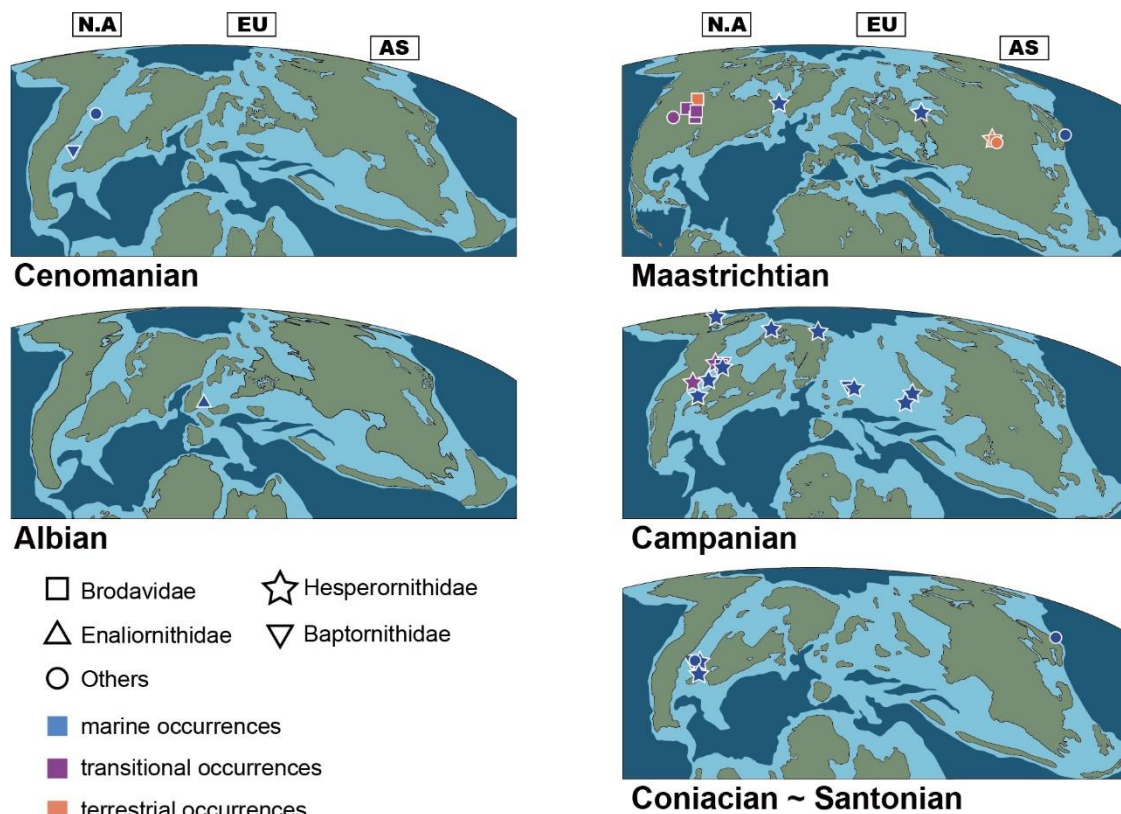


Fig. 2.10 Palaeogeographic map during the Cretaceous showing distribution of hesperornithiform localities in the Northern Hemisphere. Blue, purple, and orange stars show marine, transitional, and terrestrial occurrences, respectively. Maps are modified from (Scotese, 2014a, b). Abbreviations: NA, North America; EU, Europa; and AS, Asia.

Table. 2.1 Linear measurements of KID 310 and MNHAH D1-048531 and size comparisons between Hesperornithiformes.

Tibiotarsus	KID 310	MNHAH D1-048531	<i>Brodavis</i> <i>varneri</i> SDSM 68435	<i>Baptornis</i> <i>advenus</i> FMNH UC395	<i>Fumicollis</i> <i>hoffmani</i> UNSM 20030	<i>Hesperornis</i> <i>regalis</i> YPM 1476
Length	119.97	153.43	233.26	198.26	196.36	344.80
Mediolateral diameter proximal articulation	14.76	17.49	24.82	-	18.15	34.02
Anteroposterior diameter proximal articulation	16.11	18.60	28.93	-	17.71	32.23
Mediolateral diameter midshaft	9.33	12.56	16.32	10.44	11.54	22.51
Anteroposterior diameter midshaft	5.56	9.37	15.56	8.22	9.09	16.47
Circumference mid-shaft	24.42	32.59	47.85	30.98	31.99	60.63
Mediolateral diameter distal articulation	14.86	20.62	24.87	19.03	19.37	32.58

CHAPTER 3

Correlated Character Evolution of Fore- and Hindlimbs in the Oldest Diving Birds

Abstract

Mesozoic diving birds hesperonithiforms became flightless as they maximized their locomotor performance under water. Fossil evidence suggested the evolutionary reduction of forelimbs and development of hindlimbs within the group, yet the pattern of this locomotor tradeoff was not assessed quantitatively. Here we compile characters related to aquatic adaptation in Mesozoic birds and estimate their locomotor modes. We then explore the pattern of aquatic adaptation on phylogeny, and test the evolutionary tradeoff of volant and diving capabilities using fore- and hindlimb characters. Results show that Mesozoic ornithuromorphs increased their swimming and diving capability stepwise. Basal ornithuromorphs were volant and bipedal on land with elongated forelimbs and relatively small hindlimbs. More derived ornithuromorphs (e.g. hongshanornithids and songlingornithids) often exhibit several aquatic characters, such as elongated tibiotarsus and slender pedal phalanges for wading around waterside. *Gansus yumenensis* shows volant and aquatic characters that enable flying, surface-

swimming and diving. The oldest seabirds hesperornithiforms evolved robust hindlimbs for foot-propelled diving. Humerus was gracile in a basal hesperornithiform *Pasquiaornis* and was extremely reduced in more derived forms, suggesting the complete flightlessness. Hesperornithids were adapted for diving with robust and asymmetrically lobed IVth toes. The phylogenetic logistic regressions revealed the evolutionary correlations of forelimb (coracoid and humerus) and hindlimb (femur and tarsometatarsus) characters in ornithuromorphs: forelimb reduction and loss of flight ability is associated with hindlimb development to support powerful hindlimb muscles for diving. Through the evolution of hesperornithiforms, a role of humerus as a self-stabilizer might be transferred to the robust and asymmetrically lobed IVth toes in the hindlimb.

Introduction

Animals moving across different media face tradeoffs of trophic, locomotor and physiological performances (Elliott *et al.* 2013). Aquatic birds experience locomotor tradeoffs as they move between air, land, and water. They often have specialized pectoral girdle and forelimbs or the pelvic girdle and hindlimbs for wing- or foot-propelled diving (Gill 1995): flipper-like wing in wing-propelled divers (e.g. auks and penguins), far backward positioned feet in foot-propelled divers (e.g. loons and grebes), and small wings and large body size in both (Ksepka *et al.* 2011; Clifton *et al.* 2018). These morphological features for diving conflict with aerial and terrestrial locomotor capabilities (Raikow 1985; Elliott *et al.* 2013), eventually leading to flightlessness (Livezey 1988). Although the morphological evolution in wing-propelled diving birds is well-studied (e.g. Ksepka *et al.* 2015; Mayr *et al.* 2018), little is known about the evolutionary process of foot-propelled diving birds.

Mesozoic ornithuromorphs are one of the best target for examining the evolution of foot propelled diving, because the group includes volant non-swimmers (*Archaeorhynchus*; Wang *et al.* 2015), volant waders (*Hogshanornis*; Zhou and Zhang 2005), volant surface swimmers or inept divers (*Gansus yumenensis*; Hou & Liu 1984), intermediate (volant to flightless) divers

(*Pasquiaornis*; Tokaryk *et al.* 1997) , flightless divers (*Baptornis*; Martin & Tate, 1976), and flightless adept divers (*Hesperornis*; Marsh 1872). Diving adaptation was particularly pronounced in seabirds hesperornithiforms, in which derived species enlarged legs and extremely reduced wings to compromise their flight ability (Marsh 1880). However, despite 140 years of research history of hesperornithiforms (Marsh 1872), evolutionary patterns leading to flightlessness and efficient diving, and the association between those have not gained much attention.

Here, we examine evolution of diving capability in Mesozoic ornithuromorphs including hesperornithiforms on phylogeny using morphological characters of fore- and hindlimbs. Firstly, we compile characters related to aquatic adaptation in Mesozoic birds and estimate their locomotor modes. Followingly, we test the association of fore- and hindlimb evolution to see the tradeoff of volant and swimming abilities. The results provide a rare insight into the secondary aquatic adaptation in foot-propelled birds.

Material and Methods

Locomotor Modes of Mesozoic Ornithuromorpha

The 20 characters related to aquatic adaptation (Table 3.1: Martin & Tate 1976;

Raikow 1985; Livezey 1986; Clarke 2004; You *et al.* 2006; Zhou & Zhang 2005; Habib & Ruff 2008; Houssaye 2009; Hinic-Frlog & Motani 2010; O'Connor *et al.* 2011; Bell & Chiappe 2015) are compiled from the morphological dataset in Chapter 1 (see Appendix 1.1). Based on the characters, we estimate the locomotor modes of Mesozoic Ornithuromorpha including basal ornithuromorphs (e.g. *Archaeorhynchus*), hongshanornithids (e.g. *Hogshanornis*), songlingornithids (e.g. *Yanornis*), *Iteravis*, *Gansus zheni*, non-hesperornithid hesperornithiforms (e.g. *Pasquiaornis* and *Baptornis*), and hesperornithids (e.g. *Hesperornis*). The locomotor categories (surface swimmers, lesser foot-propelled divers, and highly foot-propelled divers) are referred to Clifton *et al.* (2018).

Phylogenetic Logistic Regressions

To investigate the evolutionary correlation of fore- and hindlimb characters, we conducted phylogenetic logistic regressions (Ives & Garland Jr 2009) using 19 ornithuromorphs including 2 hongshanornithids, 3 songlingornithids, and 5 hesperornithiforms, and their phylogenetic framework (Chapter 1) (Fig. 3.1). We coded characters for coracoid [strut-like (0) or trapezoidal (1): Fig. 3.2A-E] and humerus [robust (0) or stick-like (1): Fig. 3.2J-O] as discrete variables, and femur (distal width / maximum length along the shaft: Fig. 3.3A-E) and tarsometatarsus

(ratio of mediolateral width of trochlear IV/trochlea III: Fig. 3.3K-O) as continuous variables. Character data used in this study are found in Appendix 3.1. The phylogenetic logistic regressions require phylogenies with the terminal ages and estimated internal branch durations. Geological age for 19 taxa was determined as the median of the first appearance data (FADs) and the last appearance data (LADs) from the primary literature with reference to Walker *et al.* (2013) (see Appendix 3.2). We used minimum branch length method (minimum internal branch length of 2Ma) (Laurin *et al.* 2004) for internal node calibration with *DatePhylo* function in the R package Strap (Bell & Lloyd 2015). FADs are used for determining internal node ages (Brusatte 2011). The phylogenetic logistic regressions were conducted using R package phylolm (Ho & Ané 2014). Bootstrap resampling (100 times) was conducted for generating 95 % confidence intervals.

Results

Distribution of Characters Related to Aquatic Adaptation in Ornithuromorpha

Distribution of 20 morphological characters related to aquatic adaptation in Mesozoic ornithuromorphs are shown in Fig. 3.4. Basal ornithuromorphs exhibit no aquatic characters, while hongshanornithids, songlingornithids, *Changzuiornis*, *Gansus zheni*, and *Iteravis* show several aquatic characters. *Gansus yumenensis*

and hesperornithiformes, particularly hesperornithids, show higher degrees of aquatic adaptation.

Locomotor Modes of Mesozoic birds

Ornithuromorpha shares forelimb characters such as the triosseal canal, the sternum with a keel extending over the entire length of the bone, and the high degree of fusion of the carpals (Wang *et al.* 2015), suggesting that early ornithuromorphs were powerful volant birds (Chiappe 2007; Mayr 2016). Basal ornithuromorphs, such as *Archaeorhynchus* and *Patagopteryx* have no aquatic characters and are considered as terrestrial birds as opposed to arboreal Enantiornithes (Chiappe 1996; O'Connor *et al.* 2011) (Fig. 3.4). Hongshanornithids, songlingornithids, *Iteravis*, and *Gansus zheni* have relatively elongated tibiotarsus (character #9 in Table 3.1), slender and long toes (#15), and weak and short claws (#14) with flexor tubercles (#16; except for songlingornithids), indicating their wading lifestyle (Zhou & Zhang 2005; O'Connor *et al.* 2010; Wang *et al.* 2015; Chiappe & Qingjin 2016). Direct evidence of swimming for these birds are currently unknown (Fig. 3.4).

Gansus yumenensis was considered as a powerful volant bird based on its developed forelimbs as seen modern birds (You *et al.* 2006) (Fig. 3.2D), while they

also show several aquatic features. The relatively narrow pelvis (#3) allows to bring legs closer to the sagittal plane of the trunk and is interpreted as an adaptation for effective underwater propulsion (Hinic-Frlog & Motani, 2010). The elongated pelvis (#4) and the enlarged rotular process of the tibiotarsus (#8) increase the attachment area of thigh muscles for holding the femora stationary (Hinic-Frlog & Motani 2010). The elongated tibiotarsus (#9) allows the ankle joint to be positioned caudally for effective foot paddling (Clifton *et al.* 2018). The IVth toe is the longest (#17; Fig. 3.6C), increasing the area of totipalmate feet (You *et al.* 2006; Li *et al.* 2011; Y-M. Wang *et al.* 2015). These characters are unknown in the closely related species such as *Iteravis* and *G. zheni* (Fig. 3.4). Although *G. yumenensis* does have some of the features of foot-propelled diving birds, its femur is gracile and lacks enlarged patella (You *et al.* 2006; Nudds *et al.* 2013) as in dabbling ducks. These anatomical features suggest that *G. yumenensis* was a transitional form between surface swimmers (e.g. dabbling ducks) and an inept foot-propelled diver (e.g. cormorants).

Hesperornithiforms share osteosclerotic (thick cortical area) bones (#19) (Chinsamy *et al.* 1998; Wilson & Chin 2014) for providing ballast under water (De Ricqlès 2001). Some hesperornithiforms (e.g. *Baptornis* and *Hesperornis*) have extremely reduced wings (#1; Fig. 3.5H, K) (Marsh, 1880; Martin & Tate 1976). A

basal hesperornithiform *Pasquiaornis* (Tokaryk *et al.* 1997) has a strut-like coracoid (typical shape of volant birds: Fig. 3.2B), and the glenoid facet, the procoracoid process, and the acrocoracoidal process (Fig. 3.2B, F) as in *G. yumenensis* (Fig. 3.2A). The humerus of *Pasquiaornis* is more gracile than in *G. yumenensis*, yet the deltopectoral crest, the medial and lateral condyles, the brachial fossa, and well-defined distal condyles clearly exist (Fig. 3.2K, L) (Sanchez 2010). Although flight ability of *Pasquiaornis* is unknown because their sternum and articulated forelimbs have never been found, *Pasquiaornis* might retain volant ability based on their forelimbs (Fig. 3.5G) (Sanchez 2010). The hindlimbs of *Pasquiaornis* have been reported abundantly, but mostly fragmentally and incomplete (Sanchez 2010). Since some of hindlimb characters in *Pasquiaornis* are shared with *Baptornis* and *Fumicollis* (Tokaryk *et al.* 1997), They might have similar diving ability.

Baptornis, a more derived hesperornithiform, has a stick-like humerus (Fig. 3.2M) and rudimentary forearms (Fig. 3.5H). The coracoid of *Baptornis* is not slender (Fig. 3.2C), and the acrocoracoid processes, the procoracoid process and the glenoid facet are not defined (Fig. 3.2C, G). The extremely reduced forelimbs suggest that they were flightless birds (Martin & Tate 1976). *Pasquiaornis* and *Baptornis* share the acutely angled antitrochanter of ilium (#2), robust and short

femur (#6; Fig. 3.3B, C), and equal-sized distal condyles of pedal phalanges (suggesting webbed-feet; Martin and Tate 1976) (Fig. 3.3P, Q). The angled antitrochanter allows the femora to elevate (Fig. 3.5J) during power stroke for the efficient foot-propelled diving (Kurochkin & Vasiliev 1966). *Baptornis* has an enlarged pyramidal patella (Fig. 3.5I) as in cormorants (Owre 1967), and elongated tibiotarsus with a large rotular process (Martin & Tate 1976). These knee structures indicate development of *m. femorotibialis medius*, *gastrocnemius* heads, and digital flexor muscles (Clifton *et al.* 2018). The increased mass of these muscles is critical for stabilization of knee joint and powerful planterflexion for paddling (Zinoviev 2011; Clifton *et al.* 2018). The enlarged knee area reduces the range of motion around the knee joint (Ribak *et al.* 2004). The tibiotarsi are held close to the body by *m. iliofibularis*, *m. femorotibialis*, and *m. iliotibialis lateralis* (Zinoviev 2011), and increase propulsive forces transmitted by the tarsometatarsus (Hinic-Frlog & Motani 2010). The extant foot-propelled divers with the elongated pelvis, elevated femora, enlarged knee structure, and caudally positioned tarsal joint share similar swimming styles: during underwater locomotion, knee joint and crus are held stationary, and tarsometatarsus and the parts distal to it are used for propulsion (Hinic-Frlog & Motani 2010; Fish 2016). Morphologies of hindlimbs in *Baptornis* and other non-hesperornithid

heperornithiforms suggest that their underwater locomotion was similar to that in extant foot-propelled divers (e.g. loons) (Marsh 1880; Martin & Tate 1976; Hinic-Frlog & Motani 2010; Zinoviev 2011) .

Hesperornithids (e.g. *Parahesperornis* and *Hesperornis*) are the most specialized foot-propelled divers (Martin 1984; Zinoviev 2011; Bell & Chiappe 2015). The humerus is more gracile than that of *Baptornis* (Fig. 3.2N, O), and forearms are extremely reduced or lost (Fig. 3.5K) (Marsh 1880). The coracoid of hesperornithids is expanded mediolaterally with an angular lateral margin, giving it a blunt trapezoidal appearance (Fig. 3.2D, E) (Marsh 1880). The coracoid of *Parahesperornis* (Fig. 3.2D) is slightly slender than that of *Hesperornis* (Fig. 3.2E) (Martin 1984), and their acrocoracoid processes and the glenoid facet are not defined (Fig. 3.2D, E). Their non-keeled sternum and the rudimentary forelimbs suggested that they were flightless divers (Marsh 1880). Their hindlimbs are highly adapted for foot-propelled diving than in non-hesperornithid hesperornithiforms (Fig. 3.5L). Hesperornithids have a pachyostotic femur (#20; Fig. 3.3D, E). The pelvis and patella of *Hesperornis* are more enlarged (Fig. 3.5L) than that of *Baptornis* and *Fumicollis* (Fig. 3.5I) (Martin & Tate 1976; Bell & Chiappe 2015). The antitrochanter of the ilium is dorsally directed (#2), which allows the femora to elevate above the body (Fig. 3.5M; Zinoviev 2011). The

articular surfaces of IVth pedal phalanges in hesperornithids are ball and socket structure specialized for toe-rotation (#18; Fig. 3.3R, S, V, W) as in grebes (Stolpe 1935). Hesperornithids might have lobed-feet (Fig. 3.6E) (Stolpe 1935; Martin & Tate 1976; Zinoviev 2011) unlike non-hesperornithid hesperornithiforms (Fig. 3.3P, Q, T, U), suggesting that hesperornithids were more efficient foot-propelled divers (Zinoviev 2011; Bell & Chiappe, 2015; Fish 2016). In hesperornithids, the metatarsal trochleae IV of the tarsometatarsus are almost twice wider than that of IIIrd (Fig. 3.3N, O), and the IVth toes are the most robust (Marsh 1880) (Fig. 3.3R, S). Such enlarged IVth toes are never seen in any other birds (Fig. 3.6).

Phylogenetic Logistic Regressions

The phylogenetic logistic regressions identified 4 pairs of fore- and hindlimb character correlations (Table 3.2). The morphological changes in the coracoid (from strut-like to trapezoidal shape) and the humerus (from robust to extremely reduced stick-like appearance) are correlated with the changes in the femur (shorter and expanded distal end) and the tarsometatarsus (wider metatarsal trochlea IV).

Discussion

Evolution of Aquatic Locomotion in Ornithuromorpha

The estimation of locomotor modes shows a stepwise evolution of foot-propelled diving behavior in Mesozoic ornithuromorphs. In the Early Cretaceous, ornithuromorphs (e.g. hongshanornithids) had slender hindlimbs and pedal phalanges (Fig. 3.6B) for wading (Zhou & Zhang 2005; O'Connor *et al.* 2010). More derived *Gansus yumenensis* shows a combination of fore- and hindlimb features (elongated pelvis, posteriorly positioned knee joint, and large totipalmate hindlimbs) that enable powerful flapping, surface swimming and active foot-propelled diving (You *et al.* 2006; Li *et al.* 2011; Nudds *et al.* 2013) (Figs 3.5D, E, 3.6D). Their forelimbs might also be used for underwater propulsion (Nudds *et al.* 2013). Such foot-and-wing-propelled diving style is seen in extant diving ducks (e.g. *Mergus* and *Melanitta*; Brooks, 1945) and shearwaters (e.g. *Puffinus* and *Fulmarus*; Ashmole 1971). A basal hesperornithiform *Pasquiaornis* exhibits a set of hindlimb characters for foot-propelled diving (e.g. osteosclerotic bones, robust and short femur, and sharp angled ilium antitrochanter). Their reduced forelimbs (Fig. 3.5G) might be held slightly away from the body as lateral stabilizers during swimming as in extant cormorants and shags (Ross 1976; Livezey 1992). The robust hindlimbs and reduced forelimbs in *Pasquiaornis* indicate a trade-off

between active aerial flight and foot-propelled diving. *Baptornis* has a similarly robust hindlimbs as in *Pasquiaornis* (Fig. 3.5I) and much reduced forelimbs (stick-like humerus and diminished ulna and radius) (Fig. 3.5H), indicating it was a non-volant foot-propelled diver. Probably, tiny wing of *Baptornis* would have a stabilizing and steering functions (Martin & Tate 1976).

All hesperornithids are highly adapted for foot-propelled diving (Martin & Tate 1976; Bell & Chiappe 2015a). The specialized articular surfaces of pedal phalanges imply the presence of lobed-feet (at least IVth toe) that function as efficient propellers (Stolpe, 1935; Martin & Tate 1976). Hindlimbs of extant foot-propelled divers are also known to stabilize the body under water. For example, loons extend the toes of inboard foot as a rudder during tight turning (Clifton & Biewener 2018), and extant grebes use the asymmetrically lobed toes as a self-stabilizing multislotted hydrofoil during the power stroke (Johansson & Norberg 2000). The possibly lobed IVth toes of hesperornithids (Marsh, 1880) would function similarly.

Phylogenetic logistic regressions revealed correlated evolution of forelimb (coracoid and humerus) and hindlimb (femur and tarsometatarsus) characters (Table 3.2). The reduction of forelimb is associated with stouter hindlimb to support powerful hindlimb muscles in ornithuromorphs, which were culminated

in hesperornithiforms, adept foot-propelled divers. The robustness of humerus is correlated with wider IVth toes, which means it could be possible that the role of humerus as a self-stabilizer was gradually transferred to the IVth toe through the evolution of decreased flight and increased diving capabilities in ornithuromorphs.

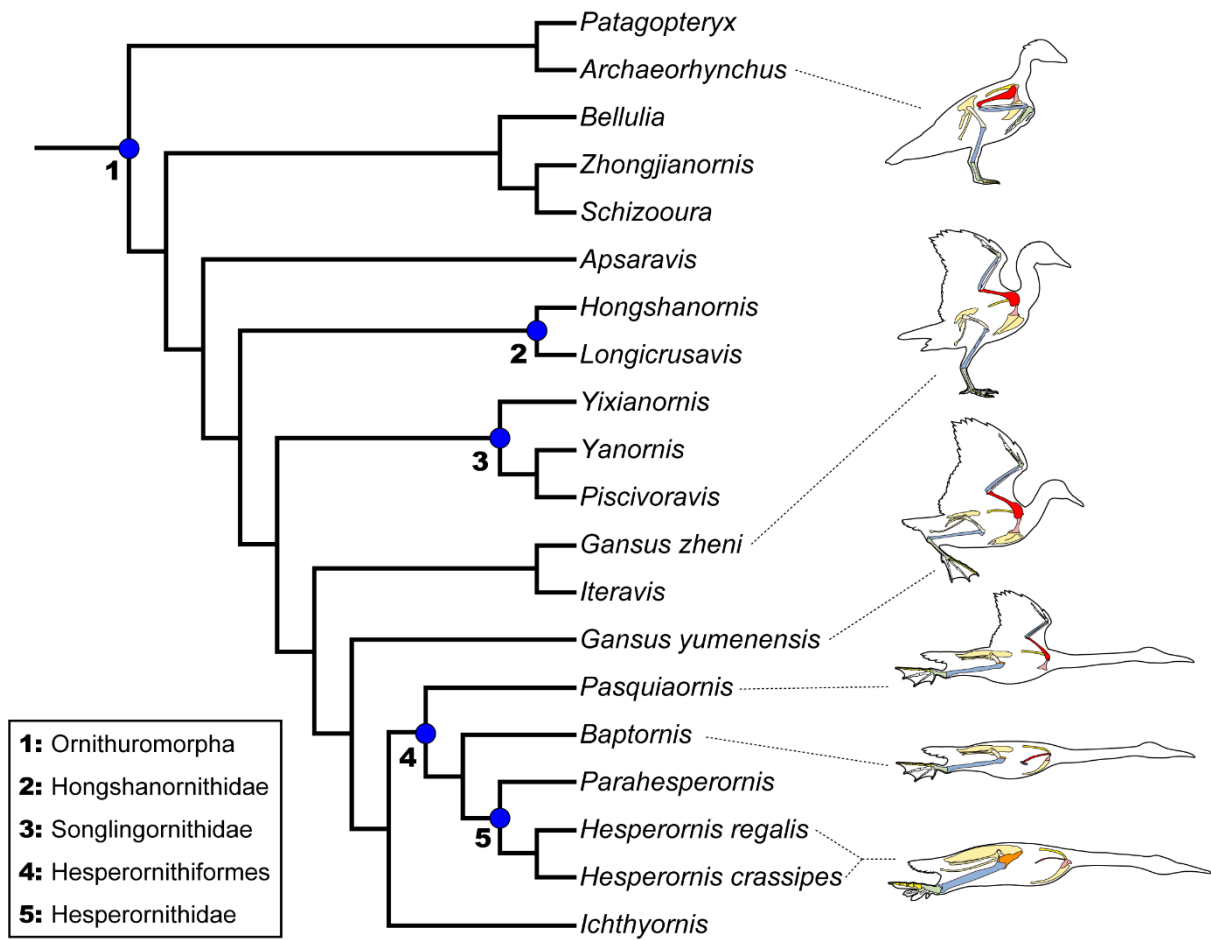


Fig. 3.1 Phylogenetic relationships of Mesozoic ornithuromorphs. Phylogenetic framework is modified from Chapter 1.

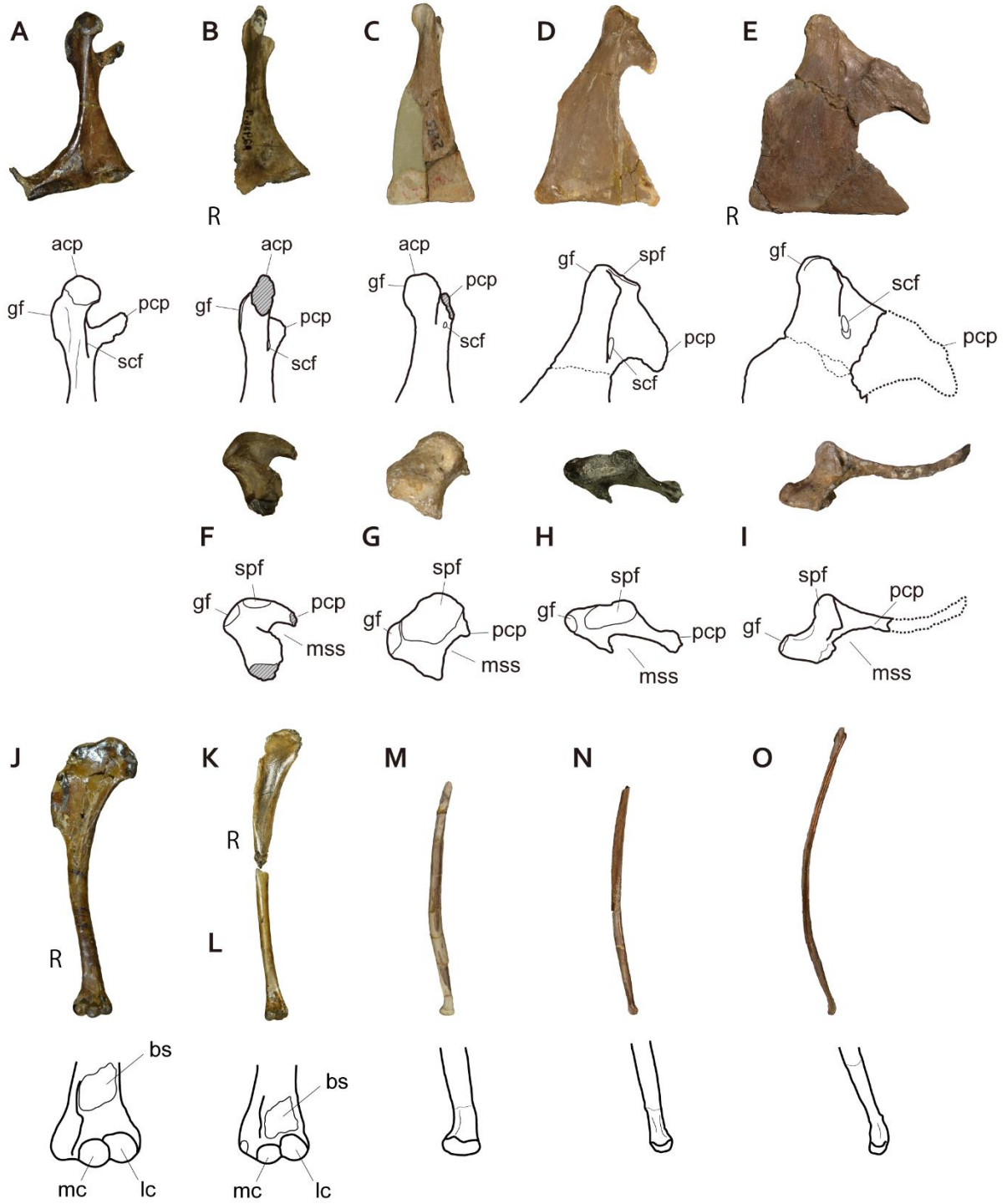


Fig. 3.2 Morphological comparisons of forelimb module. The right coracoid in anterior (**A-E**) and proximal (**F-I**) aspects in: **A**, *Gansus yumenensis* (CAGS 04-CM-004); **B, F**, *Pasquiaornis tankei* (RSM P2988.9); **C, G**, *Baptornis advenus* (KUVVP 2290); **D, H**, *Parahesperornis alexi* (KUVVP 2287) **E, I**, *Hesperornis regalis* (FHSM VP-). The right humerus in anterior (**J-O**) aspects in: **J**, *Gansus yumenensis* (CAGS-04-CM-004); **K**, *Pasquiaornis tankei* (RSM P2989.11 in reverse); **L**, *Pasquiaornis tankei* (RSM P2987.2); **M**, *Baptornis advenus* (KUVVP 2290); **N**, *Parahesperornis alexi* (KUVVP 2287); and **O**, *Hesperornis regalis* (FHSM VP-2069). Abbreviations: acp, acrocoracoid process; gf, glenoid fossa; mss, sulcus *m. supracoracoideus*; pcp, procoracoid process; scf, supracoracoid foramen; and spf, scapular fossa. Figures are not to scale.

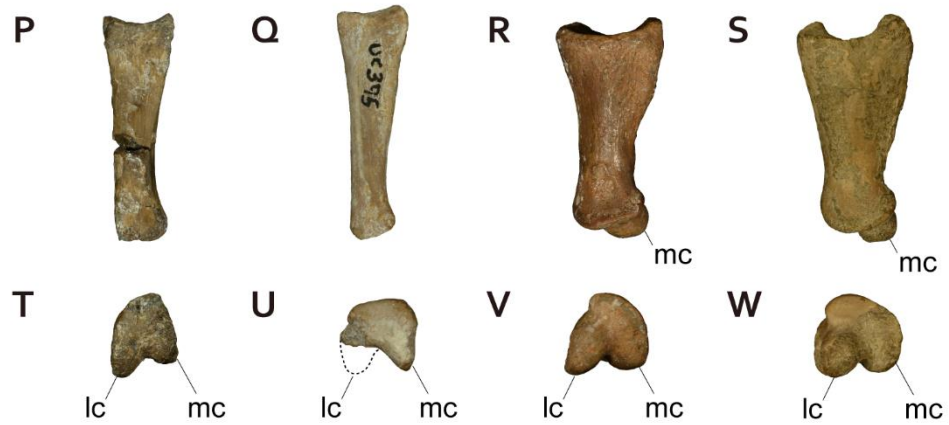
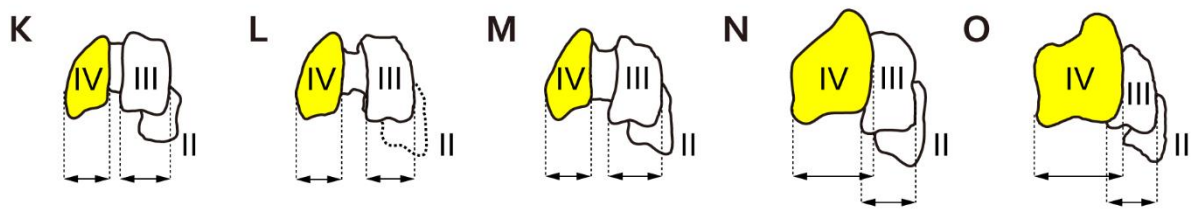
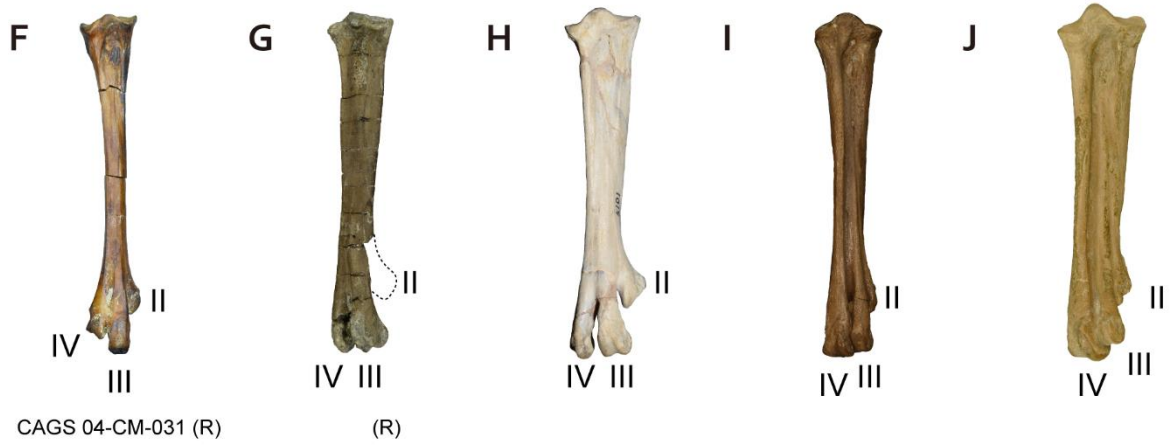
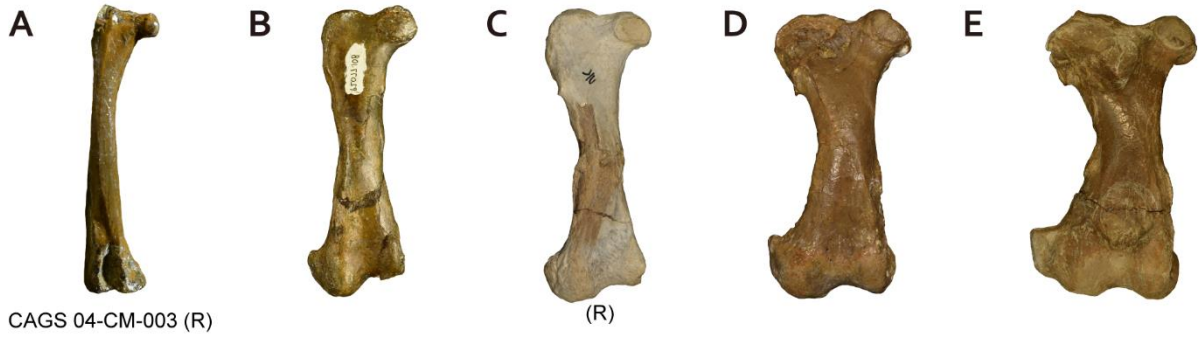


Fig. 3.3 Morphological comparisons of hindlimb module. The right femur in anterior (**A-E**) aspects in: **A**, *Gansus yumenensis* (CAGS 04-CM-003 in reverse); **B**, *Pasquiaornis tankei* (RSM P2077.108 in reverse); **C**, *Baptornis advenus* (KUV P 2290 in reverse); **D**, *Parahesperornis alexi* (KUV P 2287); and **E**, *Hesperornis regalis* (YPM 1200). The right tarsometatarsus in plantar (**F-J**) aspects and line drawing of distal (**K-O**) aspects in: **F, K**, *Gansus yumenensis* (CAGS-04-CM-031 in reverse); **G, L**, *Pasquiaornis tankei* (RSM P2957.27 in reverse); **H, M**, *Baptornis advenus* (AMNH 5101); **I, N**, *Parahesperornis alexi* (KUV P 2287); and **J, O**, *Hesperornis regalis* (YPM 1200). The right phalanx of the IVth digit in medial (**P-S**) and distal (**T-W**) aspects in: **P, T**, *Pasquiaornis tankei* (RSM P2997.68); **Q, U**, *Baptornis advenus* (FMNH UC395); **R, V**, *Parahesperornis alexi* (KUV P 2287); and **S, W**, *Hesperornis regalis* (YPM 1200). Abbreviations: lc, lateral condyle; mc, medial condyle; II, metatarsal trochlea II; III, metatarsal trochlea III; and IV, metatarsal trochlea IV.

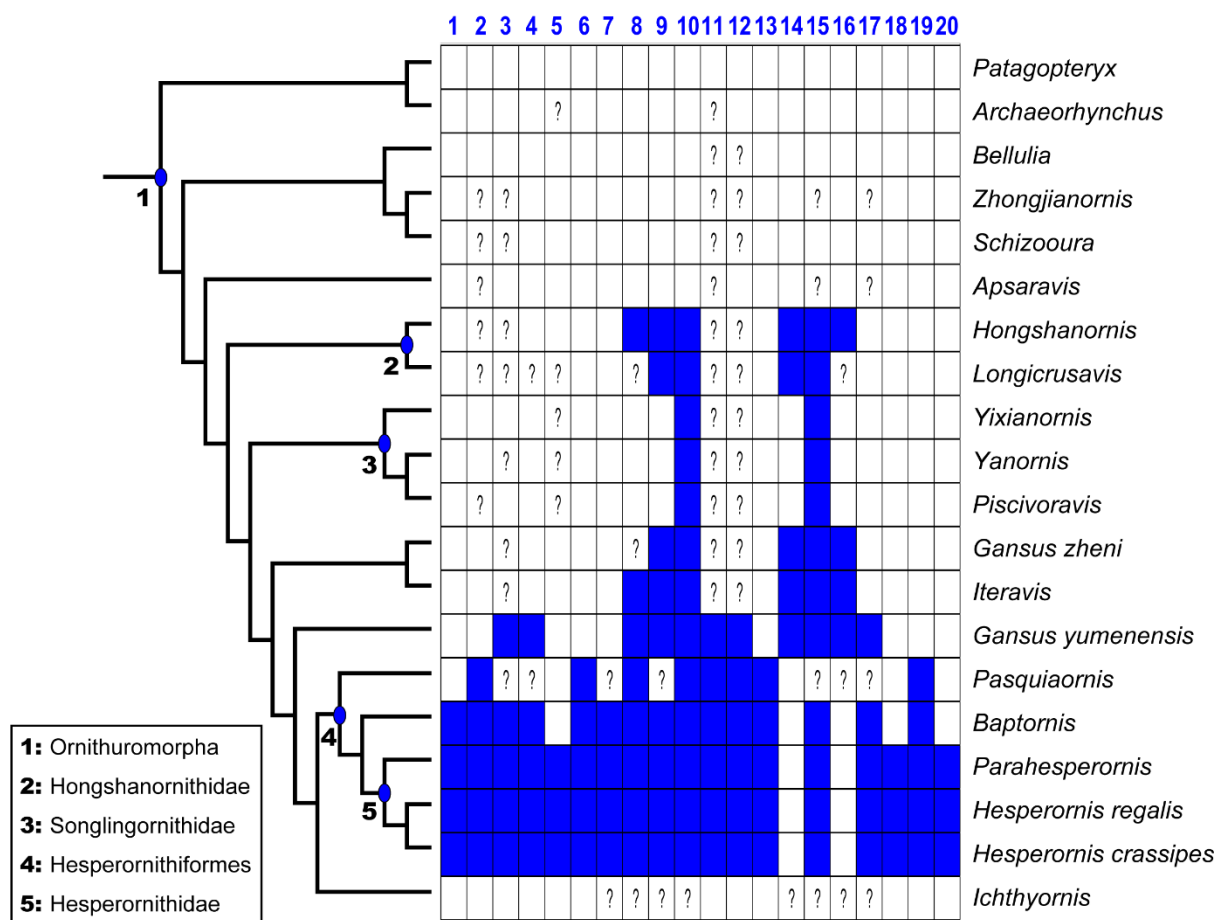


Fig. 3.4 Distribution of 20 characters that are related to aquatic adaptation on the phylogenetic tree of Mesozoic Ornithuromorpha. Character numbers correspond to Table 3.1.

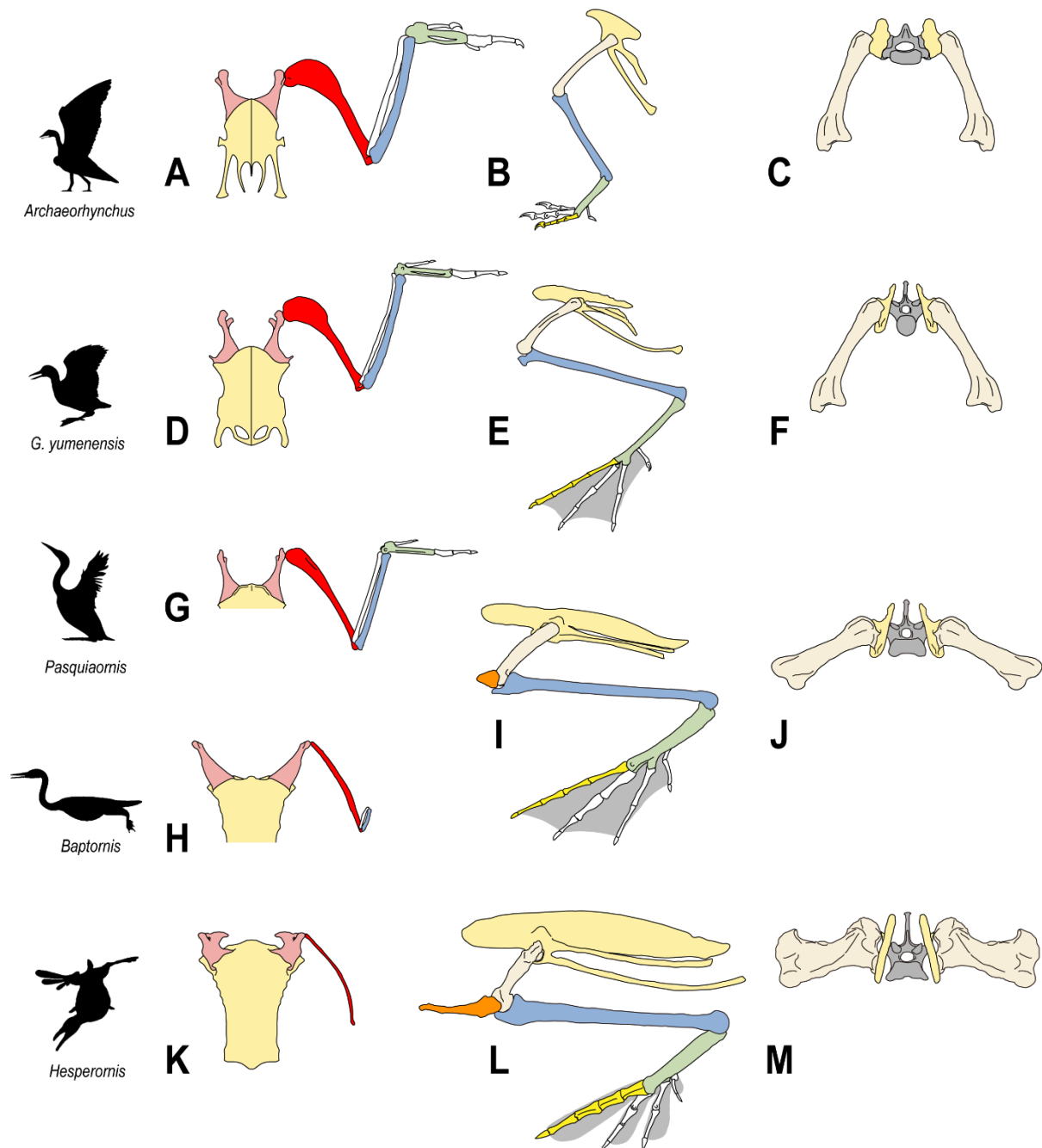


Fig. 3.5 The morphological changes of the forelimb module in anterior (A, D, G, H, K) aspect, the hindlimb modules in left lateral (B, E, I, J) aspect, and the hip and thigh in anterior (C, F, J, M) in: A, B, *Archaeopteryx spatula*; C, *Patagopteryx deferrariisi*; D, E, F, *Gansus yumenensis*; G, *Pasquiaornis tankei*; H, I, J, *Baptornis advenus*; and K, L, M, *Hesperornis regalis*.

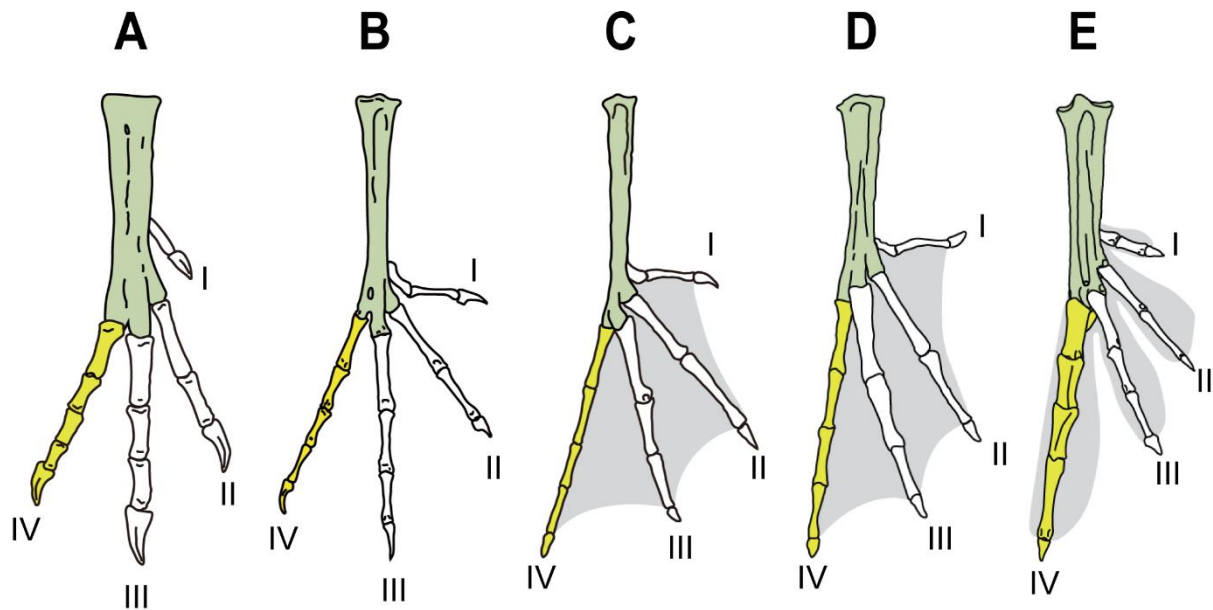


Fig. 3.6 Comparative drawing of the right feet. **A**, *Bellulia rectusunguis*; **B**, *Hongshanornis longicresta*; **C**, *Gansus yumenensis*; **D**, *Baptornis advenus*; and **E**, *Hesperornis regalis*. Grey silhouettes show probable totipalmate webbed-feet for *Gansus* and *Baptornis* and probable lobed-feet for *Hesperornis*. Abbreviations; I, Ist toe; II, IInd toe; III, IIIrd toe; and IV, IVth toe. The tarsometatarsi are shown in green, and the IVth toes are shown in yellow.

Table 3.1 Morphological characters related to aquatic adaptation of foot-propelled diving Ornithuromorpha.

No.	Character descriptions	References	Character number of Appendix 1.1
1	Extremely reduced forelimbs	Marsh 1880; Bell & Chiappe 2015	148
2	Acute antitrochanter	Zinoviev 2011	230
3	Narrow hip	Raikow 1985	231
4	Elongated pelvis	Raikow 1985	223
5	Ossified acetabulum	Zinoviev 2011; Bell & Chiappe 2015	224
6	Short and robust femur	Bell & Chiappe 2015	248, 249, 250, 266
7	Enlarged patella	Heilmann 1926	269
8	Remarkably enlarged rotular process	Livezey 1986	275
9	Elongated tibiotarsus	Clarke 2004	271
10	Elongated tarsometatarsus	Zhou & Zhang 2005	
11	mediolaterally compressed tarsometatarsus	Raikow 1985	
12	Plantar and proximal positioned metatarsal trochlear II	Martin & Tate 1976	330, 332
13	Approximately same distal positioned metatarsal trochlear III and IV	Clarke 2004	317
14	Slender and elongated pedal phalanges	O'Connor et al. 2011	
15	Small pedal claws	Clarke 2004	346
16	Unrecurved unguals with large flexor tubercula	You et al. 2006	
17	The IVth toe is longer than IInd and IIIrd toes	This study	335
18	Ball and socket articular surface of proximal IVth pedal phalanges	Stolpe 1935	336
19	Osteosclerosis	Habib & Ruff 2008	268, 298
20	Pachyostosis	Houssaye 2009	248, 249, 250, 266

Table 3.2 Results of phylogenetic logistic regression analysis. Abbreviation: MTT, metatarsal trochlea.

Character	p. value	AIC	lower bootstrap CI	upper bootstrap CI
Coracoid × Femur	0.03254*	9.875	-1.0922	18.2812
Coracoid × MTT IV/III	0.04975*	7.6179	1.636	9.2555
Humerus × Femur	0.04617*	11.291	-0.90303	17.6917
Humerus × MTT IV/III	0.04921*	12.388	-0.30444	6.9989

CHAPTER 4

A New Small Hesperornithidae from the Pierre Shale

(Campanian) of Manitoba: Body Mass Evolution in the Oldest

Diving Birds

Abstract:

Hesperornithiformes, the oldest diving birds, are the predominant sea-going birds in the Northern Hemisphere during the Cretaceous. While the derived clade Hesperornithidae is well known for several giant taxa, fossil records of small hesperornithids are scarce and limited to isolated remains. Here we describe the first associated skeleton of a new small size hesperornithid MM V-2487 from the Gammon Ferruginous Member (early Campanian) of the Pierre Shale in Manitoba, Canada. Despite of its small size, skeletal maturity of MM V-2487 is suggested by the complete ossification of the tibiotarsus and the tarsometatarsus. The phylogenetic analysis demonstrates that MM V-2487 is a sister taxon of *Hesperornis*. Our regression analyses based on the tarsometatarsus of foot-propelled diving birds revealed that MM V-2487 is one of the smallest Hesperornithidae with

its body mass estimated as 4.54 kg. Its small body mass might have contributed to foraging depth separation with gigantic taxon *Hesperornis* known from the same region, since body mass is one of the key factors affecting diving abilities. Ancestral state reconstruction demonstrates gradual body mass increase in non-hesperornithid Hesperornithiformes and rapid increase in Hesperornithidae in late Santonian to earliest Campanian. The timing is not associated with the starting period of the late Cretaceous global cooling. Instead, the Cretaceous marine high productivities might have been one of the major driving forces of body mass increase on Hesperornithiformes.

Introduction

Hesperornithiformes is a group of highly specialized foot-propelled diving seabirds (Marsh 1880; Chiappe & Dyke 2002) which is known as one of the most dominant birds during the Cretaceous (Galton & Martin 2002). Although the group distributed widely in the Northern Hemisphere of Cretaceous including England, Sweden, Russia, Kazakhstan, Mongolia, and Japan (Seeley 1876; Rees & Lingden 2005; Nesov & Yakov 1993; Kurochkin 2000; Nesov & Prizemlin 1991; Tanaka *et al.* 2017), the majority of the remains have been unearthed from the Western Interior Seaway deposits of North America (Everhart 2017). Among the Western Interior Seaway deposits, the Upper Cretaceous Pierre Shale, a geologic formation that crops out on southwestern Manitoba of Canada and South Dakota of U.S.A. (Fig. 4.1), is known for one of the most diverse Mesozoic marine faunas including that of hesperornithiforms (Nicholls 1989; Nicholls & Russel 1990; Martin & Lim 2002; Martin & Codes-Person 2007; Carpenter 2008; Aotsuka & Sato 2016).

The Pierre Shale hesperornithiforms collected from the Morden-Miami area, southwestern Manitoba, are primarily assigned to genus *Hesperornis* (Nicholls 1989). Later, Martin & Lim (2002) named a new species, *H. mengeli*,

from the Pierre Shale crops out in the same area. A recent study by Aotsuka & Sato (2016) updated the taxonomy of 251 Pierre Shale hesperornithiform remains from the same area. They identified five species of two genera, *H. regalis*, *H. lungairi*, *H. chowi*, *H. macdonaldi*, *H. rossicus*, and *Brodavis* sp., and suggested a higher avifaunal diversity in the area than previously considered. While these works revealed the high diversity of the Pierre Shale hesperornithiformes, phylogenetic analysis was never conducted due to the fragmentally and isolated natures of the bird remains.

Here we describe a new hesperornithiform remains (MM V-2487) from the Pierre Shale in the southwestern Manitoba. MM V-2487 is represented by well-preserved hind limb elements unlike other hesperornithiform remains from the Pierre Shale (Martin & Lim 2002; Aotsuka & Sato 2016). It is also worth noting that MM V-2487 is one of the smallest known Hesperornithiformes (Martin & Lim 2002; Aotsuka & Sato 2016). The relatively well-preserved nature and the small size of MM V-2487 offer a great opportunity to investigate the evolutionary history of hesperornithiform body mass.

Body mass is known to have a positive correlation with diving depth in

lung breathing vertebrates such as extant marine mammals and diving birds (Piatt & Nettleship 1985; Watanuki & Burger 1999; Halsey *et al.* 2006; Chiaradia *et al.* 2007; Wienecke *et al.* 2007). Similarly, body mass is strongly correlated to diving duration in extant foot-propelled diving birds (Cooper 1986; Watanuki & Burger 1999) because heavier animals are capable of making longer breath-hold dives (Kooyman 1992). Furthermore, large diving animals can swim faster and could travel longer distance (Watanabe *et al.* 2011). Therefore, estimating hesperornithiform body mass and reconstructing their body mass evolutionary history is expected to provide insights on transition in their diving ability and accompanied changes in foraging strategies. This study further discusses on possible driving forces of hesperornithiform body mass evolution such as global climate change and marine productivity change, which are the major driving forces of body size evolution on Cenozoic birds (Yom-Tov *et al.* 2006; Clarke *et al.* 2007; Clave & Morlon 2017; Crouch & Clarke 2019).

As such, the main purposes of this study are to (1) describe the newly discovered small hesperornithid skeletal remain from Manitoba in detail and investigate its phylogenetic position, (2) establish a body mass estimation

method for hesperornithiforms, and (3) investigate evolutionary history of hesperornithiform body mass on its phylogenetic framework and speculate on driving force of their body mass evolution.

Geology

MM V-2487 is collected from southwestern Manitoba of Canada (Fig. 4.4.1A, B) by Kevin Conlin, a local fossil collector. This bird skeleton was collected from the Western Interior Seaway deposit in the Vermillion River locality (township 23, range 20 west of the second meridian) of the north flank of Riding Mountain (Fig. 4.1C). The locality belongs to the Gammon Ferruginous Member (lower Campanian), the lowermost member of the Pierre Shale (Campanian to the lower Maastrichtian) (Fig. 4.1D). McNeil and Caldwell (1981) inferred that the age of this member is early Campanian based on biostratigraphy of foraminifera. The Gammon Ferruginous Member is composed of organic-rich grey noncalcareous shale that contains numerous red-weathered ferruginous concretions and sideritic concretions, thin bentonite layers, and clay-rich swelling grey shale (McNeil & Caldwell, 1981; Bamburak & Nicolas, 2010; Bamburak *et al.* 2012). The lower to middle

Gammon Ferruginous Member has produced numerous vertebrate remains including Cretaceous fishes (*Clidastes* and *Xiphactinus*), large mosasaurs, and microvertebrate fossils (fish teeth, scales, and vertebrae) (Bamburak & Nicolas 2010). On the other hand, the upper part of the member has produced several hesperornithiform remains including a gigantic taxon *Hesperornis regalis* and a small taxon *H. macdonalidi*, have previously been reported from (Bamburak *et al.* 2012; Aotsuka & Sato 2016). The lithology, rare earth element concentration, the abnormal concentration of flightless bird fossils, and the palynological analysis of the bentonite layers imply that the sedimentation of the Gammon Ferruginous Member occurred in the shallow pools of a nearshore environment (Bamburak *et al.* 2012).

Material and Methods

Fossil material

The Manitoba specimen described herein (MM V-2487) is a semi-articulated partial skeleton represented by the distal end of the left femur, the right patella, left and right tibiotarsi, distal end of the left tarsometatarsus, proximal end of the right tarsometatarsus, and several pedal phalanges. This

bird remain is housed in the collection of the Manitoba Museum, Winnipeg, Manitoba, Canada. Anatomical nomenclature used here largely follows Baumel & Witmer (1993) using the English equivalent of the Latin term.

Phylogenetic analysis

The method of the present phylogenetic analysis (47 taxa including 10 hesperornithiforms and 349 characters) including MM V-2487 is described in Chapter 1. The character coding of MM V-2487 can be seen in Appendix 1.2.

Body mass estimation

Bell & Chiappe (2015) recently attempted hesperornithiform body mass estimation using an empirical equation based on femoral lengths of extant birds including land birds (Maloiy *et al.* 1979; Prange *et al.* 1979; Alexander & Jays 1983). Here we develop empirical equations based solely on foot-propelled diving birds in order to eliminate any possible biases that originate from the unique locomotion and lifestyles of foot-propelled diving birds (Fjelds  2005). In addition to Phalacrocoracidae (cormorant), recently proposed most appropriate morphological modern analogue of

Hesperornithiformes (Bell *et al.* 2019), this study employs Gaviidae (loons) and Podicipedidae (grebes), the groups traditionally considered as ecological analogues of hesperornithiform (Marsh 1880; Martin & Tate 1976), in order to construct empirical equations for body mass estimation.

Eighty-three skeletal specimens (33 phalacrocoracids, 20 gaviids, and 30 podicipedids) were measured using a digital caliper sensitive to 0.01 mm from the ornithological collections of the Field Museum (Chicago) and the Royal Ontario Museum (Toronto). Only osteological matured specimens, identified based on completely ossified epiphyses of the measured elements, are utilized. All measurements were taken from specimens whose live body mass is recorded in the databases of the responsible museums. For paired materials, the left skeletal element was measured. Prior works generally suggest that body mass is highly correlated with length and circumference (proxy of cross-sectional area) of weight-bearing bones in terrestrial vertebrates (Anderson *et al.* 1985; Campione & Evans 2012; Campione *et al.* 2014). Therefore, following skeletal measurements were taken for each specimen: maximum length of femur (Lf), minimum femur shaft circumference (Cf), maximum length of tibiotarsus (Ltbt), minimum

tibiotarsus shaft circumference (Ctbt), maximum length of tarsometatarsus (Ltmt), proximal transverse (mediolateral) width of tarsometatarsus (PWtmt), proximal sagittal (dorsoplantar) width without hypotarsus of tarsometatarsus (PStmt), transverse width of tarsometatarsal midshaft (MWtmt), and sagittal width of tarsometatarsal midshaft (MStmt) (see Appendix 4.1). Sagittal and transverse widths of the proximal end of the tarsometatarsus are utilized as the proxy of cross-sectional area of the element since circumference cannot be measured accurately due to the irregular morphology at the midshaft.

Prior to statistical analyses, all raw measurement data were log 10 transformed. Single regression analyses for Lf, Cf, Ltbt, Ctbt and Ltmt and multiple regression analyses for Lf+Cf, Ltbt+Ctbt, Ltmt+PWtmt+PStmt, MWtmt+MStmt, and PWtmt+PStmt were conducted using statistic software JMP Pro 14.0.0 (SAS Institute Inc., Cary, NC, USA). The best fit equation was determined based on R square value, the percent prediction error (PPE), and Akaike's information criterion (AIC) values following Campione *et al.* (2014). We also provided the variance inflation factor (VIF) for each explanatory variable of multiple regression analyses.

Using the scaling equation derived from extant foot-propelled diving bird data (see Appendix 4.2), body mass of nineteen hesperornithiform taxa and *Gansus yumenensis* (volant non-hesperornithiform foot-propelled diving bird; You *et al.* 2006; Nudds *et al.* 2013; Wang *et al.* 2015) were estimated. The hesperornithiforms whose weight-bearing bones are not preserved (e.g. *Chupkaornis keraorum* and *Canadaga arctica*) are excluded from this analysis. The measurements are taken by the first author except for *Brodavis mongoliensis* and *Asiahesperornis bazhanovi* which were taken from Martin *et al.* (2012) and Dyke *et al.* (2006), respectively.

Ancestral state reconstruction

Subsequent to the body mass estimation, parsimony based ancestral state reconstruction of the estimated body masses was conducted using the software Mesquite version 2.75 (Maddison 2008). In order to investigate a finer-scale evolutionary history of hesperornithiform body mass, a combined tree was constructed based on the present phylogenetic framework of hesperornithiforms. The taxa whose phylogenetic positions are ambiguous are added to the combined tree by grouping to their corresponding genus:

Enaliornis barretti in *Enaliornis*, *Pasquiaornis tankei* and *P. hardiei* in *Pasquiaornis* (the clade Pasquiaornithidae), *Brodavis varneri* and *B. mongoliensis* in *Brodavis* (the clade Brodavidae), and *Hesperornis mengeli*, *H. bairdi*, *H. lumgairi*, *H. chowi*, and *H. rossicus* in *Hesperornis*. *Asiahesperornis bazhanovi* is excluded from the analysis since their phylogenetic positions are under debates (Dyke *et al.* 2006). The branch lengths of the combined tree are calculated following the method provided by Brusatte (2011).

Institutional abbreviations. **AMNH**, American Museum of Natural History, New York, USA; **CAGS**, Chinese Academy of Geological Sciences, Beijing, China; **CAMSM (SMC)**, Sedgwick Museum of Earth Sciences, The University of Cambridge, Cambridge, England; **CFDC**, Canadian Fossil Discovery Centre, Morden, Manitoba, Canada; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **IGM**, Institute of Geology, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **IZASK**, Institute of Zoology, Ministry of Science and Education, Almaty, Kazakhstan; **KUVP**, The

University of Kansas, Vertebrate Paleontology, Museum of Natural History, Lawrence, Kansas, USA; **NHMUK (BMNH)**, British Museum of Natural History, London, England; **PIN**, Borissjak Paleontological Institute of the Russian Academy of Sciences; **RSM (SMNH)**, Royal Saskatchewan Museum, Saskatchewan, Canada; **SDSM**, Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota, USA; **SGU**, Geological Survey of Sweden, Uppsala, Sweden; **SMNH**, Sternberg Museum of Natural History, Hays, Kansas, USA; **MM**, the Manitoba Museum, Winnipeg, Manitoba, Canada; **UNSM**, University of Nebraska state Museum, Lincoln, Nebraska, USA; **YPM**, Yale Peabody Museum, New Haven, Connecticut, USA.

Systematic Paleontology

AVIALAE Gauthier 1986

ORNITHUROMORPHA Chiappe 2002

Order HESPERORNITHIFORMES Fürbringer 1888

Family HESPERORNITHIDAE Marsh 1872

Locality and horizon. Riding Mountain region, Vermillion River, Manitoba, Canada; Gammon ferruginous Member (lower Campanian), Pierre Shale.

Diagnosis. A hesperornithid Hesperornithiformes with single unique character: a strong groove for *m. ambiens* on anterior surface of the patella. Also diagnosed by the unique combination of following characters: remarkably flat femur with strong lateral orientation of fibular condyle, an anteriorly positioned foramen for *m. ambiens* of the patella in medial view, a prominent intercondylar eminence on tarsometatarsus, and trochlea IV positioned slightly further than trochlea III.

Description

Femur. Distal end of left femur is preserved (Fig. 4.2). The fibular condyle is expanded laterally (Fig. 4.2A) as in other hesperornithiforms as well as modern foot-propelled diving bird loons and grebes (Cracraft 1982). The distal end of the femur is compressed anteroposteriorly, giving it a remarkably flat appearance (Fig. 4.2E). The fibular trochlea is wide and showing a remarkable lateral orientation (Fig. 4.2E). On the anterior distal surface, the

patellar groove is present and is interrupted distally by a slight ridge (Fig. 4.2A) as in other hesperornithids (*Parahesperornis*, *Hesperornis*, and *Asiahesperornis*). The medial condyle is kidney-shaped in posterior view (Fig. 4.2B). The popliteal fossa is present on the posterior distal surface. The fossa is distally bordered by transverse ridge that connects the medial and the lateral condyles (Fig. 4.2B). In distal view, the lateral condyle of the femur has the distinct fossa for attachment of the *m. tibialis cranialis* (Fig. 4.2E). The transverse width of the distal end of the femur is slightly larger than that of *H. macdonaldi* (LACM 9728) (Table 4.2).

Patella. Proximal end of the right patella is preserved (Figs 4.3A–E). The patella is anteroposteriorly compressed triangular in shape as in *Parahesperornis* and *Hesperornis* (Figs 4.9B, D), but differs from the short, trihedral patella of *Baptornis advenus* (KUV 2290) and *Fumicollis hoffmani* (UNSM 20030) (Fig. 4.9A). Its articular facet for the lateral condyle of the femur bears a single concavity as in *Parahesperornis* and *Hesperornis* (Martin and Tate 1976). The foramen for the tendon of the *m. ambiens* at the medial surface of the patella is present, even though its cranial margin is not preserved (Fig. 4.3D). The foramen is as large as those of *B. advenus* (KUV

2290), *F. hoffmani* (UNSM 20030), and *Parahesperornis alexi* (KUVP 2287) (Figs 4.9A–C), differing from the small foramen of *Hesperornis regalis* (YPM 1200) (Fig. 4.9D). At the anterior surface, a deep groove for the *m. ambiens* is present (Fig. 4.3A), which is unique in *MM V-2487*. The patella of *MM V-2487* is smaller than those of *P. alexi* (KUVP 2287) and *H. regalis* (YPM 1200) but is larger than that of *F. hoffmani* (UNSM 20030) (Table 4.2).

Tibiotarsus. Both left and right tibiotarsi are nearly complete except for the proximal end of right and the cnemial crest of the left tibiotarsus (Fig. 4.4). Both lateral and medial articular surfaces at the proximal surfaces are strongly inclined laterally (Fig. 4.4B). The medial articular surface is slightly concave, while the lateral articular surface is convex and well rounded (Fig. 4.4D). The cranial cnemial crest is low and the intercnemial groove is shallow and broad (Fig. 4.4I). In the proximal view, the tibial incision is deep as in that of other hesperornithids (Fig. 4.4I). In the lateral surface of shaft, the fibular crest is present (Figs 4.4A, B, E, F). The proximal tarsals (the astragalus and the calcaneum) are completely fused to the distal end of the tibia. In distal view, both lateral and medial condyles extend anteriorly, forming a deep anterior intercondylar groove (Figs 4.4J, K). The posterior

intercondylar groove is also deep unlike in *Parahesperornis alexi* (KUVVP 2287) and *Hesperornis regalis* (YPM 1200). The lateral condyle is more anteriorly extended than the medial condyle does (Figs 4.4J, K). The posterior intercondylar groove is well developed (Figs 4.4J, K). The lateral condyle is slightly more expanded mediolaterally and anteroposteriorly than the medial condyle. In lateral view, the lateral condyle exhibits half-moon shape (Figs 4.4D, G), which is a synapomorphy of hesperornithids. The extensor groove is exposed anteriorly without the supratendinal bridge (Figs 4.4A, E), which is a common condition in Mesozoic birds (Clarke 2004). The distal shaft of the left tibiotarsus curves anteriorly but is straight in the left tibiotarsus (Figs 4.4G, H).

Fibula. Proximal end of the left and partially eroded mid-shaft of the right fibulae are preserved (Figs 4.5A–D). The articular surface for the fibular crest of the right tibiotarsus is present on posterior proximal surface of the middle shaft. In medial and lateral views, the head is rectangular (Figs 4.5A, B) as in other hesperornithiforms. The posterior edge of the proximal head hangs over the shaft (Figs 4.5A, B). A deep depression is present on the ventral surface of the posteriorly overhanging head (Figs 4.5A, B). This feature

resembles to *Parahesperornis alexi* (KUVP 2287) and *Hesperornis regalis* (YPM 1200) but differs from *Pasquiaornis* (RSM P.2985.35) and *Fumicollis hoffmani* (UNSM 20030).

Tarsometatarsus. Right tarsometatarsus is nearly complete other than the distal end while the distal end of the left tarsometatarsus is preserved (Fig. 4.6). Compared to *Hesperornis regalis* (YPM 1200), the tarsometatarsus of *MM V-2487* is slender and is compressed mediolaterally. The distal tarsals and metatarsals are completely fused, forming a true tarsometatarsus. The dorsolateral ridge on the dorsal surface of metatarsal IV is well defined and extends to the trochlea IV (Fig. 4.6A). This is one of the unique characters of Hesperornithidae. A distinct groove runs proximodistally along the dorsal surface of the shaft (Fig. 4.6A). The proximal foramens are unclear due to preservation condition. The intercotylar eminence is remarkably projected and inclined laterally in dorsal view (Fig. 4.6A) unlike in *P. alexi* (KUVP 2289) (Figs 4.10G, I). The hypotarsus is absent and the plantar surface of the proximal end bears a flat hypotarsal area (Fig. 4.6B). The medial and lateral cotylae are ovoid shaped in proximal view (Fig. 4.6I) and they are approximately equal in size. The lateral and medial cotylae are inclined

dorsally (Figs 4.6C, D). In dorsal view, the proximal articular surface is inclined laterally as in *H. regalis* (YPM 1200) and *H. chowi* (YPM PU 17208), but the angle is not as steep as in *H. bairdi* (YPM PU 17208A) and *Asiahesperornis bazhanovi* (IZASK 1/KM 97). The outline of the proximal articular surface is rounded in proximal view (Fig. 4.6I) as in *H. mengeli* (CFDC B.78.01.08) and *H. lungairi* (CFDC B.78.02.07), but differs from the quadrilateral outlines of *P. alexi* (KUV 2289), *H. regalis* (YPM 1200), *H. chowi* (YPM PU 17208), *H. gracilis* (YPM 1473), *H. bairdi* (YPM PU 17208A), and *A. bazhanovi* (IZASK 1/KM 97). A deep and ovoid fossa for metatarsal I is present on the medial surface of the shaft (Fig. 4.6B).

In the distal end, the metatarsal trochlea II is positioned farthest proximally (Fig. 4.6E) as in *Gansus yumenensis* (CAGS-04-CM-031) and other Hesperornithiformes. The metatarsal trochlea IV is remarkably larger and wider than the metatarsal trochleae II and III (Fig. 4.6K). It is slightly more extended distally than the metatarsal trochlea III as in *P. alexi* (KUV 2289) (Figs 4.10H, J). Lateral twist of the metatarsal trochlea IV is weaker than that in *H. regalis* (YPM 1200). The distal foramen is located in between the metatarsal trochleae III and IV (Fig. 4.6E). The intertrochlear incision

between the metatarsal trochleae III and IV is enclosed (Fig. 4.6E) and exhibits tear-drop shape in plantar view (Fig. 4.6F) as seen in *Fumicollis*, *Parahesperornis*, and *Hesperornis*. In distal view, the metatarsal trochlea II is displaced plantarly in respect to the metatarsal trochleae III and IV and is triangular shaped (Fig. 4.6K). The former character is seen in all hesperornithiforms, while the latter is unique to hesperornithids.

Pedal phalanges. The first phalanx of right IVth toe, the second phalanx of left IVth toe, the third phalanx of left IIIrd toe, and the first phalanx of left IInd toe are preserved (Fig. 4.7). The first phalanx of right IVth toe (IV-1) is short and stout (Figs 4.7A–F). Its proximal end is somewhat compressed laterally, and there are two cotylae on the proximal articular surface, separated by a ridge that runs dorsoplantarly (Fig. 4.7D). The medial cotyla is larger than the lateral cotyla. The shaft of the bone is rounded on the dorsal surface. The plantar surface possesses a remarkably high flange and a deep plantar groove (Fig. 4.7F). The distal articular surface is sub-triangular in distal view (Fig. 4.7B). Its lateral trochlea is greatly hypertrophied and enlarged much more distally than its medial trochlea, giving it a rounded peg-like appearance (Fig. 4.7B). These characters are common in other

hesperornithids. On the other hand, distal articular surface of the IV-1 toe in *Pasquiaornis tankei* (RSM P.2997.68) and *Baptornis advenus* (FMNH UC 395) is ginglymoid with the equally sized medial and lateral trochleae that are arranged in parallel.

The second phalanx of the left IVth toe (IV-2) (Figs 4.7G–L) resembles in size and proportion to the right IV-1, except for the proximal articular surface which is rounded rather than laterally compressed. The proximal articular surface has a well-developed lateral cotyla and a less developed medial cotyla (Fig. 4.7J). The medial cotyla is a deep cavity for articulation with the peg-like medial trochlea of the preceding phalanx (Fig. 4.7J). The plantolateral surface of the IV-2 bears a deep plantar groove that runs proximodistally (Fig. 4.7L). A prominent flange that reaches the medial trochlea runs along the lateral surface (Fig. 4.7K). The medial surface of the shaft is well rounded. Distally, the lateral trochlea is greatly hypertrophied and expanded dorsoplantarly while the peg-like rounded medial trochlea is protruded distally (Fig. 4.7H) as in the IV-1 toe.

The third phalanx of left IIIrd toe (III-3) is mediolaterally compressed (Figs 4.7M–R), especially at its distal end. The proximal articular surface is

subcircular in outline. It does not have distinct medial and lateral cotylae (Fig. 4.7P). The plantar surface of the shaft gradually tapers distally. The distal articular surface does not have distinct medial and lateral trochleae (Fig. 4.7N).

The first phalanx of left IIInd toe (II-1) is slender than the IV-1 and IV-2 (Fig. 4.7S–X). The proximal articular surface is triangular in outline (Fig. 4.7V). The medial and lateral cotylae are separated by a distinct vertical ridge which runs dorsoventrally. The lateral cotyla is slightly larger than the medial cotyla. The shaft gradually tapers distally (Fig. 4.7U). A shallow plantar groove runs proximodistally on the plantar surface (Fig. 4.7W). The distal articulation facet is ginglymoid (Fig. 4.7T) unlike the phalanges of the IVth toe. The medial trochlea is slightly larger than the lateral trochlea.

Results

Phylogenetic analysis

The present phylogenetic analysis produced a two most parsimonious tree with 777 steps (consistency index = 0.58, retention index = 0.79) (see Chapter 1, Fig. 1.5). This analysis recovered MM V-2487 as a member of

Hesperornithidae, more derived than *Parahesperornis alexi* and more basal than the clade of *Hesperornis regalis* + *H. gracilis*. Hesperornithiformes is recovered as a monophyletic clade supported by 15 synapomorphies. The derived clade Hesperornithidae is supported by 35 synapomorphies (Fig. 1.7, node 7). The complete synapomorphy list of the most parsimonious tree with corresponding node numbers is provided in Appendices 1.3.

The clade of MM V-2487 and *Hesperornis* (Fig. 1.7, node 8) is supported by following three unambiguous synapomorphies: the strong lateral orientation of the fibular condyle of the femur (Figs 4.8E, F; character 259:1); the remarkably flat femur (Fig. 4.8E; character 267:0); and the high and sharp intercotylar eminence of the tarsometatarsus (Figs 4.10I, K; character 305:2). MM V-2487 is distinguished from the clade of *H. regalis* and *H. gracilis* which is supported by following four unambiguous synapomorphies (Fig. 1.7, node 9): the distally extended lateral condyle of the femur past the medial condyle (character 257:1); the remarkably concave lateral surface of the fibular condyle (Fig. 4.8F; character 260:1); the foramen for *m. ambiens* of the patella located at the center of the patella (Fig. 4.9C; character 270: 1), and the distal extension of the metatarsal trochlea IV of the tarsometatarsus

past the metatarsal trochlea III (Fig. 4.10L; character 317:3).

Body mass estimation

In the present analyses, the seven single regression analyses (Fig. 4.11, Table 4.3) and the five selective multivariate regression analyses (Fig. 4.12, Table 4.4) demonstrate correlations between linear measurements of extant bird skeletons and the body masses ($p < 0.0001$). VIF values are lower than 10 in all the multivariate regression analyses except for the analysis based on Ltmt+PWtmt+PStmt (Table 4.4). Among the regression analyses conducted, the multivariate analysis based on PWtmt+PStmt as the predictor represents the best fit ($R^2 = 0.95$, PPE = 16.8, AIC = -132) over the other analyses (Table 4.4). Analyses with Ltmt+PWtmt+PStmt, Ltbt+Ctbt, and Ctbt also demonstrate good fits, whereas those with element lengths as the predictor (Lf, Ltbt, Ltmt) have the lowest fits.

The body masses of Mesozoic foot-propelled diving bird including nineteen hesperornithiforms and *Gansus yumenensis* were estimated based on the empirical equations (Appendix 4.3). Estimations based on the best fit equation (PWtmt+PStmt) (Table 4.5) demonstrates that the EBM of

hesperornithiforms has a large range from 0.72kg of *Pasquiaornis hardiei* (RSM P2077.117), to 42.66kg of *Hesperornis rossicus* (SGU 3442 Ve01), with the average of 13.72kg (standard deviation: 12.94). While members of Hesperornithidae have high EBM with average of 20.39kg (Table 4.5), the EBM of MM V-2487 is 4.54kg (Table 4.5). This is the lowest value among the hesperornithids estimated herein other than *H. mengeli* (3.49kg, CFDC B.78.02.07).

Ancestral body mass reconstruction

Ancestral state reconstruction utilizing the EBM values based on PWtmt+PStmt suggest that Hesperornithiformes evolved from an ancestral lineage with a reconstructed body mass of 1.85 kg (Fig. 4.14). The estimated ancestral body mass of Pasquiaornithidae is 2.64kg, Brodavidae is 8.04kg, and the Hesperornithidae is 13.83kg (Fig. 4.14).

Discussion

Morphology of MM V-2487 and Anatomical Comparison

Although MM V-2487 is smaller than most of the known hesperornithids

(Table 4.5), the completely ossified distal end of the tibiotarsus and the proximal end of the tarsometatarsus, together with the relatively small nutrient foramen of the tibiotarsus (Fig. 4.4B), indicate that MM V-2487 was osteologically matured at the time of its death (e. g. Watanabe 2018). MM V-2487 is morphologically unique in having a strong groove for *m. ambience* on anterior surface of the patella. This character is not seen in any other hesperornithiforms. Additionally, MM V-2487 have unique combination of following characters: the anteriorly positioned foramen for *m. ambience* on medial aspect of the patella (Fig. 4.9), shared with *Baptornis advenus*, *Fumicollis hoffmani*, and *Parahesperornis alexi*; the remarkably flat femur with a strong lateral orientation of the fibular condyle (Fig. 4.8) and a prominent intercondylar process of the tarsometatarsus (Fig. 4.10), shared with *Hesperornis regalis* and *H. gracilis*; and the distally positioned metatarsal trochlea IV relative to the metatarsal trochlea III (Fig. 4.10), shared with *Parahesperornis*.

MM V-2487 also shows morphological differences with previously known small hesperornithid taxa, *H. mengeli* and *H. macdonaldi*, in which phylogenetic relationships cannot be investigated due to their incompleteness

(Martin & Lim 2002). MM V-2487 differs from *H. mengeli* in the flared and pointed medial and lateral ridges of the proximal end of the tarsometatarsus (Fig. 4.13A) and the medially expanded metatarsal trochlea II (Fig. 4.13C). MM V-2487 also differs from the type specimen of *H. macdonaldi* (LACM 9728) in the remarkably flat femur, in which the anteroposterior width of medial condyle is only 41% of the width of the distal end, while the ratio is 47% in *H. macdonaldi* (LACM 9728). The strong lateral orientation of the fibular trochlea (Fig. 4.13E) of MM V-2487 also differs from *H. macdonaldi* (LACM 9728). These differences show that MM V-2487 is a unique hesperornithid distinct from the previously known small sized hesperornithid.

Body mass estimation of foot-propelled diving birds

The better fits in proxies for the cross-sectional area over bone length demonstrated in the present analyses are concordant with the trend in terrestrial extant birds and mammals (Campione & Evans, 2012). On the other hand, the better fits in the distal elements than the proximal elements differ from the trend in extant volant birds (Field *et al.* 2013). Unlike volant birds, most foot-propelled diving birds spend most of their lives in water thus

their hind limbs are liberated from the stress of supporting body weight on ground. On the other hand, the underwater paddling locomotion, which is mainly performed by autopodium without much move of femora and tibiotarsi (Willcox 1952; Zinoviev 2011), might be putting continuous stress mainly on tarsometatarsus. Therefore, the unique ecology may have resulted in relative high stress on tarsometatarsus among hind limb elements. The best fit in PWtmt+PStmt may be reflecting the unique hind limb stress distribution of foot-propelled diving birds, although further investigation is mandatory to reveal the mechanism.

Diving Ability of MM V-2487

Multiple osteological features of MM V-2487 suggest that it was highly adapted for powerful swimming as in other hesperornithids. Its remarkably deep tibial incision of proximal end of the tibiotarsus (Fig. 4.4I) implies presence of a well-developed *m. tibialis cranialis*, which functions for dorsal flexion of the intertarsal joint during the recovery stroke. The intertarsal joint have wide range of motion as in *Hesperornis regalis*, indicating presence of well-developed menisci for supination of the tarsometatarsus as in

Gaviiformes but unlike Podicipediiformes (Zinoviev 2011). The phalanges of IVth toe have peculiar distal articular surfaces (Fig. 4.6B; the elongated medial trochlea and the rounded, peg-like projected lateral trochlea) for toe-rotation as in Podicipediiformes (Stolpe 1935; Fjeldså 2005). The specialized articular surface of the IVth toe may suggest that *MM V-2487* had lobed feet as in Podicipediiformes (Zinoviev 2011), which allows speedy and energy efficient lift-based paddling (Johansson & Lindhe Norberg 2001).

Despite of these osteological features that provide *MM V-2487* high ability to swim, its relatively light body mass among hesperornithids (Table 4.5) was a disadvantage for diving, since larger body mass improves diving duration (Piatt & Nettleship 1985; Burger 1991). The combination of high swimming ability and low diving ability might have allowed *MM V-2487* to forage for target resources mainly in shallow water, where food-resources were abundant (Furness & Monaghan 1987) but buoyance would increase thus the energy expenditures would be high (Wilson *et al.* 1992). The powerful hind limb of *MM V-2487* may have effectively utilized for working against the high buoyance during underwater locomotion in shallow water. Therefore, the small hesperornithid *MM V-2487* was likely to have inhabited mainly in

shallow water. Its inhabitation in shallow water was likely to be beneficial for spatial niche partitioning with the giant hesperornithids of the Gammon Ferruginous Member, *H. regalis* or *H. chowi* (Aotsuka & Sato 2015), which is likely to have hunted their targets in deeper water where buoyance is low and could spend their energy for searching, capturing, and manipulating prey during long breath holding diving enabled by large body mass.

Evolutionary history of Hesperornithiform Body Mass

Notably, the ancestral state reconstruction demonstrates that the ancestral body mass increased gradually in the initial stage of hesperornithiform evolution, and it increase abruptly in Hesperornithidae during Santonian to early Campanian (Fig. 4.14). Although global cooling is considered as a major factor that accelerated body size evolutionary rate in Cenozoic Neornithes and mammals (Clavel & Morlon 2017) and caused gigantism of Paleognathae (Crouch & Clarke 2019), it is unlikely the case in hesperornithiforms since the timing of their body mass increase does not match with the starting period of the late Cretaceous global sea surface cooling which begun in Coniacian (Fig. 4.14; O'Brien *et al.* 2017). The absence of clear correlation between body

size and temperature in North American hesperornithiforms (Wilson *et al.* 2011) also supports the assumption that hesperornithiforms body mass evolution was not sensitive to their surrounding temperatures unlike majority of the Cenozoic avian groups.

Instead, hesperornithid body mass increase may be triggered by increased ocean productivity. The occurrences of remarkably large hesperornithiforms (*Hesperornis regalis*, *H. rossicus*, *H. rossicus*, and *Asiahesperornis*) are limited only to the deposits of epicontinental seas where ocean productivity is higher than open seas (Diaz & Rosenberg 2008). These epicontinental seas developed as a result of sea level rise completed in early Campanian (Haq 2014), which is concordant with the occurrence ages of the remarkably large hesperornithids. For instance, previous works suggested that Cenozoic flightless diving seabird Sphenisciformes and large marine reptile mosasaurs are also considered to have established large body mass triggered by increase in ocean productivity (Clarke *et al.* 2007; Polcyn *et al.* 2014). Therefore, although further investigations on the interactions of physiological and ecological factors are mandatory, we hypothesize that the abundant food resources in the late Cretaceous epicontinental sea is one of

the major driving forces of hesperornithiform body mass evolution.

Conclusion

A new hesperornithiform, MM V-2487 from the Late Cretaceous of south Manitoba, Canada, is described herein. This specimen is the best-preserved bird remains in the Pierre Shale of the Morden-Manitoba region. The phylogenetic analysis recovers MM V-2487 as a member of Hesperornithidae more derived than *Parahesperornis alexi* and a sister taxon of *Hesperornis*.

The body mass estimation based on the linear measurements of tarsometatarsus of extant foot-propelled diving birds suggested that the estimated body mass of MM V-2487 is 4.54kg, indicating that this new small sized hesperornithiform is one of the smallest Hesperornithidae. Its small body mass and the body plan adapted for powerful swimming are likely to allowed MM V-2487 shallow water inhibition, which might have contributed to spatial niche partitioning with sympatric giant taxa *Hesperornis regalis*.

Ancestral body mass reconstruction in the phylogenetic framework suggests a gradual body mass increase in non-hesperornithid hesperornithiforms and a rapid body mass increase within the clade of

Hesperornithidae. The timing of abrupt body mass increase in hesperornithiforms is not associated with the late Cretaceous global cooling unlike in Cenozoic Neornithes and mammals. On the other hand, the Cretaceous marine high productivities might have been one of the major driving forces of the hesperornithiform body mass increase.

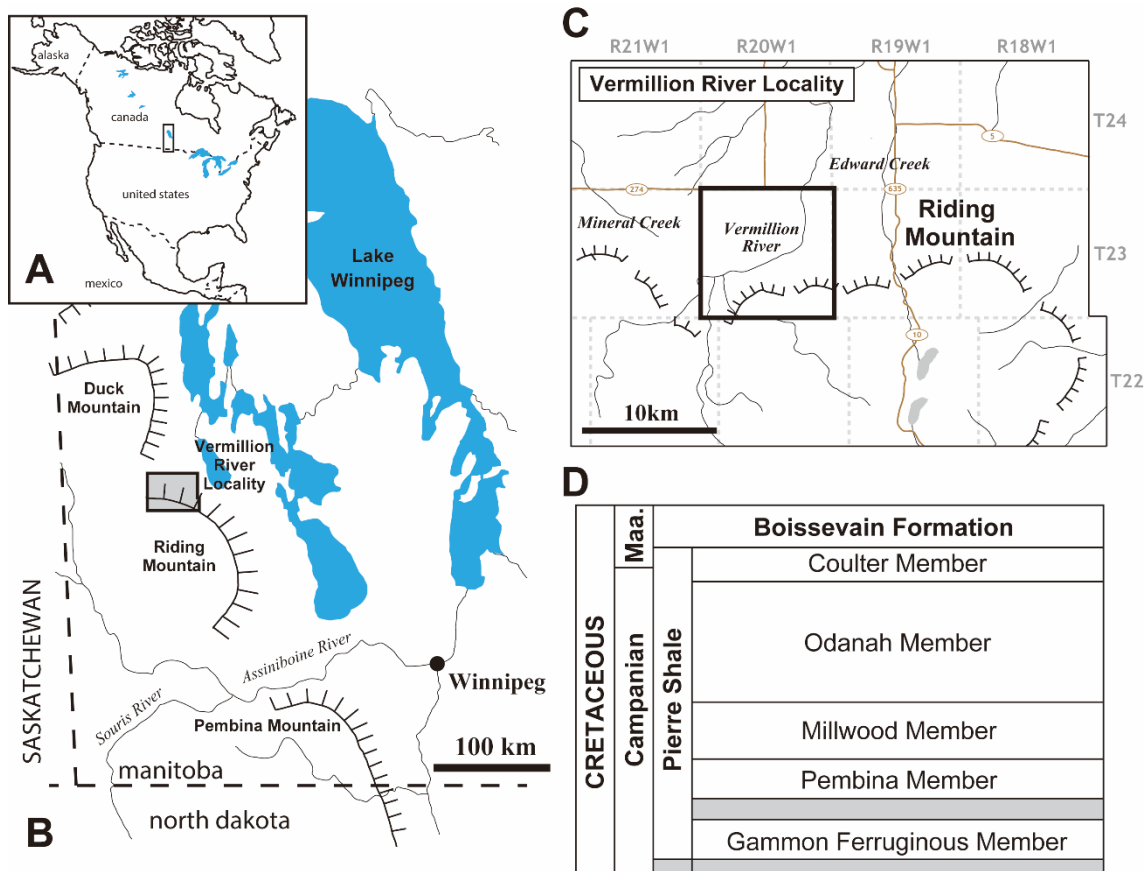


Fig. 4.1 Locality maps of MM V-2487. Map of **A**, the North America and **B**, the Manitoba Escarpment, modified from Schroder-Adams *et al.* (2001). **C**, Black square indicate that the Vermillion River locality, modified from Bamburak & Nicolas (2010). **D**, the local stratigraphy based on Bamburak & Nicolas (2010).

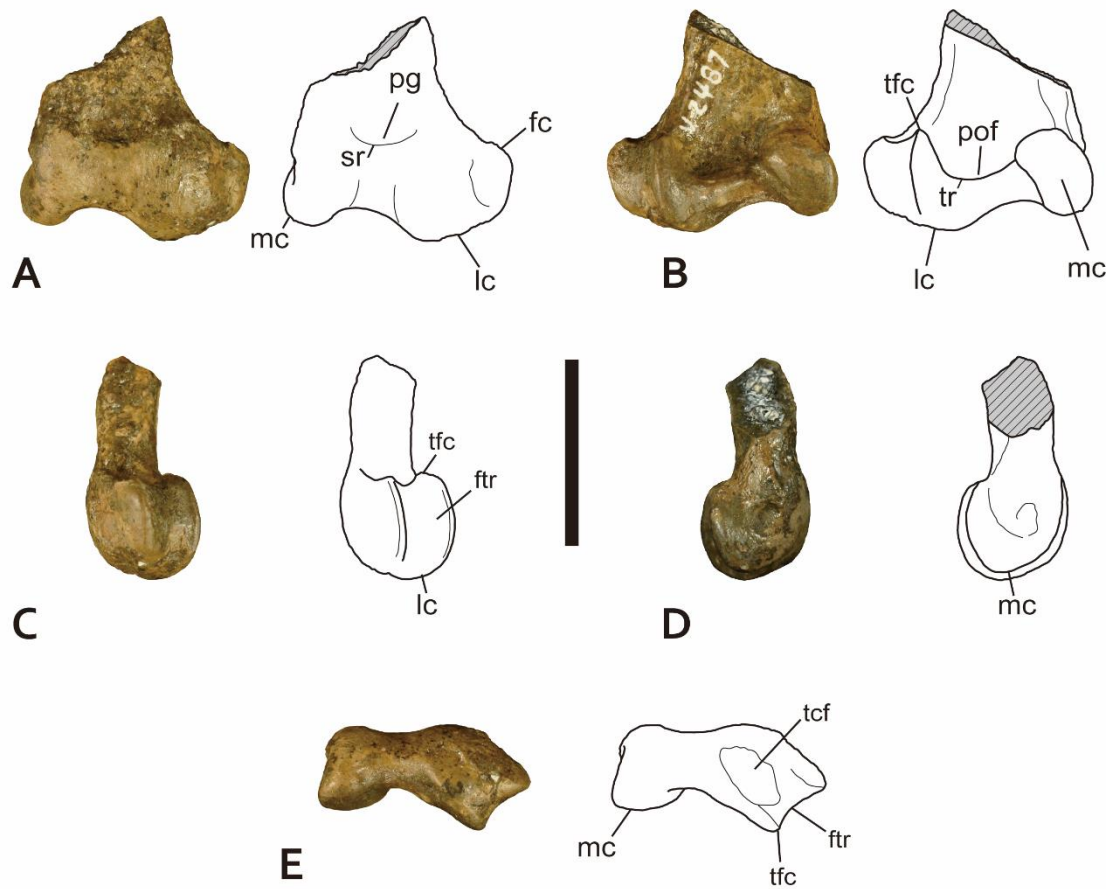


Fig. 4.2 MM V-2487. Distal end of right femur in **A**, anterior, **B**, posterior, **C**, lateral, **D**, medial, and **E**, distal views. Abbreviations: fc, fibular condyle; ftr, fibular trochlea; lc, lateral condyle; mc, medial condyle; pg, patellar groove; pof, popliteal fossa; r, ridge; tcf, fossa for *m. tibialis cranialis*; tfc, tibiofibular crest; tr, transverse ridge. Scale bar = 2cm.

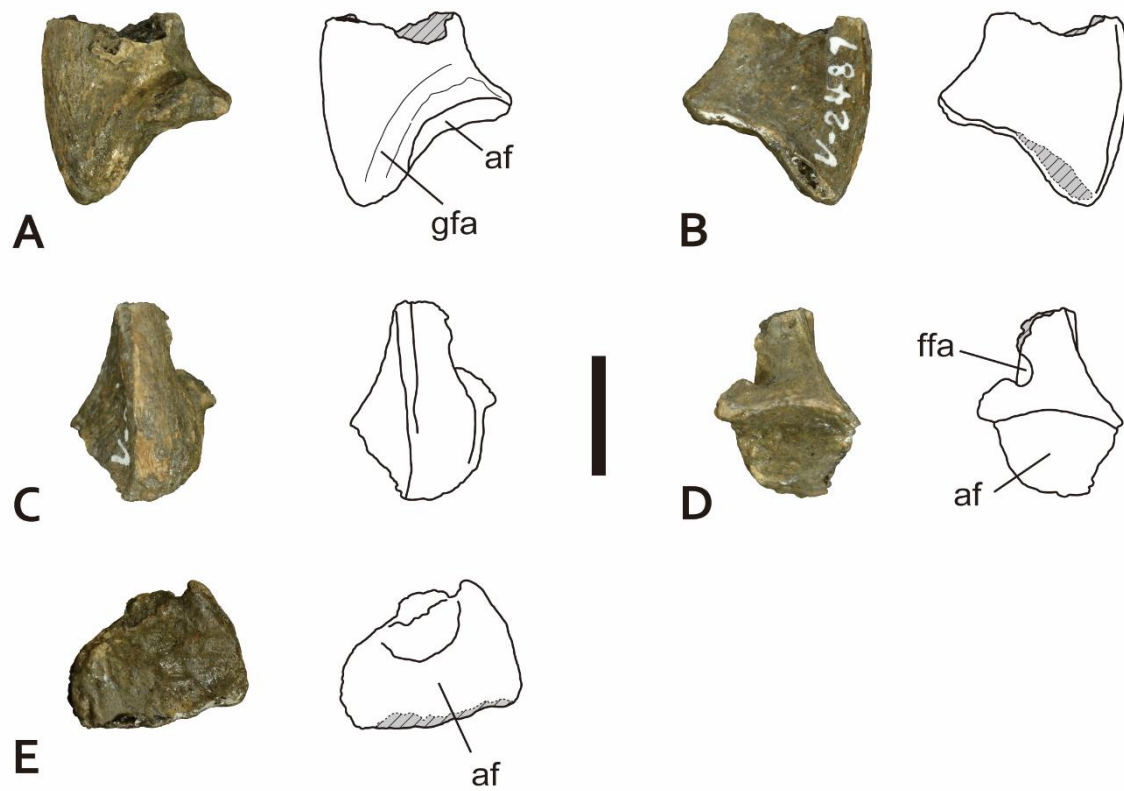


Fig. 4.3 MM V-2487. Proximal end of left patella in **A**, anterior, **B**, posterior, **C**, lateral, **D**, medial, and **E** distal views. Abbreviations: af, articular facet; gfa, groove for *m. ambiens*; ffa, foramen for *m. ambiens*. Scale bar = 2cm.

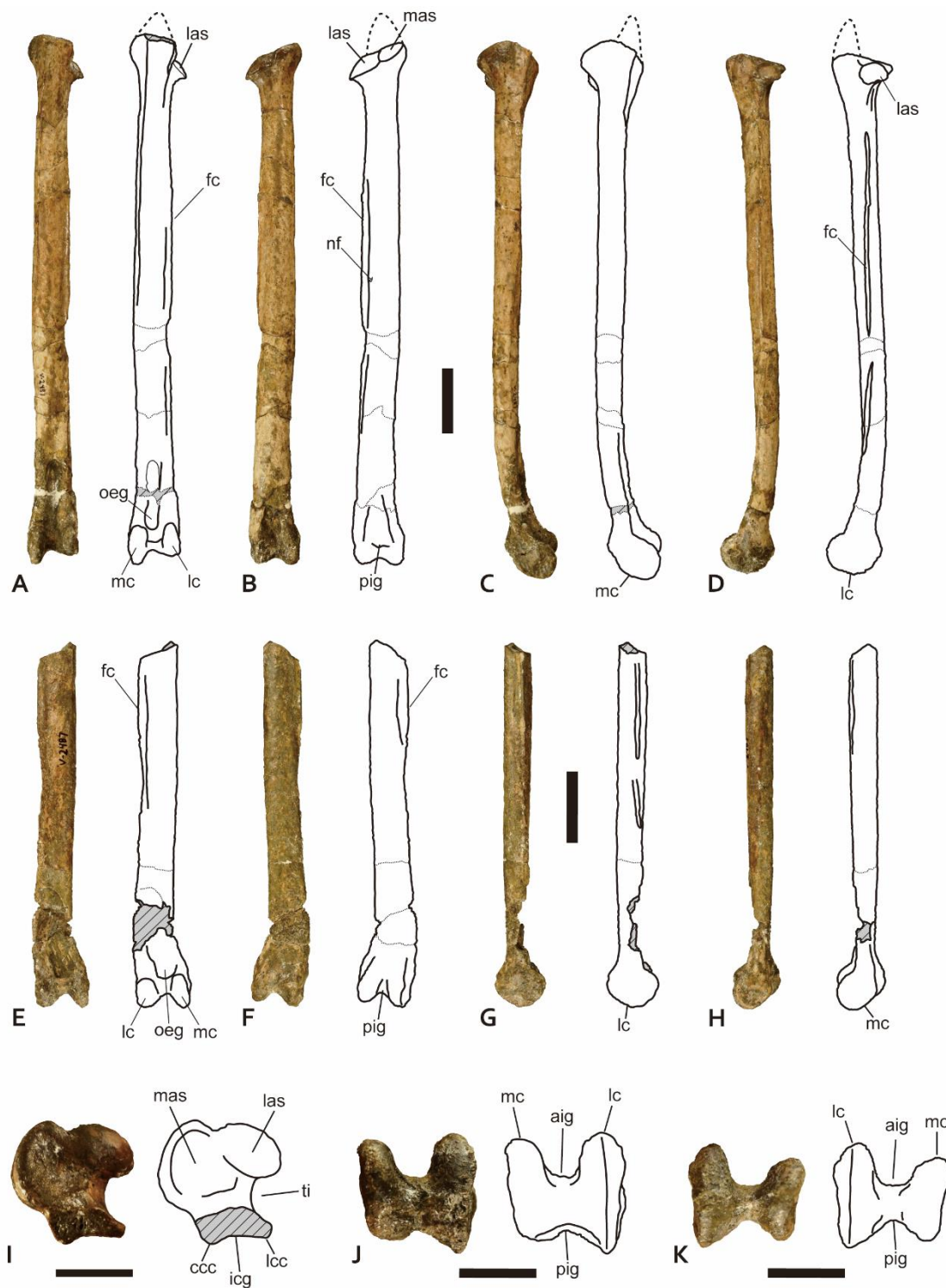


Fig. 4.4 MM V-2487. Left tibiotarsus in **A**, anterior, **B**, posterior, **C**, medial, and **D**, lateral, **I**, proximal, and **J**, distal views. Right tibiotarsus in **E**, anterior, **F**, posterior, **G**, lateral, **H**, media, and **K**, distal views. Abbreviations: aig, anterior intercondylar groove; ccc, cranial cneial crest; fc, fibular crest; icg, intercnemial groove; las, lateral articular surface; lc, lateral condyle; lcc, lateral cnemial crest; mas, medial articular surface; mc, medial condyle; oeg, open extensor groove; pig, posterior intercondylar groove. Scale bar = 2cm.

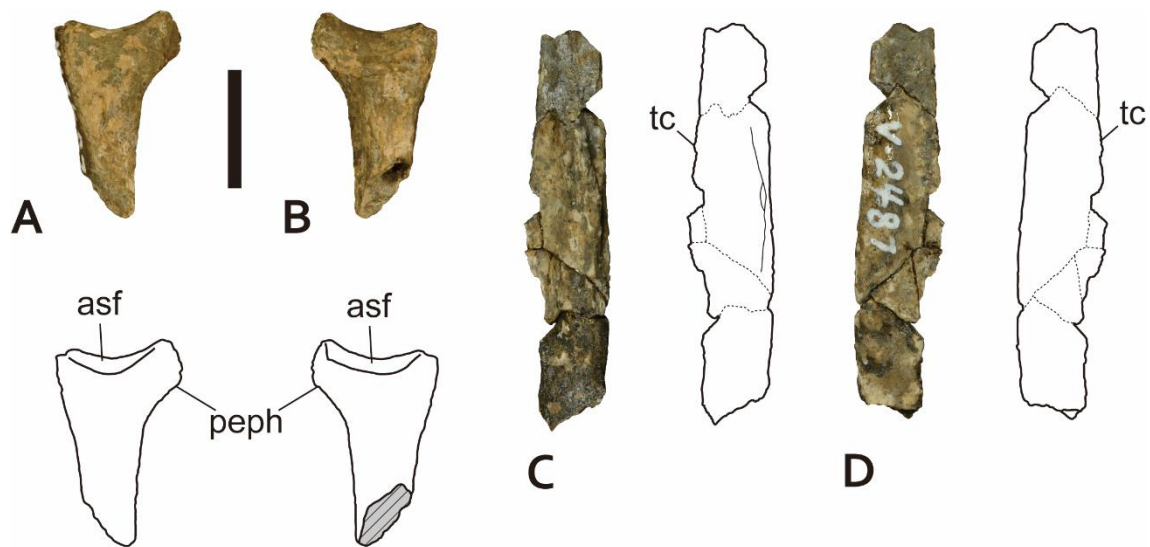


Fig. 4.5 MM V-2487. Left fibula in **A**, lateral and **B**, medial views. Right fibula in **C**, lateral and **D**, medial views. Abbreviations: asf, articular surface for femur; tc, tibial crest; peph, posterior edge of the proximal head. Scale bar = 2cm.

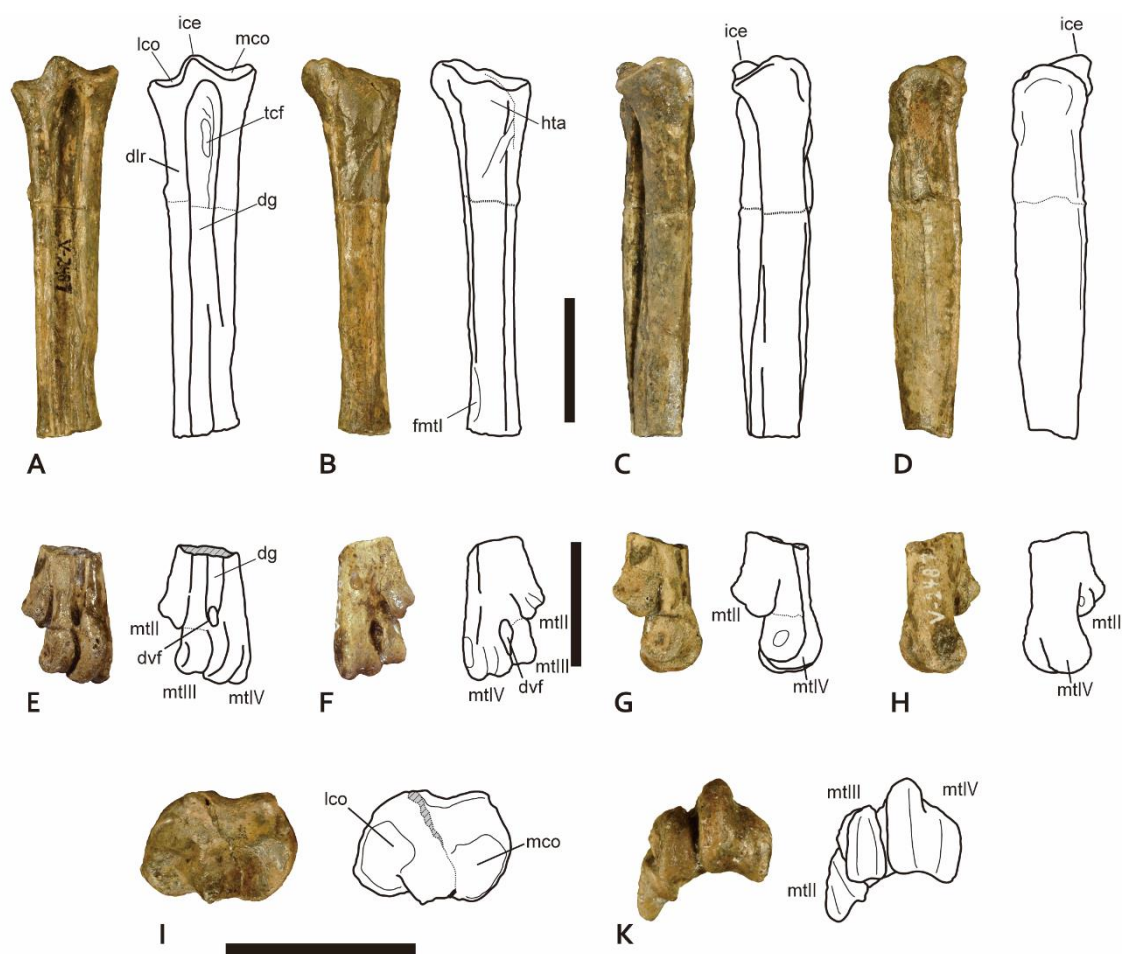


Fig. 4.6 MM V-2487. Right tarsometatarsus in **A**, dorsal, **B**, plantar, **C**, medial, **D**, lateral, and **I**, distal views. Left tarsometatarsus in **E**, dorsal, **F**, plantar, **G**, medial, **H**, lateral, and **K**, distal views. Abbreviations: ice, intercotylar eminence; dg, distinct ridge; dlr, dorsolateral ridge; dvf, distal vascular foramen; fmtI, fossa for metatarsal I; hta, hypotarsal-like area; mtII, metatarsal trochlea II; mtIII, metatarsal trochlea III; mtIV, metatarsal trochlea IV; tcf, fossa for *m. tibialis cranialis*. Scale bar = 2cm.

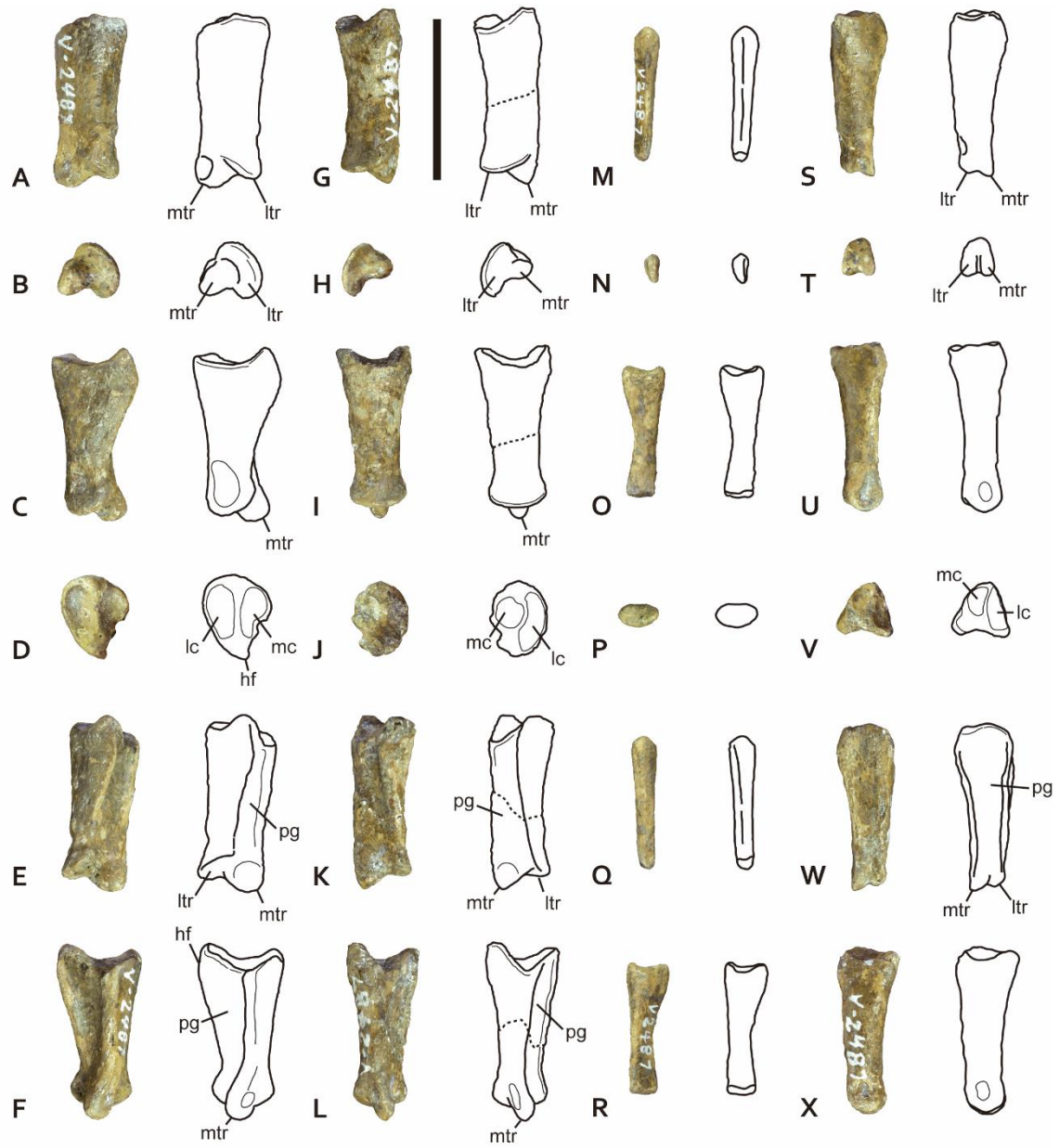


Fig. 4.7 MM V-2487. First digit of right fourth toe in **A**, dorsal, **B**, distal, **C**, medial, **D**, proximal, **E**, plantar, and **F**, lateral views. Second digit of left fourth toe in **G**, dorsal, **H**, distal, **I**, medial, **J**, proximal, **K**, plantar, and **L**, lateral views. Third digit of left third toe in **M**, dorsal, **N**, distal, **O**, medial, **P**, proximal, **Q**, plantar, **R**, lateral views. First digit of left second toe in **S**, dorsal, **T**, distal, **U**, medial, **V**, proximal, **W**, plantar, **X**, lateral views. Abbreviations: hf, high flange; lc, lateral cotyla; ltr, lateral trochlea; medial cotyla; mtr, medial trochlea; pg, plantar groove. Scale bar = 2cm.

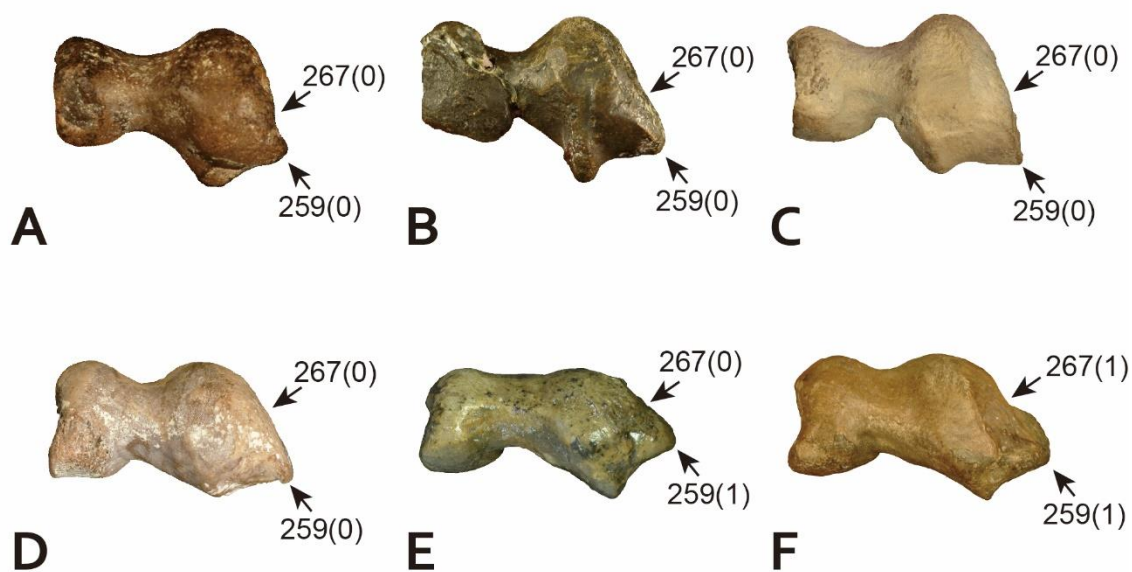


Fig. 4.8 Left femora in distal views of **A**, *Enaliornis sedgwicki* (CAMSM B55295); **B**, *Pasquiaornis tankei* (RSM P2077.108); **C**, *Baptornis advenus* (KUVF 2290); **D**, *Parahesperornis alexi* (KUVF 2287); **E**, MM V-2487; and **F**, *Hesperornis regalis* (YPM 1200).

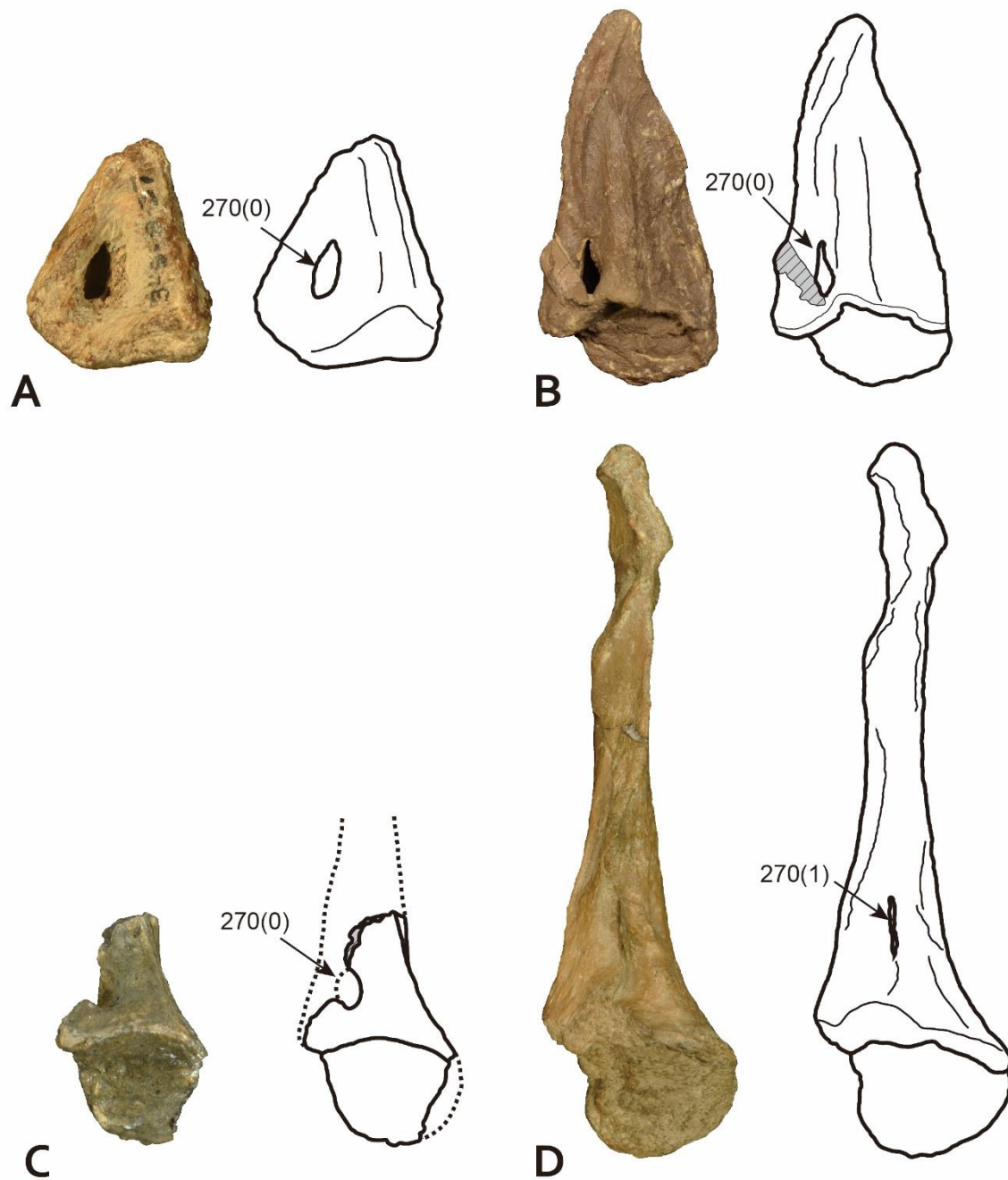


Fig. 4.9 Right patellae in medial views of **A**, *Fumicollis hoffmani* (UNSM 20030); **B**, *Parahesperornis alexi* (KUV 24090); **C**, MM V-2487; and **D**, *Hesperornis regalis* (YPM 1200). Note that the position of the foramen for *m. ambiens*.

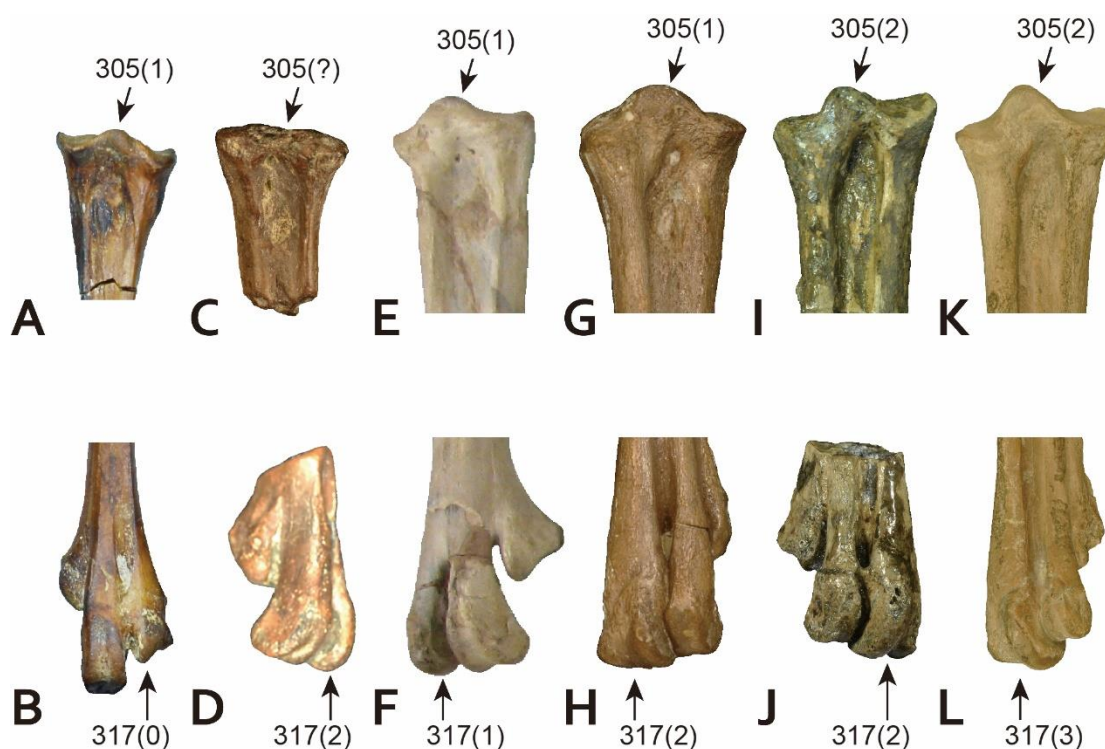


Fig. 4.10 Proximal ends of left tarsometatarsi in dorsal views in **A**, *Gansus yumenensis* (CAGS-04-CM-031); **C**, *Enaliornis barretti* (CAMSM B55331). Proximal ends of right tarsometatarsi in dorsal views in **E**, *Baptornis advenus* (AMNH 5101); **G**, *Paraesperornis alexi* (KUV 2287); **I**, MM V-2487; and **K**, *Hesperornis regalis* (YPM 1200). Distal ends of left tarsometatarsi in dorsal views in **B**, *Gansus yumenensis* (CAGS-04-CM-031); **D**, *Enaliornis barretti* (NHMUK A477); and **J**, MM V-2487. Distal ends of right tarsometatarsi in dorsal views in **F**, *Baptornis advenus* (AMNH 5101); **H**, *Paraesperornis alexi* (KUV 2287); and **L**, *Hesperornis regalis* (YPM 1200).

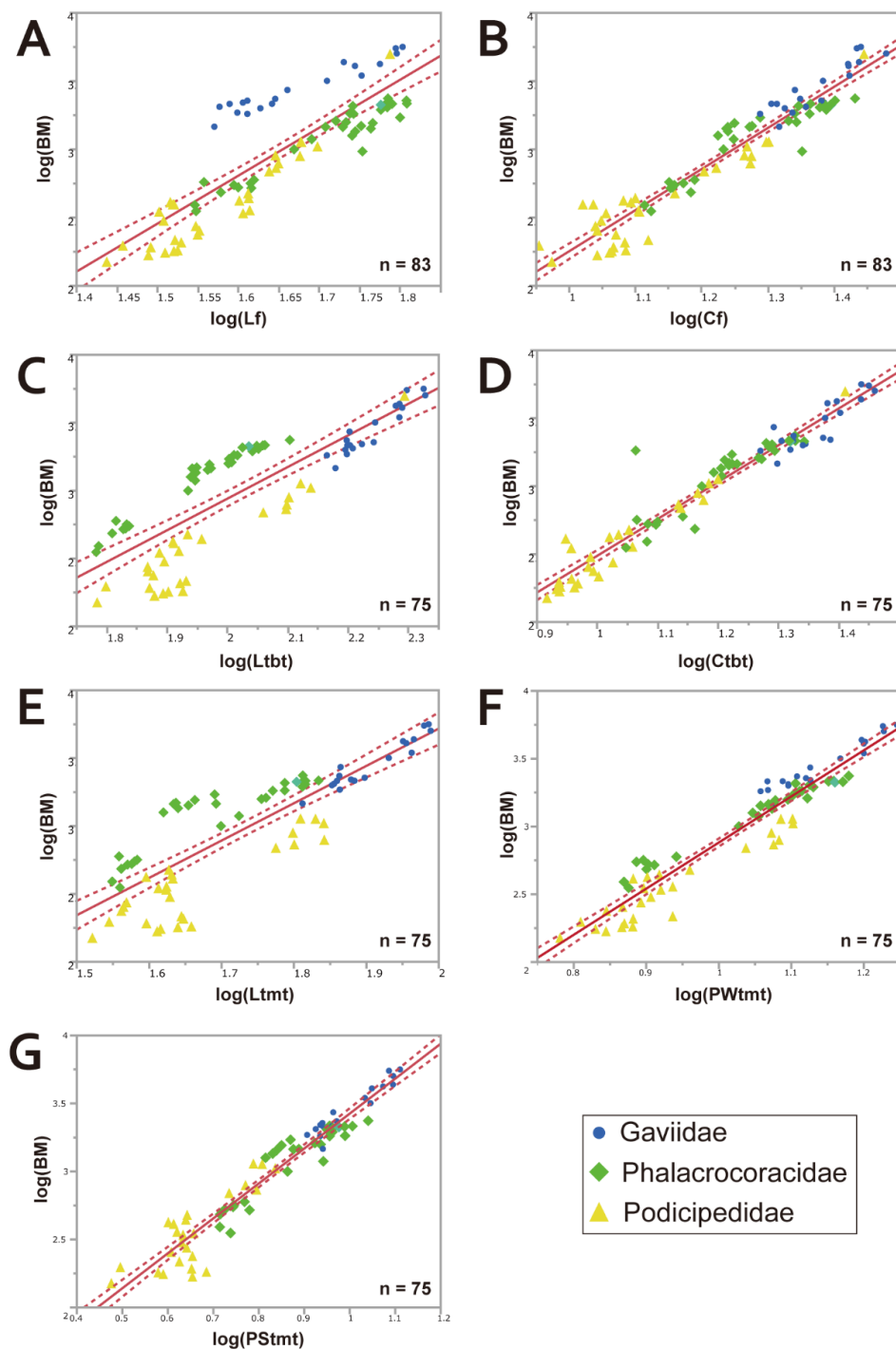


Fig. 4.11 Plot and single regression of **A**, maximum length of femora (Lf); **B**, least circumference of femora (Cf); **C**, maximum length of tibiotarsi (Ltbt); **D**, least circumference of tibiotarsi; and **E**, maximum length of tarsometatarsi (Ltmt).

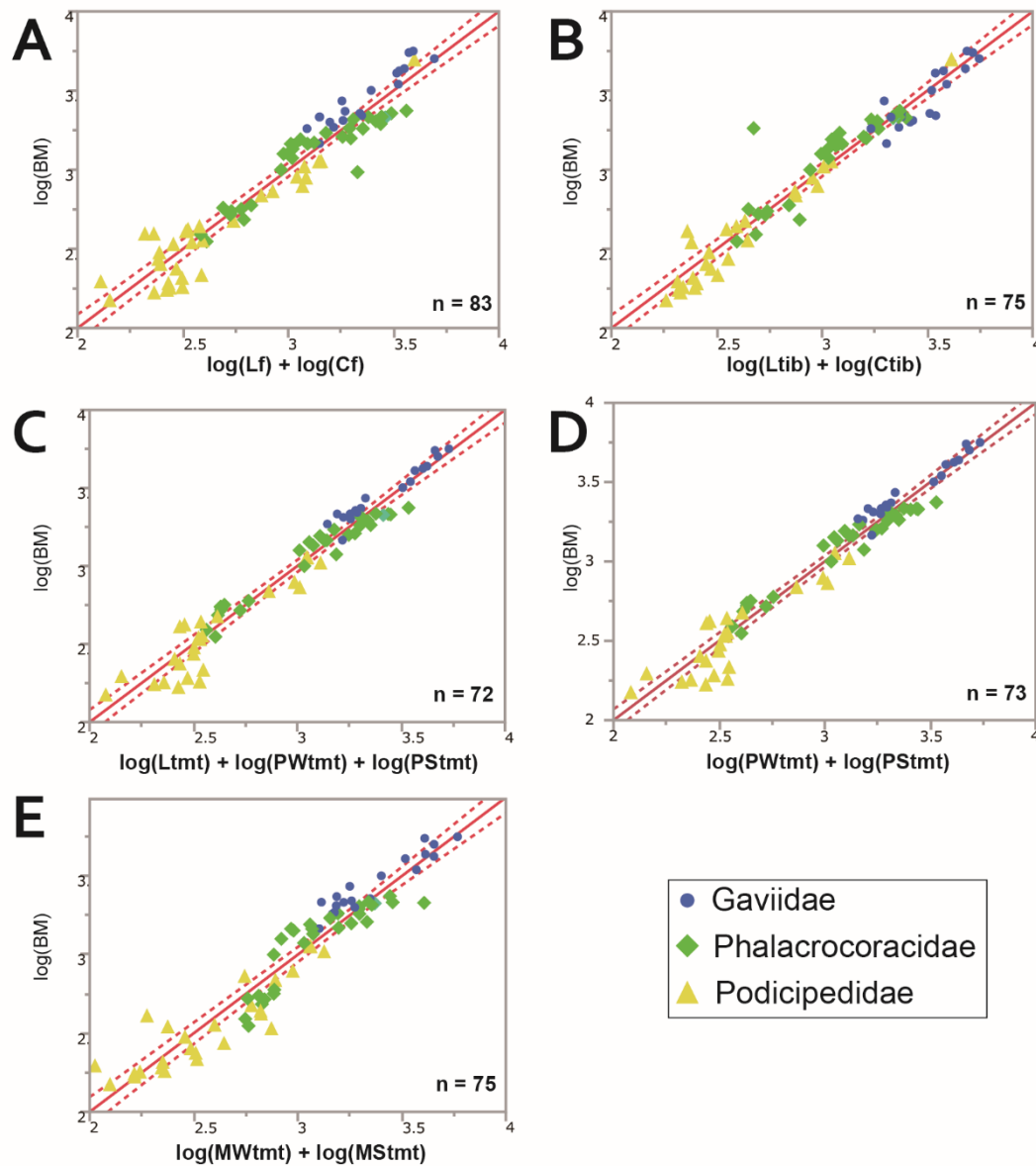


Fig. 4.12 Plot and multivariate regression of **A**, maximum length and least circumference of femora (Lf+Cf), **B**, maximum length and least circumference of tibiotarsi (Ltbt+Ctbt), **C**, maximum length, proximal transverse and saggital width of tarsometatarsi (Ltmt+PWtmt+PStmt), **D**, proximal transverse and saggital width of tarsometatarsi (PWtmt+PStmt), **E**, transverse and saggital width of middle shaft of tarsometatarsi (MWtmt+MStmt).

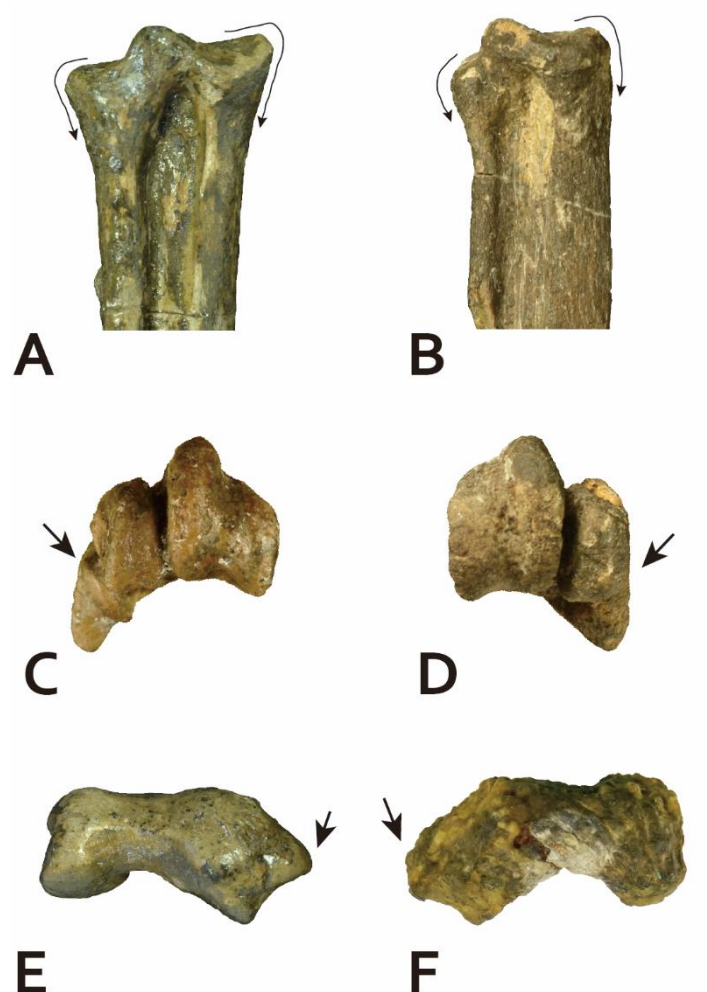


Fig. 4.13 Comparisons between small hesperornithiforms. Proximal ends of tarsometatarsi in **A**, MM V-2487 and **B**, *H. mengeli* in dorsal views. Distal ends of tarsometatarsi in **C**, MM V-2487 and **D**, *H. mengeli* in distal views. Distal ends of femora in **E**, MM V-2487 and **F**, *H. macdonaldi* in distal views.

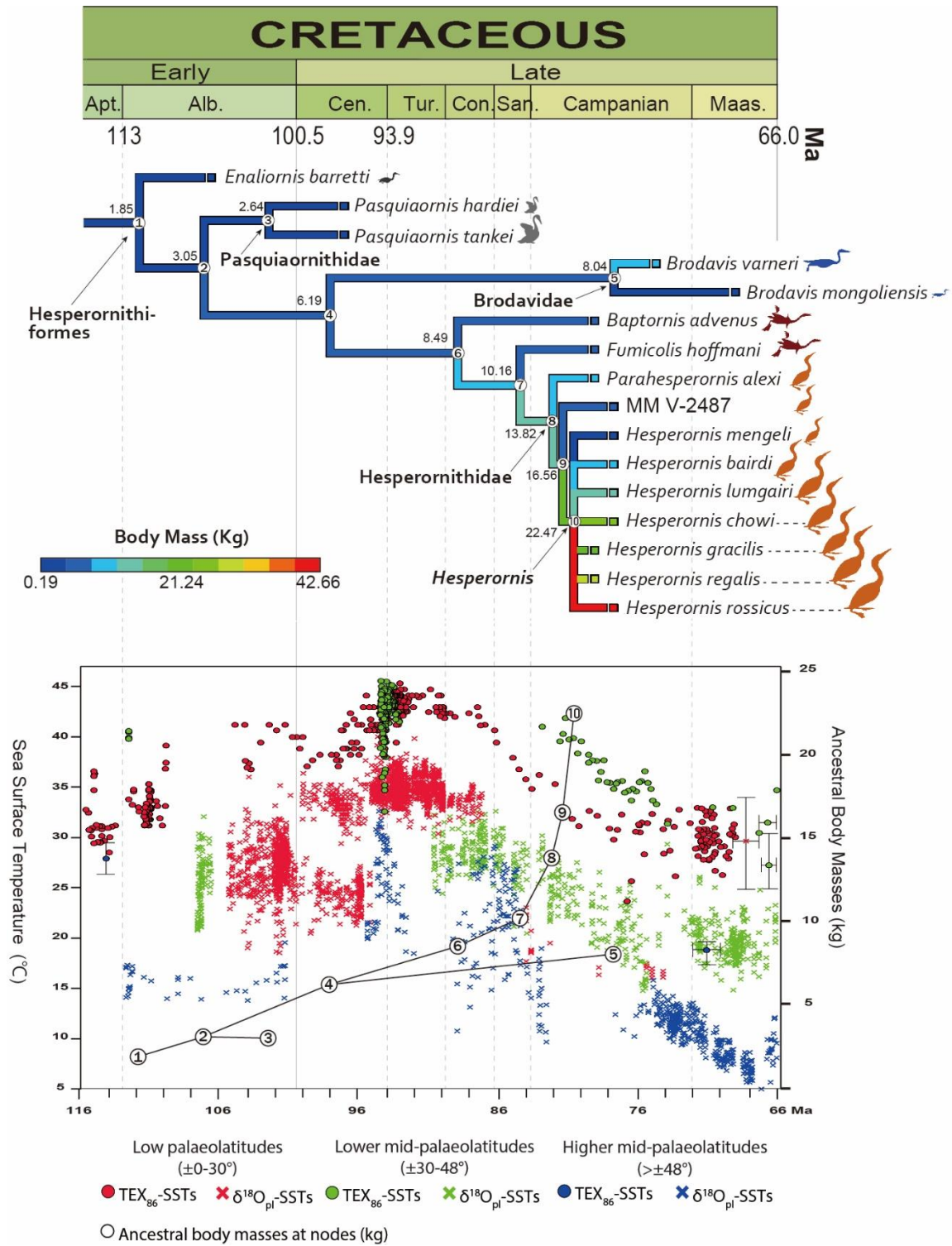


Fig. 4.14 A time scaled phylogeny and reconstruction of ancestral body mass based on transverse width and sagittal diameter of tarsometatarsi (PWtmt+PStmt) for Hesperornithiformes. Note that a small body mass in non-hesperornithid hesperornithiforms and a greater diversity in body mass within the clade of Hesperornithidae. Fluctuation of sea surface temperature follows O'Brien *et al.* (2017) and reconstructed ancestral body masses (kg) are also showing.

Table 4.1. Linear measurements of MM V-2487 (in mm).**Femur**

	L	R
Mediolateral diameter distal articulation	-	23.88

Tibiotarsus

character	L	R
Mediolateral diameter proximal articulation	17.25	-
Anteroposterior diameter proximal articulation	17.04	-
Mediolateral diameter midshaft	11.37	11.26
Anteroposterior diameter midshaft	7.91	8.65
Mediolateral diameter distal articulation	11.41	12.06
Anteroposterior diameter medial condyle	12.4	11.55
Anteroposterior diameter lateral condyle	15.82	14.63

Tarsometatarsus

	L	R
Anteroposterior diameter proximal articulation	-	11.71
Mediolateral diameter proximal articulation	-	17.07
Anteroposterior diameter midshaft	-	11.04
Mediolateral diameter midshaft	-	10.08
Anteroposterior diameter MTTII	6.53	-
Mediolateral diameter MTTII	4.5	-
Anteroposterior diameter MTTIII	7.22	-
Mediolateral diameter MTTIII	3.88	-
Anteroposterior diameter MTT IV	9.98	-
Mediolateral diameter MTT IV	6.98	-
Tip of MTTII to distal end	6.78	-

* MTT: metatarsal trochlea

Table 4.2. Size comparisons between MM V-2487 and other hesperornithiforms based on width of distal mediolateral articulation of femur, length without cnemial process of tibiotarsus, and width of proximal mediolateral articulation.

Femur		<i>Enaliornis barretti</i>	<i>Pasquiaornis tankei</i>	<i>Baptornis</i>	<i>Fumicollis</i>	<i>Paraesperornis</i>	<i>Hesperornis regalis</i>	<i>H. macdonaldi</i>
	MM V-2487 (R)	NHМУK A163 (R)	RSM P2077.108 (L)	KUVP 2290 (R)	UNSM 20030 (R)	KUVP 2287 (R)	YPM 1200 (R)	LACM 9728
Distal mediolateral articulation	23.88	20.09	21.29	25.74	24.48	30.19	52.58	21.14
Ratio (MM V-2487 = 1.00)	1.00	0.84	0.89	1.08	1.03	1.26	2.20	0.89

Tibiotarsus		<i>Baptornis</i>	<i>Fumicollis</i>	<i>Paraesperornis</i>	<i>H. regalis</i>
	MM V-2487 (L)	FMNH 395 (L)	UNSM 20030 (L)	KUVP 2287 (L)	YPM 1200 (L)
Length without cnemial process	156.72	191.58	180.65	203.7	314.35
Ratio (MM V-2487 = 1.00)	1.00	1.22	1.15	1.30	2.01

Tarsometatarsus		<i>E. barretti</i>	<i>P. tankei</i>	<i>Baptornis</i>	<i>Fumicollis</i>	<i>Paraesperornis</i>	<i>H. regalis</i>	<i>H. mengeli</i>
	MM V-2487 (R)	CAMSM B55331	RSM P2077.63	AMNH 5101 (R)	UNSM 20030 (R)	KUVP 2287 (R)	YPM 1200 (R)	CFDC B78.01.08
Proximal mediolateral articulation	17.07	11.37	16.71	19.21	18.77	21.20	35.21	16.18
Ratio (MM V-2487 = 1.00)	1.00	0.67	0.98	1.13	1.10	1.24	2.06	0.95

Table 4.3. Ordinary least squares single regression results between linear measurements of skeletal elements (x-axis) and body mass (y-axis) in extant foot-propelled diving birds. Scaling equation in format $y = mx + b$. Abbreviations: AIC, Akaike information criterion; Lf, maximum length of femora; Cf, least circumference of femora; Ltbt, maximum length of tibiotarsi; Ctbt, least circumference of tibiotarsi; Ltmt, maximum length of tarsometatarsi; PWtmt, transverse width of proximal end of tarsometatarsi; PStmt, sagittal diameter of proximal end of tarsometatarsi; MWtmt, transverse width of middle shaft of tarsometatarsi; MStmt, sagittal width of middle shaft of tarsometatarsi; PPE, mean per cent prediction error (Campione *et al.* 2014).

Proxy	N	m	b	R ²	P value	AIC	PPE
Lf	83	3.51	-2.81	0.69	< 0.0001	1.59343	53.8
Cf	83	3.01	-0.76	0.91	< 0.0001	-105.06	23.7
Ltbt	75	2.33	-1.71	0.69	< 0.0001	5.73091	51.2
Ctbt	75	2.71	-0.22	0.93	< 0.0001	-108.23	20.2
Ltmt	75	2.75	-1.78	0.72	< 0.0001	-3.9464	44.0
PWtmt	75	3.4	-0.51	0.91	< 0.0001	-95.458	22.8
PStmt	73	2.57	0.85	0.93	< 0.0001	-101.89	20.4

Table 4.4 Ordinary least squares multivariate regression results between linear measurements of skeletal elements (x-axis) and body mass (y-axis) in extant foot-propelled diving birds. Scaling equation in format $y = mx_1 + nx_2 + ox_3 + b$. Abbreviations: AIC, Akaike information criterion; Lf, maximum length of femora; Cf, least circumference of femora; Ltbt, maximum length of tibiotarsi; Ctbt, least circumference of tibiotarsi; Ltmt, maximum length of tarsometatarsi; PWtmt, transverse width of proximal end of tarsometatarsi; PStmt, sagittal diameter of proximal end of tarsometatarsi; MWtmt, transverse width of middle shaft of tarsometatarsi; MStmt, sagittal width of middle shaft of tarsometatarsi; PPE, mean per cent prediction error (Campione *et al.* 2014); and VIF, variance inflation factor.

Proxy	N	m	n	o	b	R ²	p value	AIC	PPE	VIF
Lf + Cf	83	0.48	2.71	-	-1.17	0.92	< 0.0001	-106.91	22.8	Lf: 3.289 Cf: 3.289
Ltbt + Ctbt	75	0.17	2.57	-	-0.39	0.93	< 0.0001	-107.38	20.1	Ltbt: 3.484 Ctbt: 3.484
Ltmt + PWtmt + PStmt	72	-0.12	1.78	1.39	0.21	0.95	< 0.0001	-128.51	16.8	Ltmt: 5.390 PWtmt: 12.137 PStmt: 8.533
PWtmt + PStmt	73	1.64	1.41	-	0.13	0.95	< 0.0001	-132.26	16.8	PWtmt: 8.345 PStmt: 8.345
MWtmt + MStmt	75	1.16	2.14	-	0.84	0.91	< 0.0001	-88.821	24.0	MWtmt: 1.444 MStmt: 1.444

Table 4.5. Estimated body mass based on proxies of PWtmt + PStmt for Mesozoic birds.

Taxon	Specimen ID	EBM (kg)
<i>Enaliornis barretti</i>	CAMSM B55331	1.51
<i>Pasquiaornis hardiei</i>	RSM P.2077.117	0.72
<i>Pasquiaornis tankei</i>	RSM P2077.63	4.14
<i>Brodavis vernerii</i>	SDSM 68430	10.27
<i>Brodavis mongoliensis</i>	PIN 4491-8	0.72
<i>Baptornis advenus</i>	AMNH 5101	7.49
<i>Fumicollis hoffmani</i>	UNSM 20030	4.49
<i>Paraesperornis alexi</i>	KUVP 2287	9.30
	MM V-2487	4.54
<i>Hesperornis regalis</i>	YPM 1200	33.02
<i>Hesperornis gracilis</i>	YPM 1473	21.60
<i>Hesperornis rossicus</i>	SGU 3442 Ve01	42.66
<i>Hesperornis bairdi</i>	YPM PU 17208A	10.96
<i>Hesperornis chowi</i>	YPM PU 17208	29.51
<i>Hesperornis mengeli</i>	CFDC B.78.01.08	3.58
<i>Hesperornis lumgairi</i>	CFDC B.78.02.07	15.18
<i>Asiahesperornis bazhanovi</i>	IZASK 1/KM_97	33.58
<i>Gansus yumenensis</i>	CAGS 04-CM-031	0.19

CHAPTER 5

Morphological Evolutionary Rates and Disparity of Mesozoic

Aquatic Birds

Abstract

The adaptive radiation model predicts that organisms' invasion of a new adaptive zone involves an initial rapid morphological evolution followed by a relative stasis. However, previous works suggested that this “early burst” pattern may not be applied to some of the ecological transitions such as aquatic adaptation in vertebrates. In this study, we measure rates of morphological evolution and disparity in Mesozoic Ornithuromorpha, focusing on the adaptation from terrestrial, freshwater through marine realms using a new morphological data set. The rate analysis shows that evolutionary rates were relatively lower for the non-aquatic to freshwater transition. However, rates were relatively higher at the origin of the oldest seabirds Hesperornithiformes, indicating that these birds experienced rapid anatomical evolution when they first invaded marine realm in the Early Cretaceous. Within Hesperornithiformes, there are two more bursts of evolutionary rates in derived nodes. The disparity analysis shows that non-aquatic and freshwater birds are overlapped in morphospace, whereas marine

hesperornithiforms occupy a distinctive and remarkably wide area due to their unique hindlimbs.

Introduction

Ecological transition in vertebrates are often associated with changes in tempo and mode of morphological evolution (Simpson 1944). The adaptive radiation model predicts that organisms' invasion of a new adaptive zone involves an initial rapid morphological evolution followed by a stasis, since the adaptive zone is eventually filled by competitors and the evolutionary rates become lower (Simpson 1944; Schluter 2000; Losos 2010) . Although many paleontological works supported early bursts in adaptive radiation (Foote 1994; Wagner 1997; Hughes *et al.* 2013) , some neontological works argued otherwise (Cooper & Purvis 2010; Harmon *et al.* 2010). Recent methodological advancements using large morphological data set and phylogenies allow us to quantitatively test patterns and processes of morphological evolution in geological time scale (Brusatte *et al.* 2008; Brusatte *et al.* 2014; Close *et al.* 2015; Lloyd 2016; Stubbs *et al.* 2019).

The organisms' return to the aquatic environment is one of the major macroevolutionary event that involves great morphological and physiological changes (Vermeij & Dudley 2000; Dial *et al.* 2015). This “secondary” aquatic adaptation occurred multiple times in tetrapod evolution (Carroll 1988). Several reptile lineages invaded marine habitats and diversified since the Early Triassic (Motani 2009; Pyenson *et al.* 2014; Kelley *et al.* 2015). Sauropterigia,

Ichthyopteria, and Mosasauridae were the most successful marine reptiles during the Mesozoic (Carroll 1988), yet intermediate forms connecting these aquatic animals with terrestrial ancestors are unknown (Carroll 1997; Rieppel & Zaher 2000) except for the possibly amphibious ichthyopterygiform *Cartorhynchus* (Motani *et al.* 2015). On the other hand, fossil marine mammals, such as cetaceans (whales), provides an excellent example of morphological transformation following the marine invasion because sequences of terrestrial to fully aquatic forms via freshwater intermediates are well known (Marx *et al.* 2016; Berta *et al.* 2018). Although transitional forms have been reported in mammals (Gingerich & Russel 1981; Thewissen *et al.* 1994; Domning 2001; Rybczynski *et al.* 2009), little is known about tempo and mode of their morphological character evolution associated with aquatic adaptation. Jones *et al.* (2015) measured disparity and evolutionary rates through the terrestrial-aquatic transition in Pinnipeds and found no major rate change at the origin of the clade.

Non-avian dinosaurs were dominant tetrapods in terrestrial ecosystems during the Jurassic and the Cretaceous (Brusatte *et al.* 2008; Weishampel *et al.* 2007). However, they have never adapted to ocean as sea-dwellers, and only two theropods are potentially semi-aquatic (Ibrahim *et al.* 2014; Cau *et al.* 2017). In avialan lineages, on the other hand, several fully aquatic taxa emerged during the

Early Cretaceous (Zhou & Zhang 2005; O'Connor *et al.* 2010; You *et al.* 2006; Chiappe & Qingjin 2016) . The pioneer among those was Hesperornithiformes, the toothed foot-propelled diving birds (Marsh 1880). These oldest marine birds were widely distributed in the Northern Hemisphere, especially in the Western Interior Seaway of North America (Bell & Chiappe 2015b). All aquatic and diving birds including hesperornithiforms belong to Ornithuromorpha, the largest clade of Avialae (Gauthier 1987; Chiappe 1996; Prum *et al.* 2015) . Recently, our understanding of early avialan evolution has been remarkably progressed (Chiappe 1995; Benton *et al.* 2008; Zhou 2014; O'Connor & Zhou 2015) , and several aquatic birds were reported from the Lower Cretaceous Jehol Group in China (You *et al.* 2006; Zhou & Zhang 2005; O'Connor *et al.* 2010; Y-M. Wang *et al.* 2015; M. Wang *et al.* 2015; Chiappe & Qingjin 2016; X. Wang 2018) . The Cretaceous seabird Hesperornithiformes is one of the most diversified group among the Mesozoic birds (Marsh 1880; Seeley 1876; Martin 1984; Tokaryk *et al.* 1997; Martin & Lim 2002; Martin & Codes-Person 2007; Bell & Chiappe 2015a; Bell & Chiappe 2015b) . The rich fossil record of them can provide critical insights into how Mesozoic birds invaded freshwater and finally marine realm.

This study aims to understand the association of a major ecological transition with morphological evolutionary rates and disparity in Ornithuromorpha. Wang

& Lloyd (2016) examined morphological evolutionary rates using the early Cretaceous avian phylogeny and revealed that rates were accelerated when Ornithuromorpha split from Enantiornithes. However, Wang & Lloyd (2016) only used early Cretaceous birds, and their data matrix did not comprehensively include aquatic characters related to aquatic adaptation. Here, we establish a new morphological data set including aquatic characters to reconstruct the ornithuromorph phylogeny. We then explore the morphological evolutionary rate and disparity dynamics with the particular focus on fore- and hindlimbs.

Material and Methods

Ornithuromorph Phylogeny

The new morphological dataset (43 taxa and 349 characters, see Chapter 1) is used for the present morphological rates and disparity analyses. The most parsimonious tree and strict consensus tree that is used in the present analyses is shown in Fig. 1.5 and 1.6 of Chapter 1, respectively. The complete character description and data matrix are provided in Appendix 1.1 and 1.2.

Ecological categories of Ornithuromorpha

Because the current rate and disparity analyses focus on Mesozoic

ornithuromorphs, *Archaeopteryx*, *Protopteryx*, *Pengornis*, and five modern neornithine species were removed from the data matrix. Each ornithuromorph is assigned to 3 ecological categories, terrestrial, freshwater, marine, or unknown, based on the descriptions of ecological relevance in previous studies: 9 ornithuromorphs *Archaeorhynchus*, *Patagopteryx*, *Vorona*, *Bellulia*, *Shizoura*, *Apsaravis*, *Jianchangornis*, *Zhoungianornis*, and *Dingavis* to terrestrial, 5 hongshanornithids, 3 songlingornithids, *Changzuiornis*, *Iteravis*, *Gansus zheni*, and *G. yumenensis* to the freshwater, and 9 hesperornithiforms to marine categories. Hesperornithiforms share osteosclerosis seen in highly specialized diving birds (Chinsamy *et al.* 1998; Wilson & Chin 2014) . An anseriform *Vegavis iaai* from the Late Cretaceous also shows an osteosclerotic femur (Clarke *et al.* 2005; Marsà *et al.* 2017) and their hindlimb morphology suggest foot-propelled diving behavior (Agnolín *et al.* 2017), yet their paleoecology is still under debate. Although *Ichthyornis dispar* was a traditionally considered as a seabird (Marsh *et al.* 1880; Chiappe 2007; Mayr 2016) , no morphological feature supports swimming capability as a sea-dweller (Clarke 2004; Hinic-Frlog & Motani 2010). For these reasons, *Vegavis* and *Ichthyornis* were assigned to the unknown category.

Phylogenetic Time-Scaling

The evolutionary rate analyses require a time calibrated phylogenies (Lloyd 2016). Geological age or epoch boundaries for 35 terminal taxa were compiled as first appearance data (FADs) and last appearance data (LADs) based on the primary literature and the geological time scale (Walker *et al.* 2013) (see Appendix 5.1). In this study, we used “equal” branch length approaches (Laurin 2004; Brusatte 2011) for the internal node calibration, using the *DatePhylo* function in R package Strap (Bell & Lloyd 2015). In accordance with previous studies, we performed 100 replicates of dating randomization, where terminal ages were determined randomly between FAD and LAD. These 100 trees with different terminal ages and internal branch lengths were subjected to the morphological rate analysis described below.

Morphological Data

Our discrete morphological data set include 349 morphological characters from the whole skeleton (see Chapter 1 and Appendix 1.1). In addition to the whole skeleton data set, forelimb [scapula, coracoid, furcula, sternum, humerus, ulna, radius, carpometacarpus, and manual digits (122 characters)], and hindlimb [pelvis, femur, tibiotarsus, tarsometatarsus, and pedal phalanges (131 characters)] data sets

were used to examine evolutionary rates in each anatomical subregion. Evolutionary rate and disparity analyses were performed separately on these 3 partitions (whole skeleton, forelimbs, and hindlimbs).

Rates of Morphological Evolution

Evolutionary rates were examined using maximum-likelihood methods using the protocols established by previous studies (Brusatte *et al.* 2008; Brusatte *et al.* 2014; Wang & Lloyd, 2016). Rates were calculated separately for 3 data sets (whole skeleton, forelimbs, and hindlimbs) with *DiscreteCharacterRate* function in R package Claddis (Lloyd 2016). Rates are based on the number of character changes along a branch relative to its duration (Brusatte 2011). We tested whether each branch or clade has a higher or lower evolutionary rate than the rest of the tree as in previous studies (Brusatte *et al.* 2014; Wang & Lloyd 2016; Stubbs *et al.* 2019). The absolute evolutionary rates are shown in Appendix 3. To identify branches with significantly high/low rates, branch likelihood test was conducted (Lloyd *et al.* 2012). In this test, character changes were modeled with the Poission process, and goodness of fit for two models (single rate model: homogeneous rate across the entire phylogenetic tree; two-rate model: individual branch rates are different to that of the rest of the phylogenetic tree) are assessed based on their likelihood

ratios. Individual branch tests give a p-value (alpha threshold of 0.01) to assess significance of the result. The branch likelihood test was conducted using 100 randomized trees, and the results were summarized as pie charts on the strict consensus tree, illustrating the proportion of trees that showed significantly high or low rates for each branch.

Disparity

Disparity analyses were conducted for assessing the skeletal morphological diversity in ornithuromorphs. 3 morphological character-taxon matrices (whole skeleton, fore-, and hindlimb matrices) were converted into pairwise distance matrices, based on maximum observable rescaled distance (MORD), using *MorphDistMatrix* function of R package Claddis (Lloyd 2016). To visualize morphological variation, we generated phylomorphospaces of Mesozoic birds for each anatomical region. The pairwise distance matrix based on MORD were subjected to principal coordinate analysis (PCoA), and morphospace were constructed based on PCoA axes 1 and 2, which are the major axes of morphological variation. Followingly, disparity was quantified in three ecological categories, terrestrial, freshwater, and marine, from the pairwise distance matrices. We calculated within-category weighted mean pairwise dissimilarity

(WMPD), the variance-based disparity metric (Close *et al.* 2015) using 3 pairwise distance matrices. Bootstrap resampling was conducted for generating 95% confidence intervals.

Results

Rates of Morphological Evolution

Rates of morphological evolution were highly heterogeneous among different avialan lineages. For the whole skeleton analysis, higher evolutionary rates are identified at the base of Ornithuromorpha, *Vegavis* (Neornithes), Hesperornithiformes, the clade of *Fumicollis* + Hesperornithidae, and Hesperornithidae (Fig. 5.2). When fore- and hindlimbs were analyzed separately, higher rates are recognized at the base of Ornithuromorpha for forelimbs, and at the base of Ornithuromorpha, Hesperornithiformes, the clade of *Fumicollis* + Hesperornithidae, and Hesperornithidae for hindlimbs (Figs 5.3, 5.4). There is no significant rate change at the base or within the freshwater clades, whereas rates were considerably elevated at the origin of marine hesperornithiforms. Within hesperornithiforms, two accelerated evolution were seen at the origin of *Fumicollis* + Hesperornithidae and Hesperornithidae (Fig. 5.4).

Morphospace Occupation

The morphospace of terrestrial taxa is not clearly separated from that of freshwater taxa for either whole skeleton or fore- and hindlimbs (Fig. 5.5A, B, C). On the contrary, marine taxa occupy a large area for whole skeleton and fore- and hindlimbs (Fig. 5.5A, B, C). In particular, forelimbs for marine taxa are non-overlapped with terrestrial and freshwater taxa along PCO axes 1 and 2 (Fig. 5.5B) due to a large forelimb variation in hesperornithiforms. A basal hesperornithiform *Pasquiaornis* was the transitional form between volant and flightless, having strut-like coracoids and relatively developed forelimbs (Tokaryk *et al.* 1997), whereas more derived *Baptornis* and *Hesperornis* were obviously flightless birds, having blunt triangular coracoids and extremely reduced forelimbs (Marsh 1880; Martin & Tate 1976) (Fig. 5.5B). A terrestrial and flightless *Patagopteryx* was plotted close to hesperornithiforms, reflecting its reduced forelimbs (Chiappe 1996). The morphospace occupations for the whole skeleton and hindlimbs are similar, where marine taxa are separated on PCO axis 1 (Fig. 5.5A, C).

Disparity

Disparity (WMPD) of whole skeleton and hindlimbs show similar trends, where marine taxa exhibit greater disparity followed by terrestrial and freshwater taxa

(Fig. 5.5D, F). For forelimbs, terrestrial taxa exhibit the greatest disparity (Fig. 5.5E).

Discussion

The results of evolutionary rate analyses demonstrated that morphological adaptation for freshwater environment was gradual in Mesozoic birds. Overlapped morphospaces of terrestrial and freshwater taxa (Fig. 5.5A) supported this view. Most of terrestrial and freshwater taxa in the current data set were reported from the Jehol Group (O'Connor *et al.* 2011). Michell & Makovicky (2014) concluded that the ecological diversity of early Cretaceous birds from the Jehol Group is unexpectedly low, which is congruent with the current results.

The relatively high rates at the origin of hesperornithiforms imply that the first avian invasion into marine realm was achieved rapidly. The adaptive radiation model predicts that invasion of a new environment is characterized by initially higher evolutionary rates followed by gradually slower rates as the niche fills (Simpson 1944; Schluter 2000). The current analysis of Mesozoic birds lends support to this model. Higher disparity of hesperornithiforms might be achieved by rapid morphological change associated with freshwater-marine transition at the base of Hesperornithiformes. For hindlimbs, two further accelerate rates can

be found at the origin of Hesperornithidae (Figs 5.3, 5.4). These might coincide with rapid hindlimb evolution for more powerful, speedy, and energetically efficient foot-propelled diving.

The different patterns of land to freshwater and freshwater to marine transitions are probably due to differences in predation pressure. In general, freshwater environment is thought to involve lower predation pressure than in marine and terrestrial environments. The safe terrestrial environment offers less biological resistance to invaders than ocean (Vermeij & Dudley 2000). In fact, large marine reptiles such as ichthyopterygians and sauropterygians dominated marine ecosystems during the Early Cretaceous (Motani 2009). The high predation pressure in marine realm might accelerate hindlimb evolution of early hesperornithiforms for escaping large predators.

The accelerated morphological changes during the aquatic adaptation of Mesozoic birds contradict results from some previous works that suggested otherwise (e.g. Harmon et al. 2010). Jones *et al.* (2015) investigated tempo and mode of morphological evolution in the skull of pinnipeds (seals, sea lions and walruses) to see the evolutionary process of terrestrial-aquatic transitions, finding no accelerate evolution at the base of the pinniped radiation. They concluded that pinnipeds have more diverse cranial disparity than that of terrestrial relatives,

but the increased disparity was not achieved through higher rates of evolution in the terrestrial-aquatic transition. It might be possible that patterns of morphological evolution during marine invasion are different among tetrapod lineages. Future studies focusing on evolutionary rate and disparity for other marine tetrapods including freshwater intermediates may provide further insights into the adaptive radiation across different environments.

Conclusion

The aquatic adaptation of Mesozoic birds provides an ideal example for understanding the processes of morphological changes during the secondary aquatic adaptation. This study used a new morphological data set of Mesozoic birds including characters related to aquatic adaptation, and provided a solid phylogenetic framework of Ornithuromorpha upon which evolutionary rates were calculated. The result suggests that evolutionary rates in freshwater clades are relatively stable, whereas higher rates are found at the origins of Hesperornithiformes and derived clades of hesperornithiforms, including hesperornithids. These indicate that the first avialan marine invasion by hesperornithiforms was achieved through rapid morphological evolution, whereas the invasion into freshwater environment did not involve accelerated

morphological change. The differences between two ecological transitions may be due to differences in predation pressure. Since freshwater environment is generally associated with lower predation pressure than in marine and terrestrial environments, biological resistance to invaders is smaller in the former. Harsher marine environment might accelerate evolution of hindlimbs in hesperornithiforms for escaping large predators. The rapid morphological evolution at the origin of the oldest seabirds contradicts the pattern observed in marine mammals (pinnipeds), indicating that evolutionary patterns of tetrapod marine invasion might be diverse.

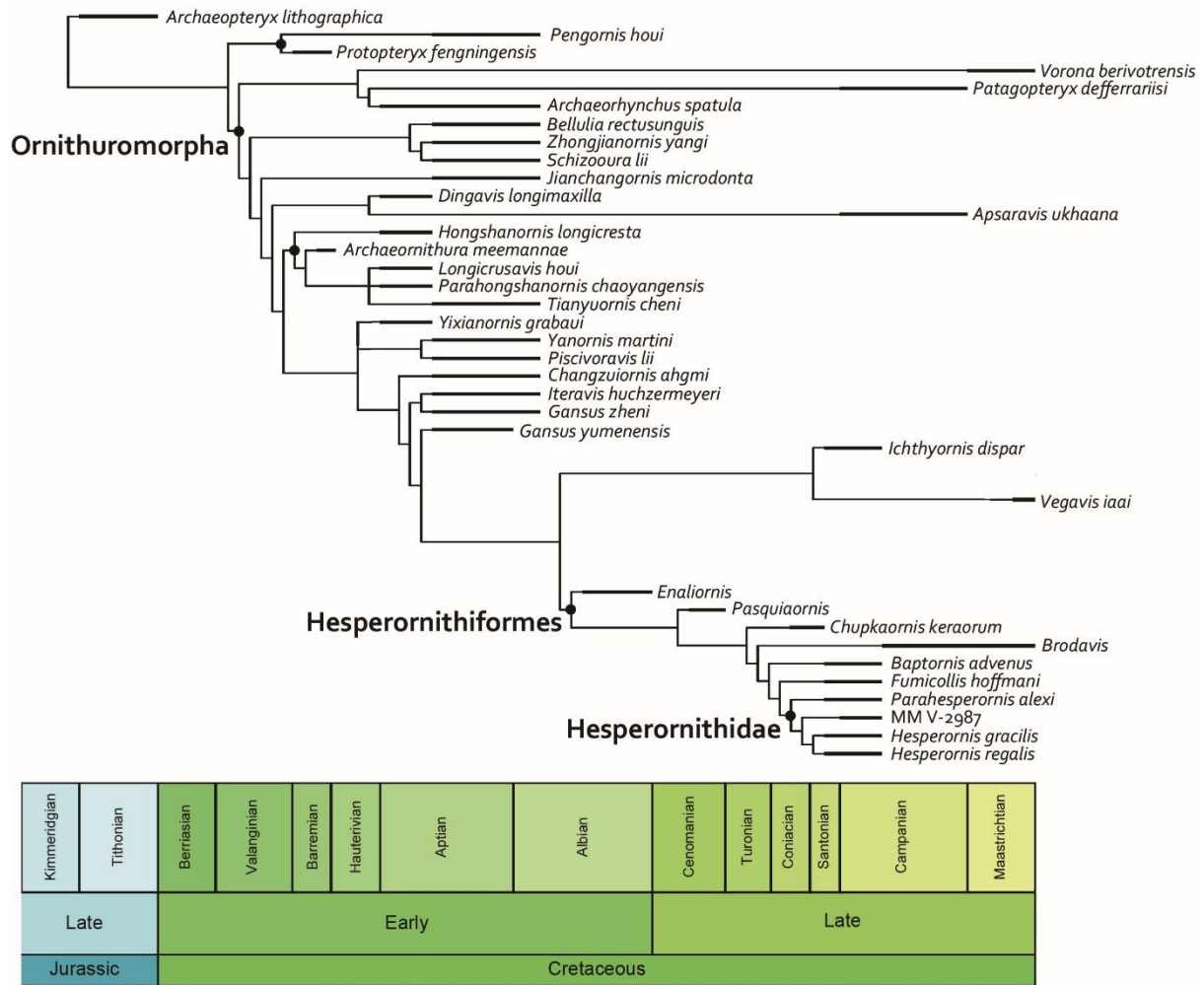
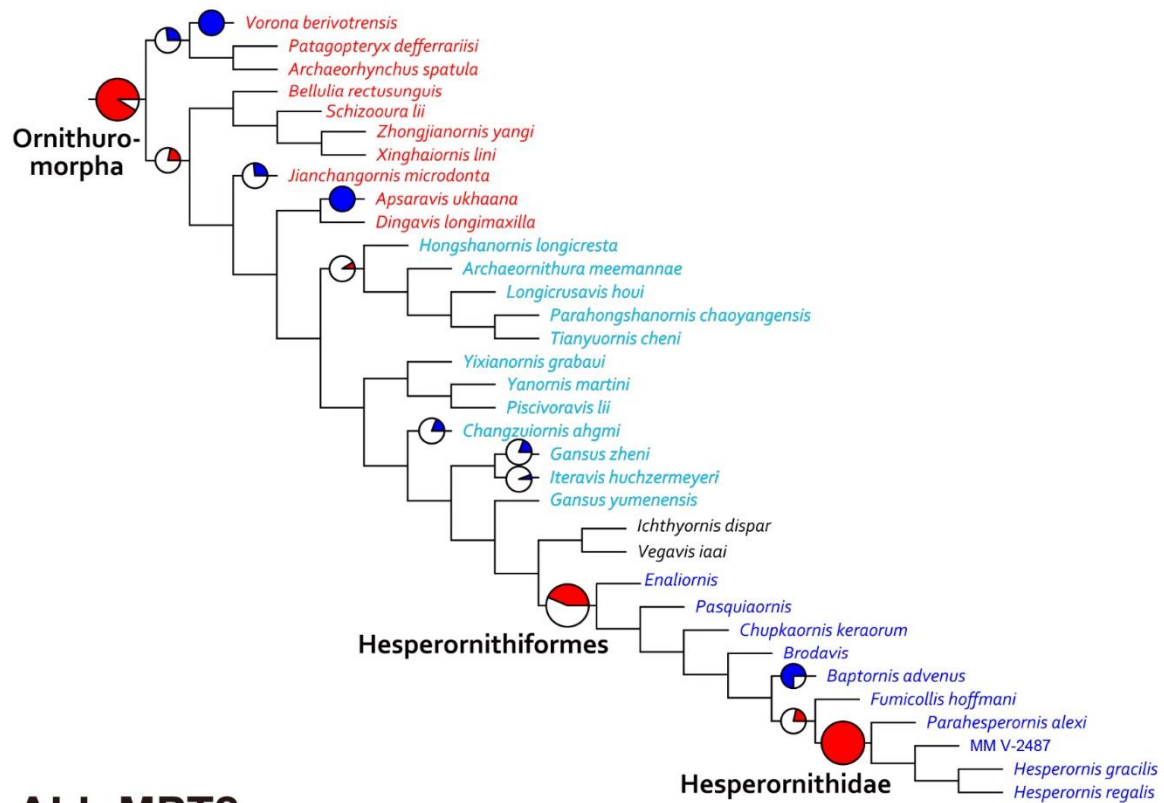


Fig. 5.1 Time-scaled phylogeny of ornithuromorphs. The phylogenetic tree is a strict consensus tree generated using the three most parsimonious tree (see Appendix 01).

ALL MPT1



ALL MPT2

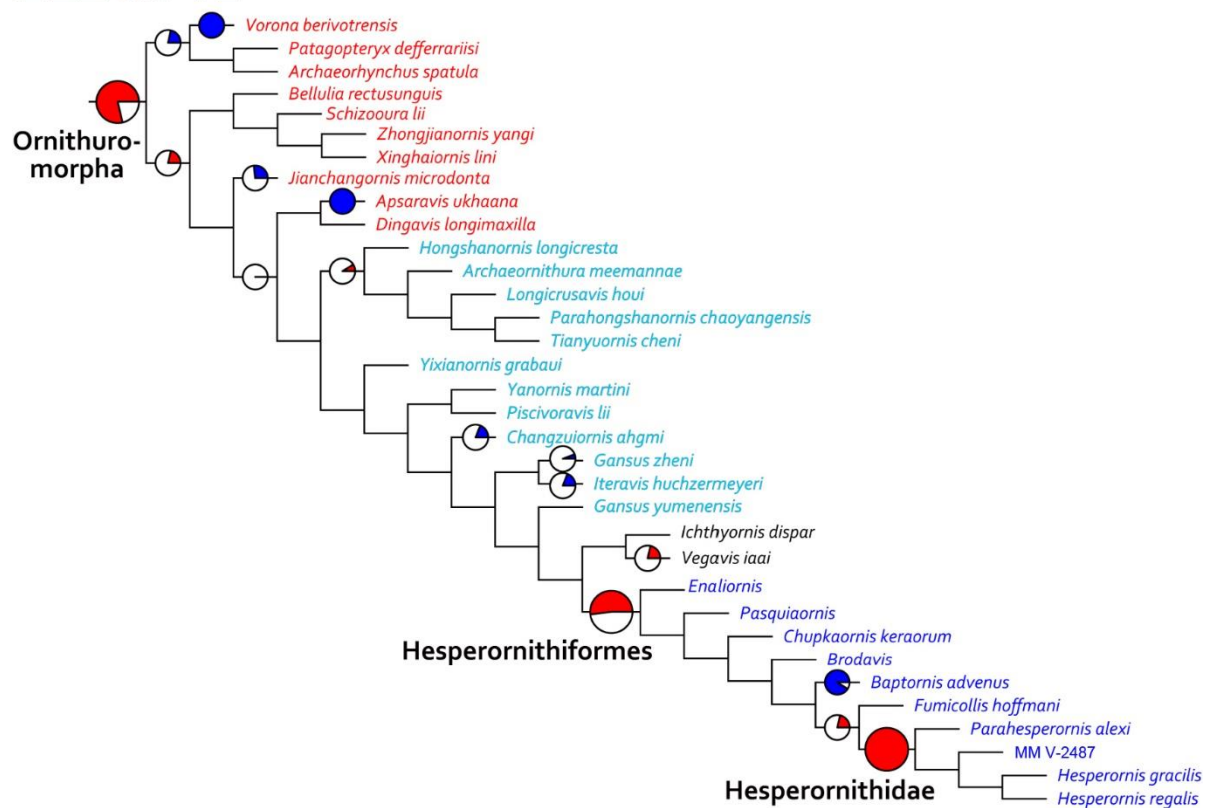
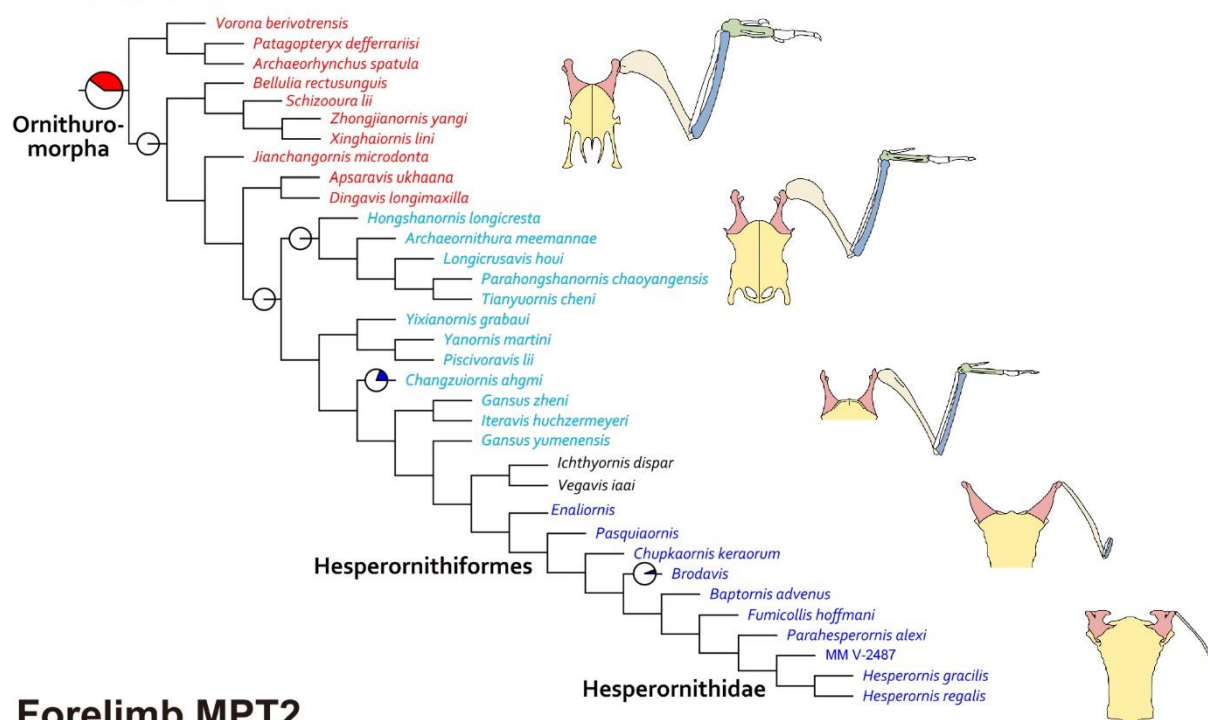


Fig. 5.2 Rates of morphological evolution in the whole body of ornithuromorphs. Cladograms generated the results from branch likelihood tests with 100 dating replications. Pie charts on branches illustrate the proportion of dating replicates that showed significantly high rates (red), slow rates (blue), and non-significant average rates (white). No pie charts are plotted on branches that showed non-significant rates in 100% of dating replicates. Branches that showed high rates (red) in more than 25% of dating replicates are doubled in length.

Forelimb MPT1



Forelimb MPT2

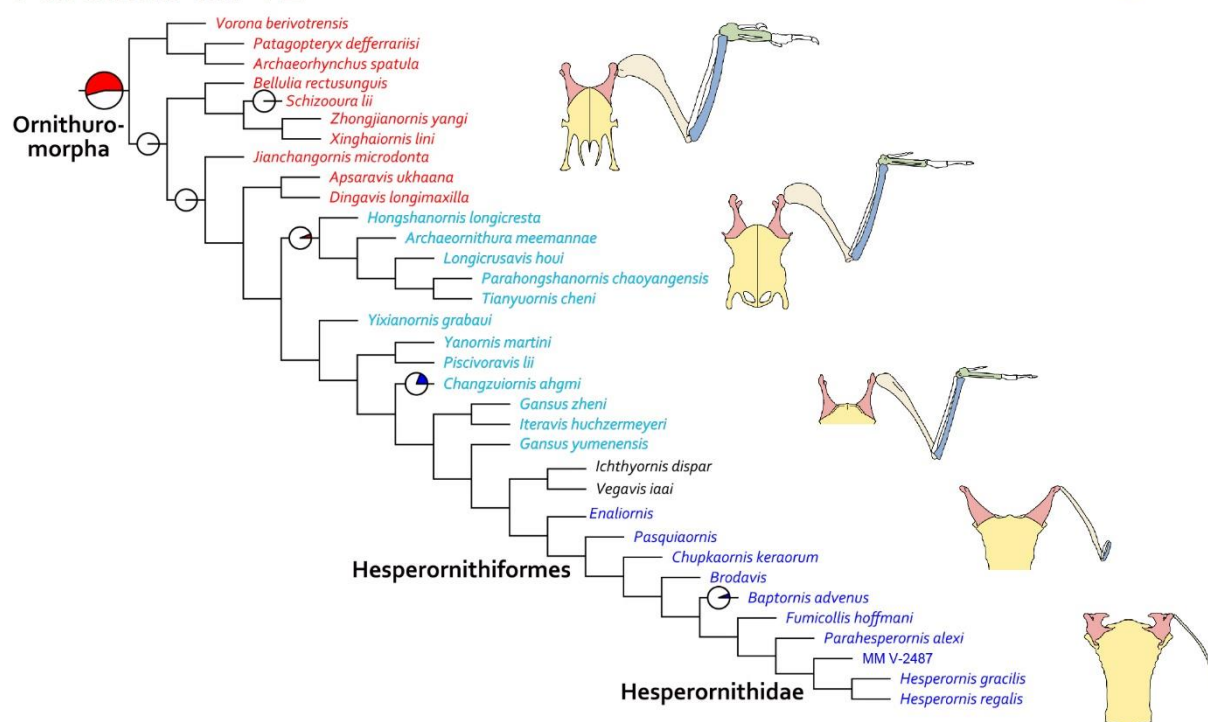
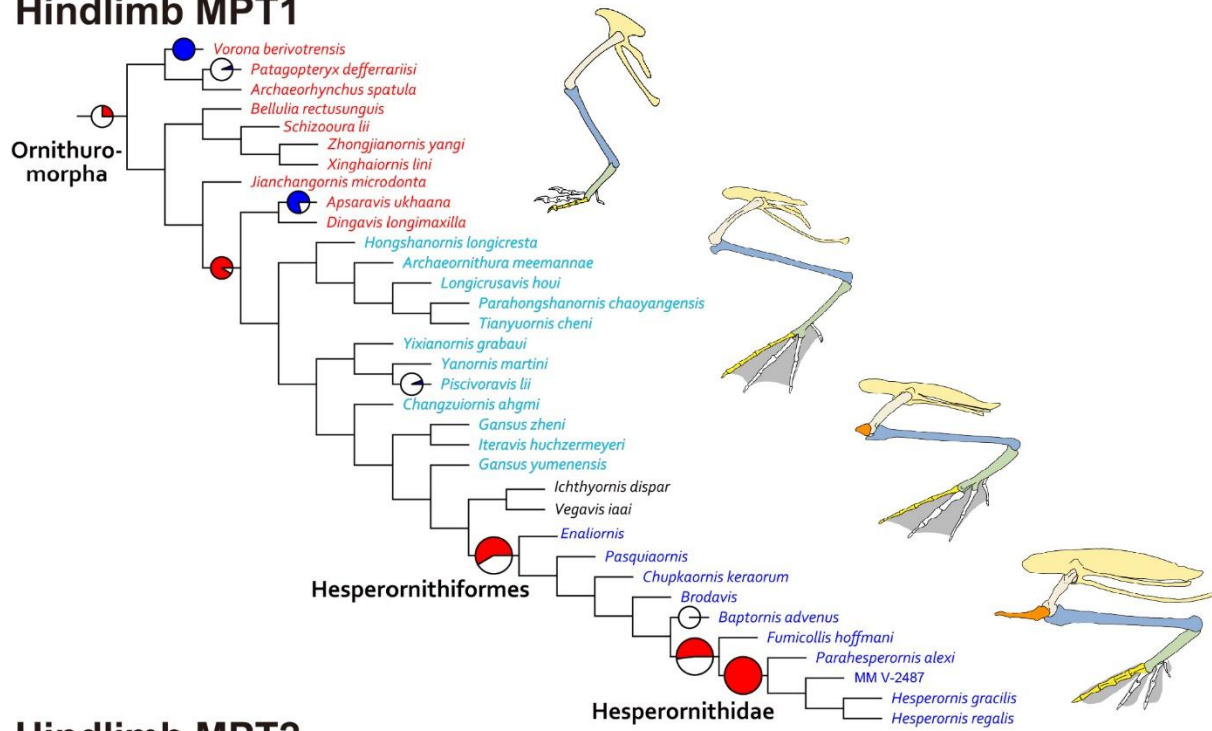


Fig. 5.3 Rates of morphological evolution in the forelimb module of ornithuromorphs. Cladograms generated the results from branch likelihood tests with 100 dating replications. Pie charts on branches illustrate the proportion of dating replicates that showed significantly high rates (red), slow rates (blue), and non-significant average rates (white). No pie charts are plotted on branches that showed non-significant rates in 100% of dating replicates. Branches that showed high rates (red) in more than 25% of dating replicates are doubled in length.

Hindlimb MPT1



Hindlimb MPT2

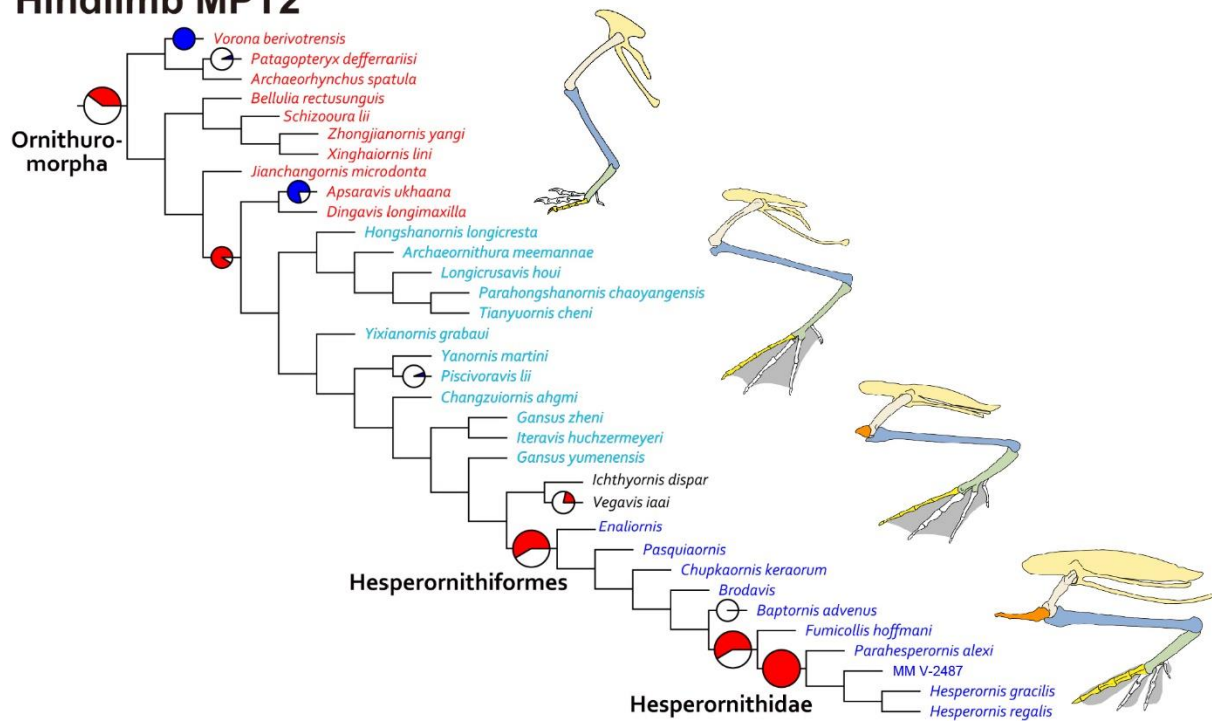


Fig. 5.4 Rates of morphological evolution in the hind limb module of ornithuromorphs. Cladograms generated the results from branch likelihood tests with 100 dating replications. Pie charts on branches illustrate the proportion of dating replicates that showed significantly high rates (red), slow rates (blue), and non-significant average rates (white). No pie charts are plotted on branches that showed non-significant rates in 100% of dating replicates. Branches that showed high rates (red) in more than 25% of dating replicates are doubled in length.

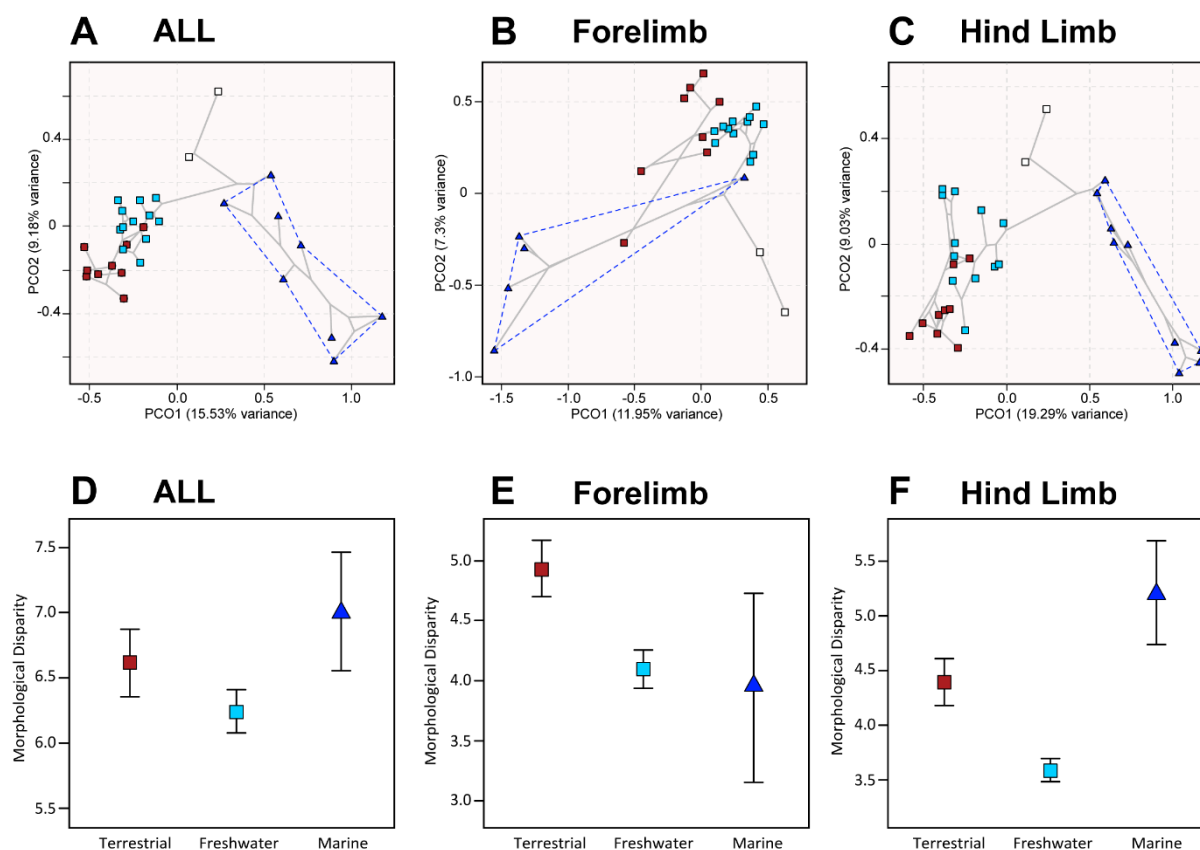


Fig. 5.5 Morphospace trends in Ornithuromorpha. Phylomorphospace plots are based on PCoA axes 1 and 2 for three morphological character partitions: **A**, the whole body; **B**, forelimb module; and **C**, hind limb module. Disparity is weighted mean pairwise dissimilarity (WMPD) calculated from maximum observable rescaled distance (MORD). Results and plotted for **D**, the whole body; **E**, forelimb module; and **F**, hind limb module. Disparity was calculated for three ecological bins: terrestrial (red squares), freshwater (sky blue squares), and marine (blue triangles) taxa. Error bars represent 95% confidence intervals generated using a bootstrapping procedure.

Appendix 1.1

Morphological Character Description

The 349 morphological characters used for present phylogenetic analysis are listed. The character list is built upon the three large datasets for Mesozoic birds: 165 characters from Huang et al. (2017) (enhanced version of Clarke *et al.* 2006), 95 characters from Wang et al. (2015) (enhanced version of Gao *et al.* 2008), and 50 characters from Bell & Chiappe (2015). Characters 68, 69, 73, 77, 86, 87, 100, 129, 136, 155, 118, 168, 177, 184, 195, 198, 200, 203, 215, 228, 230, 258, 273, 278, 291, 292, 295, 301, 302, 311, 323, 330, 332, 334, and 336 in the present list have been modified from original description of previous studies. In addition, 39 new characters are included. The 40 characters are ordered.

Skull and Mandibular

1. Premaxillae in adults:

(0) unfused in adults;

(1) fused anteriorly in adults, posterior nasal [frontal] processes not fused to each other;

(2) frontal processes completely fused as well as anterior premaxillae. *Ordered*

Remarks: Character #1 of Huang et al. (2017).

2. Premaxillary teeth:

(0) present throughout premaxillae;

(1) absent;

(2) anteriorly reduced, posteriorly present;

(3) anteriorly present, posteriorly reduced;

Remarks: Character #2 of Huang et al. (2017).

3. Tooth crown serration:

(0) present;

(1) vestigial or absent.

Remarks: Character #5 of Huang et al. (2017).

4. Frontal process of the premaxilla:

- (0) short;
- (1) relatively long, approaching the rostral border of the antorbital fenestra;
- (2) very long, extending caudally near the level of lacrimals. *Ordered*

Remarks: Character #5 of Wang et al. (2015).

5. Maxillary process of the premaxilla:

- (0) restricted to its rostral portion;
- (1) subequal or longer than the facial contribution of the maxilla.

Remarks: Character #2 of Wang et al. (2015).

6. Maxillary teeth:

- (0) present;
- (1) absent.

Remarks: Character #3 of Huang et al. (2017).

7. Nasal process of maxilla, dorsal ramus:

- (0) prominent, exposed medially and laterally;
- (1) absent or reduced to slight medial, and no lateral, exposure.

Remarks: Character #10 of Huang et al. (2017).

8. Dorsal (ascending) ramus of the maxilla:

- (0) present with two fenestrae (the promaxillary and maxillary fenestra);
- (1) present with one fenestra;
- (2) unfenestrated;
- (3) ramus absent. *Ordered*

Remarks: Character #8 of Wang et al. (2015).

9. Caudal margin of naris:

- (0) far rostral than the rostral border of the antorbital fossa;
- (1) nearly reaching or overlapping the rostral border of the antorbital fossa.

Remarks: Character #5 of Wang et al. (2015).

10. Naris longitudinal axis:

- (0) considerably shorter than the long axis of the antorbital fossa;
- (1) subequal or longer.

Remarks: Character #6 of Wang et al. (2015).

11. Caudal margin of choana:

- (0) located rostrally, not overlapping the region of the orbit;
- (1) displaced caudally, at the same level or overlapping the rostral margin of the orbit.

Remarks: Character #9 of Wang et al. (2015).

12. Rostral margin of the jugal:

- (0) away from the caudal margin of the naris;
- (1) very close to (leveled with) the caudal margin of the naris.

Remarks: Character #10 of Wang et al. (2015).

13. Contact between palatine and maxilla/premaxilla:

- (0) palatine contact maxilla only;
- (1) contacts premaxilla and maxilla.

Remarks: Character #11 of Wang et al. (2015).

14. Articulation between vomer and pterygoid:

- (0) present, well developed;
- (1) reduced, narrow process of pterygoid passes dorsally over palatine to contact vomer;
- (2) absent, pterygoid and vomer do not contact.

Remarks: Character #14 of Huang et al. (2017).

15. Ectopterygoid:

- (0) present;
- (1) absent.

Remarks: Character #13 of Huang et al. (2017).

16. Jugal process of palatine:

(0) present;

(1) absent.

Remarks: Character #13 of Wang et al. (2015).

17. Palatine and pterygoid:

(0) long, anteroposteriorly-overlapping, contact;

(1) short, primarily dorsoventral, contact.

Remarks: Character #15 of Huang et al. (2017).

18. Palatine contacts:

(0) maxillae only;

(1) premaxillae and maxillae.

Remarks: Character #16 of Huang et al. (2017).

19. Vomer contacts premaxilla:

(0) present;

(1) absent.

Remarks: Character #17 of Huang et al. (2017).

20. Postorbital:

(0) present;

(1) absent.

Remarks: Character #17 of Wang et al. (2015).

21. Jugal/postorbital contact:

(0) present;

(1) absent.

Remarks: Modified from #50 of Huang et al. (2017).

22. Quadratojugal:

(0) sutured to the quadrate;

(1) joined through a ligamentary articulation.

Remarks: Modified from #19 of Wang et al. (2015).

23. Lateral, round cotyla on the mandibular process of the quadrate (quadratojugal articulation):

(0) absent;

(1) present.

Remarks: Character #20 of Wang et al. (2015).

24. Contact between the quadratojugal and squamosal:

(0) present;

(1) absent.

Remarks: Character #21 of Wang et al. (2015).

25. Squamosal incorporated into the braincase, forming a zygomatic process:

(0) absent;

(1) present.

Remarks: Character #22 of Wang et al. (2015).

26. Squamosal, ventral or “zygomatic” process:

(0) variably elongate, dorsally enclosing otic process of the quadrate and extending cranioventrally along shaft of this bone, dorsal head of quadrate not visible in lateral view;

(1) short, head of quadrate exposed in lateral view.

Remarks: Character #23 of Wang et al. (2015).

27. Frontal/parietal suture in adults:

(0) open;

(1) fused.

Remarks: Character #24 of Wang et al. (2015).

28. Quadrate orbital process (pterygoid ramus):

(0) broad;

(1) sharp and pointed.

Remarks: Character #25 of Wang et al. (2015).

29. Quadrate, pneumaticity:

(0) absent;

(1) present.

Remarks: Character #38 of Huang et al. (2017).

30. Quadrate, quadratojugal articulation:

(0) overlapping;

(1) peg and socket articulation.

Remarks: Character #34 of Huang et al. (2017).

31. Quadrate, dorsal process, articulation:

(0) with squamosal only;

(1) with squamosal and prootic.

Remarks: Character #35 of Huang et al. (2017).

32. Otic articulation of the quadrate:

(0) articulates with a single facet (squamosal);

(1) articulates with two distinct facets (prootic and squamostal);

(2) articulates with two distinct facets and quadrate differentiated into two heads.

Ordered

Remarks: Character #28 of Wang et al. (2015).

33. Quadrate distal end:

- (0) with two transversely aligned condyles;
- (1) with a triangular, condylar pattern, usually composed of three distinct condyles.

Remarks: Character #29 of Wang et al. (2015).

34. Quadrate/ pterygoid contact:

- (0) as a facet, variably with slight anteromedial projection cradling base;
- (1) condylar, with a well-projected tubercle on the quadrate.

Remarks: Character #32 of Huang et al. (2017).

35. Quadrate, well-developed tubercle on anterior surface of dorsal process:

- (0) absent;
- (1) present.

Remarks: Character #33 of Huang et al. (2017).

36. Quadrate, dorsal process, development of intercotylar incisure between prootic and squamosal cotylae:

- (0) absent, articular surfaces not differentiated;
- (1) two distinct articular facets, incisure not developed;
- (2) incisure present, “double headed.”

Remarks: Character #36 of Huang et al. (2017).

37. Quadrate, mandibular articulation:

- (0) bicondylar articulation with mandible;
- (1) tricondylar articulation, additional posterior condyle or broad surface.

Remarks: Character #37 of Huang et al. (2017).

38. Projecting basisphenoid articulation with pterygoid:

- (0) present;
- (1) absent.

Remarks: Character #19 of Huang et al. (2017).

39. Basipterygoid processes:

- (0) long;
- (1) short (articulation with pterygoid sub-equal to, or longer than, amount projected from the basisphenoid rostrum).

Remarks: Character #20 of Huang et al. (2017).

40. Basisphenoid-ptyerygoid articulations:

- (0) located basal on basisphenoid;
- (1) located markedly anterior on basisphenoid (parasphenoid rostrum) such that the articulations are subadjacent on the narrow rostrum (the “rostrompterygoid articulation” of Weber, 1993).

Remarks: Character #21 of Huang et al. (2017).

41. Basisphenoid/ptyerygoid articulation, orientation of contact:

- (0) anteroventral;
- (1) mediolateral;
- (2) entirely dorsoventral.

Remarks: Character #22 of Huang et al. (2017).

42. Pterygoid, articular surface for basisphenoid:

- (0) concave “socket,” or short groove enclosed by dorsal and ventral flanges;
- (1) flat to convex;
- (2) flat to convex facet, stalked, variably projected. *Ordered*.

Remarks: Character #23 of Huang et al. (2017).

43. Pterygoid, kinked:

- (0) present, surface for basisphenoid articulation at high angle to axis of palatal process of pterygoid;
- (1) absent, articulation in line with axis of pterygoid.

Remarks: Character #24 of Huang et al. (2017).

44. Osseous interorbital septum (mesethmoid):

(0) absent;

(1) present.

Remarks: Character #25 of Huang et al. (2017).

45. Eustachian tubes:

(0) paired, lateral, and well-separated from each other;

(1) paired, close to each other and to cranial midline or forming a single cranial opening.

Remarks: Character #32 of Wang et al. (2015).

46. Eustachian tubes ossified:

(0) absent;

(1) present.

Remarks: Character #28 of Huang et al. (2017).

47. Prementary element:

(0) absent;

(1) present.

Remarks: Character #205 of Huang et al. (2017).

48. Dentary teeth:

(0) present;

(1) absent.

Remarks: Character #4 of Huang et al. (2017).

49. Dentary tooth implantation:

(0) teeth in individual sockets;

(1) teeth in a communal groove.

Remarks: Modified from #35 of Wang et al. (2015).

50. Symphysial portion of dentaries:

(0) unfused;

(1) fused.

Remarks: Character #36 of Wang et al. (2015).

51. Small ossification present at the rostral tip of the mandibular symphysis (intersymphysial ossification):

(0) absent;

(1) present.

Remarks: Character #40 of Wang et al. (2015).

52. Dentary strongly forked posteriorly:

(0) unforked, or with a weakly developed dorsal ramus;

(1) strongly forked with the dorsal and ventral rami approximately equal in posterior extent.

Remarks: Character #42 of Huang et al. (2017).

53. Coronoid ossification:

(0) present;

(1) absent.

Remarks: Character #18 of Huang et al. (2017)

54. Mandibular ramus sigmoidal such that the rostral tip is dorsally convex and the caudal end is dorsally concave:

(0) absent;

(1) present.

Remarks: Character #42 of Wang et al. (2015).

55. Mandibular symphysis, symphyseal foramina:

- (0) absent;
- (1) single;
- (2) paired.

Remarks: Character #38 of Wang et al. (2015).

56. Deeply notched rostral end of the mandibular symphysis:

- (0) absent;
- (1) present.

Remarks: Character #37 of Wang et al. (2015).

57. Mandibular symphysis, symphyseal foramen/foramina:

- (0) opening on posterior edge of symphysis;
- (1) opening on dorsal surface of symphysis.

Remarks: Character #47 of Huang et al. (2017).

58. Cranial extent of splenial:

- (0) stops well caudal to mandibular symphysis;
- (1) extending to mandibular symphysis, though non-contacting;
- (2) extending to proximal tip of mandible, contacting on midline. *Ordered*

Remarks: Character #43 of Wang et al. (2015).

59. Splenial, anterior extent:

- (0) splenial stops well posterior to mandibular symphysis;
- (1) extending to mandibular symphysis, though non-contacting;
- (2) extending to proximal tip of mandible, contacting on midline.

Remarks: Character #43 of Huang et al. (2017).

60. Meckel's groove:

(0) not completely covered by splenial, deep and conspicuous medially;

(1) covered by splenial, not exposed medially.

Remarks: Character #48 of Huang et al. (2017).

61. Anterior external mandibular fenestra:

(0) absent;

(1) present.

Remarks: Character #49 of Huang et al. (2017).

62. Caudal mandibular fenestra:

(0) present;

(1) absent.

Remarks: Character #46 of Wang et al. (2015).

63. Surangular:

(0) not as follows;

(1) dorsal margin concave and ventral margin convex;

(2) sigmoid.

Remarks: Character #262 of Wang et al. (2015).

64. Articular pneumaticity:

(0) absent;

(1) present.

Remarks: Character #41 of Huang et al. (2017).

Columnar Vertebrae

65. Cervical vertebrae:

- (0) variably dorsoventrally compressed, amphicoelous ('biconcave': flat to concave articular surfaces),
- (1) anterior surface heterocoelous (i.e. mediolaterally concave, dorsoventrally convex), posterior surface flat,
- (2) heterocoelous anterior (i.e. mediolaterally concave, dorsoventrally convex) and posterior (i.e. mediolaterally convex, dorsoventrally concave) surfaces. *Ordered*

Remarks: Character #52 of Huang et al. (2017).

66. Prominent (50% or more of the height of the centrum's cranial articular surface) ventral processes of the cervicothoracic vertebrae:

- (0) absent;
- (1) present. (Chiappe 2002)

Remarks: Character #24 of Bell & Chiappe (2015).

67. Thoracic vertebrae (with ribs articulating with the sternum), one or more with prominent hypapophyses:

- (0) absent,
- (1) present.

Remarks: Character #53 of Huang et al. (2017).

68. Thoracic vertebrae, count:

- (0) 12 or more;
- (1) 11;
- (2) 10 to 8;
- (3) 7 or fewer. *Ordered*

Remarks: Modified from character #54 of Huang et al. (2017).

69. Thoracic vertebrae:

- (0) at least part of series with subround, central articular surfaces (e.g. amphicoelous/opisthocoelous) that lack the dorsoventral compression seen in heterocoelous vertebrae;
- (1) central articular surfaces are compressed dorsoventrally and lack the saddle-shaped, concave on one axis and convex on the other;
- (2) series completely heterocoelous.

Remarks: Modified from character #55 of Huang et al. (2017).

70. Thoracic vertebrae, parapophyses:

- (0) rostral to transverse processes,
- (1) directly ventral to transverse processes (close to midpoint of vertebrae).

Remarks: Character #56 of Huang et al. (2017).

71. Thoracic vertebrae, centra, length, and midpoint width:

- (0) approximately equal in length and midpoint width;
- (1) length markedly greater than midpoint width.

Remarks: Character #57 of Huang et al. (2017).

72. Wide vertebral foramen in the mid-caudal thoracic vertebrae, vertebral foramen/articular cranial surface ratio (vertical diameter) larger than 0.40:

- (0) absent;
- (1) present.

Remarks: Character #59 of Wang et al. (2015).

73. Thoracic vertebrae, lateral sides of the centra, lateral excavation:

- (0) excavation with a pronounced and sharply defined edge of the ventral margin,
- (1) excavation without a pronounced and sharply defined edge of the ventral margin,
- (2) not depressed or only slightly depressed.

Remarks: Modified from character #58 of Huang et al. (2017).

74. Thoracic vertebrae with ossified connective tissue bridging transverse processes:

(0) absent;

(1) present.

Remarks: Character #59 of Huang et al. (2017).

75. Notarium:

(0) absent;

(1) present.

Remarks: Character #60 of Huang et al. (2017).

76. Synsacrum, cranial articular surface of synsacrum:

(0) flat or amphicoelous,

(1) hetelocoelous.

Remarks: This character is newly added in the present study (Fig. A1.3).

77. Sacral vertebrae, number ankylosed (synsacrum):

(0) less than 7,

(1) 7,

(2) 8,

(3) 9,

(4) 10,

(5) 11-14,

(6) 15 or more. *Ordered*

Remarks: Modified from character #61 of Huang et al. (2017).

78. Sacral vertebrae, series of short vertebrae, number of fused vertebrae that are positioned anterior to the anterior margin of the acetabulum:

(0) two or three,

(1) four or five,

(2) six or more.

Remarks: This character is newly added in the present study (Fig. A1.3).

79. Sacrum shape (in lateral view):

- (0) straight,
- (1) slight convex curve (dorsal edge at peak of curve).

Remarks: Character #33 of Bell & Chiappe (2015).

80. Series of short sacral vertebrae with dorsally directed parapophyses just cranial to the acetabulum:

- (0) absent;
- (1) present, three such vertebrae;
- (2) present, four such vertebrae. *Ordered*

Remarks: Character #62 of Huang et al. (2017).

81. Degree of fusion of distal caudal vertebrae:

- (0) fusion absent,
- (1) few vertebrae partially ankylosed (intervening elements are well discernable),
- (2) vertebrae completely fused into a pygostyle. *Ordered*

Remarks: Character #69 of Wang et al. (2015).

82. Free caudal vertebrae, number:

- (0) more than 8,
- (1) 8 or less.

Remarks: Character #63 of Huang et al. (2017).

83. Caudal vertebrae, chevrons, fused on at least one anterior caudal:

- (0) present;
- (1) absent.

Remarks: Character #64 of Huang et al. (2017).

84. Free caudals; length of transverse processes:

- (0) subequal to width of centrum,
- (1) significantly shorter than centrum width.

Remarks: Character #65 of Huang et al. (2017).

85. Procoelous caudals:

(0) absent;

(1) present.

Remarks: Character #71 of Wang et al. (2015).

86. Anterior free caudal vertebrae:

(0) elongate pre/postzygapophyses,

(1) pre- and postzygapophyses short or negligible.

Remarks: Modified from character #66 of Huang et al. (2017).

87. Fused distal caudals, morphology:

(0) fused element length equal or greater than 4 free caudal vertebrae,

(1) length less than 4 caudal vertebrae,

(2) less than 2 caudal vertebrae in length,

(3) unfused. *Ordered*

Remarks: Modified from character #68 of Huang et al. (2017).

88. Pygostyle:

(0) longer than or equal to the combined length of the free caudals;

(1) shorter.

Remarks: Character #75 of Wang et al. (2015).

89. Cranial end of pygostyle dorsally forked:

(0) absent,

(1) present.

Remarks: Character #76 of Wang et al. (2015).

90. Cranial end of pygostyle with a pair of laminar, ventrally projected processes:

(0) absent;

(1) present.

Remarks: Character #77 of Wang et al. (2015).

91. Pygostyle, well developed transverse processes throughout length of pygostyle:

(0) absent;

(1) present.

Remarks: Character #206 of Huang et al. (2017).

92. Ossified uncinat processes:

(0) absent,

(1) present and unfused to ribs,

(2) fused to ribs. *Ordered*

Remarks: Character #69 of Huang et al. (2017).

93. Gastralia:

(0) present,

(1) absent.

Remarks: Character #70 of Huang et al. (2017).

Pectoral girdle

94. Ossified sternal plates:

(0) unfused,

(1) fused, flat,

(2) fused, with slightly raised midline ridge,

(3) fused with projected carina. *Ordered*

Remarks: Character #71 of Huang et al. (2017).

95. Sternal carina:

- (0) near to, or projecting rostrally from, the cranial border of the sternum;
- (1) not reaching the cranial border of the sternum.

Remarks: Character #110 of Wang et al. (2015).

96. Sternal carina, location of apex:

- (0) posterior to anterior margin;
- (1) equal or surpassing anterior margin.

Remarks: Character #210 of Huang et al. (2017).

97. Sternum, dorsal surface, pneumatic foramen (or foramina):

- (0) absent;
- (1) present.

Remarks: Character #73 of Huang et al. (2017).

98. Sternum, caudal margin, number of paired caudal trabecula:

- (0) none;
- (1) one;
- (2) two.

The use of “lateral” and “medial” to identify the specific sternal processes is abandoned here due to the difficulty of identifying trabecula when only one is present.

Remarks: Character #111 of Wang et al. (2015).

99. Sternum, outermost trabecula, shape:

- (0) tips terminate cranial to caudal end of sternum;
- (1) tips terminate at or approaching caudal end of sternum;
- (2) tips extend caudally past the termination of the sternal midline.

Remarks: Character #112 of Wang et al. (2015).

100. Prominent distal expansion in the outermost trabecula of the sternum:

- (0) absent or simple bulb-like;
- (1) fan-shaped expansion;
- (2) triangular expansion with an acute medial angle;
- (3) branched.

Remarks: Modified from character #113 of Wang et al. (2015).

101. Sternum, outermost trabecula:

- (0) mainly parallel to the long axis of the sternum;
- (1) clearly directed laterally.

Remarks: Character #246 of Wang et al. (2015).

102. Sternal incisures, anterior extent relative to rib articulations:

- (0) terminate sub-equal with posterior-most rib facet;
- (1) terminate well posterior to the posterior-most rib facet.

Remarks: Character #209 of Huang et al. (2017).

103. Sternum, rostral margin of the sternum broad and rounded:

- (0) absent;
- (1) present.

Remarks: Character #114 of Wang et al. (2015).

104. Sternum, pneumatic foramina in the depressions (*loculi costalis*, Baumel & Witmer, 1993) between rib articulations (*processi articularis sternocostalis*, Baumel & Witmer, 1993):

- (0) absent,
- (1) present.

Remarks: Character #74 of Huang et al. (2017).

105. Sternum, coracoidal sulci spacing on anterior edge:

- (0) widely-separated mediolaterally,
- (1) adjacent,
- (2) crossed on midline.

Remarks: Character #75 of Huang et al. (2017).

106. Sternum, number of processes for articulation with the sternal ribs:

- (0) three;
- (1) four;
- (2) five;
- (3) six;
- (4) seven or more. *Ordered*

Remarks: Character #76 of Huang et al. (2017).

107. Sternum, raised, paired intermuscular ridges (*linea intermuscularis*, Baumel & Witmer, 1993) parallel to sternal midline:

- (0) absent,
- (1) present.

Remarks: Character #77 of Huang et al. (2017).

108. Sternal midline, caudal end:

- (0) blunt W-shape;
- (1) V-shape;
- (2) elongate straight projection (xiphoid process);
- (3) xiphoid process slightly flared mediolaterally;
- (4) xiphoid process distal end strongly flared with prominent medial and lateral projections;
- (5) rounded.

Remarks: Character #118 of Wang et al. (2015).

109. Sternum, caudal half, paired enclosed fenestra:

(0) absent;

(1) present.

Remarks: Character #119 of Wang et al. (2015).

110. Sternum, lateral margin, well-developed zyphoid process (Clarke et al. 2006):

(0) absent,

(1) present as a projection,

(2) present and squared in shape.

Remarks: **Remarks:** This character is newly added in the present study (Fig. A1.4).

111. Clavicles:

(0) fused;

(1) unfused.

Remarks: Character #79 of Huang et al. (2017).

112. Furcular, shape:

(0) boomerang-shaped;

(1) V to Y-shaped;

(2) U-shaped.

Remarks: Character #104 of Wang et al. (2015).

113. Furcula interclavicular angle:

(0) approximately 90°;

(1) less than 70°.

The interclavicular angle is measured as the angle formed between three points, one at the omal end of each rami and the apex located at the clavicular symphysis.

Remarks: Character #105 of Wang et al. (2015).

114. Furcula, dorsal furrow:

- (0) present,
- (1) absent.

Remarks: This character is newly added in the present study (Fig. A1.5).

115. Furcula, clavicular rami:

- (0) broad mediolaterally,
- (1) slender.

Remarks: This character is newly added in the present study (Fig. A1.5).

116. Hypocleideum:

- (0) absent;
- (1) present as a tubercle or short process;
- (2) present as an elongate process approximately 30% rami length;
- (3) hypertrophied, exceeding 50% rami length. *Ordered*

Remarks: Modified from #107 of Wang et al. (2015).

117. Distal end of furcula relative to sternal margin of coracoid:

- (0) proximal to or level with the sternal margin of the coracoid;
- (1) well beyond the sternal end of the coracoid.

When coracoid and furcula are not remained in natural position, then their proximodistal lengths are compared.

Remarks: Character #247 of Wang et al. (2015).

118. Furcula, ventral margin of apophysis:

- (0) curved, angling;
- (1) with a truncate or squared base.

Remarks: Character #84 of Huang et al. (2017).

119. Scapula and coracoid:

- (0) fused,
- (1) unfused.

Remarks: Character #85 of Huang et al. (2017).

120. Coracoid and scapula:

- (0) articulate through a wide, sutured articulation,
- (1) articulate through more localized facets. (Chiappe 2002)

Remarks: Character #42 of Bell & Chiappe (2015).

121. Scapula, glenoid facet:

- (0) present as a sub-circular facet,
- (1) absent, or present as an extremely reduced facet.

Remarks: This character is newly added in the present study (Fig. A1.6).

122. Angle between coracoid and scapula at glenoid:

- (0) more than 90 degrees;
- (1) 90 degrees or less, probably but see orientation of scapular cotyla.

Remarks: Character #99 of Huang et al. (2017).

123. Scapula, posterior end:

- (0) wider or approximately the same width as proximal dorsoventral shaft width,
- (1) tapering distally.

Remarks: Character #100 of Huang et al. (2017).

124. Scapula:

- (0) straight,
- (1) dorsoventrally curved.

Remarks: Character #101 of Huang et al. (2017).

125. Scapula, length:

- (0) shorter than humerus,
- (1) as long as or longer than the humerus.

Remarks: Character #102 of Huang et al. (2017).

126. Scapula, acromion process:

- (0) projected anteriorly to surpass the articular surface for coracoid (facies articularis coracoidea, Baumel & Witmer, 1993),
- (1) projected less anteriorly than the articular surface for coracoid.

Remarks: Character #103 of Huang et al. (2017).

127. Scapula, acromion process:

- (0) straight,
- (1) laterally hooked tip.

Remarks: Character #104 of Huang et al. (2017).

128. Scapula, proximal end, peg-shaped coracoidal tubercle,

- (0) absent,
- (1) present.

Remarks: This character is newly added in the present study (Fig. A1.6).

129. Coracoid, procoracoid process:

- (0) absent or extremely reduced,
- (1) present.

Remarks: Modified from character #87 of Wang et al. (2015).

130. Coracoid:

- (0) trapezoidal,
- (1) strut-like,
- (2) blunt triangle with short neck.

Remarks: Character #53 of Bell & Chiappe (2015).

131. Coracoid, lateral margin:

- (0) strongly concave,
- (1) nearly straight,
- (2) convex,
- (3) angular shape.

Remarks: This character is newly added in the present study (Fig. A1.7).

132. Coracoid, width at the sternal articulation:

- (0) broad flares markedly;
- (1) very narrow.

Remarks: Character #211 of Huang et al. (2017).

133. Coracoid, dorsal surface (= posterior surface of basal maniraptoran theropods):

- (0) strongly concave,
- (1) flat to convex.

Remarks: Character #90 of Huang et al. (2017).

134. Coracoid, pneumatized:

- (0) absent,
- (1) present.

Remarks: Character #91 of Huang et al. (2017).

135. Coracoid, pneumatic foramen:

- (0) proximal,
- (1) distal.

Remarks: Character #5 of Huang et al. (2017).

136. Coracoid, lateral process:

- (0) absent,
- (1) present, expanded laterally,
- (2) present as a hooked projection.

Remarks: Modified from character #93 of Wang et al. (2015).

137. Coracoid, ventral surface, lateral intermuscular line or ridge:

- (0) absent,
- (1) present.

Remarks: Character #94 of Huang et al. (2017).

138. Coracoid, glenoid facet:

- (0) dorsal to, or at approximately same level as, acrocoracoid process/ “biceps tubercle”;
- (1) ventral to acrocoracoid process.

Remarks: Character #95 of Huang et al. (2017).

139. Coracoid, glenoid facet, position relative to the scapular cotyla:

- (0) extends to sternal margin of the cotyla in lateral view;
- (1) over half of the glenoid facet lies omal to the cotyla in lateral view.

Remarks: Character #212 of Huang et al. (2017).

140. Coracoid, glenoid facet:

- (0) well-subrounded concave facet;
- (1) flat or slightly convex.

Remarks: This character is newly added in the present study (Fig. A1.7).

141. Coracoid, scapular cotyla:

- (0) absent or flat to convex;
- (1) present as a pit-shaped cotyla.

Remarks: This character is newly added in the present study (Fig. A1.7).

142. Coracoid, glenoid facet and scapular cotyla:

- (0) glenoid facet is larger than scapular cotyla;
- (1) scapular facet is larger than glenoid facet, or both of them are the same size.

Remarks: This character is newly added in the present study (Fig. A1.7).

143. Coracoid, glenoid and scapular facets:

- (0) located near the proximal end of the coracoid,
- (1) displaced distally.

Remarks: Character #48 of Bell & Chiappe (2015).

144. Coracoid, acrocoracoid:

- (0) absent,
- (1) present, straight,
- (2) present, hooked medially.

Remarks: Character #96 of Huang et al. (2017).

145. Coracoid, n. supracoracoideus passes through coracoid:

- (0) present,
- (1) absent.

Remarks: Character #97 of Huang et al. (2017).

146. Coracoid, medial surface, area of the foramen n. supracoracoideus (when developed):

- (0) strongly depressed,
- (1) flat to convex.

Remarks: Character #98 of Huang et al. (2017).

147. Coracoid, medial surface, strongly depressed elongate furrow at the level of the passage of n. supracoracoideus:

- (0) absent;
- (1) present.

Remarks: Character #93 of Wang et al. (2015).

Forelimbs

148. Humerus, shape:

- (0) robust, with large, expanded proximal and/or distal ends;
- (1) elongate or slender.

Remarks: Character #63 of Bell & Chiappe (2015).

149. Humerus and ulna, length:

- (0) humerus longer than ulna;
- (1) ulna and humerus approximately the same length;
- (2) ulna significantly longer than humerus. *Ordered.*

Remarks: Character #105 of Huang et al. (2017).

150. Proximal and distal humeral ends:

- (0) twisted;
- (1) expanded nearly in the same plane.

Remarks: Character #121 of Wang et al. (2015).

151. Humerus, proximal end, head in anterior or posterior view:

- (0) strap-like, articular surface flat, no proximal midline convexity;
- (1) head domed proximally.

Remarks: Character #106 of Huang et al. (2017).

152. Humerus, proximal end, proximal projection:

- (0) dorsal edge projected farthest;
- (1) midline projected farthest.

Remarks: Character #107 of Huang et al. (2017).

153. Humeral head:

- (0) concave cranially and convex caudally;
- (1) globe shaped, craniocaudally convex.

Remarks: Modified from #122 of Wang et al. (2015).

154. Humerus, proximocranial surface, well-developed circular fossa on midline:

- (0) absent;
- (1) present.

Remarks: Modified from #124 of Wang et al. (2015).

155. Humerus, the impression of the lig. acrocoracohumerale on the proximal surface of the bicipital crest:

- (0) absent,
- (1) present, develop as a discreet fossa,
- (2) present, developed as a slight transverse groove.

Remarks: Modified from character #155 of Wang et al. (2015).

156. Humerus, ventral tubercle projected caudally, separated from humeral head by deep capital incision:

- (0) absent;
- (1) present.

Remarks: Character #126 of Wang et al. (2015).

157. Humerus, capital incisure:

- (0) an open groove;
- (1) closed by tubercle associated with a muscle insertion just distal to humeral head.

Remarks: Character #109 of Huang et al. (2017).

158. Humerus, deltopectoral crest:

- (0) projected dorsally (in line with the long axis of humeral head);
- (1) projected anteriorly.

Remarks: Character #112 of Huang et al. (2017).

159. Humerus, deltopectoral crest:

- (0) less than shaft width;
- (1) approximately same width;
- (2) prominent and subquadrangular (i.e., subequal length and width).

Remarks: Character #129 of Wang et al. (2015).

160. Humerus, deltopectoral crest, proximoposterior surface:

- (0) flat to convex;
- (1) concave.

Remarks: Character #114 of Huang et al. (2017).

161. Humerus, deltopectoral crest:

(0) not perforate;

(1) with a large fenestra.

Remarks: Character #115 of Huang et al. (2017).

162. Humerus, deltopectoral crest, distal end recedes abruptly with the humeral shaft:

(0) present;

(1) absent.

Remarks: Character #253 of Wang et al. (2015).

163. Humerus, bicipital crest, pit-shaped scar/fossa for muscular attachment on proximal or anteroproximal surface:

(0) absent;

(1) present.

Remarks: This character is newly added in the present study (Fig. A1.8).

164. Humerus, bicipital crest:

(0) little or no ventral projection;

(1) developed as a ventral projection relative to shaft surface in anterior view;

(2) hypertrophied, rounded tumescence. *Ordered*

Remarks: Modified from character #118 of Huang et al. (2017).

165. Pneumatic fossa in the caudoventral corner of the proximal end of the humerus:

(0) absent or rudimentary;

(1) well developed.

Remarks: Character #127 of Wang et al. (2015).

166. Humerus, distal condyles:

- (0) developed distally;
- (1) developed on anterior surface of humerus.

Remarks: Character #32 of Huang et al. (2017).

167. Humerus, long axis of dorsal condyle:

- (0) at low angle to humeral axis, proximodistally oriented;
- (1) at high angle to humeral axis, almost transversely oriented.

Remarks: Character #121 of Huang et al. (2017).

168. Humerus, distal condyles:

- (0) sub-round, bulbous,
- (1) weakly defined, “strap-like”,
- (2) extremely reduced.

Remarks: Modified from character #122 of Huang et al. (2017).

169. Humerus, distal condyles, remarkable intercondylar incision:

- (0) present,
- (1) absent.

Remarks: This character is newly added in the present study (Fig. A1.8).

170. Humerus in cranial view, ventral epicondyle extends:

- (0) to a similar extent as condyles;
- (1) epicondyles absent.

Remarks: Character #76 of Bell & Chiappe (2015).

171. Humerus, distal margin:

- (0) approximately perpendicular to long axis of humeral shaft;
- (1) ventrodistal margin projected significantly distal to dorsodistal margin,
- (2) distal margin angling strongly ventrally (sometimes described as a well-projected flexor process).

Remarks: Character #123 of Huang et al. (2017).

172. Humerus, brachial fossa:

(0) absent;

(1) present, developed as a flat scar or as a scar-impressed fossa.

Remarks: Character #124 of Huang et al. (2017).

173. Humerus, ventral condyle:

(0) length of long axis of condyle less than the same measure of the dorsal condyle;

(1) same or greater.

Remarks: Character #125 of Huang et al. (2017).

174. Humerus, ventral condyle:

(0) length of long axis of condyle less than the same measure of the dorsal condyle;

(1) same or greater.

Remarks: Character #126 of Huang et al. (2017).

175. Humerus, demarcation of muscle origins (e.g., m. extensor metacarpi radialis in Aves) on the dorsal edge of the distal humerus:

(0) no indication of origin as a scar, a pit, or a tubercle;

(1) indication as a pit-shaped scar or as a variably projected scar-bearing tubercle or facet.

Remarks: Character #127 of Huang et al. (2017).

176. Humerus, distal end, posterior surface, groove for passage of m. scapulotriceps:

(0) absent;

(1) present.

Remarks: Character #128 of Huang et al. (2017).

177. Humerus, m. humerotricipitalis groove:

(0) absent or shallow,

(1) present as a remarkable ventral depression contiguous with the olecranon fossa.

Remarks: Modified from character #129 of Huang et al. (2017).

178. Well-developed olecranon fossa on the caudal face of the distal end of the humerus:

(0) absent;

(1) present.

Remarks: Character #136 of Wang et al. (2015).

179. Ulnar shaft, radial-shaft/ulnar-shaft ratio:

(0) larger than 0.70;

(1) smaller than 0.70.

Remarks: Character #145 of Wang et al. (2015).

180. Ulna, cotylae:

(0) dorsoventrally adjacent;

(1) widely separated by a deep groove.

Remarks: Character #130 of Huang et al. (2017).

181. Ulna, dorsal cotyla convex:

(0) absent;

(1) present.

Remarks: Character #131 of Huang et al. (2017).

182. Ulna, distal end, dorsal condyle, dorsal trochlear surface developed as a semilunate ridge:

(0) absent;

(1) present.

Remarks: Character #132 of Huang et al. (2017).

183. Ulna, distal end, dorsal condyle, dorsal trochlear surface, extent along posterior margin:

(0) less than transverse measure of dorsal trochlear surface;

(1) approximately equal in extent.

Remarks: Character #133 of Huang et al. (2017).

184. Ulna, bicipital tubercle (Clarke 2004):

(0) absent;

(1) present.

Remarks: Modified from character #134 of Huang et al. (2017).

185. Proximal end of the ulna with a well-defined area for the insertion of m. brachialis anticus (brachial impression):

(0) absent;

(1) present.

Remarks: Character #149 of Wang et al. (2015).

186. Radius, ventroposterior surface:

(0) smooth;

(1) with muscle impression along most of surface;

(2) deep longitudinal groove.

Remarks: Character #136 of Huang et al. (2017).

187. Ulnare:

(0) absent;

(1) present.

Remarks: Character #137 of Huang et al. (2017).

188. Ulnare:

(0) “heart-shaped,” little differentiation into short dorsal and ventral rami;

(1) V-shaped, well-developed dorsal and ventral rami.

Remarks: Character #138 of Huang et al. (2017).

189. Ulnare, ventral ramus (crus longus, Baumel and Witmer, 1993):

(0) shorter than dorsal ramus (crus brevis);

(1) same length as dorsal ramus;

(2) longer than dorsal ramus.

Remarks: Character #139 of Huang et al. (2017).

190. Semilunate carpal and proximal ends of metacarpals in adults:

- (0) unfused;
- (1) semilunate fused to the alular (I) metacarpal;
- (2) semilunate fused to the major (II) and minor (III) metacarpals;
- (3) fusion of semilunate and all metacarpals.

Any specimen that is inferred to be a juvenile should be scored as a “?” in order to account for the possibility of ontogenetic change.

Remarks: Character #154 of Wang et al. (2015).

191. Distal end of metacarpals:

- (0) unfused;
- (1) partially or completely fused.

Remarks: Character #166 of Wang et al. (2015).

192. Semilunate carpal, position relative to the alular metacarpal (I):

- (0) over entire proximal surface;
- (1) over less than one-half proximal surface or no contact present.

Remarks: Character #155 of Wang et al. (2015).

193. Metacarpal III, anteroposterior diameter as a percent of same dimension of metacarpal II:

- (0) approximately equal or greater than 50%;
- (1) less than 50%.

Remarks: Character #142 of Huang et al. (2017).

194. Metacarpal I, extensor process:

- (0) absent,
- (1) present as a small knob (tip of extensor process just surpasses the distal articular facet for phalanx 1 in cranial extent),
- (2) present as a pronounced process (tip of extensor surpasses the articular facet by approximately the width of the facet or more).

Remarks: This character is newly added in the present study (Fig. A1.9).

195. Metacarpal I, anterior surface:

- (0) flat or slightly convex,
- (1) anterior surface broadly convex,
- (2) roughly hourglass-shaped proximally, at least moderately expanded anteroposteriorly, and constricted just before flare of articulation for phalanx 1.

Remarks: Modified from character #144 of Huang et al. (2017).

196. Metacarpal I, distal articulation with phalanx I:

- (0) ginglymoid;
- (1) shelf.

Remarks: Character #145 of Huang et al. (2017).

197. Pisiform process:

- (0) absent;
- (1) present.

Remarks: Character #146 of Huang et al. (2017).

198. Carpometacarpus, ventral surface, infratrochlear fossa excavating proximal surface of pisiform process:

- (0) absent;
- (1) present.

Remarks: Modified from character #147 of Huang et al. (2017).

199. Intermetacarpal space (between metacarpals II and III):

- (0) reaches proximally as far as the distal end of metacarpal I;
- (1) terminates distal to end of metacarpal I.

Remarks: Character #148 of Huang et al. (2017).

200. Intermetacarpal space (between metacarpals II and III),

(0) at least as wide as the maximum width of major metacarpal (II) shaft: absent;

(1) present.

Remarks: Modified from character #164 of Wang et al. (2016).

201. Minor metacarpal (III) projecting distally more than the major metacarpal (II):

(0) absent;

(1) present.

Remarks: Character #167 of Wang et al. (2016).

202. Intermetacarpal process or tubercle:

(0) absent;

(1) present as scar;

(2) present as tubercle or flange. *Ordered*

Remarks: Character #150 of Huang et al. (2017).

203. Alular digit (I), phalanx 1, distal extension relative to the major metacarpal (II):

(0) beyond the distal end of major metacarpal or approximately equal in distal extension;

(1) shorter than the distal end but beyond half of the major metacarpal;

(2) terminating less than half of the major metacarpal. *Ordered*

Remarks: Modified from character #168 of Wang et al. (2015).

204. Ungual phalanx of alular digit (I):

(0) present;

(1) absent.

Remarks: This character is newly added in the present study (Fig. A1.9).

205. Manual digit II, phalanx 1:

(0) subcylindrical to subtriangular;

(1) strongly dorsoventrally compressed, flat caudal surface.

Remarks: Character #151 of Huang et al. (2017).

206. Manual digit II, phalanges:

(0) length of phalanx II-1 less than or equal to that of II-2;

(1) longer.

Remarks: Character #152 of Huang et al. (2017).

207. Manual digit II, phalanx 2, "internal index process" (Stegmann, 1978) on posterodistal edge:

(0) absent;

(1) present.

Remarks: Character #153 of Huang et al. (2017).

208. Ungual phalanx of major digit (II):

(0) present;

(1) absent.

Remarks: Character #172 of Wang et al. (2015).

209. Ungual phalanx of major digit (II):

(0) larger or subequal to other manual unguals;

(1) smaller than the alular ungual but larger than that of the minor (III) digit, and the ungual of the minor digit may or may not present;

(2) smaller than the unguals of the alular and minor digits.

Remarks: Character #173 of Wang et al. (2015).

210. Manual phalanx III-1, flexor tubercle:

(0) absent or indistinct, not developed as a tubercle;

(1) present.

Remarks: Character #214 of Huang et al. (2017).

211. Manual digit III, number of phalanges:

- (0) four;
- (1) two;
- (2) one;
- (3) three.

Remarks: Character #215 of Huang et al. (2017).

212. Proximal phalanx of the minor digit (III) much shorter than the remaining non-ungual phalanges of this digit:

- (0) absent;
- (1) present.

Remarks: Character #174 of Wang et al. (2015).

213. Ungual phalanx of minor digit (III):

- (0) present;
- (1) absent.

Remarks: Character #175 of Wang et al. (2015).

214. Length of manus (semilunate carpal + major metacarpal and digit) relative to humerus:

- (0) longer;
- (1) subequal;
- (2) shorter. *Ordered*

Remarks: Character #176 of Wang et al. (2015).

215. Intermembral index = (length of humerus + ulna)/(length of femur + tibiotarsus):

- (0) less than 0.7, flightless;
- (1) between 0.7 and 1.0;
- (2) greater than 1.0.

Remarks: Modified from character #177 of Wang et al. (2015).

Pelvic Girdle

216. Pelvic elements in adults, at the level of the acetabulum:

- (0) unfused or partial fusion;
- (1) completely fused.

Remarks: Character #178 of Wang et al. (2015).

217. Ilium/ischium, distal co-ossification to completely enclose the ilioischadic fenestra:

- (0) absent;
- (1) present.

Remarks: Character #155 of Huang et al. (2017).

218. Preacetabular ilium:

- (0) approach on midline, open, or cartilaginous connection;
- (1) co-ossified, dorsal closure of “iliosynsacral canals”.

Remarks: Character #161 of Huang et al. (2017).

219. Preacetabular ilium extends anterior to first sacral vertebrae:

- (0) no free ribs overlapped;
- (1) one or more ribs overlapped.

Remarks: Character #162 of Huang et al. (2017).

220. Postacetabular ilium:

- (0) dorsoventrally oriented;
- (1) mediolaterally oriented.

Remarks: Character #163 of Huang et al. (2017).

221. Postacetabular ilium, ventral surface, renal fossa developed:

- (0) absent;
- (1) present.

Remarks: Character #164 of Huang et al. (2017).

222. Ilium, m. cuppedicus fossa as broad, mediolaterally-oriented surface directly anteroventral to acetabulum:

- (0) present;
- (1) surface absent, insertion variably marked by a small entirely lateral fossa anterior to acetabulum.

Remarks: Character #165 of Huang et al. (2017).

223. Ilium, length of preacetabular ilium compared to postacetabular ilium:

- (0) preacetabular longer;
- (1) equal;
- (2) postacetabular ilium longer. *Ordered*

Remarks: Character #216 of Huang et al. (2017).

224. Pelvis, acetabular foramen,

- (0) large and completely open,
- (1) extremely reduced by ossification.

Remarks: This character is newly added in the present study (Fig. A1.11).

225. Small acetabulum, acetabulum/ilium length ratio equal to or smaller than 0.11:

- (0) absent;
- (1) present.

Remarks: Character #184 of Wang et al. (2015).

226. Iliac brevis fossa:

- (0) present;
- (1) absent.

Remarks: Character #187 of Wang et al. (2015).

227. Ischium:

- (0) forked (dorsal process present);
- (1) straight, no dorsal process.

Remarks: Character #156 of Huang et al. (2017).

228. Ischium:

- (0) does not contact ilium;
- (1) contacts ilium.

Remarks: Modified from character #157 of Huang et al. (2017).

229. Ischium and pubis:

- (0) not subparallel, pubis directed ventrally;
- (1) subparallel, pubis posteriorly directed;
- (2) pubis appressed to ischium. *Ordered*

Remarks: Character #158 of Huang et al. (2017).

230. Prominent antitrochanter:

- (0) incipient or absent;
- (1) present, directly posterior to acetabulum;
- (2) present, dorsal to acetabulum.

Remarks: Modified from character #159 of Huang et al. (2017).

231. The ratio (width of antitrochanter/synsacrum length):

- (0) more than 0.61;
- (1) 0.41 to 0.60;
- (2) less than 0.40.

Remarks: This character is newly added in the present study (Fig. A1.10).

232. Preacetabular pectineal process (Baumel and Witmer, 1993):

- (0) absent;
- (1) present as a small flange;
- (2) present as a well-projected flange. *Ordered*

Remarks: Character #160 of Huang et al. (2017).

233. Ischium, posterior demarcation of the obturator foramen:

(0) absent;

(1) present, developed as a small flange or raised scar contacting / fused with pubis and demarcating the obturator foramen distally.

Remarks: Character #166 of Huang et al. (2017).

234. Ischium, length relative to that of pubis:

(0) 1/3 or greater total pubis length extends posterior to end of ishium;

(1) less than 1/3 pubis extends farther than end of ishium.

Remarks: Character #167 of Huang et al. (2017).

235. Obturator process of ischium:

(0) prominent;

(1) reduced or absent.

Remarks: Character #189 of Wang et al. (2015).

236. Ischiadic terminal processes forming a symphysis:

(0) present;

(1) absent.

Remarks: Character #192 of Wang et al. (2015).

237. Pubis:

(0) sub-oval in cross section;

(1) compressed mediolaterally.

Remarks: Character #168 of Huang et al. (2017).

238. Pubes, distal contact:

(0) contacting, variably co-ossified into symphysis;

(1) non-contacting.

Remarks: Character #169 of Huang et al. (2017).

239. Distal end of pubis:

- (0) expanded, flared;
- (1) straight, subequal, in proportion with rest of pubis.

Remarks: Character #170 of Huang et al. (2017).

Hind limbs

240. Femur: fossa for insertion of lig. capitis femoris:

- (0) absent;
- (1) present.

Remarks: Character #171 of Huang et al. (2017).

241. Femur:

- (0) neck absent;
- (1) head merges into neck without sharp margin;
- (2) head forms distinct knob separated from neck. *Ordered*

Remarks: Character #123 of Bell & Chiappe (2015).

242. Femur, trochanter and head:

- (0) nearly continuous or separated by a shallow notch;
- (1) separated by a deep notch.

Remarks: Character #122 of Bell & Chiappe (2015).

243. Femur: posterior trochanter:

- (0) present, developed as a slightly projected tubercle or flange;
- (1) hypertrophied, “shelf-like” conformation (in combination with development of the trochanteric shelf; see Hutchinson, 2001);
- (2) absent (Chiappe, 1991). *Ordered*

Remarks: Character #172 of Huang et al. (2017).

244. Femoral anterior (lessor) trochanter:

- (0) separated from the greater trochanter;
- (1) fused to it, forming a trochanteric crest with a laterally curved edge;
- (2) fused to it, forming a trochanteric crest with a flattened edge.

Remarks: Character #201 of Wang et al. (2015).

245. Femoral trochanteric crest:

- (0) projects proximally beyond femoral head;
- (1) equal in proximal projection;
- (2) does not project beyond femoral head.

Remarks: Character #202 of Wang et al. (2015).

246. Femur, lateral view, margin of trochanter:

- (0) smooth, flattened surface;
- (1) lumpy, irregular surface;
- (2) sharp ridge with highly irregular margin.

Remarks: Character #130 of Bell & Chiappe (2015).

247. Femur, in proximal view, anterior margin of the trochanteric crest:

- (0) well developed and positioned anterior to the anterior margin of femoral head,
- (1) moderately developed and positioned at the same level with the anterior margin of femoral head,
- (2) less developed and positioned posteriorly to the anterior margin of the femoral head.

Remarks: This character is newly added in the present study (Fig. A1.13).

248. Femur, ratio of width of proximal end / length:

- (0) less than 0.30,
- (1) between 0.31 and 0.44,
- (2) more than 0.45.

Remarks: This character is newly added in the present study (Fig. A1.13).

249. Femur, lateral margin of shaft (between trochanter and fibular condyle):

- (0) relatively straight;
- (1) slightly concave;
- (2) highly concave.

Remarks: Character #35 of Bell & Chiappe (2015).

250. Femur, ratio of mediolateral width of the mid-shaft / length:

- (0) less than or approximately 0.10;
- (1) Between 0.12 to 0.19;
- (2) more than 0.20.

Remarks: This character is newly added in the present study (Fig. A1.13).

251. Femur, medial margin of shaft, tubercle for *m. iliofemoralis* and *m. caudofemoralis* (Zinoviev, 2011):

- (0) absent or faint,
- (1) sub-rounded and concave,
- (2) well-defined.

Remarks: This character is newly added in the present study (Fig. A1.13, A1.14).

252. Femur in medial or lateral view, "hunched", thickened appearance along shaft:

- (0) absent;
- (1) present.

Remarks: Character #119 of Bell & Chiappe (2015).

253. Femur, intramuscular lines:

- (0) absent or faint;
- (1) well-developed,
- (2) with high relief.

Remarks: Character #120 of Bell & Chiappe (2015).

254. Femur, shaft: cranially convex (in medial view, proximal and distal ends inflected caudally):

- (0) absent or slight inflection;
- (1) dramatic curvature.

Remarks: Character #121 of Bell & Chiappe (2015).

255. Femur with prominent patellar groove:

- (0) absent;
- (1) present as a continuous extension onto the distal shaft;
- (2) present and separated from the shaft by a slight ridge, giving it a pocketed appearance.

Remarks: Character #204 of Wang et al. (2015).

256. Femur, medial condyle in caudal view:

- (0) sub-circular or oval;
- (1) kidney bean shaped.

Remarks: Character #136 of Bell & Chiappe (2015).

257. Femur, lateral condyle:

- (0) similar distal extent as medial;
- (1) extends distally past medial.

Remarks: Character #137 of Bell & Chiappe (2015).

258. Femur:

- (0) ectocondylar tubercle and lateral condyle separated by deep notch;
- (1) ectocondylar tubercle and lateral condyle contiguous but without developing a tibiofibular crest;
- (2) developed tibiofibular crest present, defining laterally a fibular trochlea. *Ordered*

Remarks: Modified from character #205 of Wang et al. (2015).

259. Femur, face of fibular condyle oriented:

- (0) caudally or slightly laterally;
- (1) nearly entirely laterally.

Remarks: Character #141 of Bell & Chiappe (2015).

260. Femur, in distal view, lateral surface of fibular condyle:

- (0) smooth,
- (1) remarkably concave.

Remarks: This character is newly added in the present study (Fig. A1.13).

261. Femur, distal view, depressed medial margin of medial condyle:

- (0) faint or absent,
- (1) present.

Remarks: This character is newly added in the present study (Fig. A1.13).

262. Femur, lateral view, lateral condyle:

- (0) merges smoothly into shaft;
- (1) constricts into neck before widening at shaft.

Remarks: Character #142 of Bell & Chiappe (2015).

263. Femur, popliteal fossa:

- (0) a groove open distally and bounded medially and laterally by narrow condyles;
- (1) closed distally by expansion of both condyles (primarily the medial).

Remarks: Character #178 of Huang et al. (2017).

264. Fossa for the femoral origin of m. tibialis cranialis:

- (0) absent;
- (1) present.

Remarks: Character #208 of Wang et al. (2015).

265. Femur, distal surface of lateral condyle:

- (0) featureless curve;
- (1) small bump or rounded prominence;
- (2) projected, flattened prominence. *Ordered*

Remarks: Character #143 of Bell & Chiappe (2015).

266. Femur, ratio of width of distal end / length:

- (0) less than 0.25,
- (1) between 0.25 and 0.41,
- (2) more than 0.41.

Remarks: This character is newly added in the present study (Fig. A1.13)

267. Femur, the ratio of anteroposterior width of medial condyle / width of distal end:

- (0) less than 0.45,
- (1) between 0.46 and 0.55,
- (2) more than 0.56.

Remarks: This character is newly added in the present study.

268. Femur, thick cortical area:

- (0) absent,
- (1) present.

Remarks: This character is newly added in the present study.

269. Patella shape:

- (0) roughly pyramidal;
- (1) laterally compressed, nearly flat and highly elongate.

Remarks: Character #148 of Bell & Chiappe (2015).

270. Patella in medial view, foramen for *m. ambiens*:

- (0) located cranially,
- (1) located at around the center.

Remarks: This character is newly added in the present study (Fig. A1.15).

271. The ratio (femur length/tibiotarsus length):

- (0) more than 0.61;
- (1) 0.41 ~ 0.60;
- (2) less than 0.40.

Remarks: This character is newly added in the present study.

272. Tibia, calcaneum and astragalus:

- (0) unfused to each other or tibia in adult;
- (1) fused to each other, unfused to tibia;
- (2) complete fused to each other and tibia. *Ordered*

Remarks: Character #179 of Huang et al. (2017).

273. Tibiotarsus, cnemial crest(s):

- (0) absent;
- (1) lateral cnemial crest only;
- (2) lateral and medial cnemial crests present.

Remarks: Modified from character #180 of Huang et al. (2017).

274. Tibiotarsus, proximal articular surface:

- (0) both medial and lateral cotylae are flat;
- (1) lateral cotyla is tilted laterally;
- (2) both medial and lateral cotylae are strongly tilted laterally.

Remarks: This character is newly added in the present study (Fig. A1.18).

275. Tibiotarsus, rotularl process:

- (0) absent or low relief;
- (1) High relief, well-projected proximally.

Remarks: This character is newly added in the present study (Fig. A1.16).

276. Tibiotarsus, proximal articular surface, central depression between cotylae:

(0) absent;

(1) present.

Remarks: Character #152 of Bell & Chiappe (2015).

277. Tibiotarsus, proximal view, lateral incision (incisura lateralis, Baumel and Witmer, 1993):

(0) shallow,

(1) remarkably deep.

Remarks: This character is newly added in the present study (Fig. A1.18).

278. Tibiotarsus, medial view, roughened triangular surface covers proximo-cranial portion of shaft and cnemial expansion:

(0) absent,

(1) faint,

(2) well-developed and bounded by a diagonal ridge.

Remarks: Modified from Bell & Chiappe (2015).

279. Tibiotarsus, in anterior view, lateral margin of lateral cnemial crest:

(0) well-flared laterally, hiding the lateral cotyla;

(1) slightly flared laterally, not hiding the lateral cotyla.

Remarks: This character is newly added in the present study (Fig. A1.18).

280. Tibiotarsus, cnemial crests on cranial surface of cnemial expansion:

(0) asymmetric, medial crest forms sharp angle distal to the slight flare of lateral crest;

(1) fairly symmetric, medial and lateral crests both curve outward slightly;

(2) asymmetric, medial crest projects cranially, lateral has sharp angle.

Remarks: Character #156 of Bell & Chiappe (2015).

281. Tibiotarsus, caudal view, lateral border of lateral cotylae:

- (0) smooth bulge;
- (1) abrupt lip outward from shaft.

Remarks: Character #159 of Bell & Chiappe (2015).

282. Tibiotarsus, fibular crest extends approximately:

- (0) over half-way;
- (1) half-way down shaft;
- (2) restricted to upper 1/3 of shaft.

Remarks: Character #161 of Bell & Chiappe (2015).

283. Tibiotarsus, distal fibular crest is interrupted by a transverse groove extending across the lateral border of the tibial shaft:

- (0) absent;
- (1) present.

Remarks: Character #162 of Bell & Chiappe (2015).

284. Tibiotarsus, groove runs along caudal surface of shaft adjacent to fibular crest:

- (0) faint;
- (1) well-developed.

Remarks: Character #164 of Bell & Chiappe (2015).

285. Tibiotarsus, cranial view, intercondylar sulcus:

- (0) symmetric;
- (1) asymmetric, medial margin steeper than lateral margin.

Remarks: Character #157 of Bell & Chiappe (2015).

286. Tibiotarsus, cranial view, intercondylar sulcus:

- (0) slightly;
- (1) deeply indented.

Remarks: Character #158 of Bell & Chiappe (2015).

287. Tibia/tarsal formed condyles, extensor canal:

- (0) absent;
- (1) an emarginate groove;
- (2) groove bridged by an ossified supratendinal bridge. *Ordered*

Remarks: Character #182 of Huang et al. (2017).

288. Tibia/tarsal formed condyles, tuberositas retinaculi extensoris (Baumel and Witmer, 1993) indicated by short medial ridge or tubercle proximal to the condyles close to the midline and a more proximal second ridge on the medial edge:

- (0) absent;
- (1) present.

Remarks: Character #183 of Huang et al. (2017).

289. Tibia/tarsal formed condyles, mediolateral widths:

- (0) medial condyle wider;
- (1) approximately equal;
- (2) lateral condyle wider. *Ordered*

Remarks: Character #184 of Huang et al. (2017).

290. Tibia/tarsal formed condyles, intercondylar groove:

- (0) mediolaterally broad, approximately 1/3 width of anterior surface;
- (1) less than 1/3 width of total anterior surface.

Remarks: Character #186 of Huang et al. (2017).

291. Tibiotarsus, distal view, intercondylar incision:

- (0) excavated by a notch,
- (1) broad and shallow,
- (2) deep with sloped sides.

Remarks: Modified from #172 of Huang et al. (2017).

292. Tibia, extension of articular surface for distal tarsals/tarsometatarsus:

- (0) no posterior extension of trochlear surface, or restricted to distal-most edge of posterior surface;
- (1) well-developed, posteriorly projecting, medial and lateral crests. *Ordered*

Remarks: Modified from #187 of Huang et al. (2017).

293. Tibiotarsus, lateral view, lateral condyle:

- (0) roughly circular;
- (1) j-shaped;
- (2) half-circle.

Remarks: Character #171 of Bell & Chiappe (2015).

294. Tibiotarsus, distal view, lateral condyle cranio-caudally:

- (0) similar length to;
- (1) longer than;
- (2) shorter than medial condyle.

Remarks: Character #173 of Bell & Chiappe (2015).

295. Tibia, distal-most mediolateral width:

- (0) wider than mid-point of shaft, giving distal profile a weakly developed triangular form;
- (1) approximately equal to shaft width, no distal expansion of whole shaft, although condyles may be variably splayed mediolaterally;
- (2) medial condyle more expanded than lateral, distal end flares slightly medially from the midline of the shaft.

Remarks: Modified from #188 of Huang et al. (2017).

296. Fibula:

- (0) reaches tarsal joint articulating into distinct socket formed between the proximal tarsals and the tibia;
- (1) reduced in length, does not reach tarsal joint.

Remarks: Character #189 of Huang et al. (2017).

297. Proximal end of the fibula:

- (0) prominently excavated by a medial fossa;
- (1) nearly flat.

Remarks: Character #218 of Wang et al. (2015).

298. Tibiotarsus, thick cortical area:

- (0) absent.
- (1) present.

Remarks: This character is newly added in the present study.

299. The ratio (tibiotarsus length/tarsometatarsus length):

- (0) 2 or larger;
- (1) between 2 and 1.6;
- (2) smaller than 1.6.

When distal tarsals are not fused with metatarsals, metatarsal III length is used.

Remarks: Character #257 of Wang et al. (2015).

300. Distal tarsals in adults:

- (0) free;
- (1) completely fused to the metatarsals.

Any specimen that is inferred to be a juvenile should be scored as a “?” in order to account for the possibility of ontogenetic change.

Remarks: Character #221 of Wang et al. (2015).

301. Metatarsals II-IV, intermetatarsal fusion:

- (0) absent or minimal co-ossification;
- (1) proximal fusion;
- (2) Fused throughout their length, sutural contacts easily discernible;
- (3) Fused throughout their length, sutural contacts absent or poorly demarcated.

Ordered

Remarks: Modified from character #222 of Wang et al. (2015).

302. Tarsometatarsus, dorsal view, deep groove between metatarsals III and IV along entire length of shaft:

(0) absent;

(1) present.

Remarks: Modified from #195 of Bell & Chiappe (2015).

303. Metatarsal V:

(0) present;

(1) absent.

Remarks: Character #191 of Huang et al. (2017).

304. Metatarsal III:

(0) proximally in plane with II and IV;

(1) proximally displaced plantarly, relative to metatarsals II and IV.

Remarks: Character #192 of Huang et al. (2017).

305. Tarsometatarsus, intercotylar eminence:

(0) absent;

(1) low relief;

(2) high relief.

Remarks: Character #183 of Bell & Chiappe (2015).

306. Tarsometatarsus, intercotylar eminence:

(0) absent;

(1) projects symmetrically from articular surface;

(2) projects asymmetrically, such that it tilts laterally in dorsal view.

Remarks: Character #184 of Bell & Chiappe (2015).

307. Tarsometatarsus, dorsal view, articular surface forms a plane positioned, relative to the long axis of the shaft:

- (0) roughly perpendicular;
- (1) angled, medial cotyla further proximal than lateral.

Remarks: Character #186 of Bell & Chiappe (2015).

308. Tarsometatarsus, lateral view, proximal surface of lateral cotyla:

- (0) flat and perpendicular to long axis of shaft;
- (1) slopes distally at dorsal margin.

Remarks: Character #182 of Bell & Chiappe (2015).

309. Tarsometatarsus, lateral view, round depression on proximal-most face of metatarsal IV:

- (0) weakly developed;
- (1) well-developed.

Remarks: Character #189 of Bell & Chiappe (2015).

310. Tarsometatarsus, plantar view, projected surface or grooves on hypotarsus area:

- (0) flat, unprojected surface,
- (1) projected without distinct crest and groove,
- (2) projectcted with distinct two crests and one groove,
- (3) projected with at least one groove enclosed by bone posteriorly,
- (4) projected with four crests and three grooves.

Remarks: This character is newly added in the present study (Fig. A1.19).

311. Tarsometatarsus, dorsal view, proximal vascular foramen (foramina):

- (0) absent,
- (1) one, between metatarsals III and IV,
- (2) two. *Ordered*

Remarks: Modified from character #195 of Huang et al. (2017).

312. Tarsometatarsus, plantar view, proximal vascular foramen (foramina):

- (0) absent,
- (1) one perforated foramen,
- (2) two perforated foramina.

Remarks: This character is newly added in the present study (Fig. A1.19).

313. Tarsometatarsus, the ratio (mediolateral width / dorsoplantar width):

- (0) more than 2.0;
- (1) Less than 2.0.

Remarks: This character is newly added in the present study.

314. Metatarsal I:

- (0) straight;
- (1) curved or distally deflected but not twisted, ventral surface convex “J shaped”;
- (2) deflected and twisted such that the ventromedial surface is concave proximal to trochlear surface for phalanx I. *Ordered*

Remarks: Character #196 of Huang et al. (2017).

315. Metatarsal II tubercle (associated with the insertion of the tendon of the m. tibialis cranialis in Aves):

- (0) absent;
- (1) present, on approximately the center of the proximodorsal surface of metatarsal II;
- (2) present, developed on lateral surface of metatarsal II, at contact with metatarsal III or on lateral edge of metatarsal III. *Ordered*

Remarks: Character #197 of Huang et al. (2017).

316. Metatarsal II, distal plantar surface, fossa for metatarsal I (fossa metatarsi I; Baumel and Witmer, 1993):

- (0) absent;
- (1) shallow notch;
- (2) conspicuous ovoid fossa. *Ordered*

Remarks: Character #198 of Huang et al. (2017).

317. Tarsometatarsus, distal extent of trochlea IV:

- (0) not as far as;
- (1) to a similar level as;
- (2) slightly further than;
- (3) or markedly further than trochlea III. *Ordered*

Remarks: Modified from #202 of Bell & Chiappe (2015).

318. Metatarsals, relative mediolateral width:

- (0) metatarsal IV approximately the same width as metatarsals II and III;
- (1) metatarsal IV narrower than MII and MIII;
- (2) metatarsal IV greater in width than either metatarsal II or III.

Remarks: Character #200 of Huang et al. (2017).

319. Tarsometatarsus, ridge on the dorsal surface of metatarsal IV:

- (0) absent;
- (1) extends to midshaft;
- (2) extends to trochlea.

Remarks: Character #196 of Bell & Chiappe (2015).

320. Tarsometatarsus, lateral view, metatarsal IV shaft:

- (0) tapers evenly to distal end;
- (1) widest at midshaft, tapers at both proximal and distal ends.

Remarks: Character #197 of Bell & Chiappe (2015).

321. Tarsometatarsus, lateral view, shaft:

- (0) bowed;
- (1) straight.

Remarks: Character #198 of Bell & Chiappe (2015).

322. Tarsometatarsus, medial view, shaft of metatarsal II:

- (0) nearly straight;
- (1) slightly curved;
- (2) dramatically curved into an s-shape.

Remarks: Character #188 of Bell & Chiappe (2015).

323. Tarsometatarsus, plantar-medial view, medial margin of metatarsal II:

- (0) rounded edge;
- (1) sharp ridge;
- (2) well-defined plantar crest.

Remarks: Modified from character #190 of Bell & Chiappe (2015).

324. Tarsometatarsus, comparative metatarsal trochlear width:

- (0) metatarsal trochlea III is wider than II and IV,
- (1) metatarsals III and IV wider than II, IV is approximately as wide as III,
- (2) metatarsal trochlea IV remarkably wider than II and III.

Remarks: This character is newly added in the present study (Fig. A1.20).

325. Trochlea of metatarsal II broader than the trochlea of metatarsal III:

- (0) absent;
- (1) present.

Remarks: Character #238 of Wang et al. (2015).

326. Distal vascular foramen:

- (0) simple, with one exit;
- (1) forked, two exits (plantar and distal) between metatarsals III and IV.

Remarks: Character #202 of Huang et al. (2017).

327. Tarsometatarsal distal vascular foramen completely enclosed by metatarsals III and IV:

- (0) absent;
- (1) present.

Remarks: Character #231 of Wang et al. (2015).

328. Tarsometatarsus, plantar view, intertrochlear incision between III and IV:

- (0) absent, metatarsals unfused;
- (1) wedge-shaped;
- (2) enclosed oval or tear-drop shape with rounded proximal end;
- (3) round.

Remarks: Character #201 of Bell & Chiappe (2015).

329. Metatarsal III, trochlea in plantar view, proximal extent of lateral and medial edges of trochlea:

- (0) absent, trochlear edges approximately equal in proximal extent;
- (1) present, lateral edge extends farther.

Remarks: Character #203 of Huang et al. (2017).

330. Tarsometatarsus, distal extent of metatarsal II relative to metatarsal IV:

- (0) distal edge of metatarsal II extends farther than the base of metatarsal IV trochlea or similar extent as IV,
- (1) distal edge of metatarsal II does not reach the base of metatarsal IV trochlea.

Remarks: Modified from character #204 of Huang et al. (2017).

331. Plantar surface of tarsometatarsus excavated:

- (0) absent;
- (1) present.

Remarks: Character #230 of Wang et al. (2015).

332. Distal metatarsus, trochlea in distal view:

- (0) aligned in a single plane,
- (1) metatarsal trochlea II and IV roughly aligned in a single plane, III displaced dorsally in respect to II and IV,
- (2) metatarsal trochlea II strongly displaced plantarly in respect to III and IV.

Remarks: Modified from character #237 of Wang et al. (2015).

333. Tarsometatarsus, distal view:

- (0) the dorsal edge of metatarsal trochlear III is dorsal to that of trochlear IV,
- (1) the dorsal edges of metatarsal trochleae III and IV are approximately equal,
- (2) the dorsal edge of metatarsal trochlear IV is dorsal to that of trochlear III.

Remarks: This character is newly added in the present study (Fig. A1.20).

334. Tarsometatarsus, distal view, articular ridges on metatarsal trochlea II:

- (0) aligned and roughly parallel,
- (1) angled toward each other dorsally, forming a triangular shape for the trochlea.

Remarks: Modified from character #203 of Bell & Chiappe (2015).

335. Pedal digits, relative length:

- (0) digit III longest, followed by digit IV, digit II shortest;
- (1) digit III almost equal to digit IV, digit II shortest;
- (2) digit IV longest, then digit III, digit II shortest. *Ordered*

Remarks: Character #217 of Huang et al. (2017).

336. Digit IV phalanges in distal view:

- (0) the medial and lateral trochleae lie parallel and are about the same size,
- (1) medial trochlea greatly enlarged and the lateral trochlea reduced to a rounded peg.

Remarks: Modified from character #205 of Bell & Chiappe (2015).

337. Phalanx 1 of digit IV:

(0) elongate;

(1) robust, with a squat, shortened appearance.

Remarks: Character #206 of Bell & Chiappe (2015).

338. Phalanx I of Digit IV, ventral groove:

(0) absent;

(1) present.

Remarks: Character #207 of Bell & Chiappe (2015).

339. Phalanx I of Digit IV, ventral surface of phalanx:

(0) smooth;

(1) possesses a high flange.

Remarks: Character #208 of Bell & Chiappe (2015).

340. Completely reversed hallux (arch of ungual phalanx of digit I opposing the arch of the unguals of digits II-IV):

(0) absent;

(1) present.

Remarks: Character #242 of Wang et al. (2015).

341. Size of claw of hallux relative to other pedal claws:

(0) shorter, weaker, and smaller;

(1) similar in size;

(2) longer, more robust, and larger.

Remarks: Character #243 of Wang et al. (2015).

342. Pedal digit II, proportions of II-3 to II-1:

(0) II-3 subequal to or longer than II-1 and;

(1) II-3 shorter.

Remarks: Character #219 of Huang et al. (2017).

343. Pedal digit, Penultimate phalanx, longer than preceding phalanges in each digit:

- (0) absent;
- (1) present.

Remarks: Character #258 of Wang et al. (2015).

344. Phalanx in digit IV:

- (0) not as follows,
- (1) the second and the third phalanges reduced and significantly shorter than the fourth phalanx,
- (2) as before but with the proximal phalanx reduced to be nearly equal in length with the second and third phalanx.

Remarks: Character #260 of Wang et al. (2015).

345. Ungual in digit III, length relative to the tarsometatarsus:

- (0) less than 20% the length of tarsometatarsus;
- (1) 20% – 40%;
- (2) extremely elongated and measuring more than 40% the length of tarsometatarsus;

When metatarsals are not fused with distal tarsals, the length of metatarsal III is used. The length of ungual represents the linear distance between proximal end (position equivalent to flexor process) and tip of the sheath. If the sheath is not preserved or disarticulated with bony ungual, it should be scored as “?”. *Ordered*

Remarks: Character #261 of Wang et al. (2015).

346. Ungual in digit III, length relative to the digit III-3:

- (0) longer or equal to;
- (1) approximately 75%;
- (2) less than 50% the length of digit III.

Remarks: This character is newly added in the present study (Fig. A1.21).

Feathers

347. Alula:

(0) absent;

(1) present.

Remarks: Character #244 of Wang et al. (2015).

348. Fan-shaped feathered tail composed of more than two elongate retrices:

(0) absent;

(1) present.

Remarks: Character #245 of Wang et al. (2015).

349. Tail feathers, number of associated with free caudals:

(0) more than 14,

(1) none, but two associated with pygostyle;

(2) none, but more than two associated with pygostyle.

Remarks: Character #220 of Huang et al. (2017).

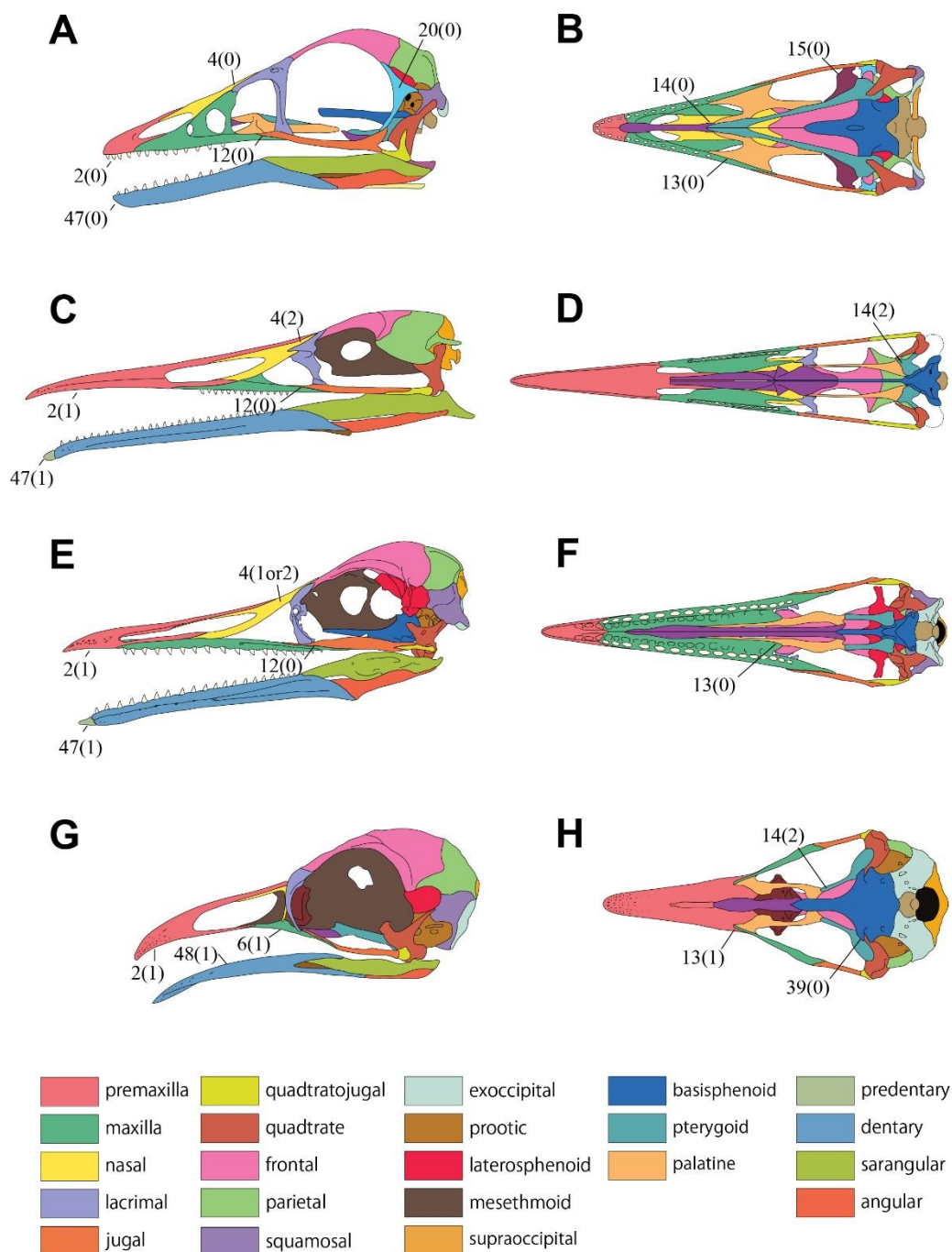


Fig. A1.1 Morphological comparisons of the skull and mandibular in lateral (A, C, E, G) and ventral (B, D, F, H) aspects in: A, B, *Archaeopteryx lithographica* (modified from Bhullar *et al.* 2018); C, D, *Hesperornis regalis* (modified from Gingerich 1973); E, F, *Ichthyornis dispar* (modified from Field *et al.* 2017); G, H, *Eudromia elegans*. Figures are not to scale.

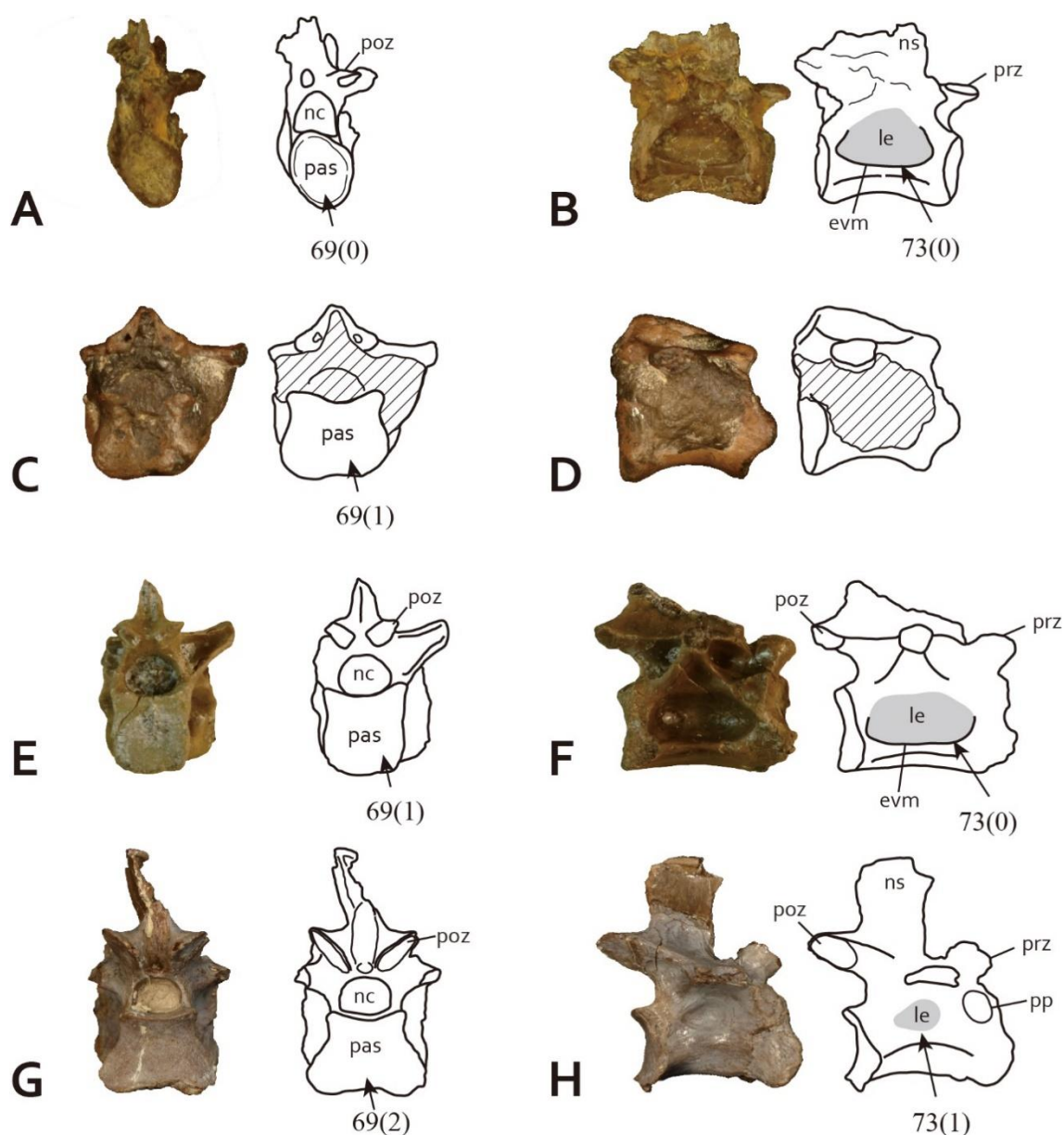


Fig. A1.2 Comparisons of the thoracic vertebra in posterior (A, C, E, G) and right lateral (B, D, F, H) aspects in: A, B, *Ichthyornis dispar* (YPM 1732); C, D, *Enaliornis barretti* (CAMSM B55277); E, F, *Pasquiaornis tankei* (RSM P2989.23); G, H, *Parahesperornis alexi* (KUVF 2287). Abbreviations: evm, edge of the ventral margin; le, lateral excavation; nc, neural canal; ns, neural spine; pas, posterior anterior articular surface; poz, postzygapophysis; pp, parapophysis; and prz, prezygapophysis. Figures are not to scale.

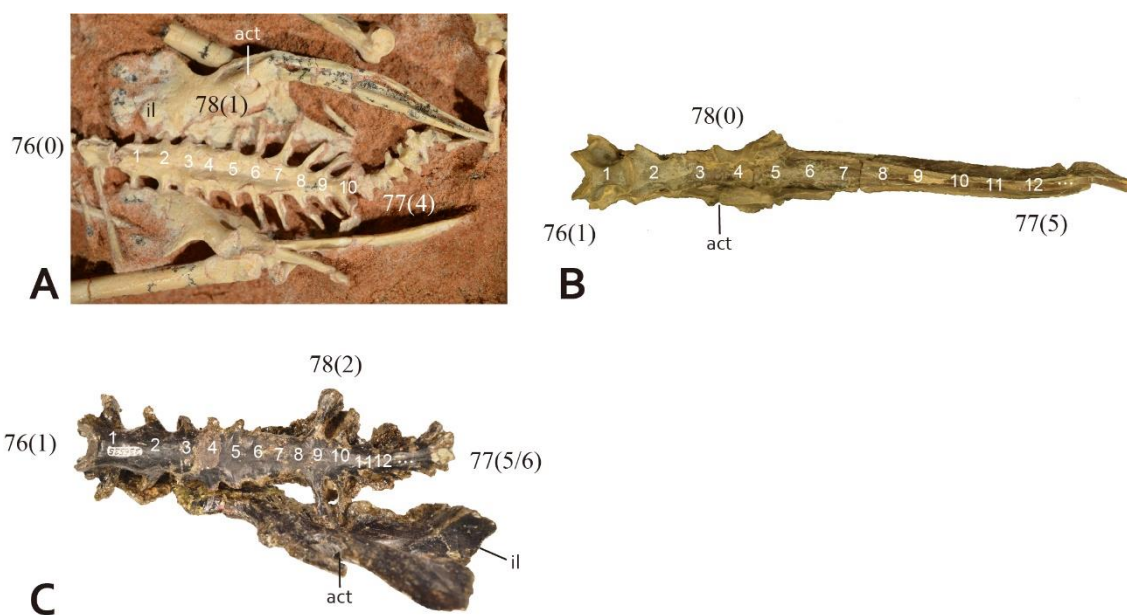


Fig. A1.3 Comparisons of the thoracic vertebra in ventral aspects in: **A**, *Apsaravis ukhaana* (IGM 100/1017); **B**, *Hesperornis regalis* (YPM 1476); **C**, *Lithornis promiscuus* (USNM 336535). Abbreviations: act, acetabulum; and il, ilium. Figures are not to scale.

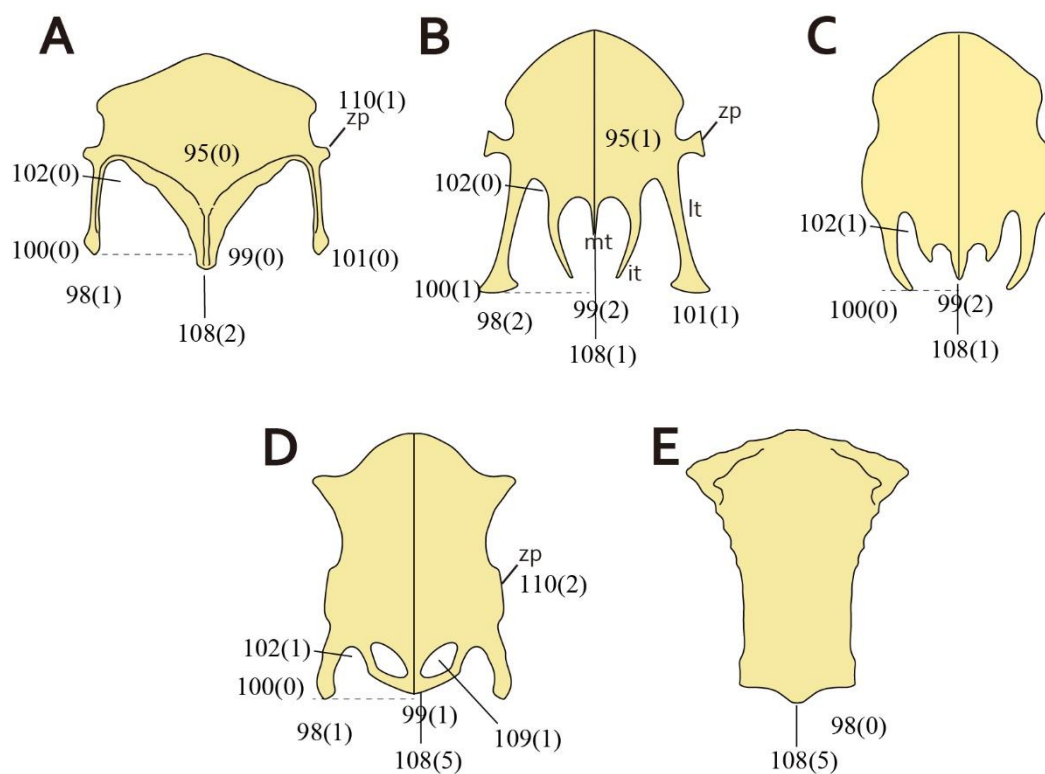


Fig. A1.4 Comparisons of the sternum in ventral aspects in: **A**, *Protopteryx fengningensis*; **B**, *Archaeorhynchus spatula*; **C**, *Hongshanornis longcresta*; **D**, *Gansus yumenensis*; **E**, *Hesperornis regalis*. Abbreviations: it, intermediate trabecula; lt, lateral trabecula; mt, medial trabecula; and zp, zyphoid process. Figures are not to scale.

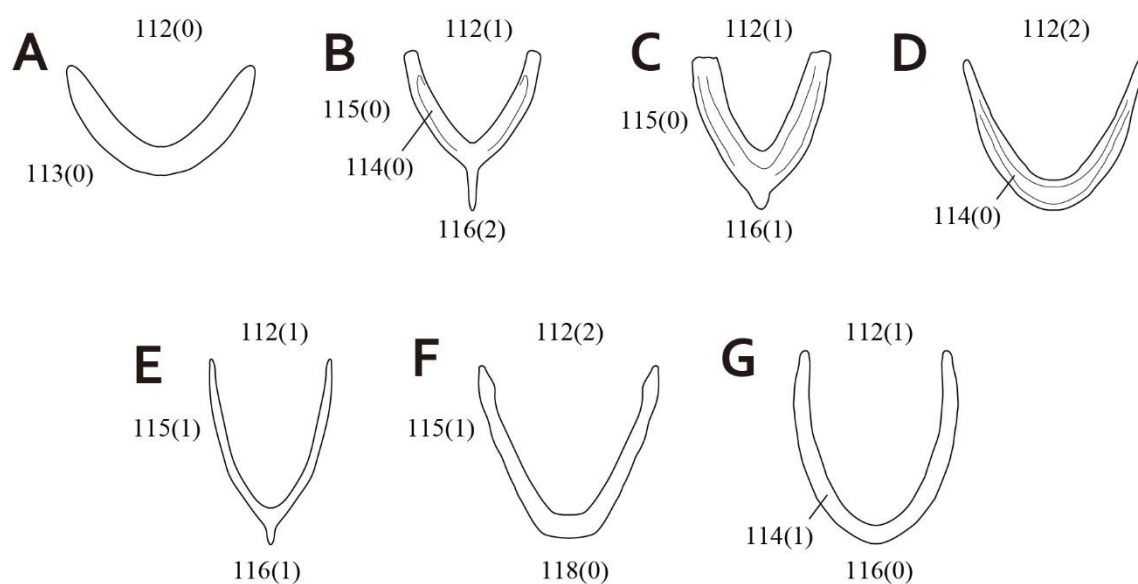


Fig. A1.5 Comparisons of the furcula in dorsal aspects in: **A**, *Archaeopteryx lithographica*; **B**, *Protopteryx fengningensis*; **C**, *Schizoura lii*; **D**, *Yanornis martinii*; **E**, *Hongshanornis longicresta*; **F**, *Yixianornis grabaui*; **G**, *Gansus yumenensis*. Abbreviations: it, intermediate trabecula; lt, lateral trabecula; mt, medial trabecula; and zp, zyphoid process. Figures are not to scale.

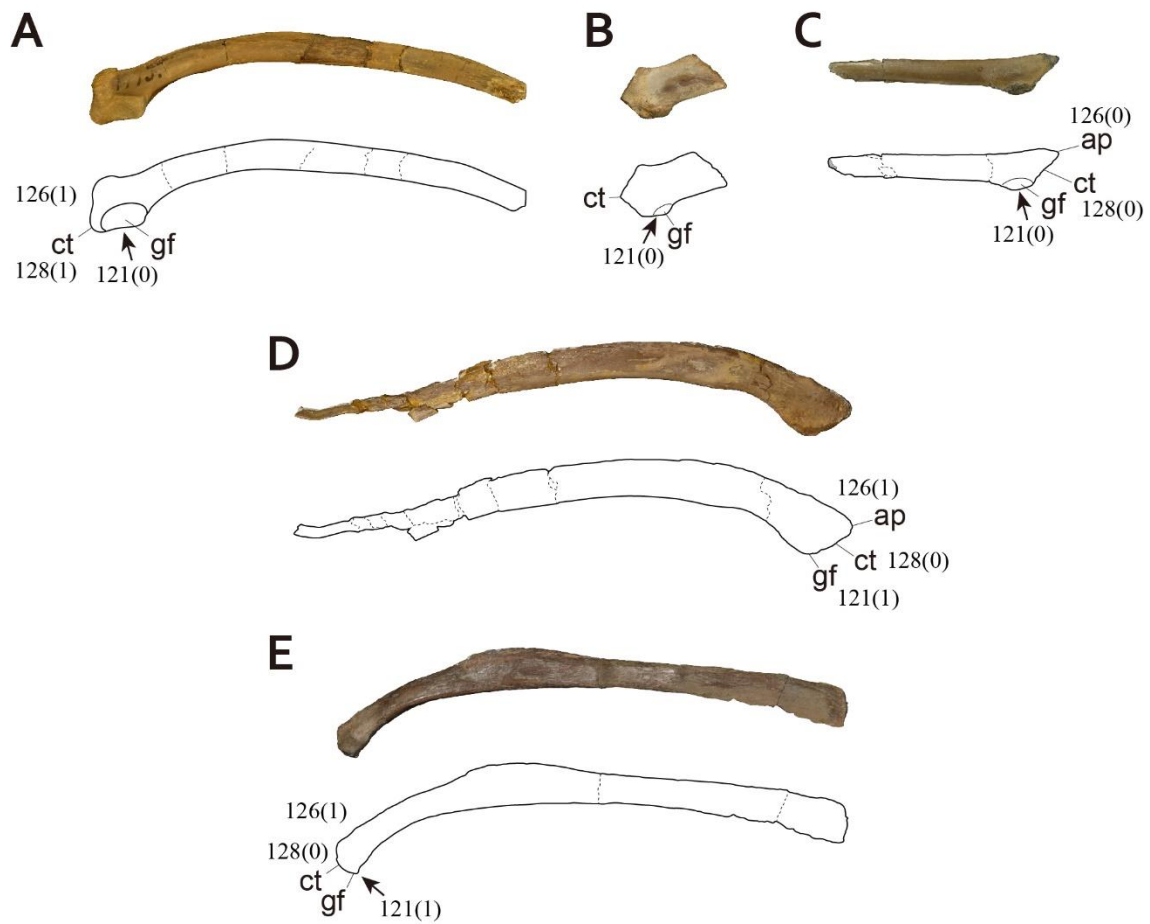


Fig. A1.6 Comparisons of the scapulae in medial aspects in: **A**, *Ichthyornis dispar* (YPM 1450); **B**, *Baptornis advenus* (KUVP 2290); **C**, *Pasquiaornis tankei* (RSM P2997.58); **D**, *Parahesperornis alexi* (KUVP 24090); **E**, *Hesperornis regalis* (FHSM VP-2069). Abbreviations: ap, acromion process; ct, coracoid tubercle; and gf, glenoid facet. Figures are not to scale.

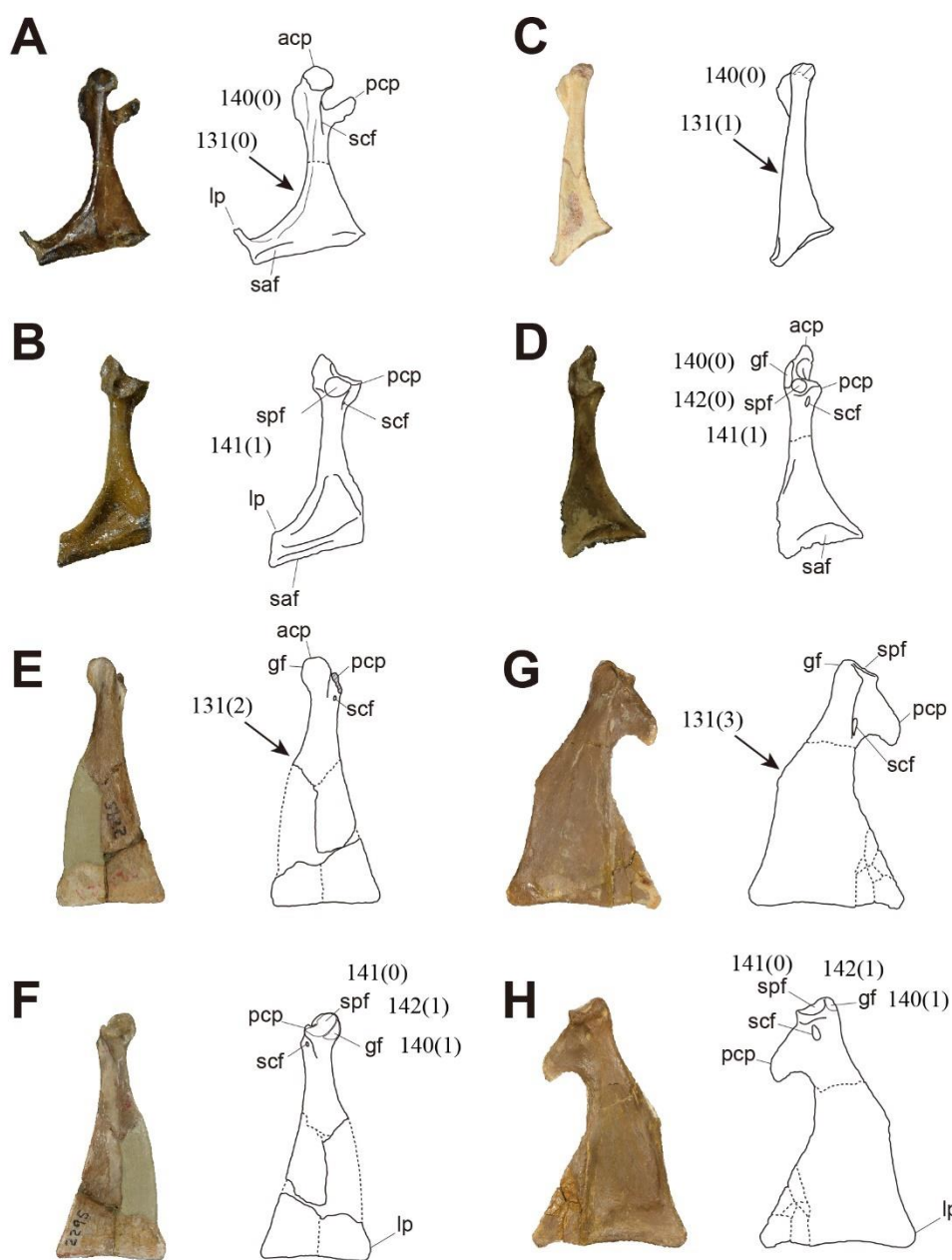


Fig. A1.7 Comparisons of the coracoids in ventral (A, C, E, G) and dorsal (B, D, F, H) aspects in: A, *Gansus yumenensis* (CAGS 04-CM-004); B, *Gansus yumenensis* (CAGS 07-CM-006); C, *Apsaravis ukhaana* (IGM 100/1017); D, *Pasquiaornis tankei* (RSM P2988.9); E, F, *Baptornis advenus* (KUV 2290); G, H, *Parahesperornis alexi* (KUV 2287). Abbreviations: acp, acrocoracoid process; gf, glenoid facet; lp, lateral process; pcpc, procoracoid process; scf, supracoracoid nerve foramen; spf, scapular foramen; . Figures are not to scale.

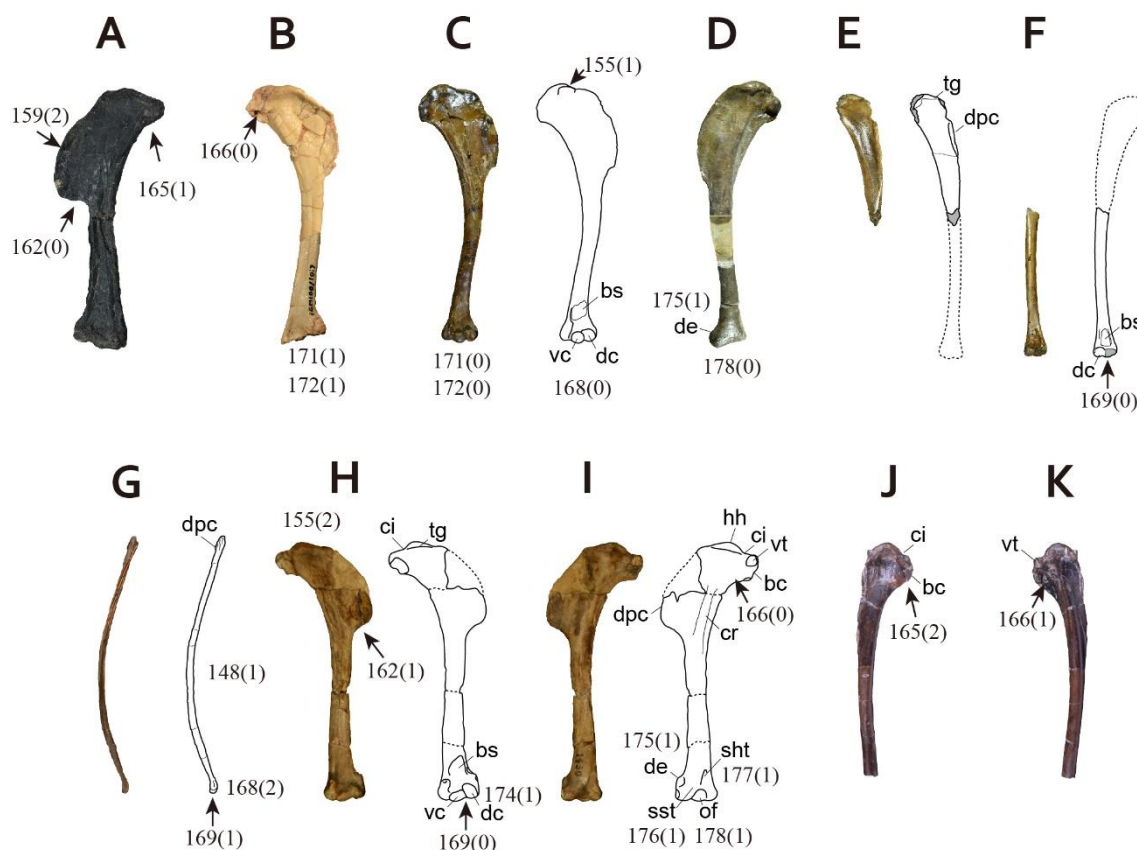


Fig. A1.8 Comparisons of the humeri in anterior (A, B, C, E, F, I) and posterior (D, G, J) aspects in: A, *Schizoooura lii* (IVPP V16708); B, *Apsaravis ukhaana* (IGM 100/1017); C, *Gansus yumenensis* (CAGS 04-CM-004); D, *Gansus yumenensis* (CAGS 05-CM-014); E, *Pasquiaornis tankei* (RSM P2987.2); F, *Pasquiaornis tankei* (RSM P2987.2); G, *Hesperornis regalis* (FHSM VP-2069); H, I, *Ichthyornis dispar* (YPM 1450); J, K, *Vegavis iaai* (MACN-PV 19.748). Abbreviations: bc, bicipital crest; bs, brachial scar; ci, capital incision; cr, capital ridge; dc, dorsal condyle; de, dorsal epicondyle; dp, deltopectoral crest; dt, dorsal tubercle; hh, humeral head; sht, sulcus *humeroatricipitalis* sulcus; sst, sulcus *m. scaplotricititalis*; of, olecranon fossa; tg, transverse groove; vc, ventral condyle; and vt, ventral tubercle. Figures are not to scale.

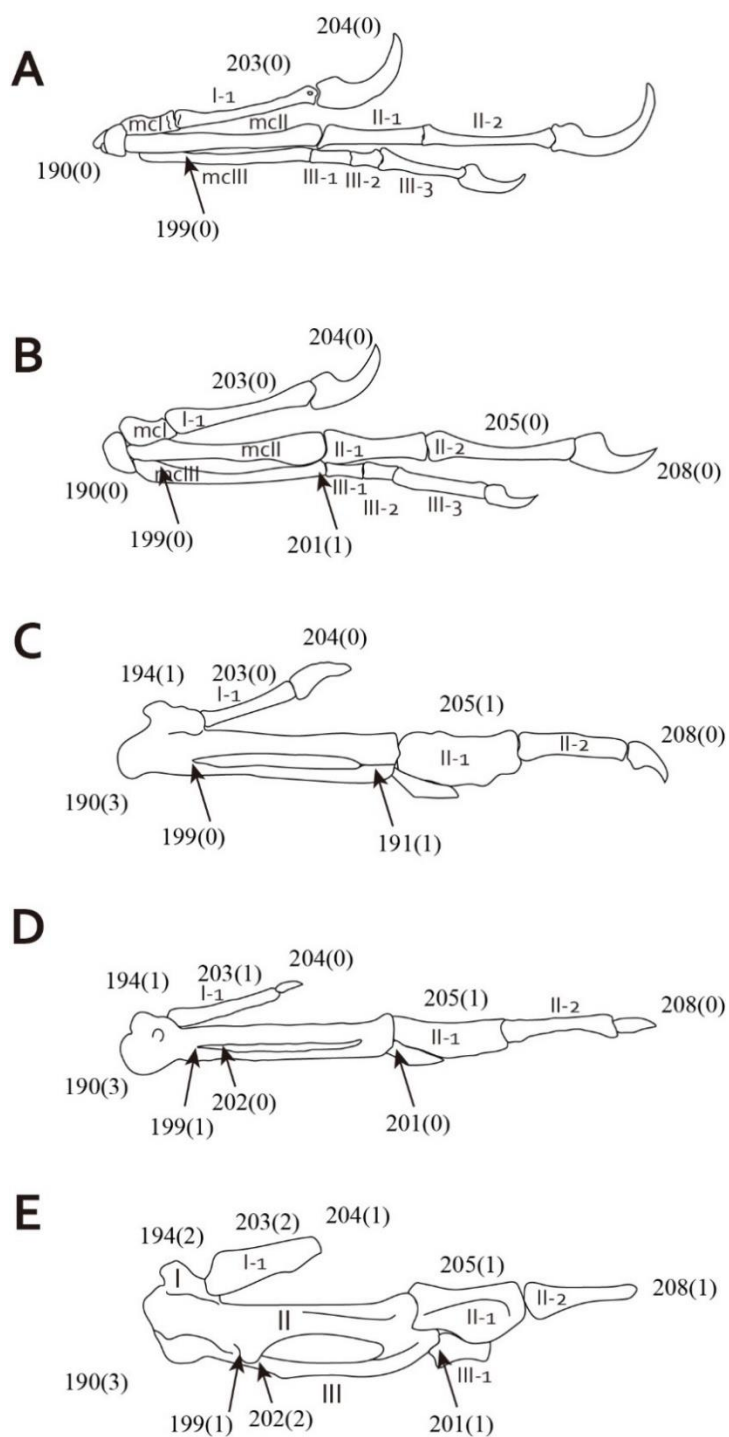


Fig. A1.9 Comparisons of the carpometacarpi in dorsal (A, B, C, E) and ventral (D) aspects in: **A**, *Archaeopteryx lithographica*; **B**, *Protopteryx fengningensis*; **C**, *Yixianornis grabaui*; **D**, *Iteravis huchzermeyeri*; **E**, *Gallus gallus*. Abbreviation: mc, metacarpal. Figures are not to scale.

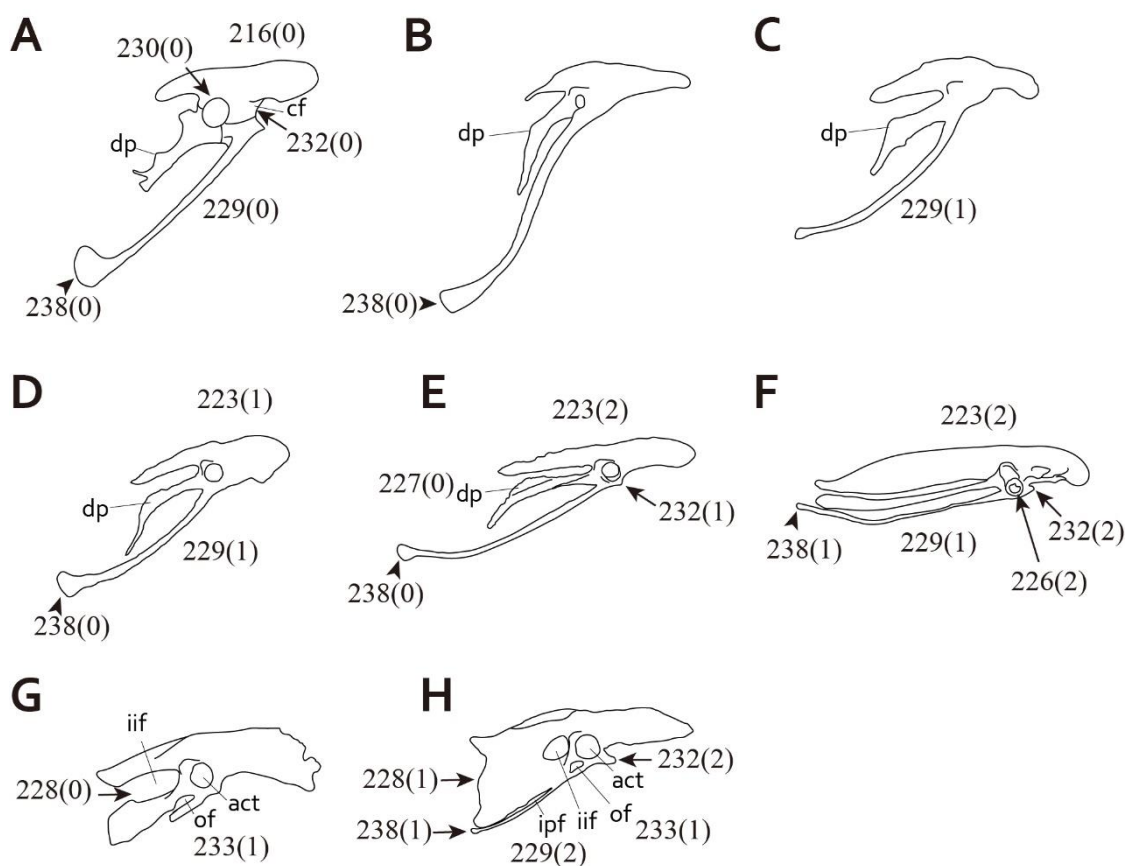


Fig. A1.10 Comparisons of the pelvises in right aspects in: **A**, *Archaeopteryx lithographica*; **B**, *Yanornis martini*; **C**, *Yixianornis grabau*; **D**, *Iteravis huchzermeyeri*; **E**, *Gansus yumenensis*; **F**, *Hesperornis regalis*; **G**, *Lithornis promiscuous*; **H**, *Gallus gallus*. Abbreviations: act, acetabulum; cf, cuppedicus fossa; dp, dorsal process; iif, ilioischadic foramen; ipf, ischiopubic fenestra of, obturator foramen. Figures are not to scale.

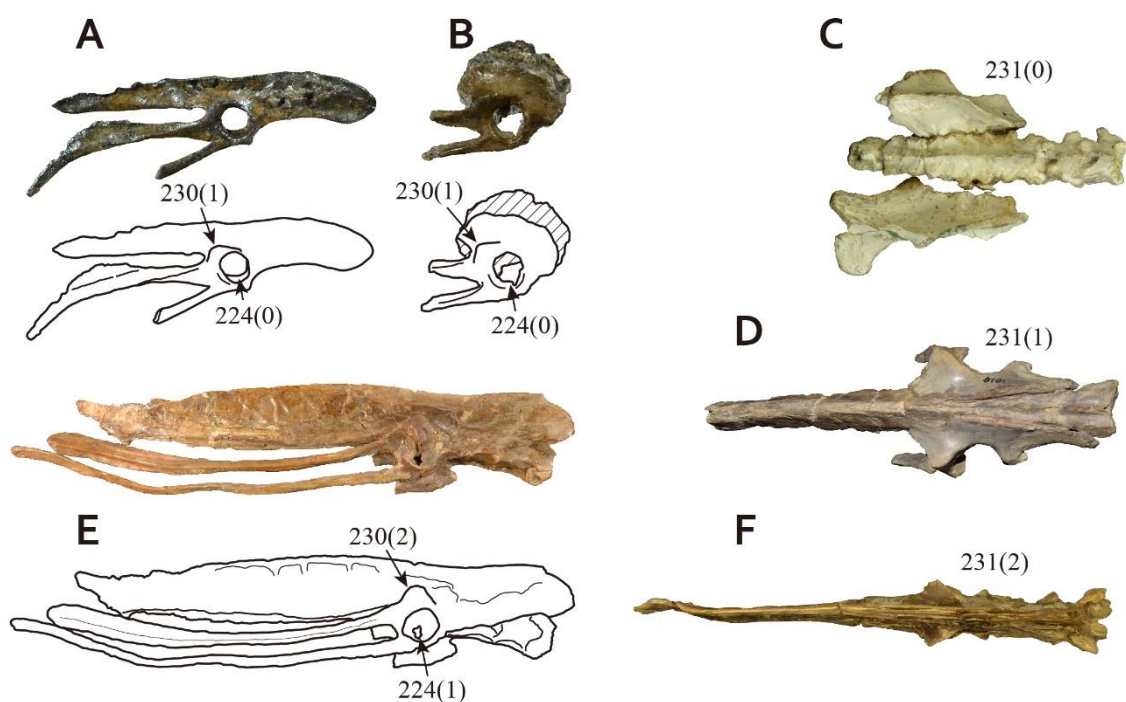


Fig. A1.11 Comparisons of the pelvises in right lateral (A, B, E) and dorsal (C, D, F) aspects in: **A**, *Gansus yumenensis* (CAGS 07-CM-009); **B**, *Pasquiaornis tankei* (RSM P2997.62); **C**, *Patagopteryx defferariisi* (MACN-N-03); **D**, *Baptornis advenus* (AMNH 5101); **F**, *Hesperornis regalis* (YPM 1476). Figures are not to scale.

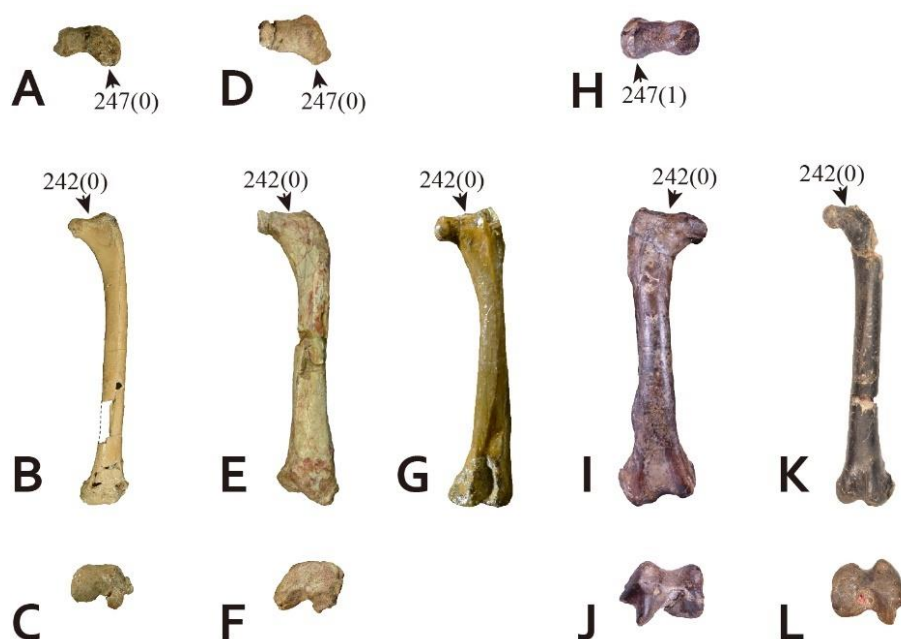


Fig. A1.12 Comparisons of the right femora in proximal (**A, D, H**), anterior (**B, E, G, I, K**), and distal (**C, F, J, L**) aspects in: **A, B, C** *Vorona berivotrensis* (FMNH PA 717); **D, E, F**, *Patagopteryx deferrariisi* (MACN-N-03); **G**, *Gansus yumenensis* (CAGS 04-CM-003); **H, I, J**, *Vegavis iaai* (MACN-PV 19.748); **K, L**, *Lithornis promiscuus* (USNM 336535). Figures are not to scale.

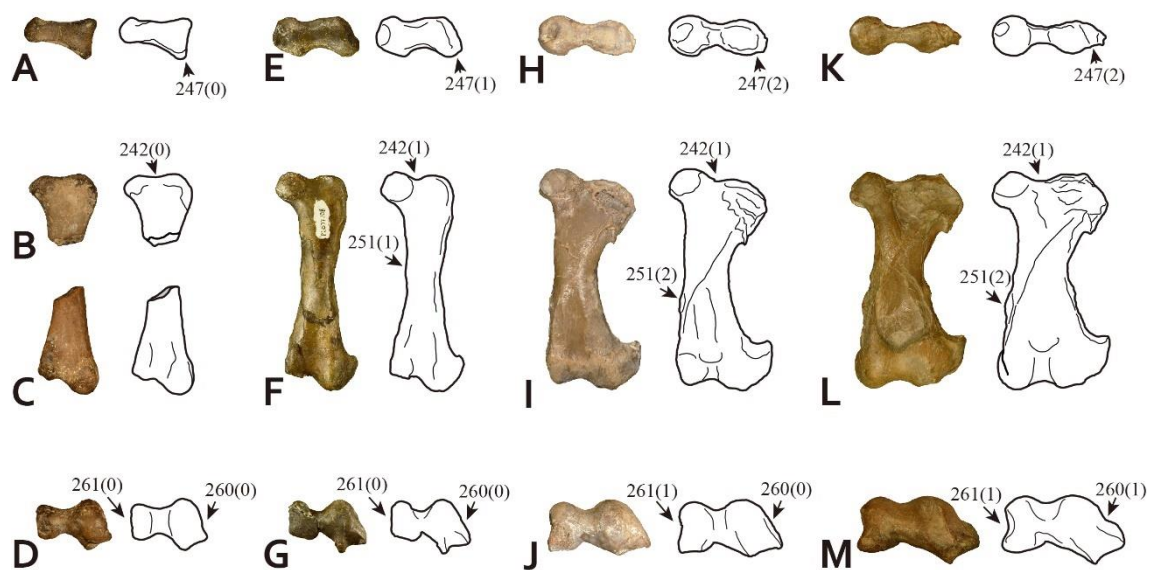


Fig. A1.13 Comparisons of the right femora in proximal (A, E, H, K), anterior (B, C, F, I, L), and distal (D, G, J, M) aspects in: A, B, *Enaliornis* sp. (CAMSM B55289); C, D, *Enaliornis sedgwicki* (CAMSM B55295); E, F, G, *Pasquiaornis tankei* (RSM P.2077.108); H, I, J, *Parahesperornis alexi* (KUVP 2287); K, L, M, *Hesperornis regalis* (YPM 1200). Figures are not to scale.

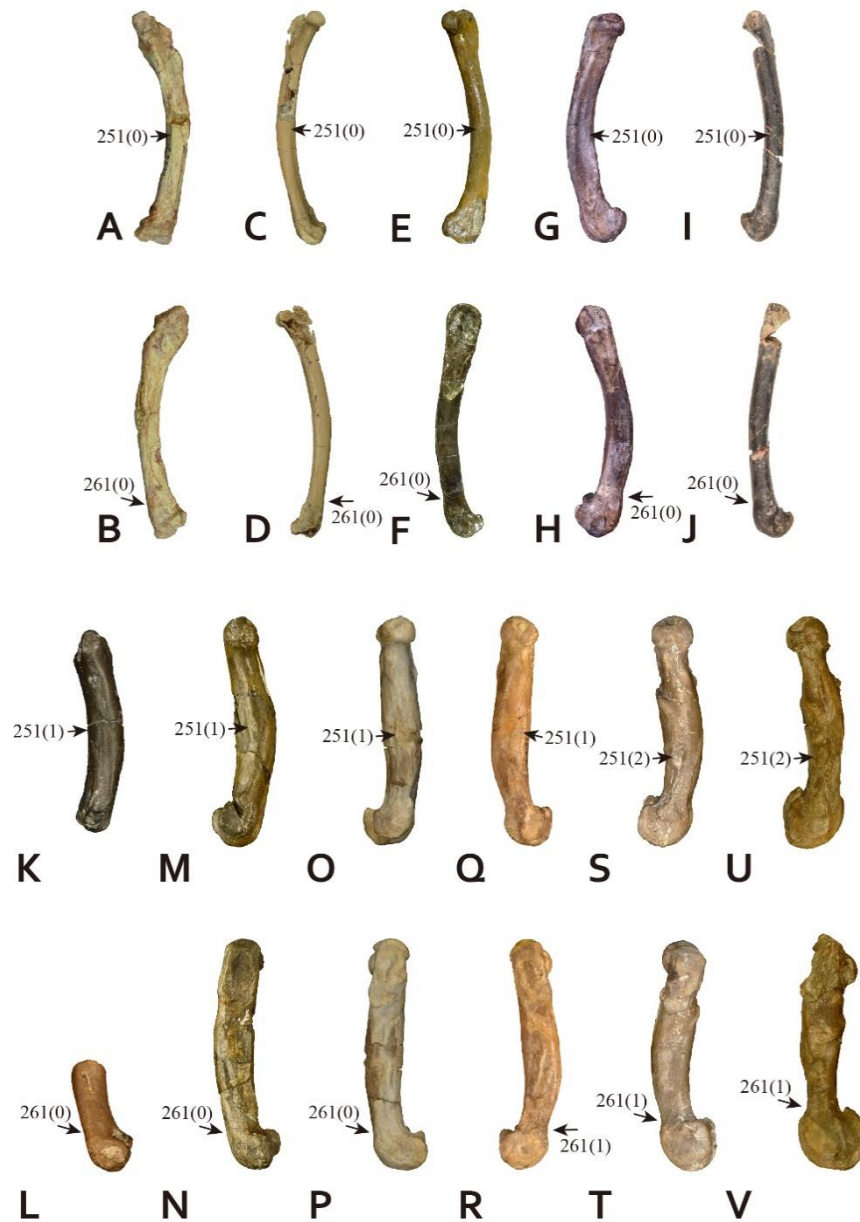


Fig. A1.14 Comparisons of the femora in medial (A, C, E, G, I, K, M, O, Q, S, U) and lateral (B, D, F, H, J, L, N, P, R, T, V) aspects in: A, B, *Patagopteryx deferrariisi* (MACN-N-03); C, D, *Vorona berivotrensis* (FMNH PA 717); E, *Gansus yumenensis* (CAGS 04-CM-003); F, *Gansus yumenensis* (CAGS 05-CM-014); G, H, *Vegavis iai* (MACN-PV 19.748); I, J, *Lithornis promiscuus* (USNM 336535); K, *Enaliornis barretti* (NHMUK A479); L, *Enaliornis sedgwicki* (CAMSM B55295); M, N, *Pasquiaornis tankei* (RSM P.2077.108); O, P, *Baptornis advenus* (KUVP 2290); Q, R, *Fumicollis hoffmani* (UNSM 20030); S, T, *Parahesperornis alexi* (KUVP 2287); U, V, *Hesperornis regalis* (YPM 1200). Figures are not to scale.

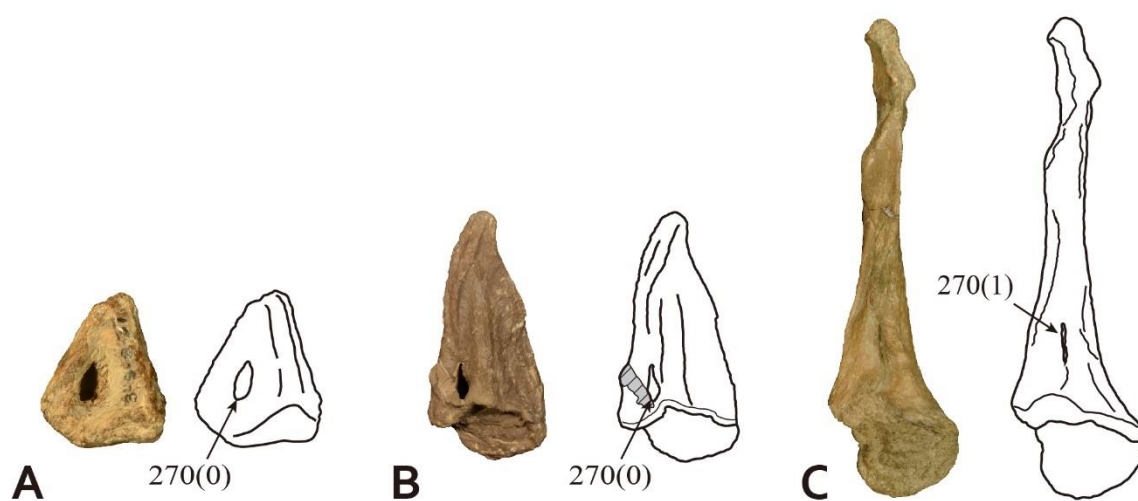


Fig. A1.15 Comparisons of the right patellae in medial aspects in: **A**, *Fumicollis hoffmani* (USNM 20030); **B**, *Parahesperornis alexi* (KUV 24090); **C**, *Hesperornis regalis* (YPM 1200). Figures are not to scale.

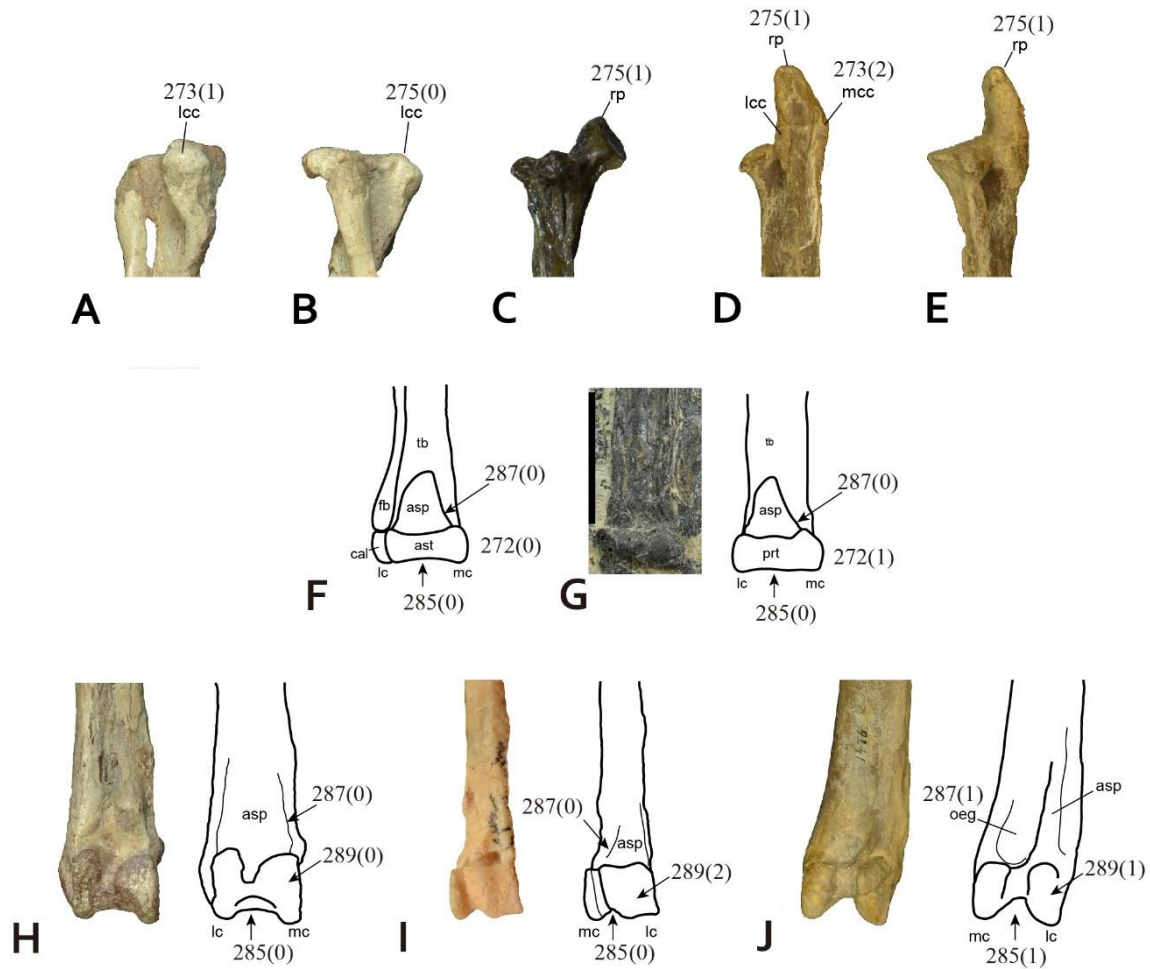


Fig. A1.16 Comparisons of the tibiotarsi in anterior (A, D, F, G, H, I, J) and lateral (B, C, E) aspects in: A, B, H, *Patagopteryx deferrariisi* (MACN-N-11); C, *Gansus yumenensis* (CAGS 04-CM-002); D, E, J, *Hesperornis regalis* (YPM 1476); F, *Archaeopteryx lithographica* (WDC-CSG-100); I, *Apsaravis ukhaana* (IGM 100/1017). Abbreviations: asp, ascending process; ast, astragalus; cal, calcaneus; fb, fibula; lc, lateral condyle; lcc, lateral cnemial crest; mc, medial condyle; mcc, medial cnemial crest; oeg, open extensor groove; rp, rotular process; and tb, tibia. Figures are not to scale.



Fig. A1. 17 Comparisons of the tibiotarsi in anterior (A, C, D, F, H, J) and distal (B, E, G, I, K, L, M, N) aspects in: A, *Patagopteryx deferrariisi* (MACN-N-03); B, *Patagopteryx deferrariisi* (MACN-N-11); C, *Gansus yumenensis* (CAGS 04-CM-018); D, E, *Fumicollis hoffmani* (UNSM 20030); F, G, *Parahesperornis alexi* (KUV 2287); H, I, *Hesperornis regalis* (YPM 1476); J, K, *Lithornis promiscuus* (USNM 336535); L, *Apsaravis ukhaana* (IGM 100/1017); M, *Enaliornis sedgwicki* (SMC B55315); N, *Pasquiaornis tankei* (RSM P2997.40). Abbreviation: lc, lateral condyle. Figures are not to scale.

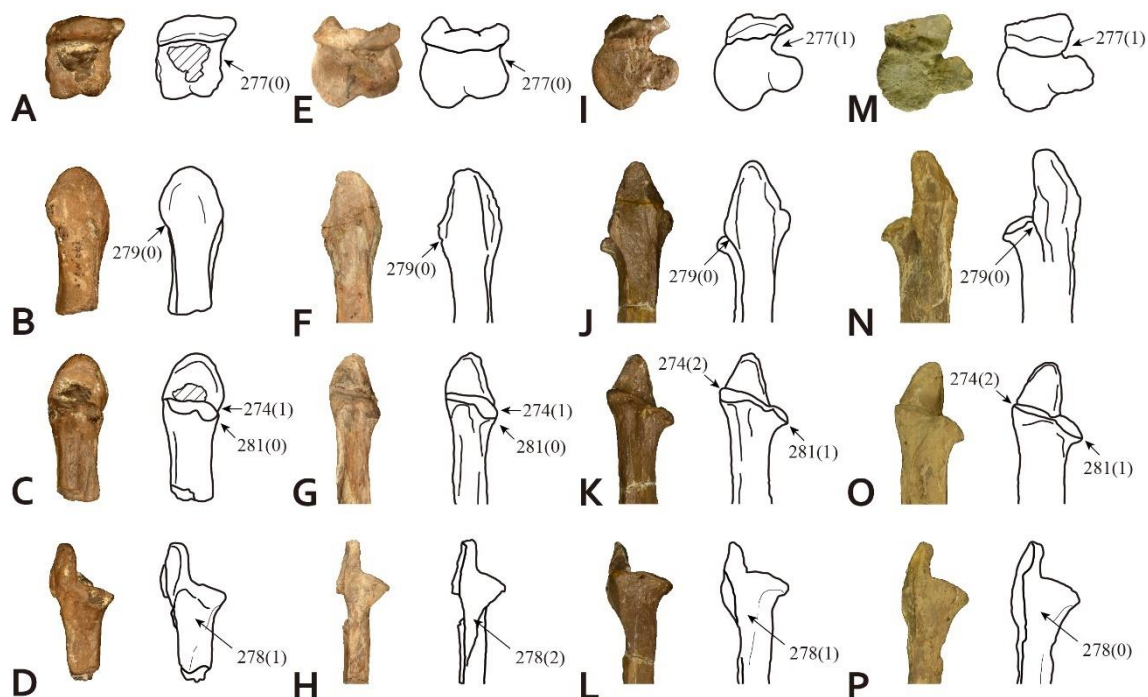


Fig. A1. 18 Comparisons of the left tibiotarsus in proximal (A, E, I, M), anterior (B, F, J, N), posterior (C, G, K, O), and medial (D, H, L, P) aspects in: A, B, C, D, *Enaliornis barretti* (NHMUK A477); E, F, G, H, *Fumicollis hoffmani* (UNSM 20030); I, J, K, L, *Parahesperornis alexi* (KUVF 2287), and M, N, O, P, *Hesperornis regalis* (YPM 1200). Figures are not to scale.

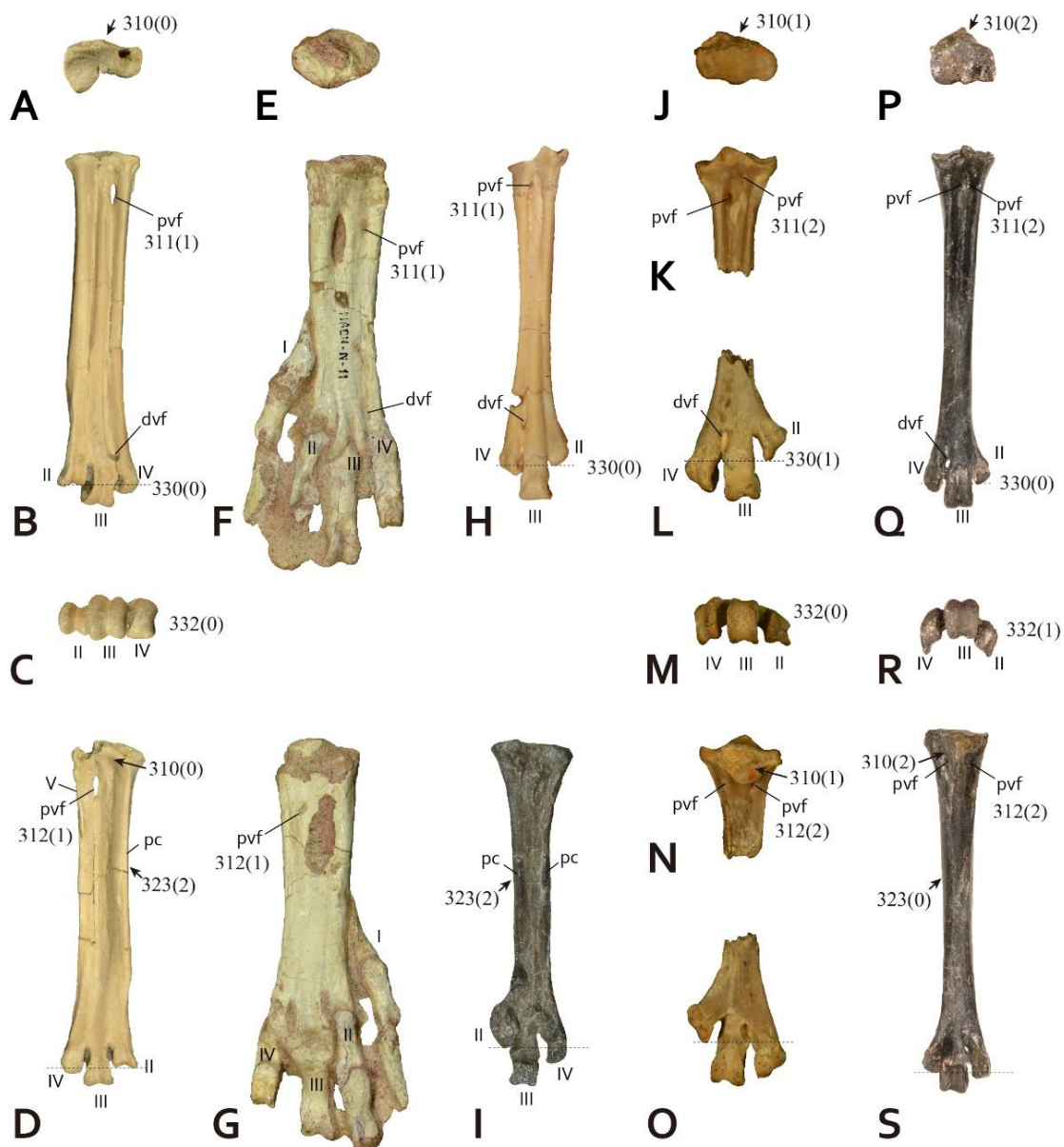


Fig. A1.19 Comparisons of the tarsometatarsus in proximal (A, E, J, P), dorsal (B, F, H, L, Q), distal (C, M, R), and plantar (D, G, I, N, O, S) aspects in: A, B, C, D, *Vorona berivotrensis* (UA 8651); E, F, G, *Patagopteryx deferrariisi* (MACN-N-11); K, L, M, N, O, *Ichthyornis dispar* (YPM 1450); P, Q, R, S, *Lithornis promiscuus* (USNM 336535). Abbreviations: dvf, dorsal vascular foramen; pc, plantar crest; pvf, proximal vascular foramen; I, metatarsal trochlea I; II, metatarsal trochlea II; III, metatarsal trochlea III; IV, metatarsal trochlea IV; and V, metatarsal trochlea V. Figures are not to scale.

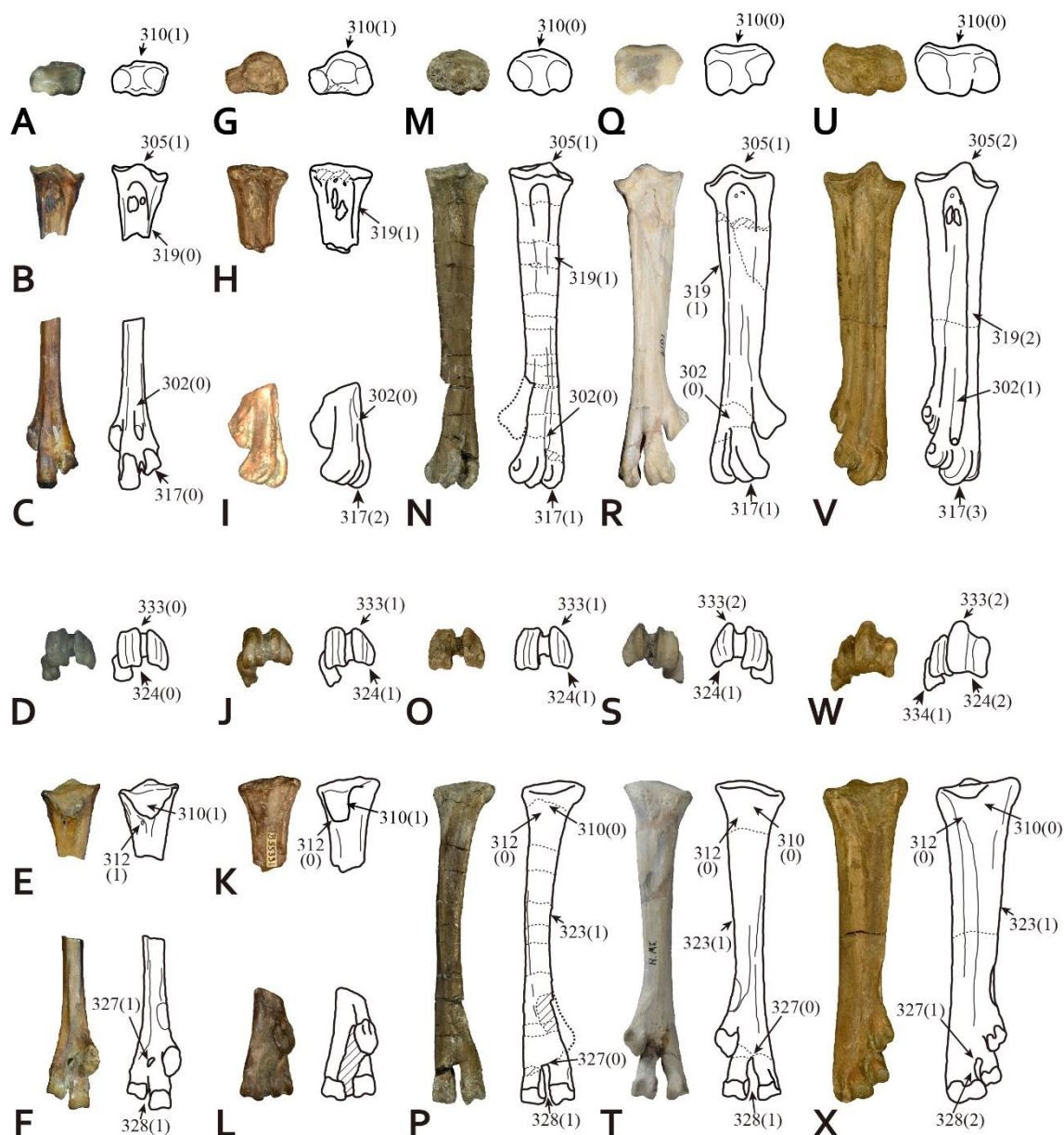


Fig. A1.20 Comparisons of the tarsometatarsus in proximal (A, G, M, Q, U), dorsal (B, C, H, I, N, R, V), distal (D, J, O, S, W), and plantar (E, F, K, L, P, T, X) aspects in: A, B, C, D, E, F, *Gansus yumenensis* (CAGS-04-CM-031); G, H, K, *Enaliornis barretti* (CAMSM B55331); I, J, L, *Enaliornis barretti* (NHMUK A477); M, N, O, P, *Pasquiaornis tankei* (RSM P2957.27); Q, R, S, T, *Baptornis advenus* (AMNH 5101; Photos of S and T courtesy of the Natural History Museum of Los Angeles County); and U, V, W, X, *Hesperornis regalis* (YPM 1200). Figures are not to scale.

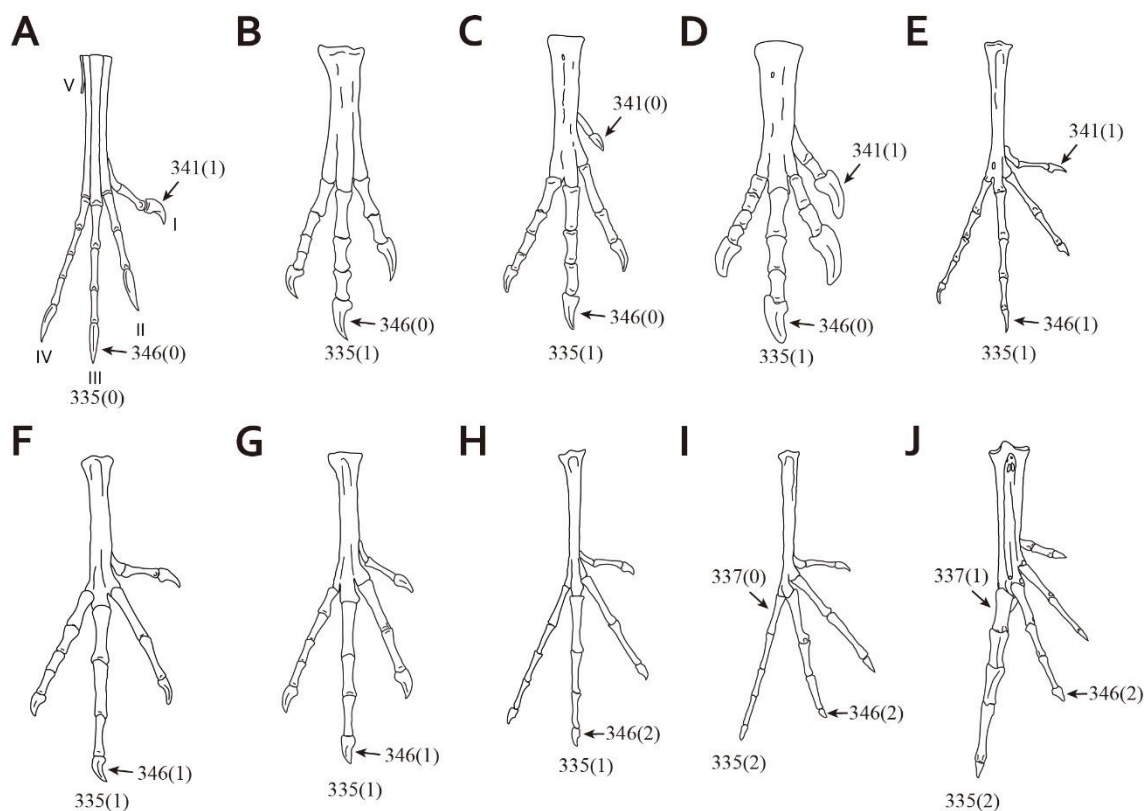


Fig. A1.21 Comparisons of the left feet in plantar aspects in: **A**, *Archaeopteryx lithographica*; **B**, *Archaeorhynchus spatula*; **C**, *Belluornis rectusunguis*; **D**, *Patagopteryx deferrariisi*; **E**, *Hongshanornis longicresta*; **F**, *Piscivoravis lii*; **G**, *Yixianornis martini*; **H**, *Hongshanornis longicresta*; **I**, *Gansus yumenensis*; **J**, *Hesperornis regalis*. Abbreviations: I, pedal digit I; II, pedal digit II; III, pedal digit III; IV, pedal digit IV; V, metatarsal V. Figures are not to scale.

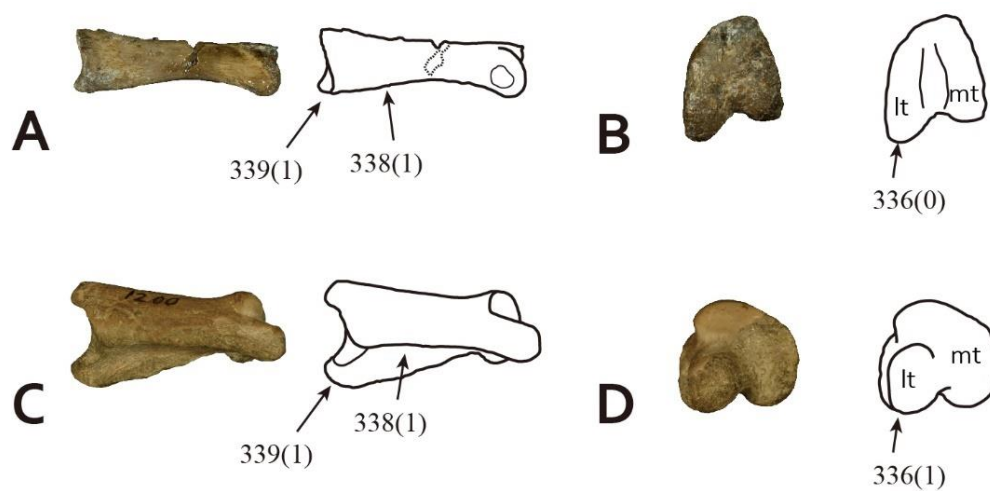


Fig. A1.22 Comparisons of the right first phalanx of IVth digit in lateral (A, C) and in distal (B, D) aspects in: A, B, *Pasquiaornis tankei* (RSM P.2997.68); C, D, *Hesperornis regalis* (YPM 1200). Abbreviations: lt, lateral condyle; mt, medial condyle. Figures are not to scale.

Appendix 1.2

Data Matrix

Appendix 1.2 Data Matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Archaeopteryx lithographica</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Protopteryx fengningensis</i>	[12]	[03]	1	[12]	?	?	?	[012]	1	?	?	?	?	?	?
<i>Pengornis houi</i>	0	0	1	[01]	0	0	?	1	1	1	?	0	?	?	?
<i>Archaeorhynchus spatula</i>	1	1	?	1	0	1	0	[12]	1	1	?	?	?	?	?
<i>Patagopteryx deferrariisi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Vorona berivotensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dingavis longimaxilla</i>	[01]	1	?	2	0	1	?	?	?	?	?	?	?	?	?
<i>Xinghaiornis lini</i>	[01]	1	?	2	1	1	?	[01]	0	1	?	1	?	?	?
<i>Bellulornis rectusunguis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Schizoura lii</i>	0	1	?	2	1	1	?	[01]	1	1	?	?	?	?	?
<i>Zhongjianornis yangi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Tianyuornis cheni</i>	1	0	1	2	0	0	?	?	?	?	?	?	?	?	?
<i>Archaeornithura meemannae</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parahongshanornis chaoyangensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hongshanornis longicresta</i>	?	0	?	2	0	0	0	?	?	1	?	?	?	?	?
<i>Longicrusavis houi</i>	1	0	?	[12]	0	0	?	?	1	?	?	?	?	?	?
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Piscivoravis lii</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Yixianornis grabaui</i>	1	2	1	2	1	?	?	?	?	?	?	?	?	?	?
<i>Yanornis martini</i>	1	2	1	[12]	0	0	?	2	1	1	?	1	?	?	?
<i>Changzuornis ahgmi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Iteravis huchzermeyeri</i>	0	1	1	2	0	0	?	2	1	1	?	0	?	?	?
<i>Gansus zheni</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Gansus yumenensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Enaliornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pasquiaornis</i>	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Baptornis varneri</i>	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?
<i>Fumicollis hoffmani</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parahesperornis alexi</i>	1	1	1	2	1	0	1	3	1	1	?	1	0	2	1
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	1	1	1	2	1	0	1	3	1	1	?	1	0	2	1
<i>Hesperornis gracilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1.2 Data Matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Ichthyornis dispar</i>	1	1	1	[12]	1	0	1	3	?	?	?	1	?	?	?
<i>Lithornis</i>	1	1	?	2	1	1	1	?	?	?	?	?	1	0	1
<i>Eudromia elegans</i>	1	1	?	2	1	1	1	?	?	?	?	?	1	[01]	1
<i>Vegavis iai</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Chauna torquata</i>	2	1	?	2	1	1	1	3	0	1	1	0	1	1	1
<i>Anas platyrhynchos</i>	2	1	?	2	1	1	1	3	0	1	1	0	1	1	1
<i>Gallus gallus</i>	1	1	?	2	1	1	1	3	1	1	1	1	1	2	1
<i>Phasianus colchicus</i>	1	1	?	2	1	1	1	3	1	1	1	1	1	2	1

Appendix 1.2 Data Matrix

	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>Archaeopteryx lithographica</i>	0	0	0	?	0	1	0	0	1	0	?	0	0	?	0
<i>Protopteryx fengningensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pengornis houi</i>	?	?	?	?	0	?	?	?	?	?	?	0	?	1	?
<i>Archaeorhynchus spatula</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Patagopteryx deferrariisi</i>	?	?	?	?	1	?	1	1	1	1	0	0	0	1	1
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dingavis longimaxilla</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Xinghaiornis lini</i>	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?
<i>Bellulornis rectusunguis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Schizoura lii</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Zhongjianornis yangi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Tianyuornis cheni</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeornithura meemannae</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parahongshanornis chaoyangensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hongshanornis longicresta</i>	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
<i>Longicrusavis houi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Piscivoravis lii</i>	?	?	?	?	?	?	?	1	?	?	?	?	1	1	?
<i>Yixianornis grabaui</i>	?	?	?	?	?	?	?	?	?	?	?	0	?	?	1
<i>Yanornis martini</i>	?	?	?	?	?	?	1	?	?	?	?	?	?	?	1
<i>Changzuornis ahgmi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Iteravis huchzermeyeri</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
<i>Gansus zheni</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Gansus yumenensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Enaliornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pasquiaornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Baptornis varneri</i>	?	?	?	?	?	?	1	1	?	?	?	0	?	?	1
<i>Fumicollis hoffmani</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parahesperornis alexi</i>	1	0	?	1	?	1	1	1	1	1	1	0	?	0	?
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	1	0	0	1	?	1	1	1	1	1	1	0	1	0	1
<i>Hesperornis gracilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1.2 Data Matrix

	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>Ichthyornis dispar</i>	?	?	?	?	1	1	1	1	1	1	?	?	1	1	1
<i>Lithornis</i>	1	0	?	0	?	?	?	?	?	?	?	?	?	?	1
<i>Eudromia elegans</i>	1	0	1	0	?	?	?	?	?	?	?	?	?	?	1
<i>Vegavis iai</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Chauna torquata</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Anas platyrhynchos</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Gallus gallus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Phasianus colchicus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Appendix 1.2 Data Matrix

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
<i>Archaeopteryx lithographica</i>	0	0	0	?	0	?	?	0	?	0	1	1	?	?	0
<i>Protopteryx fengningensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?
<i>Pengornis houi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeorhynchus spatula</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Patagopteryx deferrariisi</i>	1	1	1	?	?	1	?	0	?	0	?	?	?	?	?
<i>Vorona berivotensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dingavis longimaxilla</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Xinghaiornis lini</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Bellulornis rectusunguis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Schizooura lii</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
<i>Zhongjianornis yangi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	1	[01]	?	?	0	[01]	?	?	?	?	?	?	?	?	?
<i>Tianyuornis cheni</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeornithura meemannae</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parahongshanornis chaoyangensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hongshanornis longicresta</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Longicrusavis houi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Piscivoravis lii</i>	1	?	[01]	?	?	?	?	?	?	?	?	?	?	?	?
<i>Yixianornis grabaui</i>	?	1	?	?	?	[01]	?	?	1	0	1	?	?	?	?
<i>Yanornis martini</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
<i>Changzuiornis ahgmi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Iteravis huchzermeyeri</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Gansus zheni</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Gansus yumenensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Enaliornis</i>	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pasquiaornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Baptornis varneri</i>	1	1	1	0	0	?	0	?	?	?	?	?	?	?	?
<i>Fumicollis hoffmani</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parahesperornis alexi</i>	1	1	1	0	0	1	0	1	?	0	?	1	0	1	?
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	1	1	1	0	0	1	0	1	?	0	?	1	0	1	?
<i>Hesperornis gracilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1.2 Data Matrix

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
<i>Ichthyornis dispar</i>	1	1	?	1	0	1	0	?	?	?	?	?	?	1	0
<i>Lithornis</i>	?	?	?	0	?	[01]	1	0	0	0	1	1	1	?	0
<i>Eudromia elegans</i>	?	?	?	0	0	0	1	0	0	0	1	1	1	?	0
<i>Vegavis iai</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Chauna torquata</i>	1	2	1	1	1	1	1	0	1	0	2	2	1	1	1
<i>Anas platyrhynchos</i>	1	2	1	1	1	1	1	0	1	1	2	2	1	1	1
<i>Gallus gallus</i>	1	2	1	1	1	1	1	0	1	1	2	2	1	1	1
<i>Phasianus colchicus</i>	1	2	1	1	1	1	1	0	1	1	2	2	1	1	1

Appendix 1.2 Data Matrix

	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
<i>Archaeopteryx lithographica</i>	0	0	0	0	0	0	0	?	0	?	?	?	0	0	0
<i>Protopteryx fengningensis</i>	?	0	0	0	?	?	?	?	0	?	?	?	0	?	?
<i>Pengornis houi</i>	?	0	0	0	0	0	?	?	0	?	?	?	?	?	?
<i>Archaeorhynchus spatula</i>	?	0	1	?	0	0	0	?	?	?	0	?	0	1	0
<i>Patagopteryx deferrariisi</i>	?	?	?	?	?	?	0	?	0	?	?	?	?	?	?
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
<i>Dingavis longimaxilla</i>	?	?	1	?	1	?	0	?	0	?	0	?	0	?	?
<i>Xinghaiornis lini</i>	?	?	1	?	?	?	1	?	0	?	?	?	?	?	?
<i>Bellulornis rectusunguis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Schizoura lii</i>	?	0	1	?	0	?	0	?	0	?	?	?	?	?	?
<i>Zhongjianornis yangi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	?	?	1	?	1	?	1	?	?	?	?	?	?	?	?
<i>Tianyuornis cheni</i>	?	?	0	0	0	?	0	?	1	?	?	?	?	?	?
<i>Archaeornithura meemannae</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parahongshanornis chaoyangensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hongshanornis longicresta</i>	?	1	?	0	0	1	0	?	1	?	?	?	?	[01]	?
<i>Longicrusavis houi</i>	?	1	?	0	0	1	0	?	1	?	?	?	?	?	?
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Piscivoravis lii</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Yixianornis grabaui</i>	?	1	0	?	0	1	0	?	0	?	?	?	?	?	?
<i>Yanornis martini</i>	?	1	0	0	0	1	0	?	0	?	?	?	0	?	?
<i>Changzuiornis ahgmi</i>	?	1	?	?	?	?	0	?	?	?	?	?	?	?	?
<i>Iteravis huchzermeyeri</i>	?	1	0	0	0	1	1	?	0	?	?	?	?	?	?
<i>Gansus zheni</i>	?	1	?	?	?	?	1	?	?	?	?	?	?	?	?
<i>Gansus yumenensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Enaliornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pasquiaornis</i>	?	?	0	1	?	?	?	?	?	?	?	?	?	?	?
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Baptornis varneri</i>	?	?	?	?	?	1	?	?	0	?	0	?	?	?	1
<i>Fumicollis hoffmani</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parahesperornis alexi</i>	?	1	0	1	0	1	0	?	0	?	0	?	0	?	1
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	?	1	0	1	0	1	0	?	0	?	0	?	0	?	1
<i>Hesperornis gracilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1.2 Data Matrix

	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
<i>Ichthyornis dispar</i>	1	1	0	0	1	1	0	0	0	?	?	?	2	2	1
<i>Lithornis</i>	1	0	1	?	1	?	1	1	?	2	1	0	?	1	1
<i>Eudromia elegans</i>	1	0	1	?	1	?	1	1	?	2	1	0	?	1	1
<i>Vegavis iai</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Chauna torquata</i>	1	0	1	?	1	0	0	1	0	2	0	1	0	0	1
<i>Anas platyrhynchos</i>	1	0	1	?	1	0	0	1	0	2	0	1	0	0	1
<i>Gallus gallus</i>	1	0	1	?	1	0	0	1	0	2	0	0	0	0	1
<i>Phasianus colchicus</i>	1	0	1	?	1	0	0	1	0	2	0	0	0	0	1

Appendix 1.2 Data Matrix

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
<i>Archaeopteryx lithographica</i>	0	0	0	?	0	0	0	0	0	0	0	?	0	0	0
<i>Protopteryx fengningensis</i>	?	?	?	?	?	?	?	1	0	?	0	?	?	0	0
<i>Pengornis houi</i>	?	?	1	?	[12]	?	0	?	0	0	0	1	0	0	0
<i>Archaeorhynchus spatula</i>	?	?	[01]	1	0	?	?	?	0	?	?	?	?	?	?
<i>Patagopteryx deferrariisi</i>	0	0	0	0	2	1	1	1	0	0	0	1	2	0	0
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	?	?	1	?	1	?	?	?	0	0	0	?	0	0	0
<i>Dingavis longimaxilla</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Xinghaiornis lini</i>	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Bellulornis rectusunguis</i>	?	?	?	?	0	?	?	?	?	0	?	1	?	?	?
<i>Schizoura lii</i>	0	1	1	?	[12]	0	0	?	0	?	0	?	?	?	0
<i>Zhongjianornis yangi</i>	?	?	?	?	?	?	?	?	0	?	?	?	0	?	0
<i>Apsaravis ukhaana</i>	?	?	?	?	2	?	?	2	0	0	1	?	2	?	[01]
<i>Tianyuornis cheni</i>	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeornithura meemannae</i>	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parahongshanornis chaoyangensis</i>	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?
<i>Hongshanornis longicresta</i>	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?
<i>Longicrusavis houi</i>	0	1	?	?	1	?	?	?	?	0	?	?	?	?	?
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Piscivoravis lii</i>	?	?	?	0	2	1	1	1	0	0	1	?	0	0	0
<i>Yixianornis grabaui</i>	?	?	?	?	1	?	?	2	0	0	1	?	0	0	0
<i>Yanornis martini</i>	0	1	0	?	0	?	?	?	0	0	1	?	0	0	0
<i>Changzuornis ahgmi</i>	?	?	?	?	[12]	?	?	?	0	?	?	?	?	?	?
<i>Iteravis huchzermeyeri</i>	0	1	0	?	[12]	?	?	?	0	?	1	?	0	?	0
<i>Gansus zheni</i>	?	?	?	?	?	?	?	?	0	?	?	?	0	?	?
<i>Gansus yumenensis</i>	?	?	?	?	[01]	0	0	2	0	0	1	?	0	0	0
<i>Enaliornis</i>	?	?	?	?	2	?	?	?	1	?	1	1	?	?	0
<i>Pasquiaornis</i>	?	?	0	?	2	?	1	?	1	0	1	1	0	0	0
<i>Chupkaornis keraorum</i>	?	?	?	?	2	?	?	?	2	0	1	1	0	0	0
<i>Brodavis</i>	?	?	?	?	2	1	?	?	2	0	1	1	1	0	0
<i>Baptornis varneri</i>	0	1	?	0	2	?	1	3	2	0	1	1	1	0	0
<i>Fumicollis hoffmani</i>	?	?	?	?	2	1	1	3	2	0	1	1	1	0	0
<i>Paraesperornis alexi</i>	0	1	0	0	2	1	1	3	2	0	1	1	1	0	0
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	0	1	0	0	2	1	1	3	2	0	1	1	1	0	0
<i>Hesperornis gracilis</i>	?	?	?	?	2	?	1	?	2	?	1	?	1	0	?

Appendix 1.2 Data Matrix

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
<i>Ichthyornis dispar</i>	0	1	0	1	0	1	1	?	0	0	1	1	0	1	0
<i>Lithornis</i>	?	?	0	?	2	1	1	3	2	0	1	1	2	?	0
<i>Eudromia elegans</i>	?	?	0	?	2	?	?	?	2	?	1	?	?	?	?
<i>Vegavis iai</i>	?	?	?	?	2	1	1	3	2	0	1	?	2	1	1
<i>Chauna torquata</i>	0	1	0	1	2	1	1	3	2	0	1	1	2	1	0
<i>Anas platyrhynchos</i>	0	1	0	1	2	1	1	3	2	0	1	1	2	1	0
<i>Gallus gallus</i>	0	1	0	1	2	1	1	3	2	0	1	1	2	1	1
<i>Phasianus colchicus</i>	0	1	0	1	2	1	1	3	2	0	1	1	2	1	1

Appendix 1.2 Data Matrix

	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
<i>Archaeopteryx lithographica</i>	0	0	0	0	0	0	0	0	0	0	0	3	?	?	?
<i>Protopteryx fengningensis</i>	0	1	?	?	?	1	1	?	?	?	?	?	0	?	?
<i>Pengornis houi</i>	?	1	?	?	0	2	1	0	0	0	?	0	?	1	?
<i>Archaeorhynchus spatula</i>	0	1	0	?	?	2	1	?	1	0	?	1	?	?	?
<i>Patagopteryx deferrariisi</i>	0	[23]	0	1	0	?	?	?	1	1	1	?	?	?	?
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	0	[34]	0	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dingavis longimaxilla</i>	?	?	?	?	?	2	1	?	?	?	?	?	?	0	0
<i>Xinghaiornis lini</i>	?	?	?	?	?	[12]	1	?	0	?	?	?	1	0	0
<i>Bellulornis rectusunguis</i>	?	[234]	?	?	?	2	?	?	?	0	?	?	1	0	0
<i>Schizoura lii</i>	0	?	0	?	?	[12]	1	?	0	?	?	?	?	0	0
<i>Zhongjianornis yangi</i>	0	?	?	?	?	?	1	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	0	4	1	?	0	2	1	0	0	?	1	?	?	0	?
<i>Tianyuornis cheni</i>	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?
<i>Archaeornithura meemannae</i>	?	[34]	?	?	?	[12]	1	?	1	?	?	?	1	0	0
<i>Parahongshanornis chaoyangensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hongshanornis longicresta</i>	?	?	?	?	0	2	1	?	?	?	?	1	?	?	?
<i>Longicrusavis houi</i>	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Piscivoravis lii</i>	?	[34]	0	?	?	2	1	?	0	0	?	1	?	0	0
<i>Yixianornis grabaui</i>	?	3	0	?	0	2	1	?	?	?	?	1	1	0	0
<i>Yanornis martini</i>	0	3	1	?	0	?	?	?	?	?	?	1	?	?	?
<i>Changzuornis ahgmi</i>	?	?	?	?	?	?	1	?	?	?	?	1	?	0	?
<i>Iteravis huchzermeyeri</i>	?	?	?	?	?	2	1	?	?	?	?	1	1	0	0
<i>Gansus zheni</i>	?	?	?	?	?	?	1	?	?	?	?	1	?	?	?
<i>Gansus yumenensis</i>	0	4	1	?	1	2	1	?	0	?	1	1	1	0	0
<i>Enaliornis</i>	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?
<i>Pasquiaornis</i>	0	5	?	0	0	?	?	?	?	?	?	?	?	?	?
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Baptornis varneri</i>	1	5	0	1	0	1	?	0	0	0	1	2	?	?	0
<i>Fumicollis hoffmani</i>	1	?	?	?	?	?	?	?	?	?	?	?	?	0	?
<i>Parahesperornis alexi</i>	1	5	0	1	0	1	?	?	0	0	1	2	1	0	0
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	1	5	0	1	0	1	0	0	0	0	1	2	1	0	0
<i>Hesperornis gracilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1.2 Data Matrix

	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
<i>Ichthyornis dispar</i>	0	[45]	2	0	1	2	1	0	0	0	2	[12]	1	0	?
<i>Lithornis</i>	1	[56]	2	1	1	2	1	?	1	0	?	[12]	1	0	0
<i>Eudromia elegans</i>	?	[56]	2	?	2	?	?	0	?	?	?	2	?	?	?
<i>Vegavis iai</i>	1	?	2	1	?	2	1	?	1	0	1	1	1	0	0
<i>Chauna torquata</i>	1	6	2	1	2	2	1	1	0	0	1	1	1	0	0
<i>Anas platyrhynchos</i>	1	6	2	1	2	2	1	1	0	0	1	1	1	0	0
<i>Gallus gallus</i>	1	6	2	1	2	2	1	0	0	0	1	1	1	0	0
<i>Phasianus colchicus</i>	1	6	2	1	2	2	1	0	0	0	1	1	1	0	0

Appendix 1.2 Data Matrix

	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105
<i>Archaeopteryx lithographica</i>	?	0	0	[01]	?	?	?	?	?	?	?	?	?	?	0
<i>Protopteryx fengningensis</i>	1	0	0	2	1	?	?	1	1	0	0	0	1	?	1
<i>Pengornis houi</i>	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeorhynchus spatula</i>	?	?	0	[23]	0	0	?	2	2	1	0	0	1	?	[12]
<i>Patagopteryx deferrariisi</i>	?	?	?	[12]	?	?	?	?	?	?	?	?	1	?	0
<i>Vorona berivotensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	?	?	0	[23]	0	0	?	3	1	0	1	1	0	?	?
<i>Dingavis longimaxilla</i>	?	?	0	[23]	?	?	?	?	?	?	?	?	?	?	?
<i>Xinghaiornis lini</i>	?	?	?	[23]	?	?	?	[12]	2	0	?	?	1	?	1
<i>Bellulornis rectusunguis</i>	0	?	?	[23]	0	?	?	1	2	1	0	1	1	?	1
<i>Schizooura lii</i>	?	?	0	[23]	0	?	?	1	?	0	?	1	1	?	1
<i>Zhongjianornis yangi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	0	?	?	3	0	?	?	?	?	?	?	?	1	?	1
<i>Tianyuornis cheni</i>	?	1	?	3	?	?	?	2	2	1	0	?	0	?	[12]
<i>Archaeornithura meemannae</i>	?	1	0	3	0	?	?	?	?	?	?	1	0	?	[12]
<i>Parahongshanornis chaoyangensis</i>	?	?	?	3	0	?	?	2	2	0	0	1	0	?	[12]
<i>Hongshanornis longicresta</i>	0	1	0	?	?	0	?	2	2	0	0	1	1	?	[12]
<i>Longicrusavis houi</i>	0	?	?	3	?	?	?	1	2	0	0	1	1	?	[12]
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Piscivoravis lii</i>	?	1	0	3	0	?	?	1	1	1	0	1	0	?	?
<i>Yixianornis grabaui</i>	0	[12]	0	3	0	0	?	1	1	1	1	1	1	?	[12]
<i>Yanornis martini</i>	0	?	0	3	0	1	0	1	1	1	0	1	1	?	[12]
<i>Changzuiornis ahgmi</i>	?	1	?	?	0	?	?	?	?	?	?	?	?	?	?
<i>Iteravis huchzermeyeri</i>	0	1	0	3	0	?	?	1	1	0	1	1	0	?	[12]
<i>Gansus zheni</i>	0	?	0	3	0	?	?	1	1	0	?	1	1	?	[12]
<i>Gansus yumenensis</i>	0	1	?	3	0	1	0	1	1	0	0	1	1	0	1
<i>Enaliornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pasquiaornis</i>	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Baptornis varneri</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Fumicollis hoffmani</i>	?	1	?	?	?	?	?	?	?	?	?	?	0	0	0
<i>Parahesperornis alexi</i>	0	1	?	?	?	?	?	?	?	?	?	?	1	0	0
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	0	1	?	1	?	?	0	0	?	?	?	?	1	0	0
<i>Hesperornis gracilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1.2 Data Matrix

	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105
<i>Ichthyornis dispar</i>	0	?	?	3	0	1	1	0	?	?	?	?	0	0	1
<i>Lithornis</i>	0	[12]	1	3	0	1	1	0	?	?	?	?	0	1	1
<i>Eudromia elegans</i>	0	?	?	?	?	1	?	?	?	?	?	0	?	?	1
<i>Vegavis iai</i>	?	2	1	?	?	?	?	?	?	?	?	?	?	?	?
<i>Chauna torquata</i>	0	1	1	3	0	1	1	1	1	0	1	1	0	1	1
<i>Anas platyrhynchos</i>	0	2	1	3	0	1	1	1	1	0	1	1	0	1	1
<i>Gallus gallus</i>	0	[12]	1	3	0	0	1	1	0	0	1	0	0	1	1
<i>Phasianus colchicus</i>	0	2	1	3	0	0	1	1	0	0	1	0	0	1	1

Appendix 1.2 Data Matrix

	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
<i>Archaeopteryx lithographica</i>	?	?	?	?	?	0	0	0	?	0	0	0	0	0	0
<i>Protopteryx fengningensis</i>	[12]	?	2	0	1	0	1	1	0	0	3	1	0	1	1
<i>Pengornis houi</i>	?	?	?	?	?	0	1	1	0	0	2	0	0	1	1
<i>Archaeorhynchus spatula</i>	[12]	?	1	0	1	0	2	1	0	0	0	0	0	1	1
<i>Patagopteryx deferrariisi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	?	?	[01]	0	0	0	2	1	0	0	0	0	0	1	1
<i>Dingavis longimaxilla</i>	?	?	?	0	?	0	?	?	?	?	?	?	?	0	1
<i>Xinghaiornis lini</i>	?	?	?	?	?	0	1	1	?	?	[23]	?	0	?	?
<i>Bellulornis rectusunguis</i>	?	?	?	?	1	0	1	1	0	0	1	0	0	1	1
<i>Schizoura lii</i>	?	?	1	?	0	0	1	1	0	0	1	0	0	1	1
<i>Zhongjianornis yangi</i>	?	?	?	?	?	0	1	?	?	0	?	?	0	1	1
<i>Apsaravis ukhaana</i>	?	?	?	?	?	?	?	?	?	?	?	0	?	1	1
<i>Tianyuornis cheni</i>	?	?	1	0	2	0	2	1	1	1	1	0	0	1	1
<i>Archaeornithura meemannae</i>	?	?	?	?	2	0	2	1	1	1	1	0	0	1	1
<i>Parahongshanornis chaoyangensis</i>	?	?	1	0	0	0	2	1	1	1	1	0	0	1	1
<i>Hongshanornis longicresta</i>	?	?	1	0	0	0	2	1	1	1	1	0	0	1	1
<i>Longicrusavis houi</i>	?	?	1	0	2	0	2	1	1	1	?	0	0	1	1
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?
<i>Piscivoravis lii</i>	?	?	5	1	0	0	2	1	0	0	0	0	0	1	1
<i>Yixianornis grabaui</i>	?	?	5	1	1	0	2	1	0	1	0	0	1	1	1
<i>Yanornis martini</i>	?	?	5	1	0	0	2	1	0	0	0	?	0	1	1
<i>Changzuiornis ahgmi</i>	?	?	?	?	?	0	2	1	?	1	0	0	0	1	1
<i>Iteravis huchzermeyeri</i>	?	?	5	1	2	0	2	1	1	1	0	0	0	1	1
<i>Gansus zheni</i>	[23]	?	5	?	2	0	2	1	1	1	0	?	0	1	1
<i>Gansus yumenensis</i>	[23]	1	5	1	2	0	2	1	1	1	0	?	0	1	1
<i>Enaliornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pasquiaornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Baptornis varneri</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1
<i>Fumicollis hoffmani</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
<i>Parahesperornis alexi</i>	1	0	?	0	0	?	?	?	?	?	?	?	?	1	1
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	1	0	5	0	0	1	?	?	?	?	?	?	?	1	1
<i>Hesperornis gracilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1.2 Data Matrix

	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
<i>Ichthyornis dispar</i>	2	0	?	0	0	0	2	1	1	1	0	?	0	1	1
<i>Lithornis</i>	2	1	1	0	0	0	2	1	1	1	0	0	[01]	1	1
<i>Eudromia elegans</i>	?	?	?	?	?	0	?	1	?	?	?	?	0	1	1
<i>Vegavis iai</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1
<i>Chauna torquata</i>	4	0	4	0	0	0	2	1	1	1	[01]	0	1	1	1
<i>Anas platyrhynchos</i>	3	1	4	0	0	0	2	1	1	1	1	0	0	1	1
<i>Gallus gallus</i>	2	1	2	0	0	0	1	1	1	1	2	0	0	1	1
<i>Phasianus colchicus</i>	2	1	2	0	0	0	1	1	1	1	2	0	0	1	1

Appendix 1.2 Data Matrix

	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135
<i>Archaeopteryx lithographica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?
<i>Protopteryx fengningensis</i>	0	1	1	1	0	0	?	0	0	1	1	0	0	0	0
<i>Pengornis houi</i>	0	?	1	1	0	0	?	0	0	1	?	0	?	0	0
<i>Archaeorhynchus spatula</i>	0	?	1	1	0	0	0	0	?	1	1	0	?	0	?
<i>Patagopteryx deferrariisi</i>	0	1	1	1	1	0	1	0	0	?	0	0	?	?	?
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	?	1	1	1	0	1	0	0	1	1	0	0	1	?	?
<i>Dingavis longimaxilla</i>	?	?	1	1	0	0	0	0	?	?	?	?	?	?	?
<i>Xinghaiornis lini</i>	?	1	?	?	?	?	?	?	1	1	?	?	?	?	?
<i>Bellulornis rectusunguis</i>	?	?	1	1	?	?	?	0	1	1	1	0	?	?	?
<i>Schizoura lii</i>	?	?	1	1	0	?	?	?	1	1	1	0	?	?	?
<i>Zhongjianornis yangi</i>	?	?	1	1	0	0	0	?	0	1	1	?	?	?	?
<i>Apsaravis ukhaana</i>	0	1	1	1	1	0	1	0	0	1	1	1	?	0	?
<i>Tianyuornis cheni</i>	0	?	1	1	0	0	?	0	1	1	0	0	?	?	?
<i>Archaeornithura meemannae</i>	0	1	1	1	?	0	?	0	1	1	0	0	?	?	?
<i>Parahongshanornis chaoyangensis</i>	0	?	1	1	0	0	?	0	1	1	0	0	?	?	?
<i>Hongshanornis longicresta</i>	0	1	1	1	0	0	?	0	1	1	0	0	?	0	?
<i>Longicrusavis houi</i>	0	1	1	1	0	0	?	0	?	1	0	0	?	?	?
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Piscivoravis lii</i>	0	?	1	1	0	?	?	0	?	1	0	0	?	?	?
<i>Yixianornis grabaui</i>	0	1	1	1	1	0	0	0	1	1	0	0	1	0	?
<i>Yanornis martini</i>	0	1	1	1	?	0	0	0	1	1	0	0	?	0	?
<i>Changzuiornis ahgmi</i>	0	?	1	1	?	0	0	0	1	1	0	0	?	0	?
<i>Iteravis huchzermeyeri</i>	0	?	1	1	?	0	0	0	1	1	0	0	?	0	?
<i>Gansus zheni</i>	0	?	1	1	0	0	0	0	1	1	0	0	?	0	?
<i>Gansus yumenensis</i>	0	1	1	1	0	0	0	0	1	1	0	0	1	0	0
<i>Enaliornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pasquiaornis</i>	0	1	?	1	?	0	0	0	1	1	0	0	1	0	0
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Baptornis varneri</i>	1	1	?	?	?	1	0	0	0	1	[23]	0	1	0	0
<i>Fumicollis hoffmani</i>	1	1	?	?	?	?	?	?	0	?	?	?	?	?	?
<i>Parahesperornis alexi</i>	1	1	?	?	0	0	0	0	?	2	3	0	1	0	0
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	1	1	0	1	0	1	0	0	1	2	3	0	1	0	0
<i>Hesperornis gracilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1.2 Data Matrix

	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135
<i>Ichthyornis dispar</i>	0	1	1	1	1	1	0	1	1	1	0	0	1	0	0
<i>Lithornis</i>	0	1	1	1	0	0	1	0	1	1	0	0	1	1	0
<i>Eudromia elegans</i>	0	1	1	1	0	0	?	1	?	1	0	0	1	0	?
<i>Vegavis iai</i>	0	1	1	1	1	1	0	0	1	1	1	0	1	1	0
<i>Chauna torquata</i>	0	1	1	1	0	1	0	1	1	1	0	0	1	1	1
<i>Anas platyrhynchos</i>	0	1	1	1	0	0	0	1	1	1	0	0	1	0	?
<i>Gallus gallus</i>	0	1	0	1	1	0	0	0	1	1	1	1	1	1	1
<i>Phasianus colchicus</i>	0	1	0	1	1	0	0	0	1	1	1	1	1	1	1

Appendix 1.2 Data Matrix

	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150
<i>Archaeopteryx lithographica</i>	0	0	0	?	0	?	?	0	0	0	0	0	0	0	0
<i>Protopteryx fengningensis</i>	0	?	0	0	?	?	?	?	?	?	?	?	0	1	?
<i>Pengornis houi</i>	0	0	0	?	?	?	?	?	0	?	?	?	0	2	0
<i>Archaeorhynchus spatula</i>	1	0	1	?	0	?	?	1	1	1	?	0	0	1	?
<i>Patagopteryx deferrariisi</i>	?	0	1	0	1	1	1	?	0	1	?	0	0	0	1
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	0	?	1	?	?	0	0	1	1	0	?	0	0	2	0
<i>Dingavis longimaxilla</i>	?	?	?	?	?	?	?	?	?	?	?	?	0	2	0
<i>Xinghaiornis lini</i>	?	?	1	?	?	?	?	?	?	?	?	?	0	?	0
<i>Bellulornis rectusunguis</i>	0	0	1	?	0	?	?	1	1	0	?	0	0	2	1
<i>Schizoura lii</i>	0	?	1	?	?	?	?	?	1	0	?	?	0	2	1
<i>Zhongjianornis yangi</i>	0	?	?	?	0	?	?	?	1	0	?	?	0	2	?
<i>Apsaravis ukhaana</i>	0	0	1	1	0	0	0	0	0	0	0	1	0	?	1
<i>Tianyuornis cheni</i>	1	?	1	?	?	?	?	?	1	?	?	?	0	1	1
<i>Archaeornithura meemannae</i>	1	?	1	?	?	?	?	?	1	0	?	0	0	1	?
<i>Parahongshanornis chaoyangensis</i>	1	?	1	?	?	?	?	?	1	?	?	?	0	1	?
<i>Hongshanornis longicresta</i>	1	?	1	0	?	?	?	?	1	?	0	?	0	1	1
<i>Longicrusavis houi</i>	1	?	0	0	?	?	?	?	1	?	?	?	0	1	1
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Piscivoravis lii</i>	1	?	?	?	?	?	?	?	?	?	?	?	0	1	?
<i>Yixianornis grabaui</i>	1	1	1	0	0	0	0	1	1	0	1	0	0	1	?
<i>Yanornis martini</i>	1	?	1	?	0	0	0	1	1	?	1	0	0	1	1
<i>Changzuiornis ahgmi</i>	1	?	?	?	?	?	?	?	?	?	?	?	0	1	1
<i>Iteravis huchzermeyeri</i>	?	1	?	?	0	?	?	?	?	0	?	0	0	1	1
<i>Gansus zheni</i>	2	1	1	?	0	?	?	?	?	0	?	?	0	1	1
<i>Gansus yumenensis</i>	2	1	1	0	0	0	0	1	2	0	1	0	0	1	1
<i>Enaliornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pasquiaornis</i>	?	0	1	0	0	0	0	1	1	0	1	0	0	?	?
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Baptornis varneri</i>	0	0	?	0	1	1	1	0	0	0	0	0	1	0	?
<i>Fumicollis hoffmani</i>	?	?	?	0	1	1	1	?	0	?	?	?	?	?	?
<i>Parahesperornis alexi</i>	0	0	?	0	1	1	1	0	0	0	0	0	1	?	?
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	0	0	?	0	1	1	1	0	0	0	0	0	1	?	1
<i>Hesperornis gracilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1.2 Data Matrix

	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150
<i>Ichthyornis dispar</i>	?	0	1	0	0	0	0	1	2	0	1	0	0	1	1
<i>Lithornis</i>	1	1	1	0	0	0	0	1	2	0	1	0	0	1	1
<i>Eudromia elegans</i>	1	?	1	0	0	0	0	1	2	0	1	0	0	1	1
<i>Vegavis iai</i>	1	0	1	1	0	0	0	1	2	1	1	0	0	?	1
<i>Chauna torquata</i>	1	1	1	1	0	0	0	1	1	1	1	0	0	2	1
<i>Anas platyrhynchos</i>	1	1	1	0	0	0	0	1	2	1	1	0	0	0	1
<i>Gallus gallus</i>	1	1	1	1	0	0	0	1	2	1	1	0	0	1	1
<i>Phasianus colchicus</i>	1	1	1	1	0	0	0	1	2	1	1	0	0	1	1

Appendix 1.2 Data Matrix

	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165
<i>Archaeopteryx lithographica</i>	0	0	0	?	0	0	?	1	1	0	0	1	0	0	0
<i>Protopteryx fengningensis</i>	0	0	0	?	?	?	0	0	1	0	0	1	0	1	?
<i>Pengornis houi</i>	0	0	0	?	0	1	0	0	1	?	0	1	?	1	0
<i>Archaeorhynchus spatula</i>	1	1	1	0	?	?	?	0	1	?	0	1	?	1	?
<i>Patagopteryx deferrariisi</i>	0	?	?	1	?	?	?	1	0	?	0	1	?	1	?
<i>Vorona berivotensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	1	1	1	0	?	?	?	0	1	?	0	1	?	1	0
<i>Dingavis longimaxilla</i>	1	1	1	?	?	0	?	0	0	?	0	1	?	1	0
<i>Xinghaiornis lini</i>	1	1	1	?	?	0	?	0	2	?	0	0	?	1	0
<i>Bellulornis rectusunguis</i>	1	1	1	0	1	?	?	0	1	?	0	0	?	1	?
<i>Schizoura lii</i>	1	1	?	0	?	?	?	0	2	?	0	0	0	1	?
<i>Zhongjianornis yangi</i>	1	1	?	?	?	?	?	0	2	?	0	0	0	1	?
<i>Apsaravis ukhaana</i>	1	1	1	0	1	1	?	0	1	1	0	1	1	1	0
<i>Tianyuornis cheni</i>	1	1	1	0	?	?	?	0	1	?	0	1	?	1	?
<i>Archaeornithura meemannae</i>	1	1	?	?	?	1	?	0	1	?	0	1	?	1	0
<i>Parahongshanornis chaoyangensis</i>	1	1	1	?	?	1	?	0	1	?	0	1	?	1	?
<i>Hongshanornis longicresta</i>	1	1	1	?	1	?	0	0	1	0	0	1	1	1	?
<i>Longicrusavis houi</i>	1	1	1	?	?	1	?	0	1	1	0	1	?	1	?
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Piscivoravis lii</i>	1	1	?	?	?	?	?	0	?	?	0	?	?	1	?
<i>Yixianornis grabaui</i>	1	1	1	?	?	1	0	0	?	1	0	?	?	1	0
<i>Yanornis martini</i>	1	1	1	0	1	?	?	0	1	?	0	1	1	1	?
<i>Changzuornis ahgmi</i>	1	1	1	?	1	?	0	0	1	1	0	1	?	1	?
<i>Iteravis huchzermeyeri</i>	1	?	1	0	?	?	?	?	1	?	0	1	?	1	?
<i>Gansus zheni</i>	1	1	1	0	1	?	0	0	1	1	0	1	?	1	0
<i>Gansus yumenensis</i>	1	1	1	0	1	1	0	0	1	1	0	1	1	1	0
<i>Enaliornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pasquiaornis</i>	1	1	1	?	1	1	0	1	0	0	0	1	1	1	0
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Baptornis varneri</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Fumicollis hoffmani</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parahesperornis alexi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	?	1	1	?	0	0	?	0	0	0	0	1	0	0	0
<i>Hesperornis gracilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1.2 Data Matrix

	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165
<i>Ichthyornis dispar</i>	1	1	1	0	2	1	0	0	1	1	0	0	1	1	0
<i>Lithornis</i>	1	1	1	0	2	1	0	1	0	0	0	1	1	2	1
<i>Eudromia elegans</i>	1	1	1	0	2	1	1	1	0	0	0	1	1	2	1
<i>Vegavis iaai</i>	1	1	1	?	2	1	0	1	0	0	0	1	1	2	1
<i>Chauna torquata</i>	1	1	1	0	2	1	0	1	0	0	0	1	1	2	1
<i>Anas platyrhynchos</i>	1	1	1	0	2	1	0	1	0	0	0	1	1	2	1
<i>Gallus gallus</i>	1	1	1	0	2	1	1	1	0	0	0	1	1	2	1
<i>Phasianus colchicus</i>	1	1	1	0	2	1	1	1	0	0	0	1	1	2	1

Appendix 1.2 Data Matrix

	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180
<i>Archaeopteryx lithographica</i>	0	?	?	?	0	0	0	0	?	0	0	0	0	0	0
<i>Protopteryx fengningensis</i>	1	?	?	?	?	0	0	?	?	?	?	?	?	1	?
<i>Pengornis houi</i>	1	0	0	?	?	0	0	?	?	?	?	?	1	1	0
<i>Archaeorhynchus spatula</i>	1	0	?	?	?	0	0	0	0	?	?	?	?	0	0
<i>Patagopteryx deferrariisi</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Vorona berivotensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	1	?	?	?	?	0	0	0	?	?	?	?	?	1	?
<i>Dingavis longimaxilla</i>	1	?	?	?	?	0	0	?	?	?	?	?	1	0	?
<i>Xinghaiornis lini</i>	1	?	?	?	?	0	0	?	?	?	?	?	?	?	?
<i>Bellulornis rectusunguis</i>	1	?	?	0	?	0	0	?	?	?	?	?	?	0	?
<i>Schizoura lii</i>	1	?	?	0	?	0	0	0	?	?	?	?	?	0	?
<i>Zhongjianornis yangi</i>	1	?	?	0	?	0	0	?	?	?	?	?	?	1	?
<i>Apsaravis ukhaana</i>	1	1	1	1	?	1	1	0	0	0	0	1	1	1	0
<i>Tianyuornis cheni</i>	1	?	?	?	?	0	0	?	?	?	?	?	?	1	?
<i>Archaeornithura meemannae</i>	1	0	?	?	?	0	0	?	?	?	?	?	?	?	?
<i>Parahongshanornis chaoyangensis</i>	1	?	?	?	?	0	0	?	?	?	?	?	?	1	?
<i>Hongshanornis longicresta</i>	1	0	0	?	?	0	0	?	0	0	?	?	?	1	0
<i>Longicrusavis houi</i>	1	?	?	?	?	0	0	1	?	?	?	?	?	1	?
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Piscivoravis lii</i>	1	?	?	?	?	?	?	?	?	?	?	?	?	1	?
<i>Yixianornis grabaui</i>	1	?	0	?	?	?	?	?	?	?	0	?	?	1	0
<i>Yanornis martini</i>	1	0	0	0	?	0	0	?	0	?	?	?	?	1	?
<i>Changzuiornis ahgmi</i>	1	0	0	?	?	0	0	?	?	?	?	?	?	1	?
<i>Iteravis huchzermeyeri</i>	1	?	0	?	?	0	0	?	?	?	?	?	?	1	?
<i>Gansus zheni</i>	1	0	0	0	0	0	0	?	0	?	?	?	?	1	0
<i>Gansus yumenensis</i>	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0
<i>Enaliornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pasquiaornis</i>	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Baptornis varneri</i>	1	?	2	1	1	0	0	0	1	0	0	0	0	0	0
<i>Fumicollis hoffmani</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parahesperornis alexi</i>	1	?	2	1	1	0	0	0	1	0	0	0	0	?	?
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	1	?	2	1	1	0	0	0	1	0	0	0	0	?	?
<i>Hesperornis gracilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1.2 Data Matrix

	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180
<i>Ichthyornis dispar</i>	1	0	0	0	0	0	0	1	0	1	1	1	1	1	0
<i>Lithornis</i>	1	0	0	0	0	0	0	1	0	1	0	1	1	1	0
<i>Eudromia elegans</i>	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0
<i>Vegavis iai</i>	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?
<i>Chauna torquata</i>	1	0	0	0	0	0	0	1	0	1	1	1	1	1	0
<i>Anas platyrhynchos</i>	1	0	0	0	0	0	0	1	0	1	1	1	1	1	0
<i>Gallus gallus</i>	1	0	0	0	0	0	0	1	0	1	1	1	1	1	0
<i>Phasianus colchicus</i>	1	0	0	0	0	0	0	1	0	1	1	1	1	1	0

Appendix 1.2 Data Matrix

	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195
<i>Archaeopteryx lithographica</i>	1	0	0	0	0	0	0	?	?	0	0	0	0	0	1
<i>Protopteryx fengningensis</i>	?	?	?	?	?	?	?	?	?	0	0	1	0	0	1
<i>Pengornis houi</i>	?	0	0	?	?	?	1	0	?	[23]	0	1	1	?	?
<i>Archaeorhynchus spatula</i>	1	1	0	?	?	1	1	?	?	3	1	1	1	0	1
<i>Patagopteryx deferrariisi</i>	1	?	?	1	0	0	0	?	?	?	1	?	0	?	?
<i>Vorona berivotensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	?	?	?	?	?	?	?	?	?	?	?	1	1	1	2
<i>Dingavis longimaxilla</i>	?	?	?	?	?	?	1	?	?	2	0	1	1	1	2
<i>Xinghaiornis lini</i>	?	1	?	1	?	?	?	?	?	?	?	?	?	?	?
<i>Bellulornis rectusunguis</i>	?	?	?	?	?	?	1	0	?	3	1	1	1	0	1
<i>Schizoura lii</i>	?	?	?	?	?	?	1	0	?	3	1	1	1	0	1
<i>Zhongjianornis yangi</i>	?	?	?	?	?	?	1	?	?	3	?	1	1	0	1
<i>Apsaravis ukhaana</i>	1	1	0	1	1	1	1	0	?	3	?	1	1	2	2
<i>Tianyuornis cheni</i>	?	?	?	?	?	?	?	?	?	[23]	?	1	1	1	2
<i>Archaeornithura meemannae</i>	?	?	?	?	?	?	?	?	?	[23]	?	1	1	1	2
<i>Parahongshanornis chaoyangensis</i>	?	?	?	?	?	?	?	?	?	?	1	1	1	1	2
<i>Hongshanornis longicresta</i>	1	1	0	?	?	?	?	?	?	3	?	1	1	1	2
<i>Longicrusavis houi</i>	1	1	?	?	?	?	1	?	?	3	1	1	1	?	?
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Piscivoravis lii</i>	?	?	?	?	?	?	1	0	?	3	1	1	1	0	1
<i>Yixianornis grabaui</i>	1	1	0	1	1	?	1	0	?	3	0	1	1	1	2
<i>Yanornis martini</i>	1	1	0	1	1	?	1	0	1	3	0	1	1	0	1
<i>Changzuiornis ahgmi</i>	?	1	?	?	?	?	?	?	?	3	1	1	1	1	2
<i>Iteravis huchzermeyeri</i>	1	?	?	?	?	?	1	0	1	?	1	1	1	1	2
<i>Gansus zheni</i>	?	?	?	?	?	?	1	?	?	3	1	1	1	1	2
<i>Gansus yumenensis</i>	1	1	0	1	1	1	1	1	1	3	1	1	1	1	2
<i>Enaliornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pasquiaornis</i>	1	1	0	1	1	0	?	?	?	3	?	1	1	1	1
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Baptornis varneri</i>	1	1	?	0	0	0	?	?	?	?	?	?	?	?	?
<i>Fumicollis hoffmani</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parahesperornis alexi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis gracilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1.2 Data Matrix

	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195
<i>Ichthyornis dispar</i>	1	1	1	1	1	1	1	1	2	3	1	1	1	2	2
<i>Lithornis</i>	1	1	0	0	1	1	1	1	1	3	1	1	1	2	2
<i>Eudromia elegans</i>	1	1	0	0	1	1	1	1	0	3	1	1	1	2	2
<i>Vegavis iai</i>	?	?	?	?	?	?	?	?	?	3	1	1	1	1	2
<i>Chauna torquata</i>	1	1	0	0	1	1	1	1	2	3	1	1	1	2	2
<i>Anas platyrhynchos</i>	1	1	1	0	1	1	1	1	2	3	1	1	1	2	2
<i>Gallus gallus</i>	1	1	0	0	1	1	1	1	1	3	1	1	1	2	2
<i>Phasianus colchicus</i>	1	1	0	0	1	1	1	1	1	3	1	1	1	2	2

Appendix 1.2 Data Matrix

	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210
<i>Archaeopteryx lithographica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Protopteryx fengningensis</i>	0	?	?	0	0	1	0	0	0	0	0	0	0	0	0
<i>Pengornis houi</i>	?	1	?	0	0	1	[01]	?	?	0	?	0	0	?	?
<i>Archaeorhynchus spatula</i>	0	?	0	0	0	0	0	1	0	1	0	?	?	?	0
<i>Patagopteryx deferrariisi</i>	?	?	?	?	0	0	?	?	?	?	?	0	0	?	?
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	?	1	1	0	0	0	?	0	0	1	0	0	0	1	?
<i>Dingavis longimaxilla</i>	?	?	?	0	0	0	?	1	0	1	0	0	0	1	0
<i>Xinghaiornis lini</i>	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?
<i>Bellulornis rectusunguis</i>	0	0	?	0	0	0	?	1	0	1	0	0	0	1	0
<i>Schizoura lii</i>	0	?	?	0	0	0	?	1	0	1	0	0	0	1	0
<i>Zhongjianornis yangi</i>	?	1	1	0	0	0	?	1	0	1	0	0	0	1	?
<i>Apsaravis ukhaana</i>	1	1	1	0	0	?	1	?	?	1	0	?	?	?	?
<i>Tianyuornis cheni</i>	?	?	?	0	0	0	?	0	0	1	0	0	0	0	0
<i>Archaeornithura meemannae</i>	?	?	?	0	0	0	?	0	0	1	0	0	0	1	0
<i>Parahongshanornis chaoyangensis</i>	?	?	?	0	0	0	?	0	0	1	0	0	0	0	0
<i>Hongshanornis longicresta</i>	?	?	?	0	0	0	[01]	0	0	1	0	0	0	1	0
<i>Longicrusavis houi</i>	?	1	?	0	0	0	0	0	0	1	0	0	0	0	0
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Piscivoravis lii</i>	0	?	?	0	0	0	?	0	0	1	0	0	0	2	1
<i>Yixianornis grabaui</i>	0	1	1	0	0	0	[01]	0	0	1	0	0	0	2	1
<i>Yanornis martini</i>	0	1	1	0	0	0	[01]	0	0	1	0	0	0	2	1
<i>Changzuiornis ahgmi</i>	0	1	?	0	0	0	[01]	1	0	1	0	0	0	?	?
<i>Iteravis huchzermeyeri</i>	0	?	?	0	0	0	0	1	0	1	1	0	0	2	1
<i>Gansus zheni</i>	0	?	?	0	0	0	0	1	0	1	1	0	0	2	1
<i>Gansus yumenensis</i>	0	1	1	1	0	0	1	1	0	1	0	0	0	0	1
<i>Enaliornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pasquiaornis</i>	1	1	1	1	?	?	1	?	?	?	?	?	?	?	?
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Baptornis varneri</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Fumicollis hoffmani</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parahesperornis alexi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis gracilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1.2 Data Matrix

	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210
<i>Ichthyornis dispar</i>	1	1	1	1	0	0	1	2	1	1	1	1	1	?	1
<i>Lithornis</i>	1	1	1	1	0	0	1	2	1	1	1	0	1	?	?
<i>Eudromia elegans</i>	1	1	0	1	1	1	1	2	1	1	1	0	1	?	1
<i>Vegavis iai</i>	1	1	?	1	0	0	1	2	1	1	1	0	1	?	?
<i>Chauna torquata</i>	1	1	1	1	1	0	1	2	1	1	1	0	1	?	1
<i>Anas platyrhynchos</i>	1	1	1	1	1	0	1	2	1	1	1	0	1	?	1
<i>Gallus gallus</i>	1	1	0	1	1	1	2	2	1	1	1	0	1	?	1
<i>Phasianus colchicus</i>	1	1	0	1	1	1	2	2	1	1	1	0	1	?	1

Appendix 1.2 Data Matrix

	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225
<i>Archaeopteryx lithographica</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Protopteryx fengningensis</i>	1	0	0	0	2	?	?	?	?	?	?	?	0	?	?
<i>Pengornis houi</i>	?	0	?	?	2	?	?	?	0	?	?	?	?	?	?
<i>Archaeorhynchus spatula</i>	1	0	1	2	2	?	0	?	?	?	?	1	?	?	?
<i>Patagopteryx deferrariisi</i>	?	0	1	2	0	1	0	0	0	0	0	1	?	0	0
<i>Vorona berivotensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	2	0	1	0	2	?	?	?	?	0	0	1	0	0	?
<i>Dingavis longimaxilla</i>	2	0	1	0	2	?	0	?	?	?	?	1	?	?	?
<i>Xinghaiornis lini</i>	?	0	1	1	?	1	0	?	?	?	?	?	?	?	0
<i>Bellulornis rectusunguis</i>	2	0	1	0	2	1	?	?	?	0	0	1	?	0	?
<i>Schizoura lii</i>	2	0	1	0	2	?	0	?	?	0	0	1	?	0	1
<i>Zhongjianornis yangi</i>	2	0	1	0	2	?	0	?	?	0	?	1	1	?	?
<i>Apsaravis ukhaana</i>	?	?	?	?	?	1	0	?	0	0	0	1	1	0	1
<i>Tianyuornis cheni</i>	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?
<i>Archaeornithura meemannae</i>	0	0	1	0	1	?	?	?	?	?	?	?	?	?	?
<i>Parahongshanornis chaoyangensis</i>	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?
<i>Hongshanornis longicresta</i>	0	0	1	0	1	?	0	0	?	0	0	?	?	?	?
<i>Longicrusavis houi</i>	1	0	1	0	1	?	0	?	0	0	0	?	?	?	?
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Piscivoravis lii</i>	2	0	1	2	2	1	0	0	0	0	0	1	1	0	?
<i>Yixianornis grabaui</i>	2	0	1	1	2	1	0	0	0	0	0	1	1	?	?
<i>Yanornis martini</i>	2	0	1	2	2	1	0	0	0	0	0	1	1	?	1
<i>Changzuiornis ahgmi</i>	2	0	1	2	2	1	?	?	?	?	?	?	?	?	?
<i>Iteravis huchzermeyeri</i>	2	0	1	2	2	1	0	?	?	0	0	1	1	0	1
<i>Gansus zheni</i>	2	0	1	2	2	1	0	?	?	0	0	1	1	0	1
<i>Gansus yumenensis</i>	2	0	1	2	2	1	0	?	?	0	0	1	2	0	1
<i>Enaliornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pasquiaornis</i>	?	?	?	?	?	1	?	?	?	?	?	?	?	0	?
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	?	?	?	?	?	1	0	0	?	0	0	?	?	0	?
<i>Baptornis varneri</i>	?	?	?	?	0	1	0	0	0	0	0	1	2	0	1
<i>Fumicollis hoffmani</i>	?	?	?	?	?	1	0	?	?	0	0	1	2	0	1
<i>Parahesperornis alexi</i>	?	?	?	?	?	1	0	0	0	0	0	1	2	1	1
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	?	?	?	?	?	1	0	0	0	0	0	1	2	1	1
<i>Hesperornis gracilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 1.2 Data Matrix

	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225
<i>Ichthyornis dispar</i>	2	0	1	?	?	1	0	[01]	0	0	1	1	1	0	1
<i>Lithornis</i>	2	0	1	?	?	1	0	1	0	1	1	1	1	0	1
<i>Eudromia elegans</i>	2	0	1	2	1	1	0	1	0	1	1	1	1	0	1
<i>Vegavis iai</i>	2	0	1	?	?	1	0	?	?	?	?	?	2	?	?
<i>Chauna torquata</i>	2	0	1	2	2	1	1	1	1	1	1	1	0	0	1
<i>Anas platyrhynchos</i>	2	0	1	2	2	1	1	1	1	1	1	1	2	0	1
<i>Gallus gallus</i>	2	0	1	2	1	1	1	1	1	1	1	1	1	0	1
<i>Phasianus colchicus</i>	2	0	1	2	1	1	1	1	1	1	1	1	1	0	1

Appendix 1.2 Data Matrix

	226	227	228	229	230	231	232	233	234	235	236	237	238	239	240
<i>Archaeopteryx lithographica</i>	?	0	0	0	0	0	0	0	0	0	?	0	0	0	?
<i>Protopteryx fengningensis</i>	1	?	?	?	?	?	?	?	?	?	?	0	0	0	?
<i>Pengornis houi</i>	?	?	?	?	?	0	?	?	?	?	?	0	?	0	?
<i>Archaeorhynchus spatula</i>	?	0	?	?	?	0	?	0	0	1	?	0	0	0	?
<i>Patagopteryx deferrariisi</i>	0	0	0	?	1	0	0	0	1	1	1	0	1	?	?
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
<i>Jianchangornis microdonta</i>	1	?	?	1	?	0	?	?	?	?	?	0	0	?	?
<i>Dingavis longimaxilla</i>	1	0	?	1	1	0	?	?	?	?	1	0	0	0	?
<i>Xinghaiornis lini</i>	1	?	?	?	?	?	?	0	?	1	?	?	0	?	?
<i>Bellulornis rectusunguis</i>	?	?	?	1	1	0	0	0	?	1	1	0	?	0	?
<i>Schizoura lii</i>	1	0	?	?	?	0	?	0	0	1	?	0	0	?	?
<i>Zhongjianornis yangi</i>	?	0	?	1	?	?	0	0	?	1	?	0	0	?	?
<i>Apsaravis ukhaana</i>	1	?	0	1	1	0	0	0	1	1	1	1	1	?	1
<i>Tianyuornis cheni</i>	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?
<i>Archaeornithura meemannae</i>	?	?	?	?	?	?	?	?	?	1	1	0	?	?	?
<i>Parahongshanornis chaoyangensis</i>	?	?	?	?	?	?	?	?	?	1	?	0	?	?	?
<i>Hongshanornis longicresta</i>	?	?	?	?	?	0	?	?	0	1	1	0	0	?	1
<i>Longicrusavis houi</i>	?	?	?	?	1	?	?	?	?	1	?	0	0	?	?
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Piscivoravis lii</i>	1	0	0	1	?	0	0	0	0	1	1	0	0	?	?
<i>Yixianornis grabaui</i>	1	0	0	1	1	?	?	0	0	1	1	0	?	?	?
<i>Yanornis martini</i>	1	0	0	1	1	0	0	0	0	1	?	0	0	0	?
<i>Changzuiornis ahgmi</i>	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?
<i>Iteravis huchzermeyeri</i>	1	0	0	1	1	?	?	0	0	1	1	0	0	0	?
<i>Gansus zheni</i>	1	0	0	1	1	?	1	0	0	1	1	0	0	0	?
<i>Gansus yumenensis</i>	1	0	0	1	1	1	1	0	0	1	1	0	0	0	1
<i>Enaliornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
<i>Pasquiaornis</i>	?	?	?	?	1	?	?	0	?	?	?	?	?	?	1
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	?	?	?	1	1	?	?	0	?	?	?	1	?	?	?
<i>Baptornis varneri</i>	1	?	0	1	1	1	?	0	1	?	1	1	?	?	1
<i>Fumicollis hoffmani</i>	1	1	0	1	1	?	2	0	1	1	1	1	1	1	1
<i>Parahesperornis alexi</i>	1	1	0	1	2	2	2	0	1	1	1	1	1	1	1
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	1	1	0	1	2	2	2	0	1	1	1	1	1	1	1
<i>Hesperornis gracilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1

Appendix 1.2 Data Matrix

	226	227	228	229	230	231	232	233	234	235	236	237	238	239	240
<i>Ichthyornis dispar</i>	1	0	0	1	1	0	1	1	?	1	1	1	1	1	1
<i>Lithornis</i>	1	1	0	2	1	0	1	1	1	1	1	1	1	1	1
<i>Eudromia elegans</i>	1	1	0	2	1	0	2	1	1	1	1	1	1	1	1
<i>Vegavis iai</i>	?	?	?	?	?	?	1	1	?	1	?	1	?	?	1
<i>Chauna torquata</i>	1	1	1	2	1	0	1	1	1	1	1	1	1	1	1
<i>Anas platyrhynchos</i>	1	1	1	2	1	0	1	1	1	1	1	1	1	1	1
<i>Gallus gallus</i>	1	1	1	2	1	0	2	1	1	1	1	1	1	1	1
<i>Phasianus colchicus</i>	1	1	1	2	1	0	2	1	1	1	1	1	1	1	1

Appendix 1.2 Data Matrix

	241	242	243	244	245	246	247	248	249	250	251	252	253	254	255
<i>Archaeopteryx lithographica</i>	0	?	0	0	?	?	0	0	0	0	0	0	?	1	0
<i>Protopteryx fengningensis</i>	?	?	?	1	?	?	?	0	0	?	?	0	?	?	?
<i>Pengornis houi</i>	1	0	?	?	1	?	?	0	0	?	?	0	?	?	?
<i>Archaeorhynchus spatula</i>	?	0	?	?	?	?	?	0	0	?	?	0	?	?	?
<i>Patagopteryx deferrariisi</i>	1	0	2	1	1	0	0	0	0	0	?	0	1	1	0
<i>Vorona berivotrensis</i>	1	0	?	1	1	0	0	0	?	0	0	0	1	1	0
<i>Jianchangornis microdonta</i>	?	0	?	?	?	?	?	0	0	0	?	0	?	?	?
<i>Dingavis longimaxilla</i>	1	0	?	1	?	?	?	0	0	0	?	0	?	?	?
<i>Xinghaiornis lini</i>	?	?	?	?	?	?	?	0	0	?	?	0	?	?	?
<i>Bellulornis rectusunguis</i>	1	0	?	1	1	?	?	0	0	0	?	0	?	?	?
<i>Schizoura lii</i>	?	?	?	?	?	?	?	?	?	0	?	0	?	?	?
<i>Zhongjianornis yangi</i>	?	0	?	1	1	?	?	0	?	0	?	0	?	?	?
<i>Apsaravis ukhaana</i>	1	0	?	1	?	?	?	0	0	0	0	0	?	1	1
<i>Tianyuornis cheni</i>	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?
<i>Archaeornithura meemannae</i>	?	?	?	?	?	?	?	?	0	?	?	0	?	?	?
<i>Parahongshanornis chaoyangensis</i>	?	?	?	?	?	?	?	?	0	?	?	0	?	?	?
<i>Hongshanornis longicresta</i>	?	?	?	1	?	?	?	?	0	?	?	0	?	?	?
<i>Longicrusavis houi</i>	?	?	?	1	?	?	?	?	0	?	?	0	?	?	?
<i>Hollanda luceria</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
<i>Piscivoravis lii</i>	1	?	?	?	?	?	?	0	?	0	?	0	?	?	?
<i>Yixianornis grabaui</i>	?	?	2	1	?	0	?	?	?	?	?	0	?	1	?
<i>Yanornis martini</i>	?	0	?	1	?	?	?	0	0	0	?	0	?	?	?
<i>Changzuiornis ahgmi</i>	1	?	?	1	?	?	?	?	?	?	?	0	?	?	?
<i>Iteravis huchzermeyeri</i>	1	0	?	1	?	?	?	?	0	0	?	0	?	?	?
<i>Gansus zheni</i>	1	?	?	1	1	?	?	?	0	0	?	0	?	?	?
<i>Gansus yumenensis</i>	1	0	2	1	1	0	0	0	0	0	0	0	1	1	1
<i>Enaliornis</i>	1	0	2	1	1	0	0	1	1	?	0	1	[01]	1	1
<i>Pasquiaornis</i>	2	1	2	1	1	0	1	1	1	1	0	1	0	1	1
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
<i>Brodavis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
<i>Baptornis varneri</i>	2	1	2	1	1	1	1	1	1	1	1	1	0	0	1
<i>Fumicollis hoffmani</i>	2	1	2	1	1	1	1	1	1	1	1	1	0	1	2
<i>Parahesperornis alexi</i>	2	1	2	2	0	2	2	2	2	1	1	1	1	2	2
MM V 2487	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2
<i>Hesperornis regalis</i>	2	1	2	2	1	2	2	2	2	2	1	1	1	0	2
<i>Hesperornis gracilis</i>	2	1	2	2	1	2	2	2	2	2	1	1	1	0	2

Appendix 1.2 Data Matrix

	241	242	243	244	245	246	247	248	249	250	251	252	253	254	255
<i>Ichthyornis dispar</i>	2	0	2	1	2	0	0	0	0	0	0	0	?	?	1
<i>Lithornis</i>	2	0	2	1	1	0	0	0	0	0	0	0	1	0	1
<i>Eudromia elegans</i>	2	1	2	1	2	0	0	0	0	0	0	0	1	0	1
<i>Vegavis iai</i>	2	0	2	1	1	0	0	0	0	0	0	0	?	2	1
<i>Chauna torquata</i>	2	0	2	1	1	0	0	0	0	0	0	0	1	0	1
<i>Anas platyrhynchos</i>	2	0	2	1	1	0	0	0	0	0	0	0	1	0	1
<i>Gallus gallus</i>	2	1	2	1	2	0	0	0	0	0	0	0	1	0	1
<i>Phasianus colchicus</i>	2	1	2	1	2	0	0	0	0	0	0	0	1	0	1

Appendix 1.2 Data Matrix

	256	257	258	259	260	261	262	263	264	265	266	267	268	269	270
<i>Archaeopteryx lithographica</i>	0	0	0	0	?	?	0	0	?	0	0	?	0	?	?
<i>Protopteryx fengningensis</i>	?	0	?	?	?	?	?	?	?	?	0	?	?	?	?
<i>Pengornis houi</i>	0	0	?	0	?	?	?	?	?	?	0	?	?	?	?
<i>Archaeorhynchus spatula</i>	?	0	?	?	?	?	?	?	?	?	0	?	?	?	?
<i>Patagopteryx deferrariisi</i>	0	0	1	0	0	0	0	1	?	?	0	2	0	?	?
<i>Vorona berivotensis</i>	0	0	1	0	0	0	0	1	?	?	0	2	?	?	?
<i>Jianchangornis microdonta</i>	?	0	?	?	?	?	?	?	?	?	0	?	?	?	?
<i>Dingavis longimaxilla</i>	?	0	[12]	?	?	?	?	?	?	?	0	?	?	?	?
<i>Xinghaiornis lini</i>	?	0	?	?	?	?	?	?	?	?	0	?	?	?	?
<i>Bellulornis rectusunguis</i>	?	0	?	?	?	?	?	?	?	?	0	?	?	?	?
<i>Schizooura lii</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Zhongjianornis yangi</i>	?	0	?	?	?	?	?	?	?	?	0	?	?	?	?
<i>Apsaravis ukhaana</i>	?	0	?	0	0	0	0	1	?	?	0	?	0	?	?
<i>Tianyuornis cheni</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeornithura meemannae</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parahongshanornis chaoyangensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hongshanornis longicresta</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Longicrusavis houi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hollanda luceria</i>	0	0	1	0	0	0	0	?	?	0	?	2	?	?	?
<i>Piscivoravis lii</i>	?	0	?	?	?	?	?	?	?	?	0	?	?	?	?
<i>Yixianornis grabaui</i>	?	?	2	?	?	?	0	?	?	?	?	?	?	?	?
<i>Yanornis martini</i>	?	0	?	?	?	?	?	?	?	0	0	?	?	?	?
<i>Changzuornis ahgmi</i>	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Iteravis huchzermeyeri</i>	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Gansus zheni</i>	?	0	?	?	?	?	?	?	?	?	?	?	0	?	?
<i>Gansus yumenensis</i>	0	0	2	0	0	0	0	1	1	0	0	2	0	?	?
<i>Enaliornis</i>	0	1	2	0	0	0	0	1	1	1	1	1	1	?	?
<i>Pasquiaornis</i>	0	1	2	0	0	0	0	1	1	1	1	1	1	?	?
<i>Chupkaornis keraorum</i>	0	1	2	0	0	1	0	1	1	1	?	1	1	?	?
<i>Brodavis</i>	0	1	2	0	0	1	0	1	1	1	?	1	?	?	?
<i>Baptornis varneri</i>	0	1	2	0	0	1	0	1	1	1	1	1	?	0	0
<i>Fumicollis hoffmani</i>	0	1	2	0	0	1	1	1	1	2	1	1	?	0	0
<i>Parahesperornis alexi</i>	1	1	2	0	0	1	1	1	1	2	2	1	?	1	0
MM V 2487	1	1	2	1	0	1	1	1	1	2	?	0	1	1	0
<i>Hesperornis regalis</i>	1	0	2	1	1	1	1	1	1	2	2	0	1	1	1
<i>Hesperornis gracilis</i>	1	0	2	1	1	1	1	1	1	2	2	0	?	1	1

Appendix 1.2 Data Matrix

	256	257	258	259	260	261	262	263	264	265	266	267	268	269	270
<i>Ichthyornis dispar</i>	0	0	2	0	0	0	0	1	1	0	0	?	0	?	?
<i>Lithornis</i>	0	0	2	0	0	0	0	1	1	1	0	2	0	?	?
<i>Eudromia elegans</i>	0	0	2	0	0	0	0	1	1	1	0	2	0	?	?
<i>Vegavis iai</i>	0	1	2	0	0	0	0	1	1	1	0	2	1	?	?
<i>Chauna torquata</i>	0	1	2	0	0	0	0	1	1	0	0	2	0	?	?
<i>Anas platyrhynchos</i>	0	1	2	0	0	0	0	1	1	1	0	2	0	?	?
<i>Gallus gallus</i>	0	0	2	0	0	0	0	1	1	0	0	2	0	?	?
<i>Phasianus colchicus</i>	0	0	2	0	0	0	0	1	1	0	0	2	0	?	?

Appendix 1.2 Data Matrix

	271	272	273	274	275	276	277	278	279	280	281	282	283	284	285
<i>Archaeopteryx lithographica</i>	0	0	1	0	0	?	?	?	?	?	?	2	0	0	0
<i>Protopteryx fengningensis</i>	0	?	?	?	0	?	?	?	?	?	?	2	0	?	?
<i>Pengornis houi</i>	0	1	?	0	0	?	?	?	?	?	0	2	0	0	0
<i>Archaeorhynchus spatula</i>	0	2	2	0	0	?	?	?	?	?	0	?	0	?	0
<i>Patagopteryx deferrariisi</i>	0	2	1	0	0	?	0	?	0	?	0	2	0	0	0
<i>Vorona berivotensis</i>	1	2	1	0	0	0	0	0	0	?	0	2	0	0	0
<i>Jianchangornis microdonta</i>	0	?	?	?	0	?	?	?	?	?	?	2	0	?	?
<i>Dingavis longimaxilla</i>	0	?	?	?	0	?	?	?	?	?	?	2	0	?	0
<i>Xinghaiornis lini</i>	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?
<i>Bellulornis rectusunguis</i>	0	2	2	0	0	?	?	?	?	?	0	2	0	?	0
<i>Schizoura lii</i>	0	?	?	0	0	?	?	?	?	?	?	?	0	?	?
<i>Zhongjianornis yangi</i>	0	2	?	0	0	?	?	?	?	?	0	2	0	?	0
<i>Apsaravis ukhaana</i>	?	2	?	?	?	?	?	?	?	?	?	?	0	?	0
<i>Tianyuornis cheni</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Archaeornithura meemannae</i>	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parahongshanornis chaoyangensis</i>	0	?	?	?	?	?	?	?	?	?	?	?	0	?	?
<i>Hongshanornis longicresta</i>	1	?	?	?	0	?	?	?	?	?	?	?	0	?	?
<i>Longicrusavis houi</i>	0	2	2	?	0	?	?	?	?	?	?	?	0	?	?
<i>Hollanda luceria</i>	?	2	2	0	0	?	0	?	?	0	0	2	0	0	1
<i>Piscivoravis lii</i>	0	2	2	0	0	?	?	?	?	?	?	2	0	?	0
<i>Yixianornis grabaui</i>	0	2	2	?	0	?	?	?	?	?	0	?	0	?	0
<i>Yanornis martini</i>	0	2	?	0	0	?	?	?	?	?	0	2	0	?	0
<i>Changzuiornis ahgmi</i>	1	2	?	?	0	?	?	?	?	?	?	?	0	?	?
<i>Iteravis huchzermeyeri</i>	1	2	?	?	0	?	?	?	?	?	0	?	0	?	?
<i>Gansus zheni</i>	1	2	2	?	0	?	?	?	?	?	0	2	0	?	0
<i>Gansus yumenensis</i>	1	2	2	1	1	0	0	0	0	0	0	2	0	0	0
<i>Enaliornis</i>	?	2	2	1	1	0	0	1	0	0	0	?	?	?	1
<i>Pasquiaornis</i>	?	2	2	1	1	0	0	[01]	0	0	0	1	?	1	1
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	?	2	2	1	1	0	0	?	0	0	0	1	0	1	1
<i>Baptornis varneri</i>	2	2	2	1	1	0	0	2	0	0	0	1	0	1	1
<i>Fumicollis hoffmani</i>	2	2	2	1	1	0	0	2	0	0	0	1	0	1	1
<i>Parahesperornis alexi</i>	2	2	2	2	1	1	1	0	1	0	1	0	1	1	1
MM V 2487	?	2	2	2	1	1	1	0	1	?	1	0	1	1	1
<i>Hesperornis regalis</i>	2	2	2	2	1	1	1	0	1	1	1	0	1	1	1
<i>Hesperornis gracilis</i>	?	2	2	2	1	1	1	0	1	?	1	0	1	1	1

Appendix 1.2 Data Matrix

	271	272	273	274	275	276	277	278	279	280	281	282	283	284	285
<i>Ichthyornis dispar</i>	?	2	2	0	0	?	0	?	?	0	?	2	0	?	1
<i>Lithornis</i>	?	2	2	0	0	0	0	0	0	2	0	2	0	0	0
<i>Eudromia elegans</i>	0	2	2	0	0	0	0	1	0	2	0	2	0	0	0
<i>Vegavis iaai</i>	?	2	2	?	1	?	0	?	0	2	1	?	?	?	?
<i>Chauna torquata</i>	0	2	2	0	1	0	0	0	0	2	1	2	0	0	0
<i>Anas platyrhynchos</i>	0	2	2	0	1	0	0	1	0	2	1	2	0	0	0
<i>Gallus gallus</i>	0	2	2	0	0	0	0	0	0	2	0	2	0	0	0
<i>Phasianus colchicus</i>	0	2	2	0	0	0	0	0	0	2	0	2	0	0	0

	286	287	288	289	290	291	292	293	294	295	296	297	298	299	300
<i>Archaeopteryx lithographica</i>	0	0	0	?	?	?	?	0	0	1	0	1	0	1	0
<i>Protopteryx fengningensis</i>	?	0	?	?	?	?	?	?	?	1	?	?	?	1	0
<i>Pengornis houi</i>	0	0	?	?	0	?	?	?	?	1	0	1	?	1	1
<i>Archaeorhynchus spatula</i>	0	0	?	?	0	?	?	?	?	0	1	?	?	0	1
<i>Patagopteryx deferrariisi</i>	0	0	1	0	1	0	0	1	0	1	1	1	?	0	1
<i>Vorona berivotrensis</i>	0	0	1	0	1	0	0	1	0	1	1	1	0	0	1
<i>Jianchangornis microdonta</i>	?	0	?	?	?	?	?	?	?	1	1	?	?	0	1
<i>Dingavis longimaxilla</i>	0	0	?	?	?	?	?	?	?	?	1	1	?	2	1
<i>Xinghaiornis lini</i>	?	0	?	?	?	?	?	?	?	?	?	0	?	?	1
<i>Bellulornis rectusunguis</i>	0	0	?	?	0	?	?	?	?	0	1	?	?	1	1
<i>Schizoura lii</i>	?	0	?	?	?	?	?	?	?	1	1	?	?	1	1
<i>Zhongjianornis yangi</i>	0	0	?	?	?	?	?	?	?	1	1	?	?	0	1
<i>Apsaravis ukhaana</i>	0	0	1	2	1	0	1	1	0	1	1	?	?	?	1
<i>Tianyuornis cheni</i>	?	?	?	?	?	?	?	?	?	?	1	?	?	1	1
<i>Archaeornithura meemannae</i>	?	?	?	?	?	?	?	?	?	?	1	?	?	1	1
<i>Parahongshanornis chaoyangensis</i>	?	?	?	?	?	?	?	?	?	?	1	?	?	1	?
<i>Hongshanornis longicresta</i>	?	0	?	?	?	?	?	?	?	?	1	?	?	1	1
<i>Longicrusavis houi</i>	?	0	?	?	?	?	?	?	?	?	?	?	?	1	1
<i>Hollanda luceria</i>	0	0	?	0	1	0	1	1	2	0	1	1	0	?	1
<i>Piscivoravis lii</i>	0	?	?	?	0	?	1	1	?	?	1	1	?	1	1
<i>Yixianornis grabaui</i>	0	0	?	?	?	?	1	1	?	0	1	?	?	1	1
<i>Yanornis martini</i>	0	0	?	?	0	?	1	?	?	0	1	?	?	1	1
<i>Changzuiornis ahgmi</i>	?	?	?	?	0	?	?	?	?	?	1	?	?	2	1
<i>Iteravis huchzermeyeri</i>	?	1	?	?	0	?	?	?	?	0	1	?	0	1	1
<i>Gansus zheni</i>	0	1	?	?	0	?	?	?	?	0	1	?	0	1	1
<i>Gansus yumenensis</i>	0	1	1	1	0	1	1	1	0	0	1	1	0	1	1
<i>Enaliornis</i>	0	1	1	1	0	1	1	1	0	2	?	?	1	?	1
<i>Pasquiaornis</i>	0	1	1	1	0	1	1	1	0	2	?	1	1	?	1
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	1	1	1	1	0	2	1	1	0	2	1	0	?	0	1
<i>Baptornis varneri</i>	1	1	1	1	0	2	1	1	0	2	1	0	1	0	1
<i>Fumicollis hoffmani</i>	1	1	1	1	0	2	1	1	0	2	1	0	1	0	1
<i>Parahesperornis alexi</i>	1	1	1	1	0	2	1	2	1	2	1	0	?	0	1
MM V 2487	1	1	1	1	0	2	1	2	1	2	?	?	1	?	1
<i>Hesperornis regalis</i>	1	1	1	1	0	2	1	2	1	2	1	0	1	0	1
<i>Hesperornis gracilis</i>	1	1	1	1	0	2	1	2	1	2	1	0	?	?	1

Appendix 1.2 Data Matrix

	286	287	288	289	290	291	292	293	294	295	296	297	298	299	300
<i>Ichthyornis dispar</i>	1	1	1	1	0	2	1	1	0	2	1	1	?	?	1
<i>Lithornis</i>	0	2	1	1	0	2	1	1	2	2	1	?	?	?	1
<i>Eudromia elegans</i>	0	2	1	1	0	2	1	1	2	2	1	1	0	1	1
<i>Vegavis iai</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
<i>Chauna torquata</i>	0	2	1	1	0	2	1	1	2	2	1	1	0	1	1
<i>Anas platyrhynchos</i>	0	2	1	1	0	2	1	1	2	2	1	1	0	1	1
<i>Gallus gallus</i>	0	2	1	1	0	2	1	1	2	2	1	1	0	1	1
<i>Phasianus colchicus</i>	0	2	1	1	0	2	1	1	2	2	1	1	0	1	1

Appendix 1.2 Data Matrix

	301	302	303	304	305	306	307	308	309	310	311	312	313	314	315
<i>Archaeopteryx lithographica</i>	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
<i>Protopteryx fengningensis</i>	1	0	?	?	0	0	0	?	?	?	?	?	?	?	?
<i>Pengornis houi</i>	1	0	1	?	0	0	0	?	?	?	0	?	?	?	2
<i>Archaeorhynchus spatula</i>	1	0	1	0	0	0	0	?	?	?	1	?	?	1	0
<i>Patagopteryx deferrariisi</i>	3	0	1	0	0	0	0	0	0	?	1	1	0	0	0
<i>Vorona berivotensis</i>	2	0	0	0	0	0	0	0	0	0	1	1	0	?	2
<i>Jianchangornis microdonta</i>	?	0	1	0	0	0	0	?	?	?	1	?	?	?	?
<i>Dingavis longimaxilla</i>	3	0	1	1	?	?	0	?	?	?	?	?	?	0	2
<i>Xinghaiornis lini</i>	3	0	1	?	0	0	0	?	?	?	?	?	?	0	?
<i>Bellulornis rectusunguis</i>	3	0	1	0	0	0	0	?	?	?	1	?	?	0	2
<i>Schizoura lii</i>	3	0	1	0	0	0	0	?	?	0	1	?	?	?	2
<i>Zhongjianornis yangi</i>	?	0	1	?	0	0	0	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	2	0	1	1	1	1	0	0	0	[01]	1	?	?	?	2
<i>Tianyuornis cheni</i>	?	?	1	1	?	?	0	?	?	?	?	?	?	?	?
<i>Archaeornithura meemannae</i>	?	?	?	1	?	?	0	?	?	?	?	?	?	?	?
<i>Parahongshanornis chaoyangensis</i>	?	?	1	1	?	?	0	?	?	?	?	?	?	1	?
<i>Hongshanornis longicresta</i>	?	0	?	1	1	1	0	?	?	?	1	?	?	1	2
<i>Longicrusavis houi</i>	?	?	1	1	1	1	0	?	?	?	1	?	?	1	?
<i>Hollanda luceria</i>	2	0	1	1	1	1	0	0	0	?	?	0	?	?	0
<i>Piscivoravis lii</i>	2	0	1	1	0	0	0	?	?	?	1	0	?	?	2
<i>Yixianornis grabaui</i>	?	0	1	1	1	1	0	?	?	[01]	?	0	?	1	?
<i>Yanornis martini</i>	2	0	1	1	1	1	0	?	?	?	1	?	?	1	2
<i>Changzuornis ahgmi</i>	?	?	1	1	1	1	0	?	?	?	?	?	?	1	2
<i>Iteravis huchzermeyeri</i>	3	0	1	1	1	1	0	?	?	?	1	?	?	1	?
<i>Gansus zheni</i>	3	0	1	1	1	1	0	?	?	?	1	?	?	1	2
<i>Gansus yumenensis</i>	3	0	1	1	1	1	0	0	0	1	1	1	?	1	2
<i>Enaliornis</i>	3	0	1	1	1	?	0	0	0	1	2	0	?	?	2
<i>Pasquiaornis</i>	3	0	1	1	1	2	0	0	0	0	2	0	?	?	2
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	3	0	1	1	1	2	0	0	1	0	2	0	?	?	2
<i>Baptornis varneri</i>	3	0	1	1	1	2	0	0	1	0	?	0	1	?	2
<i>Fumicollis hoffmani</i>	3	0	1	1	1	2	0	0	1	0	2	0	?	?	2
<i>Parahesperornis alexi</i>	2	1	1	1	1	2	1	1	1	0	2	0	1	1	2
MM V 2487	2	1	1	1	2	2	1	1	1	0	2	0	1	?	2
<i>Hesperornis regalis</i>	2	1	1	1	2	2	1	1	1	0	2	0	1	1	2
<i>Hesperornis gracilis</i>	2	1	1	1	2	2	1	1	1	0	2	0	1	?	2

Appendix 1.2 Data Matrix

	301	302	303	304	305	306	307	308	309	310	311	312	313	314	315
<i>Ichthyornis dispar</i>	3	0	1	1	1	1	0	0	0	1	2	2	1	?	2
<i>Lithornis</i>	3	0	1	1	1	1	0	0	0	2	2	2	1	2	2
<i>Eudromia elegans</i>	3	0	1	1	1	1	0	0	0	2	2	2	1	2	2
<i>Vegavis iaai</i>	?	0	1	1	1	1	?	?	?	4	[12]	?	?	?	?
<i>Chauna torquata</i>	3	0	1	1	1	1	0	0	0	2	2	2	1	2	2
<i>Anas platyrhynchos</i>	3	0	1	1	1	1	0	0	0	4	2	2	1	2	2
<i>Gallus gallus</i>	3	0	1	1	1	1	0	0	0	3	2	2	1	2	2
<i>Phasianus colchicus</i>	3	0	1	1	1	1	0	0	0	3	2	2	1	2	2

Appendix 1.2 Data Matrix

	316	317	318	319	320	321	322	323	324	325	326	327	328	329	330
<i>Archaeopteryx lithographica</i>	?	0	0	0	0	?	?	?	0	0	?	0	0	?	0
<i>Protopteryx fengningensis</i>	?	0	?	0	?	?	?	?	0	1	?	0	0	?	0
<i>Pengornis houi</i>	0	0	1	0	?	?	?	?	0	1	?	0	0	?	0
<i>Archaeorhynchus spatula</i>	?	0	0	0	?	?	?	?	0	0	?	?	1	?	0
<i>Patagopteryx deferrariisi</i>	0	0	0	0	0	1	0	2	0	0	0	1	1	0	0
<i>Vorona berivotrensis</i>	1	0	0	0	0	1	0	2	0	0	0	1	1	0	0
<i>Jianchangornis microdonta</i>	?	0	0	0	?	?	?	?	0	0	?	?	?	?	0
<i>Dingavis longimaxilla</i>	?	0	0	0	?	?	?	?	?	0	?	1	?	?	?
<i>Xinghaiornis lini</i>	?	0	?	0	?	?	?	?	?	0	?	?	?	?	?
<i>Bellulornis rectusunguis</i>	?	0	0	0	?	?	?	?	0	0	?	?	1	?	0
<i>Schizoura lii</i>	?	0	0	0	?	?	?	2	?	0	?	1	1	0	0
<i>Zhongjianornis yangi</i>	?	0	0	0	?	?	?	?	0	0	?	1	1	?	0
<i>Apsaravis ukhaana</i>	0	0	0	0	0	1	0	2	0	0	0	1	1	0	0
<i>Tianyuornis cheni</i>	?	0	0	?	?	?	?	?	0	0	?	?	?	?	0
<i>Archaeornithura meemannae</i>	?	0	?	?	?	?	?	?	0	0	?	?	?	?	0
<i>Parahongshanornis chaoyangensis</i>	?	0	0	?	?	?	?	?	0	0	?	?	?	?	0
<i>Hongshanornis longicresta</i>	?	0	0	0	?	?	?	?	0	0	?	?	?	?	0
<i>Longicrusavis houi</i>	0	0	0	0	?	?	?	?	0	0	?	1	1	?	0
<i>Hollanda luceria</i>	0	0	1	0	0	1	0	2	0	0	0	1	1	0	0
<i>Piscivoravis lii</i>	?	0	0	0	?	?	?	2	0	0	?	1	1	0	0
<i>Yixianornis grabaui</i>	?	0	0	0	?	?	?	2	0	0	?	1	1	0	0
<i>Yanornis martini</i>	?	0	0	0	?	?	?	?	0	0	?	?	1	?	0
<i>Changzuiornis ahgmi</i>	?	0	0	0	?	?	?	?	0	0	?	?	1	?	0
<i>Iteravis huchzermeyeri</i>	?	0	?	0	?	?	?	?	?	0	?	1	1	?	?
<i>Gansus zheni</i>	?	0	0	0	?	?	?	?	0	0	0	1	1	?	1
<i>Gansus yumenensis</i>	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1
<i>Enaliornis</i>	1	2	0	1	0	?	?	?	1	0	0	?	1	0	1
<i>Pasquiaornis</i>	1	1	0	1	0	0	1	1	1	0	0	0	1	0	1
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	1	1	0	1	0	0	2	1	1	0	0	1	1	0	1
<i>Baptornis varneri</i>	1	1	0	1	0	0	0	1	1	0	0	0	1	0	1
<i>Fumicollis hoffmani</i>	1	2	0	1	0	0	0	1	1	0	0	1	2	0	1
<i>Parahesperornis alexi</i>	2	2	2	2	1	1	0	1	2	0	0	1	2	0	1
MM V 2487	2	2	2	2	1	1	0	1	2	0	0	1	2	0	1
<i>Hesperornis regalis</i>	2	3	2	2	1	1	0	1	2	0	0	1	2	0	1
<i>Hesperornis gracilis</i>	2	3	2	2	1	1	0	1	2	0	0	1	2	0	1

Appendix 1.2 Data Matrix

	316	317	318	319	320	321	322	323	324	325	326	327	328	329	330
<i>Ichthyornis dispar</i>	1	0	0	0	?	?	0	0	0	0	0	1	1	0	1
<i>Lithornis</i>	1	0	0	0	0	?	0	0	0	0	1	1	1	0	0
<i>Eudromia elegans</i>	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0
<i>Vegavis iai</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Chauna torquata</i>	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0
<i>Anas platyrhynchos</i>	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0
<i>Gallus gallus</i>	1	0	0	0	0	1	0	0	0	0	1	1	1	1	0
<i>Phasianus colchicus</i>	1	0	0	0	0	1	0	0	0	0	1	1	1	1	0

Appendix 1.2 Data Matrix

	331	332	333	334	335	336	337	338	339	340	341	342	343	344	345
<i>Archaeopteryx lithographica</i>	?	0	0	0	0	0	0	?	0	0	1	0	0	0	1
<i>Protopteryx fengningensis</i>	?	?	?	?	0	0	0	?	0	1	1	0	1	2	1
<i>Pengornis houi</i>	1	?	?	?	0	0	0	?	0	?	?	0	1	0	2
<i>Archaeorhynchus spatula</i>	?	?	?	?	0	0	0	?	0	?	?	1	0	0	1
<i>Patagopteryx deferrariisi</i>	1	0	0	?	0	0	1	?	0	0	1	1	0	0	?
<i>Vorona berivotensis</i>	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>Jianchangornis microdonta</i>	?	?	?	?	0	0	0	?	0	?	?	1	0	0	?
<i>Dingavis longimaxilla</i>	?	?	?	?	0	0	0	?	0	1	1	1	0	?	?
<i>Xinghaiornis lini</i>	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?
<i>Bellulornis rectusunguis</i>	?	?	?	?	0	0	0	?	0	?	0	1	0	0	0
<i>Schizoura lii</i>	?	?	?	?	0	0	0	?	0	1	0	1	0	0	0
<i>Zhongjianornis yangi</i>	?	?	?	?	0	0	0	?	0	?	?	1	0	?	?
<i>Apsaravis ukhaana</i>	1	1	0	0	?	0	0	0	0	1	1	?	0	?	0
<i>Tianyuornis cheni</i>	?	?	?	?	0	0	0	?	0	1	1	1	0	0	0
<i>Archaeornithura meemannae</i>	?	?	?	?	0	0	0	?	0	1	1	1	0	0	0
<i>Parahongshanornis chaoyangensis</i>	?	?	?	?	0	0	0	?	0	1	1	1	0	0	0
<i>Hongshanornis longicresta</i>	?	?	?	?	0	0	0	?	0	1	1	1	0	0	0
<i>Longicrusavis houi</i>	?	?	?	?	0	0	0	?	0	1	1	1	0	0	0
<i>Hollanda luceria</i>	1	?	0	0	?	0	0	0	0	1	?	?	?	0	0
<i>Piscivoravis lii</i>	1	?	?	?	0	0	0	?	0	1	0	1	1	0	0
<i>Yixianornis grabaui</i>	1	?	?	?	0	0	0	?	0	1	1	1	0	0	1
<i>Yanornis martini</i>	?	?	?	?	0	0	0	?	0	1	1	1	0	0	0
<i>Changzuornis ahgmi</i>	?	?	?	?	0	0	0	?	0	1	1	1	0	0	0
<i>Iteravis huchzermeyeri</i>	?	2	0	?	1	0	0	0	0	1	1	1	0	0	0
<i>Gansus zheni</i>	?	2	0	?	1	0	0	0	0	1	1	1	0	0	0
<i>Gansus yumenensis</i>	0	2	0	0	2	0	0	0	0	1	1	1	0	0	0
<i>Enaliornis</i>	0	2	1	0	?	?	?	?	?	?	?	?	0	?	?
<i>Pasquiaornis</i>	0	2	1	0	?	0	?	0	0	?	?	?	0	?	?
<i>Chupkaornis keraorum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brodavis</i>	0	2	1	0	?	?	?	?	?	?	?	?	?	?	?
<i>Baptornis varneri</i>	0	2	2	0	2	0	0	0	0	1	?	?	?	?	?
<i>Fumicollis hoffmani</i>	0	2	2	0	?	0	0	0	0	?	?	?	?	?	?
<i>Parahesperornis alexi</i>	0	2	2	1	2	1	1	1	1	1	1	1	0	0	0
MM V 2487	0	2	2	1	?	1	1	1	1	?	?	?	?	?	?
<i>Hesperornis regalis</i>	0	2	2	1	2	1	1	1	1	1	1	1	0	0	0
<i>Hesperornis gracilis</i>	0	2	2	1	?	1	1	1	1	?	?	?	?	?	?

Appendix 1.2 Data Matrix

	331	332	333	334	335	336	337	338	339	340	341	342	343	344	345
<i>Ichthyornis dispar</i>	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>Lithornis</i>	0	1	0	0	0	0	?	?	?	?	?	1	?	?	?
<i>Eudromia elegans</i>	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1
<i>Vegavis iai</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Chauna torquata</i>	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1
<i>Anas platyrhynchos</i>	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1
<i>Gallus gallus</i>	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1
<i>Phasianus colchicus</i>	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1

	346	347	348	349
<i>Archaeopteryx lithographica</i>	0	0	0	0
<i>Protopteryx fengningensis</i>	0	1	0	1
<i>Pengornis houi</i>	0	?	?	?
<i>Archaeorhynchus spatula</i>	0	?	?	?
<i>Patagopteryx deferrariisi</i>	0	?	?	?
<i>Vorona berivotrensis</i>	?	?	?	?
<i>Jianchangornis microdonta</i>	0	?	0	?
<i>Dingavis longimaxilla</i>	1	?	?	?
<i>Xinghaiornis lini</i>	?	?	?	?
<i>Bellulornis rectusunguis</i>	0	?	?	?
<i>Schizoura lii</i>	0	?	1	?
<i>Zhongjianornis yangi</i>	0	?	?	?
<i>Apsaravis ukhaana</i>	?	?	?	?
<i>Tianyuornis cheni</i>	1	?	?	?
<i>Archaeornithura meemannae</i>	1	1	1	?
<i>Parahongshanornis chaoyangensis</i>	1	?	?	?
<i>Hongshanornis longicresta</i>	1	1	1	2
<i>Longicrusavis houi</i>	1	?	?	2
<i>Hollanda luceria</i>	?	?	?	?
<i>Piscivoravis lii</i>	1	1	1	?
<i>Yixianornis grabaui</i>	1	?	1	2
<i>Yanornis martini</i>	1	?	?	2
<i>Changzuiornis ahgmi</i>	2	?	?	?
<i>Iteravis huchzermeyeri</i>	2	?	?	2
<i>Gansus zheni</i>	2	?	?	2
<i>Gansus yumenensis</i>	2	?	?	2
<i>Enaliornis</i>	?	?	?	?
<i>Pasquiaornis</i>	?	?	?	?
<i>Chupkaornis keraorum</i>	?	?	?	?
<i>Brodavis</i>	?	?	?	?
<i>Baptornis varneri</i>	?	?	?	?
<i>Fumicollis hoffmani</i>	?	?	?	?
<i>Parahesperornis alexi</i>	2	?	?	?
MM V 2487	?	?	?	?
<i>Hesperornis regalis</i>	2	?	?	?
<i>Hesperornis gracilis</i>	?	?	?	?

	346	347	348	349
<i>Ichthyornis dispar</i>	?	?	?	?
<i>Lithornis</i>	0	?	?	?
<i>Eudromia elegans</i>	0	1	1	2
<i>Vegavis iai</i>	?	?	?	?
<i>Chauna torquata</i>	1	1	1	2
<i>Anas platyrhynchos</i>	1	1	1	2
<i>Gallus gallus</i>	0	1	1	2
<i>Phasianus colchicus</i>	0	1	1	2

Appendix 1.3

List of Synapomorphy

Strict consensus tree (SCT) of two most parsimonious trees. Branch numbers of the SCT correspond to that of the synapomorphy list.



Tree length: 777

CI = 0.576

RI = 0.791

CR = 0.456

Synapomorphy List*Archaeopteryx_lithographica* :

No autapomorphies

Protopteryx_fengningensis :

Char. 116: 2 --> 3

Char. 117: 0 --> 1

Char. 344: 0 --> 2

Pengornis_houi :

Char. 149: 1 --> 2

Char. 345: 1 --> 2

Archaeorhynchus_spatula :

Char. 64: 0 --> 1

Char. 65: 1 --> 0

Char. 273: 1 --> 2

Char. 295: 1 --> 0

Char. 301: 2 --> 1

Char. 314: 0 --> 1

Patagopteryx_deferrariisi :

Char. 65: 1 --> 2

Char. 85: 0 --> 1

Char. 105: 1 --> 0

Char. 125: 0 --> 1

Char. 127: 0 --> 1

Char. 140: 0 --> 1

Char. 149: 1 --> 0

Char. 154: 0 --> 1

Char. 158: 0 --> 1

Char. 159: 1 --> 0

Char. 174: 0 --> 1

Char. 187: 1 --> 0

Char. 215: 2 --> 0

Char. 234: 0 --> 1

Char. 238: 0 --> 1

Char. 301: 2 --> 3

Char. 337: 0 --> 1

Vorona_berivotrensis :

Char. 271: 0 --> 1

Char. 303: 1 --> 0

Char. 316: 0 --> 1

Jianchangornis_microdonta :

Char. 98: 1 --> 3

Char. 103: 1 --> 0

Char. 126: 0 --> 1

Char. 150: 1 --> 0

Char. 299: 1 --> 0

Dingavis_longimaxilla :

Char. 150: 1 --> 0

Char. 159: 1 --> 0

Char. 179: 1 --> 0

Char. 190: 3 --> 2

Xinghaiornis_lini :

Char. 9: 1 --> 0

Char. 52: 0 --> 1

Char. 116: 1 --> 23

Char. 150: 1 --> 0

Char. 214: 0 --> 1

Bellulornis_rectusunguis :

Char. 65: 1 --> 0

Char. 100: 0 --> 1

Char. 197: 1 --> 0

Char. 295: 1 --> 0

Schizoura_lii :

No autapomorphies

Zhongjianornis_yangi :

Char. 129: 1 --> 0

Char. 179: 0 --> 1

Char. 299: 1 --> 0

Apsaravis_ukhaana :

Char. 52: 0 --> 1

Char. 125: 0 --> 1

Char. 127: 0 --> 1

- Char. 171: 0 --> 1
 Char. 172: 0 --> 1
 Char. 194: 1 --> 2
 Char. 237: 0 --> 1
 Char. 238: 0 --> 1
Tianyuornis_cheni:
 Char. 100: 0 --> 1
Archaeornithura_meemannae:
 No autapomorphies
Parahongshanornis_chaoyangensis:
 Char. 110: 2 --> 0
Hongshanornis_longicresta:
 Char. 160: 1 --> 0
 Char. 271: 0 --> 1
Longicrusavis_houi:
 Char. 98: 2 --> 1
 Char. 103: 0 --> 1
 Char. 138: 1 --> 0
Piscivoravis_lui:
 Char. 65: 1 --> 2
 Char. 103: 1 --> 0
 Char. 305: 1 --> 0
 Char. 306: 1 --> 0
 Char. 341: 1 --> 0
 Char. 343: 0 --> 1
Yixianornis_grabau:
 Char. 5: 0 --> 1
 Char. 110: 0 --> 1
 Char. 118: 0 --> 1
 Char. 125: 0 --> 1
 Char. 191: 1 --> 0
 Char. 345: 0 --> 1
Yanornis_martini:
 Char. 65: 1 --> 0
 Char. 78: 0 --> 1
 Char. 191: 1 --> 0

Changzuiornis_ahgmi:

Char. 299: 1 --> 2

Iteravis_huchzermeyeri:

Char. 103: 1 --> 0

Gansus_zheni:

No autapomorphies

Gansus_yumenensis:

Char. 78: 0 --> 1

Char. 312: 0 --> 1

Enaliornis:

Char. 317: 1 --> 2

Pasquiaornis:

Char. 158: 0 --> 1

Char. 322: 0 --> 1

Char. 327: 1 --> 0

Chupkaornis:

No autapomorphies

Brodavis:

Char. 322: 0 --> 2

Baptornis:

Char. 327: 1 --> 0

Fumicollis:

No autapomorphies

Parahesperornis:

Char. 245: 1 --> 0

MM_V_2487:

No autapomorphies

Hesperornis_regalis:

No autapomorphies

Hesperornis_gracilis:

No autapomorphies

Ichthyornis_dispar:

Char. 58: 0 --> 2

Char. 59: 01 --> 2

Char. 65: 12 --> 0

Char. 86: 1 --> 2

Char. 125: 0 --> 1

Char. 126: 0 --> 1

Char. 162: 1 --> 0

Char. 183: 0 --> 1

Char. 189: 1 --> 2

Char. 207: 0 --> 1

Char. 286: 0 --> 1

Lithornis :

No autapomorphies

Eudromia_elegans :

Char. 157: 0 --> 1

Char. 174: 0 --> 1

Char. 189: 1 --> 0

Char. 198: 1 --> 0

Char. 201: 0 --> 1

Char. 232: 1 --> 2

Char. 242: 0 --> 1

Char. 278: 0 --> 1

Vegavis_iaai :

Char. 75: 0 --> 1

Char. 84: 0 --> 1

Char. 125: 0 --> 1

Char. 131: 0 --> 1

Char. 137: 1 --> 0

Char. 194: 2 --> 1

Char. 200: 1 --> 0

Char. 217: 1 --> 0

Char. 254: 0 --> 2

Char. 268: 0 --> 1

Chauna_torquata :

Char. 107: 1 --> 0

Char. 118: 0 --> 1

Char. 144: 2 --> 1

Char. 149: 1 --> 2

Char. 223: 1 --> 0

Anas_platyrrhynchos :

Char. 134: 1 --> 0
 Char. 139: 1 --> 0
Gallus_gallus:
 No autapomorphies
Phasianus_colchicus:
 No autapomorphies
 Node 48 : Enantiornithes
 Char. 116: 0 --> 2
 Char. 179: 0 --> 1
 Char. 201: 0 --> 1
 Char. 325: 0 --> 1
 Char. 343: 0 --> 1
 Node 49 :
 No synapomorphies
 Node 50 :
 Char. 315: 2 --> 0
 Node 51 :
 Char. 299: 1 --> 0
 Char. 312: 0 --> 1
 Node 52 : Ornithuromorpha
 Char. 2: 0 --> 1
 Char. 6: 0 --> 1
 Char. 20: 0 --> 1
 Char. 48: 0 --> 1
 Char. 138: 0 --> 1
 Char. 150: 0 --> 1
 Char. 152: 0 --> 1
 Char. 153: 0 --> 1
 Char. 182: 0 --> 1
 Char. 191: 0 --> 1
 Char. 205: 0 --> 1
 Char. 213: 0 --> 1
 Char. 272: 1 --> 2
 Char. 296: 0 --> 1
 Char. 301: 1 --> 2
 Char. 311: 0 --> 1

Char. 327: 0 --> 1
Char. 328: 0 --> 1
Char. 342: 0 --> 1
Node 53 :
Char. 179: 0 --> 1
Char. 194: 0 --> 1
Char. 195: 1 --> 2
Node 54 :
Char. 4: 1 --> 2
Char. 62: 0 --> 1
Char. 102: 0 --> 1
Char. 129: 0 --> 1
Char. 149: 1 --> 2
Char. 198: 0 --> 1
Char. 211: 1 --> 2
Char. 273: 1 --> 2
Char. 345: 1 --> 0
Node 55 :
Char. 50: 0 --> 1
Char. 178: 0 --> 1
Node 56 :
Char. 71: 0 --> 1
Char. 304: 0 --> 1
Char. 305: 0 --> 1
Char. 306: 0 --> 1
Char. 346: 0 --> 1
Node 57 :
Char. 159: 1 --> 2
Node 58 :
Char. 116: 0 --> 1
Char. 162: 1 --> 0
Char. 341: 1 --> 0
Node 59 :
Char. 209: 1 --> 0
Char. 211: 0 --> 1
Node 60 :

- Char. 103: 1 --> 0
- Char. 110: 0 --> 2
- Node 61 : Hongshanornithidae
 - Char. 54: 0 --> 1
 - Char. 98: 1 --> 2
 - Char. 114: 0 --> 1
 - Char. 116: 0 --> 1
 - Char. 211: 2 --> 0
 - Char. 215: 2 --> 1
- Node 62 :
 - Char. 6: 1 --> 0
 - Char. 48: 1 --> 0
 - Char. 136: 0 --> 1
 - Char. 149: 2 --> 1
 - Char. 173: 0 --> 1
 - Char. 314: 0 --> 1
- Node 63 :
 - Char. 115: 1 --> 0
 - Char. 194: 1 --> 0
 - Char. 195: 2 --> 1
- Node 64 :
 - Char. 63: 1 --> 0
 - Char. 108: 1 --> 5
 - Char. 109: 0 --> 1
 - Char. 146: 0 --> 1
 - Char. 209: 1 --> 2
 - Char. 210: 0 --> 1
 - Char. 214: 0 --> 12
- Node 65 :
 - Char. 203: 0 --> 1
 - Char. 271: 0 --> 1
 - Char. 346: 1 --> 2
- Node 66 :
 - Char. 52: 0 --> 1
- Node 67 :
 - Char. 330: 0 --> 1

Char. 335: 0 --> 1

Node 68 :

Char. 188: 0 --> 1

Char. 199: 0 --> 1

Char. 202: 0 --> 1

Node 69 : Hesperornithiformes

Char. 69: 0 --> 1

Char. 248: 0 --> 1

Char. 249: 0 --> 1

Char. 251: 0 --> 1

Char. 252: 0 --> 1

Char. 257: 0 --> 1

Char. 265: 0 --> 1

Char. 266: 0 --> 1

Char. 267: 2 --> 1

Char. 268: 0 --> 1

Char. 298: 0 --> 1

Char. 317: 0 --> 1

Char. 319: 0 --> 1

Char. 324: 0 --> 1

Char. 333: 0 --> 1

Node 70 : Ornithurae

Char. 68: 2 --> 3

Char. 77: 4 --> 5

Char. 98: 1 --> 0

Char. 109: 1 --> 0

Char. 196: 0 --> 1

Char. 234: 0 --> 1

Char. 237: 0 --> 1

Char. 238: 0 --> 1

Char. 239: 0 --> 1

Char. 295: 0 --> 2

Char. 311: 1 --> 2

Node 71 :

Char. 242: 0 --> 1

Char. 247: 0 --> 1

Char. 310: 1 --> 0

Node 72 :

Char. 69: 1 --> 2

Char. 261: 0 --> 1

Node 73 :

Char. 73: 0 --> 1

Node 74 :

Char. 333: 1 --> 2

Node 75 :

Char. 255: 1 --> 2

Char. 262: 0 --> 1

Char. 265: 1 --> 2

Char. 317: 1 --> 2

Char. 328: 1 --> 2

Node 76 : Hesperornithidae

Char. 224: 0 --> 1

Char. 230: 1 --> 2

Char. 244: 1 --> 2

Char. 246: 1 --> 2

Char. 247: 1 --> 2

Char. 248: 1 --> 2

Char. 249: 1 --> 2

Char. 253: 0 --> 1

Char. 256: 0 --> 1

Char. 266: 1 --> 2

Char. 269: 0 --> 1

Char. 274: 1 --> 2

Char. 276: 0 --> 1

Char. 277: 0 --> 1

Char. 279: 0 --> 1

Char. 281: 0 --> 1

Char. 282: 1 --> 0

Char. 283: 0 --> 1

Char. 293: 1 --> 2

Char. 294: 0 --> 1

Char. 301: 3 --> 2

Char. 302: 0 --> 1
 Char. 307: 0 --> 1
 Char. 308: 0 --> 1
 Char. 316: 1 --> 2
 Char. 318: 0 --> 2
 Char. 319: 1 --> 2
 Char. 320: 0 --> 1
 Char. 321: 0 --> 1
 Char. 324: 1 --> 2
 Char. 334: 0 --> 1
 Char. 336: 0 --> 1
 Char. 337: 0 --> 1
 Char. 338: 0 --> 1
 Char. 339: 0 --> 1

Node 77 :

Char. 259: 0 --> 1
 Char. 267: 1 --> 0
 Char. 305: 1 --> 2

Node 78 : *Hesperornis*

Char. 257: 1 --> 0
 Char. 260: 0 --> 1
 Char. 270: 0 --> 1
 Char. 317: 2 --> 3

Node 79 :

Char. 50: 0 --> 1
 Char. 64: 0 --> 1
 Char. 74: 0 --> 1
 Char. 78: 0 --> 2
 Char. 97: 0 --> 1
 Char. 155: 1 --> 2
 Char. 177: 0 --> 1
 Char. 178: 0 --> 1
 Char. 194: 1 --> 2
 Char. 221: 0 --> 1
 Char. 233: 0 --> 1
 Char. 291: 1 --> 2

Char. 312: 0 --> 2

Node 80 :

Char. 19: 1 --> 0

Char. 39: 1 --> 0

Char. 52: 0 --> 1

Char. 56: 0 --> 1

Char. 265: 0 --> 1

Node 81 : Neornithes

Char. 6: 0 --> 1

Char. 37: 0 --> 1

Char. 47: 1 --> 0

Char. 48: 0 --> 1

Char. 69: 0 --> 2

Char. 73: 0 --> 2

Char. 76: 0 --> 1

Char. 104: 0 --> 1

Char. 158: 0 --> 1

Char. 164: 1 --> 2

Char. 165: 0 --> 1

Char. 184: 1 --> 0

Char. 220: 0 --> 1

Char. 229: 1 --> 2

Char. 280: 0 --> 2

Char. 287: 1 --> 2

Char. 294: 0 --> 2

Char. 310: 1 --> 2

Char. 326: 0 --> 1

Char. 330: 1 --> 0

Node 82 :

Char. 223: 1 --> 2

Char. 265: 0 --> 1

Char. 310: 2 --> 4

Node 83 :

Char. 1: 1 --> 2

Char. 9: 1 --> 0

Char. 12: 1 --> 0

Char. 57: 0 --> 1
 Char. 83: 0 --> 1
 Char. 189: 1 --> 2
 Char. 257: 0 --> 1
 Char. 275: 0 --> 1
 Char. 281: 0 --> 1
 Char. 346: 0 --> 1

Node 84 :

Char. 17: 0 --> 1
 Char. 35: 0 --> 1
 Char. 41: 1 --> 2
 Char. 42: 1 --> 2
 Char. 45: 0 --> 1
 Char. 98: 0 --> 1
 Char. 116: 0 --> 1
 Char. 139: 0 --> 1
 Char. 145: 0 --> 1
 Char. 217: 0 --> 1
 Char. 219: 0 --> 1
 Char. 228: 0 --> 1

Node 85 :

Char. 75: 0 --> 1
 Char. 96: 1 --> 0
 Char. 99: 1 --> 0
 Char. 112: 2 --> 1
 Char. 116: 1 --> 2
 Char. 123: 1 --> 0
 Char. 125: 0 --> 1
 Char. 131: 0 --> 1
 Char. 132: 0 --> 1
 Char. 157: 0 --> 1
 Char. 198: 1 --> 0
 Char. 201: 0 --> 1
 Char. 202: 1 --> 2
 Char. 232: 1 --> 2
 Char. 242: 0 --> 1

Char. 310: 2 --> 3

Char. 329: 0 --> 1

Appendix 2.1

List of Hesperornithiform Occurrence

Family	Genus	Species	Age	Region	Country	Env.	Formation	Member	References
Brodavidae	<i>Brodavis</i>	<i>americanus</i>	L. Maast.	North America	Saskatchewan	terrestrial	Frenchman Fm.	-	Martin <i>et al.</i> 2012
	Hesperornithiformes	indet.	L. Maast.	North America	Saskatchewan	terrestrial	Frenchman Fm.	-	Tokaryk <i>et al.</i> 1997
Brodavidae	<i>Brodavis</i>	<i>baileyi</i>	L. Maast.	North America	South Dakota	transitional	Hell Creek Fm.	-	Martin <i>et al.</i> 2012; Johnson <i>et al.</i> 2002
	Hesperornithiformes	indet.	L. Maast.	North America	North Dakota	transitional	Hell Creek Fm.	-	Pierson <i>et al.</i> 2002; Johnson <i>et al.</i> 2002
Hesperornithidae	<i>Hesperornis</i>	sp.	L. Maast.	North America	Montana	transitional	Hell Creek Fm.	-	Hutchinson 2001
	<i>cf. Fumicollis</i>		L. Maast.	North America	Montana	transitional	Hell Creek Fm.	-	Simons & Evans 2017
	<i>Potamornis</i>	<i>skutchi</i>	L. Maast.	North America	Wyoming	transitional	Lance Fm.	-	Elzanowski <i>et al.</i> 2001
Hesperornithidae	<i>Canadaga</i>	<i>arctica</i>	M. Maast.	North America	Northwest Territories	marine	-	-	Hou 1999
Hesperornithidae	<i>Asiahesperornis</i>	<i>bazhanovi</i>	Maast.	Europe	Kazakhstan	marine	-	-	Nesov & Prizemlin 1991
Baptornithidae	<i>Judinornis</i>	<i>nogontsavensis</i>	E. Maast.	Asia	Mongolia	terrestrial	Nemegt Fm.	-	Nesov & Borkin 1983
Brodavidae	<i>Brodavis</i>	<i>mongoliensis</i>	E. Maast.	Asia	Mongolia	terrestrial	Nemegt Fm.	-	Martin <i>et al.</i> 2012
	<i>cf. Parahesperornis</i>		E. Maast.	Asia	Mongolia	terrestrial	Nemegt Fm.	-	Kurochkin 2000
	Hesperornithiformes	Indet.	E. Maast.	Asia	Mongolia	terrestrial	Nemegt Fm.	-	This study (Chapter 2)

Family	Genus	Species	Age	Region	Country	Env.	Formation	Member	References
	Hesperornithiformes	indet.	E. Maast.	Asia	Japan	marine	Kita-ama Fm.	-	This study (Chapter 2)
Hesperornithidae	<i>Asiahesperornis</i>	sp.	L. Cam.	Europe	Russia	marine	-	-	Zelenkov <i>et al.</i> 2017
Hesperornithidae	<i>Hesperornis</i>	sp.	L. Cam.	North America	Arkansas	marine	Marlbook Marl Fm.	-	Bell <i>et al.</i> 2015
Baptornithidae	<i>Baptornis</i>	sp.	L. Cam.	North America	Saskatchewan	transitional	Dinosaur Park Fm.	-	Tokaryk & Harington 1992; Gilbert <i>et al.</i> 2018
	Hesperornithiformes	indet.	L. Cam.	North America	Saskatchewan	transitional	Dinosaur Park Fm.	-	Gilbert <i>et al.</i> 2018
Hesperornithidae	<i>Hesperornis</i>	sp.	Cam.	North America	Alaska	marine	Igneok Fm.	-	Bryant 1984
Hesperornithidae	<i>Canadaga</i>	<i>arctica</i>	Cam.	North America	Nunavut	marine	Kanguk Fm.	-	Wilson <i>et al.</i> 2011
Hesperornithidae	<i>Hesperornis</i>	sp.	Cam.	North America	Nunavut	marine	Kanguk Fm.	-	Wilson & Chin 2014
Hesperornithidae	<i>Hesperornis</i>	sp.	M. Cam.	North America	Nunavut	marine	Kanguk Fm.	-	Hills <i>et al.</i> 1999
Hesperornithidae	<i>Hesperornis</i>	sp.	M. Cam.	North America	Arkansas	marine	Ozan Fm.	-	Bell <i>et al.</i> 2015
Hesperornithidae	<i>Hesperornis</i>	<i>lumgairi</i>	M. Cam.	North America	Alberta	transitional	Foremost Fm.	-	Fox 1974; Aotsuka & Sato 2016
Hesperornithidae	<i>Hesperornis</i>	<i>macdonaldi</i>	M. Cam.	North America	Manitoba	marine	Pierre Shale	Millwood Mb.	Aotsuka & Sato 2016

Family	Genus	Species	Age	Region	Country	Env.	Formation	Member	References
Hesperornithidae	<i>Hesperornis</i>	cf. <i>rossicus</i>	M. Cam.	North America	Manitoba	marine	Pierre Shale	Millwood Mb.	Aotsuka & Sato 2016
Hesperornithidae	<i>Hesperornis</i>	<i>chowii</i>	M. Cam.	North America	Manitoba	marine	Pierre Shale	Millwood Mb.	Aotsuka & Sato 2016
Hesperornithidae	<i>Hesperornis</i>	sp.	M. Cam.	North America	Wyoming	transitional	Mesaverde Fm.	-	Bell <i>et al.</i> 2019
Hesperornithidae	<i>Hesperornis</i>	<i>altus</i>	E. Cam.	North America	Montana	marine	Claggett Fm.	-	Marsh 1893; Shufeldt 1915
Hesperornithidae	<i>Hesperornis</i>	<i>regalis</i>	E. Cam.	North America	Northwest Territories	marine	Smoky Hills Fm.	-	Russell 1967
Hesperornithidae	<i>Hesperornis</i>	<i>regalis</i>	E. Cam.	North America	Manitoba	marine	Vermillion River Fm.	Pembina Mb.	Bardack 1968
Brodavidae	<i>Brodavis</i>	sp.	E. Cam.	North America	Manitoba	marine	Pierre Shale	Pembina Mb.	Aotsuka & Sato 2016
Hesperornithidae	<i>Hesperornis</i>	<i>lumbairi</i>	E. Cam.	North America	Manitoba	marine	Pierre Shale	Pembina Mb.	Aotsuka & Sato 2016
Hesperornithidae	<i>Hesperornis</i>	<i>mengeli</i>	E. Cam.	North America	Manitoba	marine	Pierre Shale	Pembina Mb.	Aotsuka & Sato 2016
Hesperornithidae	<i>Hesperornis</i>	<i>chowii</i>	E. Cam.	North America	Manitoba	marine	Pierre Shale	Pembina Mb.	Aotsuka & Sato 2016
Hesperornithidae	<i>Hesperornis</i>	<i>regalis</i>	E. Cam.	North America	Manitoba	marine	Pierre Shale	Pembina Mb.	Aotsuka & Sato 2016

Family	Genus	Species	Age	Region	Country	Env.	Formation	Member	References
Hesperornithidae	<i>Hesperornis</i>	<i>macdonaldi</i>	E. Cam.	North America	Manitoba	marine	Pierre Shale	Pembina Mb.	Aotsuka & Sato 2016
Hesperornithidae	<i>Hesperornis</i>	<i>regalis</i>	E. Cam.	North America	Manitoba	marine	Pierre Shale	Gammon Ferruginous Mb.	Aotsuka & Sato 2016
Hesperornithidae	<i>Hesperornis</i>	<i>macdonaldi</i>	E. Cam.	North America	Manitoba	marine	Pierre Shale	Gammon Ferruginous Mb.	Aotsuka & Sato 2016
Hesperornithidae	<i>Hesperornis</i>	<i>regalis</i>	E. Cam.	North America	South Dakota	marine	Pierre Shale	Sharon Springs Mb.	Martin & Lim 2002
Hesperornithidae	<i>Hesperornis</i>	<i>macdonaldi</i>	E. Cam.	North America	South Dakota	marine	Pierre Shale	Sharon Springs Mb.	Martin & Lim 2002
Hesperornithidae	<i>Hesperornis</i>	<i>bairdi</i>	E. Cam.	North America	South Dakota	marine	Pierre Shale	Sharon Springs Mb.	Martin & Lim 2002
Hesperornithidae	<i>Hesperornis</i>	<i>chowi</i>	E. Cam.	North America	South Dakota	marine	Pierre Shale	Sharon Springs Mb.	Martin & Lim 2002
Brodavidae	<i>Brodavis</i>	<i>varneri</i>	E. Cam.	North America	South Dakota	marine	Pierre Shale	Sharoin Springs Mb.	Maritn & Cordes- Person 2007; Martin <i>et al.</i> 2012
Hesperornithidae	<i>Hesperornis</i>	sp.	E. Cam.	North America	Montana	marine	Claggett Fm.	-	Schufeldt 1915
Hesperornithidae	<i>Hesperornis</i>	<i>rossicus</i>	E. Cam.	Europe	Russia	marine	Rybushka Fm.	-	Panteleyev <i>et al.</i> 2004
Hesperornithidae	<i>Hesperornis</i>	sp.	E. Cam.	Europe	Russia	marine	Rybushka Fm.	-	Zelenkov <i>et al.</i> 2017
Hesperornithidae	<i>Hesperornis</i>	<i>rossicus</i>	E. Cam.	Europe	Sweden	marine	-	-	Rees & Lingden 2005
Hesperornithidae	<i>Hesperornis</i>	sp.	E. Cam.	Europe	Sweden	marine	-	-	Rees & Lingden 2005

Family	Genus	Species	Age	Region	Country	Env.	Formation	Member	References
Baptornithidae	<i>Baptornis</i>	sp.	E. Cam.	Europe	Sweden	marine	-	-	Rees & Lingden 2005
Hesperornithidae	<i>Hesperornis</i>	<i>crassipes</i>	L. San. - E. Cam.	North America	Kansas	marine	Niobrara Fm.	Smoky Hill Mb.	Marsh 1876
Hesperornithidae	<i>Hesperornis</i>	<i>gracilis</i>	L. San. - E. Cam.	North America	Kansas	marine	Niobrara Fm.	Smoky Hill Mb.	Marsh 1876
Hesperornithidae	<i>Hesperornis</i>	<i>regalis</i>	L. San. - E. Cam.	North America	Kansas	marine	Niobrara Fm.	Smoky Hill Mb.	Marsh 1872
Hesperornithidae	<i>Parahesperornis</i>	<i>alexi</i>	L. San. - E. Cam.	North America	Kansas	marine	Niobrara Fm.	Smoky Hill Mb.	Martin <i>et al.</i> 1984
Hesperornithidae	<i>Parahesperornis</i>	sp.	L. San. - E. Cam.	North America	Kansas	marine	Niobrara Fm.	Smoky Hill Mb.	Bell & Everhart 2009
	<i>Fumicollis</i>	<i>hoffmani</i>	L. San. - E. Cam.	North America	Kansas	marine	Niobrara Fm.	Smoky Hill Mb.	Martin & Tate 1976; Bell & Chiappe 2015
Baptornithidae	<i>Baptornis</i>	<i>adventus</i>	L. San. - E. Cam.	North America	Kansas	marine	Niobrara Fm.	Smoky Hill Mb.	Marsh 1874
	<i>Chupkaornis</i>	<i>keraorum</i>	Con.-San.	Asia	Japan	marine	Kashima Fm.	-	Tanaka <i>et al.</i> 2017
	<i>Pasquiaornis</i>	<i>hardiei</i>	M. Cen.	North America	Saskatchewan	marine	Ashville Fm.	Belle Fourche Mb.	Tokaryk <i>et al.</i> 1997
	<i>Pasquiaornis</i>	<i>tankei</i>	M. Cen.	North America	Saskatchewan	marine	Ashville Fm.	Belle Fourche Mb.	Tokaryk <i>et al.</i> 1997

Family	Genus	Species	Age	Region	Country	Env.	Formation	Member	References
Baptornithidae	Baptornithidae	<i>indet.</i>	Cen.	North America	Kansas	marine	Greenhorn Fm.	-	Everhart & Bell 2009
Enaliornithidae	<i>Enaliornis</i>	<i>barretti</i>	L. Alb.	Europe	England	marine	West Melbury Chalk Fm.	Cambridge Greensand Mb.	Galton & Martin 2002
Enaliornithidae	<i>Enaliornis</i>	<i>sedgwicki</i>	L. Alb.	Europe	England	marine	West Melbury Chalk Fm.	Cambridge Greensand Mb.	Galton & Martin 2002
Enaliornithidae	<i>Enaliornis</i>	<i>seeley</i>	L. Alb.	Europe	England	marine	West Melbury Chalk Fm.	Cambridge Greensand Mb.	Galton & Martin 2002

Appendix 3.1

Data for Phylogenetic Logistic Regression Analysis

Taxon Name	Specimen ID	Coracoid	Humerus	Femur			Tarsometatarsus		
		strat-like (0); trapezoidal (1)	robust (0); stick-like (1)	L (mm)	DisW (mm)	Ratio L/DisW	MTIII (mm)	MTIV (mm)	Ratio IV/III
<i>Archaeorhynchus spatula</i>	IVPP V20312	0	0	32.71	5.69	0.174	2.5	1.82	0.728
<i>Patagopteryx deferrariis</i>	MACN-N-11	0	0	98.15	19.35	0.197	6.92	4.08	0.590
<i>Bellulornis rectusunguis</i>	IVPP 17970	0	0	54.66	5.29	0.097	3	3.27	1.090
<i>Schizoura lii</i>	IVPP V16861	0	0	48.93	7.47	0.153	2.56	1.26	0.492
<i>Zhongjianornis yangi</i>	IVPP V15900	0	0	46.06	8.26	0.179	3.1	2.82	0.910
<i>Apsaravis ukhaana</i>	IGM 100/1017	0	0	37.83	4.03	0.107	2.25	1.76	0.782
<i>Hongshanornis longicresta</i>	IVPP V14533	0	0	21.56	3.26	0.151	1.52	1.07	0.704
<i>Longicrusavis houi</i>	PKUP V1069	0	0	24.45	3.6	0.147	1.37	1.3	0.949
<i>Piscivoravis lii</i>	IVPP V17078	0	0	57.08	8.33	0.146	3.76	3.14	0.835
<i>Yixianornis grabaui</i>	IVPP V12631	0	0	41.05	4.23	0.103	2.01	1.62	0.806
<i>Yanornis martini</i>	IVPP V12558	0	0	57.2	8.78	0.153	3.78	2.42	0.640
<i>Iteravis huchzermeyeri</i>	IVPP V18958	0	0	34	5.84	0.172	1.95	1.57	0.805
<i>Gansus zheni</i>	BMNHC-Ph 1342	0	0	37.84	6.8	0.180	2.48	2	0.806
<i>Gansus yumenensis</i>	CAGS 04-CM-003	0	0	34.56	7.53	0.218	-	-	-
<i>Gansus yumenensis</i>	CAGS 04-CM-031	-	-	-	-	-	2.18	2.11	0.968
<i>Pasquiaornis tankei</i>	RSM P2988.9	0	-	-	-	-	-	-	-
<i>Pasquiaornis tankei</i>	RSM P2955.1	-	0	-	-	-	-	-	-

Taxon Name	Specimen ID	Coracoid	Humerus	Femur			Tarsometatarsus		
		strat-like (0); trapezoidal (1)	robust (0); stick-like (1)	L (mm)	DisW (mm)	Ratio L/DisW	MTIII (mm)	MTIV (mm)	Ratio IV/III
<i>Pasquiaornis tankei</i>	RSM P2957.27	-	-	-	-	-	5.52	5.33	0.966
<i>Baptornis advenus</i>	KUVP 2290	0	1	74.11	25.74	0.347	6.32	6.33	1.002
<i>Paraesperornis alexi</i>	KUVP 2287	1	1	73.14	30.19	0.413	4.93	8.87	1.799
<i>Hesperornis regalis</i>	YPM 1200	-	-	98.66	53.79	0.545	7.62	14.52	1.906
<i>Hesperornis regalis</i>	FHSM VP-2069	1	1	-	-	-	-	-	-
<i>Hesperornis crassipes</i>	YPM 1679	1	1	83.93	46.93	0.559	6.72	12.86	1.914
<i>Ichthyornis dispar</i>	YPM 1450	0	0	24.65	5.77	0.234	2.51	1.91	0.761

Appendix 3.2

Geological Age for Phylogenetic Logistic Regression Analysis

Taxa	Age (Ma)
<i>Archaeorhynchus_spatula</i>	117.8
<i>Patagopteryx_deferrariisi</i>	77.85
<i>Bellulia_rectusunguis</i>	115.45
<i>Schizoooura_lii</i>	115.45
<i>Zhongjianornis_yangi</i>	115.45
<i>Apsaravis_ukhaana</i>	77.85
<i>Hongshanornis_longicresta</i>	122.65
<i>Longicrusavis_houi</i>	122.65
<i>Piscivoravis_lii</i>	115.45
<i>Yixianornis_grabau</i>	122.65
<i>Yanornis_martini</i>	115.45
<i>Iteravis_huchzermeyeri</i>	115.45
<i>Gansus_zheni</i>	115.45
<i>Gansus_yumenensis</i>	116.65
<i>Pasquiaornis tankei</i>	95.55
<i>Baptornis_advenus</i>	82.4
<i>Parahesperornis_alexi</i>	82.4
<i>Hesperornis_regalis</i>	82.4
<i>Hesperornis_crassipes</i>	82.4
<i>Ichthyornis_dispar</i>	82.4

Appendix 4.1

Measurement of Extant Foot-Propelled Diving Bird

Institution	ID	Genus	Species	Sex	Body Mass	Lf	Cf	Ltbt	Ctbt	Ltmt	PWtmt	PStmt	MWtmt	MStmt
FMNH	384663	<i>Tachybaptus</i>	<i>pelzelinii</i>	m	197	28.65	9	62.85	8.64	35.06	6.45	3.13	2.04	2.44
ROM	104352	<i>Tachybaptus</i>	<i>dominicus</i>	m	150	27.37	9.41	60.79	8.25	33.23	6.04	2.99	2.37	2.43
ROM	127526	<i>Tachybaptus</i>	<i>rufopercus</i>	f	395	33.04	10.87	-	-	-	-	-	-	-
FMNH	317234	<i>Podiceps</i>	<i>nigricolis</i>	m	182	33.5	12.17	84.32	8.68	45.53	7.61	4.84	2.05	3.49
FMNH	339458	<i>Podiceps</i>	<i>nigricolis</i>	m	208	33.83	12.13	83.42	9.06	44.39	7.62	-	2.27	3.27
FMNH	317235	<i>Podiceps</i>	<i>nigricolis</i>	f	168	30.81	11.02	75.66	8.65	40.84	6.99	4.51	1.95	3.07
FMNH	339459	<i>Podiceps</i>	<i>nigricolis</i>	f	192	31.02	11.66	74.24	9.28	39.47	7.41	4.49	2.15	3.35
FMNH	339460	<i>Podiceps</i>	<i>nigricolis</i>	f	180	33.13	11.59	79.76	9.16	43.62	7.35	3.79	1.98	3.13
FMNH	339461	<i>Podiceps</i>	<i>nigricolis</i>	f	175	32.31	11.5	78.2	8.56	41.29	6.76	3.89	1.98	3.04
ROM	110796	<i>Podiceps</i>	<i>caspicus</i>	m	410	32.79	12.39	81.46	8.86	42.92	7.62	4.1	2.22	3.05
ROM	110795	<i>Podiceps</i>	<i>caspicus</i>	m	300.5	32.18	11.17	78.54	9.74	42.53	8.06	4.27	2.54	3.45
ROM	110794	<i>Podiceps</i>	<i>caspicus</i>	f	349.1	31.76	12.76	77.11	9.05	41.01	7.88	4.54	2.34	3.3
FMNH	390692	<i>Podiceps</i>	<i>grisgena</i>	m	893	47.43	18.84	126.35	14.66	62.88	11.82	-	-	-
ROM	158471	<i>Podiceps</i>	<i>grisgena</i>	m	1130	47.61	19.83	132.16	15.84	67.57	12.18	6.42	3.76	5.34
ROM	126631	<i>Podiceps</i>	<i>grisgena</i>	m	1135.9	47.53	20.01	-	-	64.42	12.64	6.14	3.7	5.37
ROM	110067	<i>Podiceps</i>	<i>grisgena</i>	m	1050	49.85	18.55	137.39	15.29	69.38	12.66	6.86	3.97	5.56
ROM	112468	<i>Podiceps</i>	<i>grisgena</i>	f	732.2	44.31	16.67	125.03	13.62	63.15	11.9	6.24	4.46	3.46
ROM	112517	<i>Podiceps</i>	<i>grisgena</i>	f	690.8	43.45	15.98	114.6	13.74	59.56	10.9	5.43	3.84	4.4
ROM	156764	<i>Podiceps</i>	<i>cristatus</i>	m	790	44.61	18.77	125.36	14.99	69.48	12.11	5.9	3.73	4.89
ROM	127526	<i>Podiceps</i>	<i>rufopercus</i>	f	395	33.15	10.48	-	-	-	-	-	-	-
FMNH	330853	<i>Podilymbus</i>	<i>podiceps</i>	m	340	40.34	11.36	-	-	42.05	8.32	4.3	3.38	4.62
FMNH	347602	<i>Podilymbus</i>	<i>podiceps</i>	m	440	40.99	12.58	90.6	10.84	42.77	8.28	4.36	3.78	4.11
FMNH	438317	<i>Podilymbus</i>	<i>podiceps</i>	m	421.6	39.91	12.07	81.19	10.47	39.43	7.97	3.99	3.65	4.2
FMNH	496457	<i>Podilymbus</i>	<i>podiceps</i>	m	476.5	40.93	14.43	85.87	11.28	42.39	9.12	4.39	3.85	3.88

Institution	ID	Genus	Species	Sex	Body Mass	Lf	Cf	Ltbt	Ctbt	Ltmt	PWtmt	PStmt	MWtmt	MStmt
FMNH	496458	<i>Podylimbus</i>	<i>podiceps</i>	m	358.3	41.11	12.73	83.04	11.43	42.07	8.64	4.17	3.35	3.46
FMNH	429099	<i>Podylimbus</i>	<i>podiceps</i>	f	237.4	35.45	11.76	75.35	9.85	36.44	7	4.51	2.89	3.4
FMNH	451974	<i>Podylimbus</i>	<i>podiceps</i>	f	254.2	35.62	11.02	73.77	9.66	36.69	7.37	4.05	3.25	3.11
FMNH	465104	<i>Podylimbus</i>	<i>podiceps</i>	f	274.3	35.26	10.95	73.72	10.61	37.04	7.81	4.38	3.13	3.77
FMNH	475142	<i>Podylimbus</i>	<i>podiceps</i>	f	216.6	33.23	13.16	85.36	10.05	44.12	8.64	4.22	2.42	3.77
FMNH	445087	<i>Aechmophorus</i>	<i>occidentalis</i>	f	904	44.23	18.38	-	-	-	-	-	-	-
ROM	79701	<i>Gavia</i>	<i>adamsii</i>	m	4989.516	61.28	27.86	196.44	25.73	-	-	-	-	-
ROM	128672	<i>Gavia</i>	<i>adamsii</i>	m	5627	63.51	27.56	211.28	27.36	96.83	17.6	12.9	5.77	9.05
ROM	128674	<i>Gavia</i>	<i>adamsii</i>	f	4217	59.55	26.36	189.97	24.92	89.26	15.92	11.84	5.14	8.53
ROM	126596	<i>Gavia</i>	<i>arctica</i>	m	2342.5	44.2	22.32	157.58	21.13	72.9	12.82	9.36	3.73	6.14
ROM	124805	<i>Gavia</i>	<i>arctica</i>	m	2157.4	43.8	20.19	159.52	21.08	76.47	12.25	9.15	6.54	4.18
ROM	138103	<i>Gavia</i>	<i>arctica</i>	f	1820	40.83	19.41	146.09	18.62	-	11.42	8.61	3.89	5.87
ROM	128675	<i>Gavia</i>	<i>arctica</i>	f	2722	45.76	21.91	159.28	19.59	73.19	13.37	9.2	4.1	6.24
ROM	126680	<i>Gavia</i>	<i>arctica</i>	f	2000	42.37	21.15	156.74	21.89	71.2	12.47	8.91	4.15	6.36
ROM	33786	<i>Gavia</i>	<i>immer</i>	m	5035	62.46	30.1	212.64	28.8	97.47	16.89	12.46	5.19	8.49
ROM	68708	<i>Gavia</i>	<i>immer</i>	m	5500	62.28	27.18	198.14	28.16	95.43	16.84	12.2	5.51	7.83
ROM	149259	<i>Gavia</i>	<i>immer</i>	m	4354.4832	53.72	27.39	192.66	27.33	92.37	15.74	12.45	5.31	8.02
ROM	67140	<i>Gavia</i>	<i>immer</i>	f	3470	56.52	26.49	192.6	25.24	91.74	15.85	10.8	5.3	7.66
ROM	126626	<i>Gavia</i>	<i>immer</i>	f	3175.144	51.22	24.16	175.58	23.83	85.3	14.71	11.11	4.83	6.72
ROM	102162	<i>Gavia</i>	<i>immer</i>	f	4082.328	55.46	26.41	194.7	24.04	90.17	15.84	11.19	5.47	7.11
ROM	158234	<i>Gavia</i>	<i>stellata</i>	m	2049.8	37.72	22.76	161.24	22.11	71.68	12.47	8.42	3.66	6.19
ROM	158310	<i>Gavia</i>	<i>stellata</i>	m	2271.4	40.83	24.02	174.67	23.65	79	13.19	8.71	4.14	6.9
ROM	158311	<i>Gavia</i>	<i>stellata</i>	m	2200	40.32	24.25	166.98	24.32	75.66	13.38	8.62	3.72	6.64
ROM	72244	<i>Gavia</i>	<i>stellata</i>	f	1857.3	39.68	21.72	157.65	20.87	73	11.69	8.06	3.44	6.34
ROM	115485	<i>Gavia</i>	<i>stellata</i>	f	2153.2	38.82	20.58	157.97	20.18	72.35	11.67	8.73	3.59	6.5

Institution	ID	Genus	Species	Sex	Body Mass	Lf	Cf	Ltbt	Ctbt	Lmt	PWmt	PStmt	MWmt	MStmt
ROM	122474	<i>Gavia</i>	<i>stellata</i>	f	1465	37.17	20.75	150.92	19.86	64.84	11.97	8.73	3.42	5.88
FMNH	348373	<i>Phalacrocorax</i>	<i>auritus</i>	f	2120	59.68	24.86	108.45	20.86	63.63	14.46	9.47	6.63	5.47
FMNH	348374	<i>Phalacrocorax</i>	<i>auritus</i>	f	1830	54.7	21.89	102.46	11.57	61.27	13.02	9.77	5.76	4.88
FMNH	443542	<i>Phalacrocorax</i>	<i>auritus</i>	f	2164	64.29	24.21	115.32	20.76	68.23	14.41	9.03	6.53	5.34
FMNH	498239	<i>Phalacrocorax</i>	<i>auritus</i>	f	2078	55.12	22.19	105.85	19.04	61.28	12.76	9.19	6.03	5.67
FMNH	375481	<i>Phalacrocorax</i>	<i>auritus</i>	m	1950	59.7	24.44	109.92	19.24	64.82	13.5	9.16	5.99	5.32
FMNH	375489	<i>Phalacrocorax</i>	<i>auritus</i>	m	2030	60.8	23.89	112.51	19.46	65.39	13.35	8.92	6.25	5.21
FMNH	454733	<i>Phalacrocorax</i>	<i>auritus</i>	m	2154	61.65	23.13	114.43	21.28	65.45	14.17	10.14	6.35	6.14
FMNH	368736	<i>Phalacrocorax</i>	<i>carbo</i>	m	2136	60.46	24.83	111.77	22	64.91	14.83	9.74	6.95	6.88
FMNH	368737	<i>Phalacrocorax</i>	<i>carbo</i>	f	1617	52.53	21.44	101.54	18.49	57.73	13.25	8.38	6.3	5.4
FMNH	368738	<i>Phalacrocorax</i>	<i>carbo</i>	f	1819	55.23	23.06	103.81	19.66	58.98	12.93	9.03	5.8	5.43
FMNH	368739	<i>Phalacrocorax</i>	<i>carbo</i>	f	1582	54.07	22.04	100.33	18.71	56.91	12.45	8.63	5.52	5.35
FMNH	368744	<i>Phalacrocorax</i>	<i>africanus</i>	m	564.4	41.2	14.87	68.03	11.62	38.32	7.87	5.56	4.25	4.13
FMNH	368742	<i>Phalacrocorax</i>	<i>africanus</i>	m	548	39.3	14.41	68.68	12.58	37.99	7.7	5.54	4.31	3.79
FMNH	368743	<i>Phalacrocorax</i>	<i>africanus</i>	m	526.1	39.78	14.32	67.75	12.12	37.67	7.99	5.31	4.18	3.64
FMNH	369222	<i>Phalacrocorax</i>	<i>africanus</i>	m	575.6	36.09	14.15	-	-	-	-	-	-	-
FMNH	368740	<i>Phalacrocorax</i>	<i>africanus</i>	f	484.2	37.87	15.26	64.38	14.5	36.43	7.95	5.19	4.38	3.82
FMNH	368749	<i>Phalacrocorax</i>	<i>africanus</i>	f	352.5	35.29	13.29	60.56	11.15	36.28	7.51	5.47	3.84	3.83
FMNH	368750	<i>Phalacrocorax</i>	<i>africanus</i>	f	390.3	35.17	12.99	61.13	12.08	35.4	7.4	5.18	3.81	3.78
FMNH	375472	<i>Phalacrocorax</i>	<i>olivaceus</i>	m	1187	49.03	17.71	88.35	16.06	52.98	11.34	8.75	5.15	4.35
ROM	104355	<i>Phalacrocorax</i>	<i>olivaceus</i>	m	1000	46.64	17.09	86.01	14.89	50.02	10.66	7.3	4.98	3.79
ROM	138101	<i>Phalacrocorax</i>	<i>pelagicus</i>	m	1460	51.01	18.71	93.85	16.73	49.25	11.72	7.73	5.29	4.01
ROM	138102	<i>Phalacrocorax</i>	<i>penicillatus</i>	m	2360	60.92	27.01	126.78	21.25	64.9	15.11	10.98	6.54	5.96
ROM	157318	<i>Phalacrocorax</i>	<i>melanoleucos</i>	m	598	41.61	15.46	65.32	13.85	36.17	8.74	5.87	4.57	3.98

Institution	ID	Genus	Species	Sex	Body Mass	Lf	Cf	Ltbt	Ctbt	Ltmt	PWtmt	PStmt	MWtmt	MStmt
ROM	157317	<i>Phalacrocorax</i>	<i>melanoleucos</i>	f	520	41.29	14.22	67.16	12.5	37.17	8.15	6.02	4.74	3.71
ROM	105640	<i>Phalacrocorax</i>	<i>urile</i>	m	2277	64.21	25.19	-	-	-	-	-	-	-
ROM	160041	<i>Phalacrocorax</i>	<i>albiventer</i>	f	966.3	56.65	22.47	-	-	-	-	-	-	-
ROM	121169	<i>Anhinga</i>	<i>melanogaster</i>	m	1557	58.33	17.76	93.33	16.24	46.03	11.97	7.08	6.54	3.94
ROM	121170	<i>Anhinga</i>	<i>melanogaster</i>	m	1483	56.44	18.88	88.89	16.52	43.35	-	-	6.81	4.47
ROM	121174	<i>Anhinga</i>	<i>melanogaster</i>	m	1260.5	55.02	16.77	86.89	15.58	41.66	11.14	6.53	5.97	3.57
ROM	121172	<i>Anhinga</i>	<i>melanogaster</i>	m	1711	63.04	19.42	100.55	16.7	49.03	12.67	7.41	6.77	4.29
ROM	121171	<i>Anhinga</i>	<i>melanogaster</i>	f	1421	58.02	17.26	92.68	16.51	45.1	11.42	6.89	5.27	4.07
ROM	121175	<i>Anhinga</i>	<i>melanogaster</i>	f	1354.2	55.51	17.36	88.6	16.02	43.64	11.84	6.77	6.55	4
ROM	121187	<i>Anhinga</i>	<i>melanogaster</i>	f	1457	53.58	17.35	87.36	17.03	43.04	11.71	7.52	5.91	4.21

Appendix 4.2

Measurements of Fossil Foot-Propelled Diving Bird

Taxon name	specimen ID	Lf	Cf
<i>Enaliornis_barretti</i>	NHMUK A479	-	20.82
<i>Pasquiaornis_hardiei</i>	RSM P2077.60	46.83	23.87
<i>Pasquiaornis_tankei</i>	RSM P2077.108	64.81	34.76
<i>Baptornis_advenus</i>	KUVP 2290	74.11	38.07
<i>Fumicollis_hoffmani</i>	UNSM 20030	71.67	34.52
<i>Paraesperornis_alexi</i>	KUVP 2287	73.14	43.24
<i>Hesperornis_regalis</i>	YPM 1200	99.49	69.67
<i>Hesperornis_gracilis</i>	YPM 1679	83.93	61.37
<i>Hesperornis_crassipes</i>	YPM 1474	95.9	66.52
<i>Hesperornis_macdonaldi</i>	LACM 9728	43.31	28.34

Taxon name	specimen ID	Ltbt	Ctbt
<i>Gansus_yumenensis</i>	CAGS 04-CM-002	67.60	-
<i>Pasquiaornis_hardiei</i>	RSM 2957.14	-	16.78
<i>Pasquiaornis_tankei</i>	RSM P.2997.45	-	26.28
<i>Brodavis_verneri</i>	SDSM 68430	233.26	47.85
<i>Baptornis_advenus</i>	AMNH 5101	-	32.00
<i>Fumicollis_hoffmani</i>	UNSM 20030	195.33	31.87
<i>Paraesperornis_alexi</i>	KUVP 2287	218.98	39.64
	MM V-2487	-	28.78
<i>Hesperornis_regalis</i>	YPM 1200	332.43	62.50
<i>Hesperornis_crassipes</i>	YPM 1474	-	60.93

Appendix 4.2 Measurement of Fossil Bird

Taxon name	specimen ID	Ltmt	PWtmt	PStmt	MWtmt	MStmt
<i>Gansus_yumenensis</i>	CAGS 04-CM-031	34.80	6.10	4.10	-	-
<i>Enaliornis_barretti</i>	CAMSM B55331	-	11.37	8.61	-	-
<i>Pasquiaornis_hardiei</i>	RSM P.2077.117	53.42	9.68	6.12	3.65	6.12
<i>Pasquiaornis_tankei</i>	RSM P2077.63	85.89	16.71	11.24	8.98	8.88
<i>Brodavis_verneri</i>	SDSM 68430	95.92	23.72	14.24	17.29	12.17
<i>Brodavis_mongoliensis</i>	PIN 4491-8	-	9.13	6.58	-	-
<i>Baptornis_advenus</i>	AMNH 5101	89.90	19.21	14.54	8.33	9.78
<i>Fumicollis_hoffmani</i>	UNSM 20030	85.12	18.77	10.40	10.44	10.11
<i>Parahesperornis_alexi</i>	KUVP 2287	99.71	21.20	15.13	11.85	13.63
	MM V-2487	-	17.07	11.71	10.08	11.04
<i>Hesperornis_regalis</i>	YPM 1200	136.03	35.21	20.59	21.11	21.42
<i>Hesperornis_gracilis</i>	YPM 1473	-	29.73	18.55	16.67	15.76
<i>Hesperornis_rossicus</i>	SGU 3442 Ve01	-	38.36	22.35	26.72	21.01
<i>Hesperornis_bairdi</i>	YPM PU 17208A	103.03	22.92	15.52	15.64	16.47
<i>Hesperornis_chowi</i>	YPM PU 17208	137.25	31.70	21.48	21.01	18.66
<i>Hesperornis_mengeli</i>	CFDC B.78.01.08	85.68	16.18	10.53	14.01	8.49
<i>Hesperornis_lumgairi</i>	CFDC B.78.02.07	-	27.24	15.99	15.14	17.20

Appendix 4.3

Estimated Body Mass of Fossil Foot-propelled Diving Bird

Taxon Name	Specimen ID	Cf	Ctbt	Lf + Cf	Ltbt + Ctbt	Ltmt + PWtmt + PStmt	PWtmt + PStmt	MWtmt + MStmt
<i>Enaliornis_barretti</i>	NHMUK A479	1.62	-	-	-	-	-	-
<i>Enaliornis_barretti</i>	CAMSM B55331	-	-	-	-	-	1.51	-
<i>Pasquiaornis_hardiei</i>	RSM P2077.60	2.44	-	2.32	-	-	-	-
<i>Pasquiaornis_hardiei</i>	RSM 2957.14	-	1.26	-	-	-	-	-
<i>Pasquiaornis_hardiei</i>	RSM P.2077.117	-	-	-	-	0.69	0.72	1.50
<i>Pasquiaornis_tankei</i>	RSM P2077.108	7.56	-	7.51	-	-	-	-
<i>Pasquiaornis_tankei</i>	RSM P.2997.45	-	4.24	-	-	-	-	-
<i>Pasquiaornis_tankei</i>	RSM P2077.63	-	-	-	-	4.03	4.14	9.45
<i>Brodavis_verneri</i>	SDSM 68430	-	21.5	-	21.37	10.31	10.27	39.66
<i>Brodavis_mongoliensis</i>	PIN 4491-8	-	-	-	-	-	0.72	-
<i>Baptornis_advenus</i>	AMNH 5101	-	7.23	-	-	7.35	7.49	10.65
<i>Fumicollis_hoffmani</i>	UNSM 20030	7.41	7.15	7.74	7.30	4.45	4.49	14.85
<i>Parahesperornis_alexi</i>	KUVP 2287	8.61	12.91	14.39	13.03	9.13	9.30	32.61
	MM V-2487	-	5.42	-	-	-	4.54	17.22
<i>Hesperornis_regalis</i>	YPM 1200	59.87	44.34	60.76	45.09	33.34	33.02	167.63
<i>Hesperornis_gracilis</i>	YPM 1679	41.86	-	39.70	-	-	-	-
<i>Hesperornis_gracilis</i>	YPM 1473	-	-	-	-	-	21.60	66.08
<i>Hesperornis_crassipes</i>	YPM 1474	40.96	41.39	52.66	-	-	-	-
<i>Hesperornis_rossicus</i>	SGU 3442 Ve01	-	-	-	-	-	42.66	211.41
<i>Hesperornis_bairdi</i>	YPM PU 17208A	-	-	-	-	10.84	10.96	67.46
<i>Hesperornis_chowi</i>	YPM PU 17208	-	-	-	-	29.30	29.51	124.1
<i>Hesperornis_mengeli</i>	CFDC B.78.01.08	-	-	-	-	3.48	3.58	14.36
<i>Hesperornis_lumgairi</i>	CFDC B.78.02.07	-	-	-	-	-	15.18	71.33
<i>Hesperornis_macdonaldi</i>	LACM 9728	4.09	-	3.56	-	-	-	-

Taxon Name	Specimen ID	Cf	Ctbt	Lf+Cf	Ltbt+Ctbt	Ltmt+PWtmt+PStmt	PWtmt+PStmt	MWtmt+MStmt
<i>Asiahesperornis_bazhanovi</i>	IZASK 1/KM_97	-	-	-	-	-	33.58	-
<i>Gansus_yumenensis</i>	CAGS 04-CM-031	-	-	-	-	0.18	0.19	-

Appendix 5.1

Age for Morphological Rate and Disparity Analyses

Appendix. 5.1 Age for Morphological Rate and Disparity Analyses

Taxon Name	FAD	LAD
<i>Archaeopteryx lithographica</i>	152.1	145
<i>Protopteryx fengningensis</i>	132.9	129.4
<i>Pengornis houi</i>	120.3	110.6
<i>Archaeorhynchus spatula</i>	125	110.6
<i>Patagopteryx deferrariisi</i>	83.6	72.1
<i>Vorona berivotrensis</i>	72.1	66
<i>Jianchangornis microdonta</i>	120.3	110.6
<i>Dingavis longimaxilla</i>	125	120.3
<i>Bellulia rectusunguis</i>	120.3	110.6
<i>Schizoura lii</i>	120.3	110.6
<i>Zhongjianornis yangi</i>	120.3	110.6
<i>Apsaravis ukhaana</i>	83.6	72.1
<i>Tianyuornis cheni</i>	125	120.3
<i>Archaeornithura meemannae</i>	130.7	129
<i>Parahongshanornis chaoyangensis</i>	120.3	110.6
<i>Hongshanornis longicresta</i>	125	120.3
<i>Longicrusavis houi</i>	125	120.3
<i>Piscivoravis lii</i>	120.3	110.6
<i>Yixianornis grabaui</i>	125	120.3
<i>Yanornis martini</i>	120.3	110.6
<i>Changzuornis ahgmi</i>	120.3	110.6
<i>Iteravis huchzermeyeri</i>	120.3	110.6
<i>Gansus zheni</i>	120.3	110.6
<i>Gansus yumenensis</i>	120.3	113
<i>Enaliornis</i>	106.8	100.5
<i>Pasquiaornis</i>	97.2	93.9
<i>Chupkaornis keraorum</i>	88.1	85
<i>Baptornis advenus</i>	85	79.8
<i>Brodavis</i>	79.8	66
<i>Fumicollis hoffmani</i>	85	79.8
<i>Parahesperornis alexi</i>	85	79.8
MM V-2487	83.6	79.8
<i>Hesperornis regalis</i>	85	79.8
<i>Hesperornis gracilis</i>	85	79.8
<i>Ichthyornis dispar</i>	85	79.8

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