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The oldest Asian hesperornithiform from the Upper Cretaceous of Japan, and the phylogenetic reassessment of Hesperornithiformes

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Asian hesperornithiforms are extremely rare in contrast to the much more abundant record from North America. In Asia, these fossil birds are only known from fragmentary materials from Mongolia. Here we describe the skeletal remains of a new hesperornithiform *Chupkaornis keraorum* gen. et sp. nov. from the Upper Cretaceous Kashima Formation (Coniacian to Santonian) of the Yezo Group in Mikasa City, Hokkaido, Japan. This is the best-preserved hesperornithiform material from Asia and it is the first report of hesperornithiforms from the eastern margin of the Eurasian continent. *Chupkaornis* has a unique combination of characters: finger-like projected tibiofibular crest of femur, deep, emarginated lateral excavation with a sharply defined edge of the ventral margin of the thoracic vertebrae, and the heterocoelous articular surface of the thoracic vertebrae. Our new phylogenetic analysis revises the phylogenetic relationships of Hesperornithiformes. In contrast to previous studies, *Enaliornis* is assigned as the most basal taxon and *Baptornis* is positioned as more derived than *Brodavis*. *Chupkaornis* is a sister taxon to the clade of *Brodavis* and higher taxa. *Paraesperornis* and *Hesperornis* are positioned within Hesperornithidae, the derived Hesperornithiformes. Many of the skeletal character changes are concentrated at the base of Hesperornithidae (*Paraesperornis* and more derived taxa), and involve the modification of the pelvic girdle and hind limb morphology (e.g. dorsal directed antitrochanter of pelvis, short and sprawled femur, including probable lobe-toed feet suggested by the specialized distal articular surface of first digit of fourth toe, and predominantly robust digit IV phalanges). These skeletal modifications are likely adaptations for foot-propelled diving behaviour.

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Keywords: Hesperornithiformes; diving birds; fossil birds; Late Cretaceous; new species

Introduction

Hesperornithiformes were toothed, foot-propelled, diving birds and were one of the most widely distributed groups of birds in the Cretaceous of the Northern Hemisphere. These birds had extremely reduced forelimbs and powerful hind limbs, suggesting that they were flightless sea-going predatory birds (Marsh 1872a, b; Marsh 1880). To date, Hesperornithiformes is known from 30 species within at least 14 possible genera (Wilson 2012; Bell & Chiappe 2015a, b). Together with *Ichthyornis*, a tern-like toothed bird from the Upper Cretaceous, these diving birds are the closest relative or the sister clade of the crown group Neornithes (Chiappe 1996; Clarke 2004; Bell & Chiappe 2015a, b).

Most of the known hesperornithiform remains have been recovered from marine deposits of the Late Albian to Maastriichtian of the Northern Hemisphere (Galton & Martin

2002a), particularly from the Upper Cretaceous Western Interior Seaway deposits of North America. In contrast, Eurasian remains of hesperornithiforms are quite rare.

During the Cretaceous, the Turgai Strait, which extended from the modern Caspian Sea north to the Arctic region, separated western and eastern Eurasia (Duellman & Trueb 1994). Here, we refer to the western landmass as 'Europe' and the eastern landmass as 'Asia'. Several Hesperornithiformes, including *Enaliornis*, *Baptornis*, *Hesperornis rossicus* and *Asiahesperornis*, are known from Europe (Seeley 1876; Galton & Martin 2002a; Rees & Lindgren 2005; Dyke *et al.* 2006). These European forms are known from partial skeletons. In contrast, only isolated fragmentary bones are known from the Asian hesperornithiforms *Judinornis nogontsavensis* (Nessov & Borkin 1983; Kurochkin 2000) and *Brodavis mongoliensis* (L. D. Martin *et al.* 2012) from the Maastriichtian Nemegt Formation of Mongolia.

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Here we describe a new hesperornithiform from the Upper Cretaceous Kashima Formation of the Yezo Group in Hokkaido, Japan. This fossil bird (MCM.A773) is represented by nine skeletal elements from one individual, and is the best-preserved specimen of these diving birds known from Asia, unlike many hesperornithiform taxa which have been described based on a single skeletal element (see Bell & Chiappe 2015b for full discussion). It is also the first record of this group of toothed diving birds from the eastern margin of the Eurasian continent, and represents the oldest record of Hesperornithiformes from Asia.

Previously, few studies focused on the systematics of the Hesperornithiformes. Earlier work by L. D. Martin (1984) investigated the interrelationships within the Hesperornithiformes and determined that the group was monophyletic with three families: Enaliornithidae, Baptonithidae, and the most derived group, Hesperornithidae. Chiappe (2002a) and Clark (2004) conducted phylogenetic analyses of Mesozoic birds including two Hesperornithiformes taxa, *Hesperornis regalis* (Marsh 1880) and *Baptonis advenus* (Marsh 1877). Subsequent work by O'Connor *et al.* (2011) included *Enaliornis* (Galton & Martin 2002a), *Brodavis varneri* (*Baptonis varneri* in J. E. Martin & Cordes-Person 2007; see L. D. Martin *et al.* 2012) and *Parahesperornis alexi* (L. D. Martin 1984) in their panoptic phylogenetic analysis of Mesozoic birds (Fig. 1A). Using 209 morphological characters, Bell & Chiappe (2015a) attempted the first phylogenetic analysis of the group, focusing on species-level interrelationships within the Hesperornithiformes (Fig. 1B).

The morphological information from the specimen described here sheds new light on the phylogenetic

interrelationships of the oldest diving birds. Thus, this study provides a revised phylogenetic analysis of the Hesperornithiformes, based on this new data set. We discuss the tempo of morphological character changes within the group using an evolutionary rate calculation (Brusatte 2011). The Hokkaido specimen also provides new information regarding the distribution of this group in the Northern Hemisphere.

This study will: (1) describe the newly discovered hesperornithiform material from Japan in detail; (2) test the phylogenetic position of the Japanese hesperornithiform and provide a reassessment of the phylogenetic interrelationships of the clade; and (3) review the morphological characters and identify the tempo of morphological character changes in hesperornithiform evolution.

Geological setting

The partial, semi-articulated skeleton of the holotype bird described herein (MCM.A773) is from a calcareous concretion that eroded out from surrounding sedimentary strata. In 1996 Masatoshi Kera found the concretion containing the specimen described here lying on an exposure of the Kashima Formation of the Yezo Group in the Kumaoui Creek locality (Fig. 2A, B; Kakegawa & Hayakawa 2000). Because this nodule was not found in situ, the precise stratigraphical position cannot be determined. However, it can be reasonably assumed that the nodule came from the Kashima Formation as it is the only rock unit exposed in the area. The likely area of its original locality is enclosed by a square in Fig. 2B.

The Cretaceous Yezo Group crops out in a north-south band extending from central Hokkaido, Japan and into Sakhalin Island, Russia (Hoshi & Takashima 1999; Takashima *et al.* 2004; Yazykova 2004) (Fig. 2A). The rocks of this group are interpreted as forearc basin sediments deposited along the eastern margin of the Eurasian continent (Kodama *et al.* 2002). The Upper Cretaceous Kashima Formation has produced abundant invertebrate and vertebrate remains (Futakami *et al.* 2008; Caldwell *et al.* 2010). The rock unit is widely distributed along the Kumaoui Creek, one of the branches of Lake Katsurazawa in the Mikasa area of central Hokkaido (Fig. 2B).

The stratigraphical section measured in this study as well as the biostratigraphical distribution of the marine molluscs from the Kumaoui Creek locality are shown in Figure 2C. The Kashima Formation is composed mainly of bioturbated siltstones with intercalated parallel-laminated fine sandstones and greyish white tuffaceous sandstones (10~30 cm thickness). Slump beds, clastic dykes and quartz veins are common. The rocks represent outer shelf to continental slope depositional environments (Futakami *et al.* 2008).

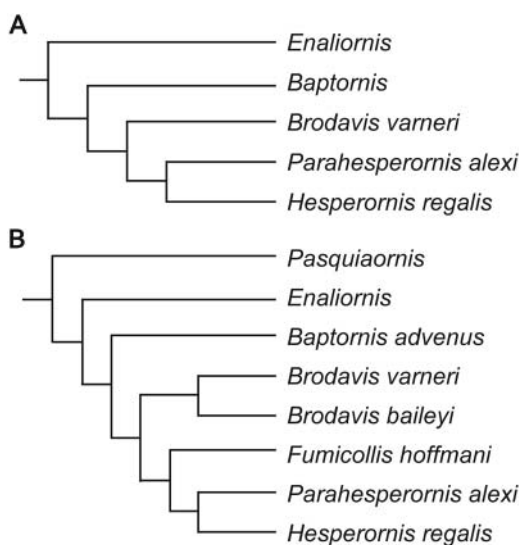


Figure 1. Phylogenetic relationship of the Hesperornithiformes presented by **A**, O'Connor *et al.* (2011); **B**, Bell & Chiappe (2015a).

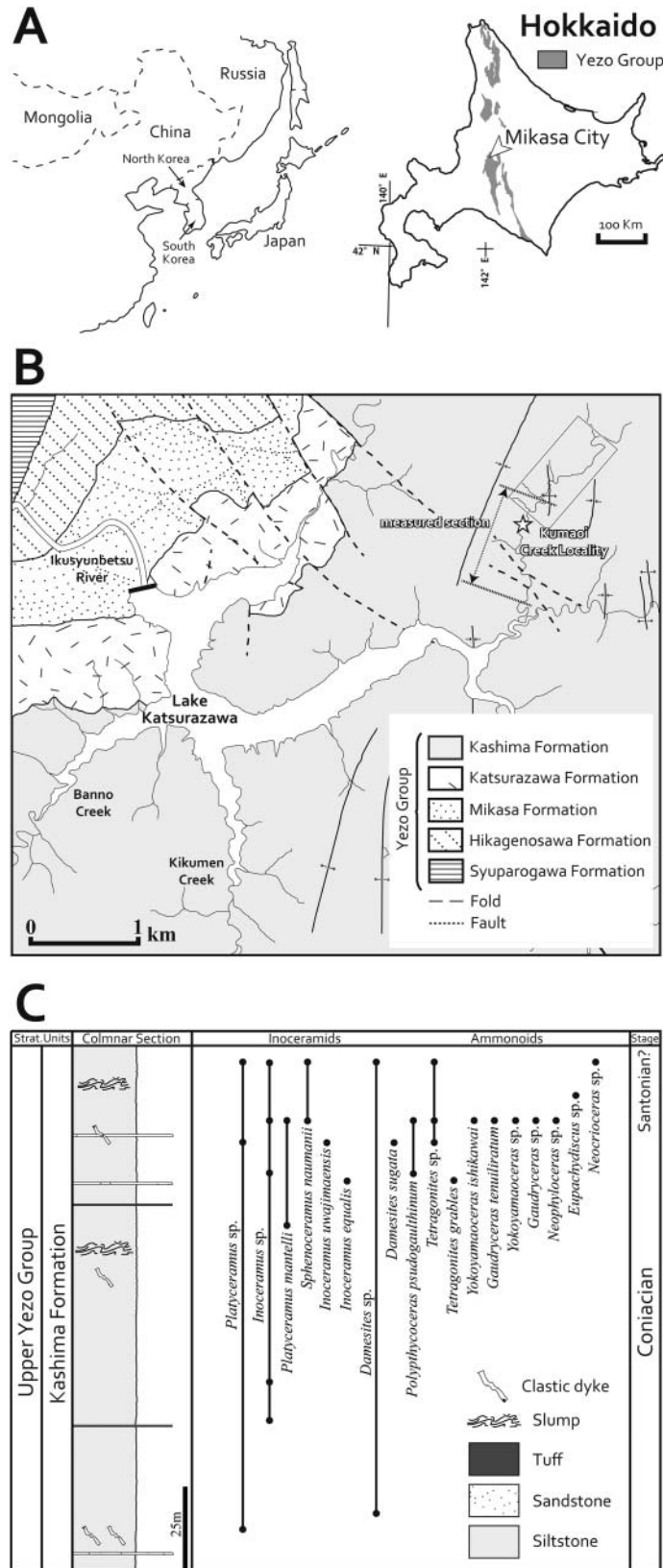


Figure 2. A, locality map and B, geological map of Mikasa area, showing Kumaoi Creek locality. Modified from Futakami *et al.* (2009). The star indicates the Kumaoi Creek locality. The square shows the possible area where the nodule including MCM.A773 came from, upstream of where it was actually recovered. C, stratigraphical section and biostratigraphical succession of marine molluscs in the Kumaoi Creek locality. Solid circles show occurrence of each species. Lines show the range of estimated occurrence.

Early work by Kakegawa & Hayakawa (2000) proposed the age of the concretion that contained MCM.A773 as early Santonian, based on the co-occurrence of the ammonoids *Polyptychoceras pseudogaultinum* and *Damesites damesi*. However, both ammonoids provide a broader age range, from the Coniacian to Lower Campanian (Toshimitsu & Hirano 2000). To refine the age range, 17 species of ammonoids and eight species of inoceramids were also collected from the calcareous concretions around the Kumaoui Creek as part of this study (Fig. 2B, C). From these newly collected specimens, the inoceramids *Platyceramus manteli* and *Inoceramus uwajimensis* are now identified. These taxa are zonal index species for the Coniacian in Japan (Toshimitsu *et al.* 1995). Although the ammonoids recognized in the concretion including MCM.A773 suggest an age range of the Coniacian to Lower Campanian, our new measured section produced no index specimens indicative of the Lower Campanian. Moreover, previous biostratigraphical work on the Kumaoui Creek (Futakami *et al.* 2008) did not report the occurrence of Campanian index species along the Kumaoui Creek. Consequently, based on these data, the age of the occurrence of MCM.A773 is inferred here to be Coniacian to Santonian.

Material and methods

Material

MCM.A773 consists of four cervical vertebrae, two thoracic vertebrae, the distal ends of the left and right femora, and the middle part of the right fibula. The material is housed in the collection of the Mikasa City Museum, Mikasa City, Hokkaido, Japan (MCM). Anatomical nomenclature used here largely follows Baumel & Witmer (1993) using the English equivalents of the Latin terms.

Analytical methods

The phylogenetic position of MCM.A773 was tested using a new data matrix of 22 taxa and 239 morphological characters. The data matrix is built upon four previous large data sets for Mesozoic birds: 13 characters from Chiappe (2002a), 135 characters from Clarke *et al.* (2006), five characters from M. Wang *et al.* (2015), and 67 characters from Bell & Chiappe (2015a). In addition, our data matrix contains 19 new characters. All new added characters were scored as unordered and were equally weighted. The 33 characters are ordered in accordance with previous studies (Clarke *et al.* 2006; Bell & Chiappe 2015a).

The data matrix used here includes two enantiornithine birds, *Protopteryx* (Zhang & Zhou 2000) and *Pengornis* (Zhou *et al.* 2008), and 19 ornithuromorphs, and *Archaeopteryx* is assigned as the outgroup. The 19

ornithuromorphs include *Apsaravis ukhaana* (Norell & Clarke 2001; Clarke & Norell 2002), *Gansus yumenensis* (You *et al.* 2006; Y. M. Wang *et al.* 2015), *Ichthyornis dispar* (Clarke 2004), seven neornithine birds, and nine Hesperornithiformes: *Enaliornis*, *Pasquiaornis*, MCM.A773, *Brodavis*, *Baptornis advenus*, *Fumicollis hoffmani*, *Parahesperornis alexi*, *Hesperornis gracilis* and *H. regalis*.

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*. The complete character list can be found in Supplemental Appendix 2, and the data matrix can be found in Supplemental Appendix 3. Specimens examined for character coding are listed in Supplemental Appendix 4.

A maximum parsimony analysis was conducted with the new data matrix, using the software TNT 1.5 (Goloboff & Catalano 2016). The tree search was performed using the Implicit Enumeration algorithm ('branch and bound' solution). Bremer support values, branch lengths, and consistency and retention indices were calculated in TNT.

After the phylogenetic analysis, evolutionary rates throughout the obtained tree were calculated using the data set. Patristic dissimilarity and time duration were calculated for each branch in the tree context (see Supplemental Appendix 7). Evolutionary rates were calculated following the methods provided by Brusatte (2011).

Institutional abbreviations

AMNH: American Museum of Natural History, New York, USA; **CAGS**: Chinese Academy of Geological Sciences, Beijing, China; **CAMSM**: 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; **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; **SMNH**: Sternberg Museum of Natural History, Hays, Kansas, 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.

Systematic palaeontology

Avialae Gauthier, 1986

Ornithuromorpha Chiappe, 2002a

Hesperornithiformes Fürbringer, 1888

Chupkaornis gen. nov.

Type species. *Chupkaornis keraorum* sp. nov.

Etymology. *Chupkaornis*, from the combination of the Ainu word ‘chupka’, meaning ‘eastern’, and the Greek ‘ornis’ for bird.

Diagnosis. As for the type and only known species.

Chupkaornis keraorum sp. nov.

(Figs 3–6)

Etymology. Named after Masatoshi and Yasuji Kera, who discovered the specimen and contributed greatly to the Mikasa City Museum.

Holotype. MCM.A773; a partial skeleton of a single individual including four cervical and two thoracic vertebrae, the distal ends of the left and right femora, and the middle part of the right fibula.

Locality and age. Kumaori Creek, one branch off Lake Katsurazawa, Mikasa City, Hokkaido, Japan; Kashima Formation (Coniacian to Santonian), Upper Cretaceous Yezo Group.

Diagnosis. A hesperornithiform differing from all other members of the clade by exhibiting the following unique combination of characters: (a) completely heterocoelous articular surface of thoracic vertebrae; (b) emarginated lateral excavation and a pronounced and sharply defined edge of the ventral margin of thoracic vertebrae; (c) slender base of ventral process, laterally expanded fibular condyle of femur; and (d) finger-like projected tibiofibular crest of femur.

Description

Cervical vertebrae. The twelfth or thirteenth cervical vertebra (Fig. 3A, B) is missing its posterior part, but the centrum is elongated anteroposteriorly. The prezygapophyses are widely separated from each other and the costal process is elongated posteriorly. These features resemble those of the twelfth or thirteenth cervical vertebra of *Pasquiaornis hardiei* (RSM P2831.8) and correspond to the thirteenth cervical vertebra of *Hesperornis regalis* (YPM 1207). The transverse foramen of this cervical vertebra is remarkably expanded dorsoventrally (Fig. 3A) as seen in *Pasquiaornis hardiei* (RSM P2831.8). In *Hesperornis regalis* (YPM 1207), the transverse foramen is more compressed dorsoventrally. The anterior articular surface is

heterocoelous and is saddle shaped, but the shape of the posterior articular surface is unknown because that part of the vertebra is missing. The cervical vertebra of *Chupkaornis keraorum* is larger and more robust than the twelfth or thirteenth cervical vertebrae of *Pasquiaornis hardiei*.

The fourteenth cervical vertebra (Fig. 3C, D) is missing most of the anterior and right lateral regions. The transverse process is developed and the postzygapophyses are widely separated from each other. The vertebra is short anteroposteriorly compared to the twelfth or thirteenth cervical vertebra. These features resemble those of the fourteenth cervical vertebra of *Pasquiaornis tankei* (RSM P2957.17) and correspond to that of *Hesperornis regalis* (YPM 1207).

The sixteenth cervical vertebra (Fig. 3E, F) is missing the ventral portion of the centrum and prezygapophysis. A large neural spine is developed dorsally and its base is anteroposteriorly wide. The postzygapophyses are positioned close together and are extended posteriorly. The transverse process is elongated laterally and the diapophysis is located at the anterolateral tip of the transverse process. On the right lateral surface, the parapophysis is located on the anteroventral margin of the transverse process. These features resemble those of the sixteenth cervical vertebra of *Fumicollis hoffmani* (UNSM 20030) and correspond to that of *Hesperornis regalis* (YPM 1207).

The seventeenth cervical vertebra (Fig. 3G, H) is missing most of the posteroventral part of the vertebra. The anterior articular surface of the centrum is heterocoelous, dorsoventrally short and transversely wide. The prezygapophyses are located close together and the remains of the transverse processes are developed laterally (Fig. 3H). The neural spine is large, and has a truncated form. These features resemble those of the seventeenth cervical vertebra of *Fumicollis hoffmani* (UNSM 20030) and correspond to that of *Hesperornis regalis* (YPM 1207).

Thoracic vertebrae. The third thoracic vertebra (Fig. 4A, B) is missing the anterior, posterior and right lateral parts. The parapophysis is deep and is located near the anterolateral edge of the transverse process. The shallow and elongated pit above the parapophysis is present as in the third thoracic vertebra of *Fumicollis hoffmani* (UNSM 20030). There is a deep lateral excavation on the lateral surface of the centrum. The neural spine is developed and truncated as in the seventeenth cervical vertebra. The transverse process is developed laterally and the diapophysis is present at its tip. The parapophysis is located moderately ventrally compared to the diapophysis of the same vertebra, indicating that this thoracic vertebra corresponds to the third thoracic vertebra of *Hesperornis regalis* (YPM 1207).

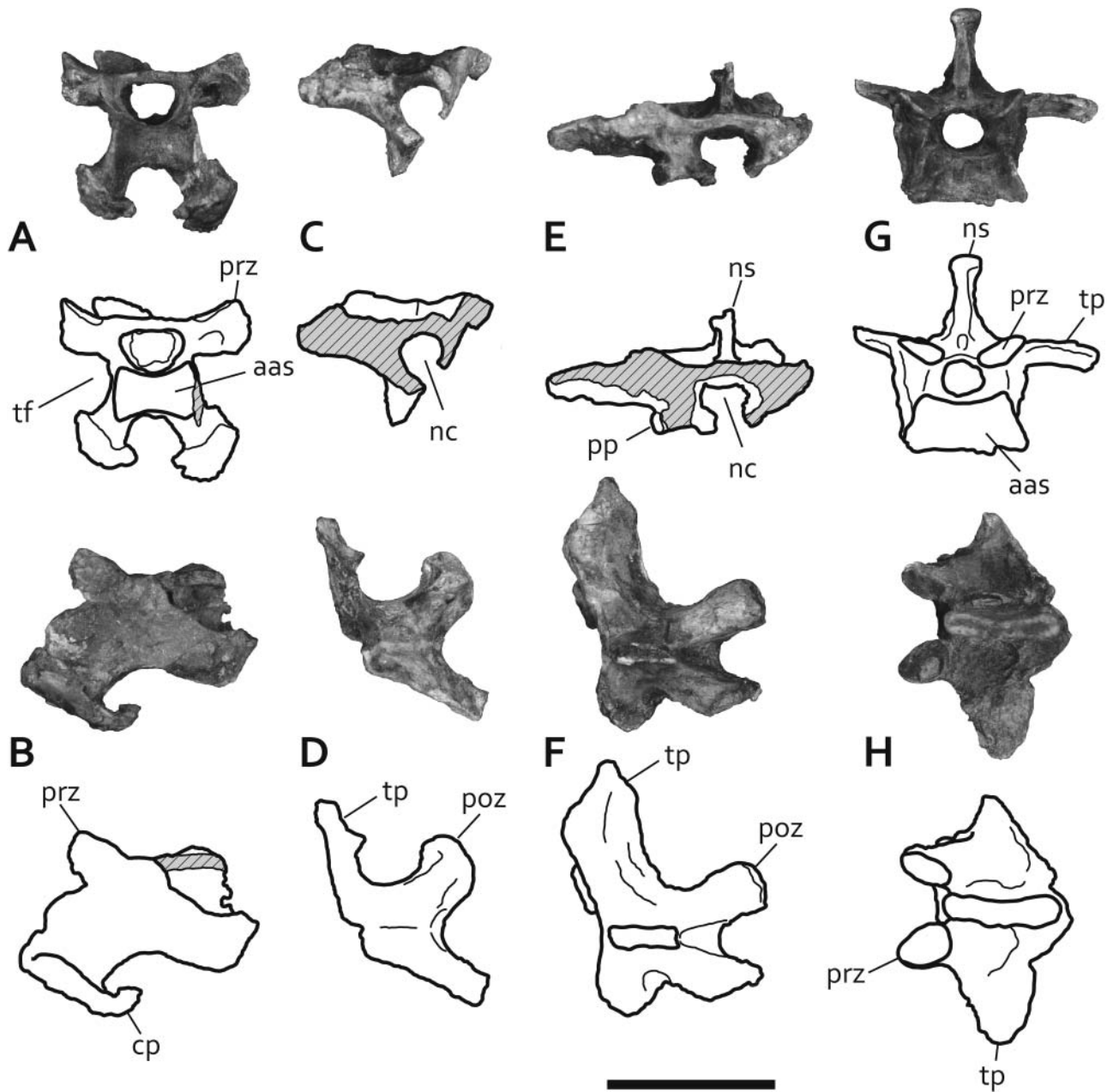


Figure 3. *Chupkaornis keraorum* gen. et sp. nov. (MCM.A773). Twelfth or thirteen cervical vertebra in **A**, anterior; **B**, left lateral views. Fourteenth cervical in **C**, anterior; **D**, dorsal views. Sixteenth cervical in **E**, anterior; **F**, dorsal views. Seventeenth cervical in **G**, anterior; **H**, dorsal views. Abbreviations: aas, anterior articular surface; cp, costal process; nc, neural canal; ns, neural spine; poz, postzygapophysis; pp, parapophysis; prz, prezygapophysis; tf, transverse foramen; tp, transverse process. Scale bar = 2 cm.

The fourth thoracic vertebra (Fig. 4C–F) is strongly heterocoelous, as seen in *Brodavis*, *Baptornis*, *Fumicollis* and hesperornithids. The prezygapophyses are located close together and are slightly inclined anteriorly. The postzygapophysis is elongated lateroposteriorly. The posterior articular surface has a slightly incised lateral margin. There is a deep concavity on the posterodorsal margin of the transverse process. The parapophysis is located near the anterior edge of the transverse process as

in the third thoracic vertebra, but it is positioned more dorsally than in the third thoracic vertebra. These features correspond to the fourth thoracic vertebra of *Hesperornis regalis* (YPM 1207). In ventral view, the centrum is spool shaped, like those of other hesperornithiforms. The lateral excavations on the lateral sides of the centrum are deep and emarginated with a pronounced and sharply defined edge of the ventral margin (Fig. 4D). *Chupkaornis* shares the character of the lateral excavation of the thoracic

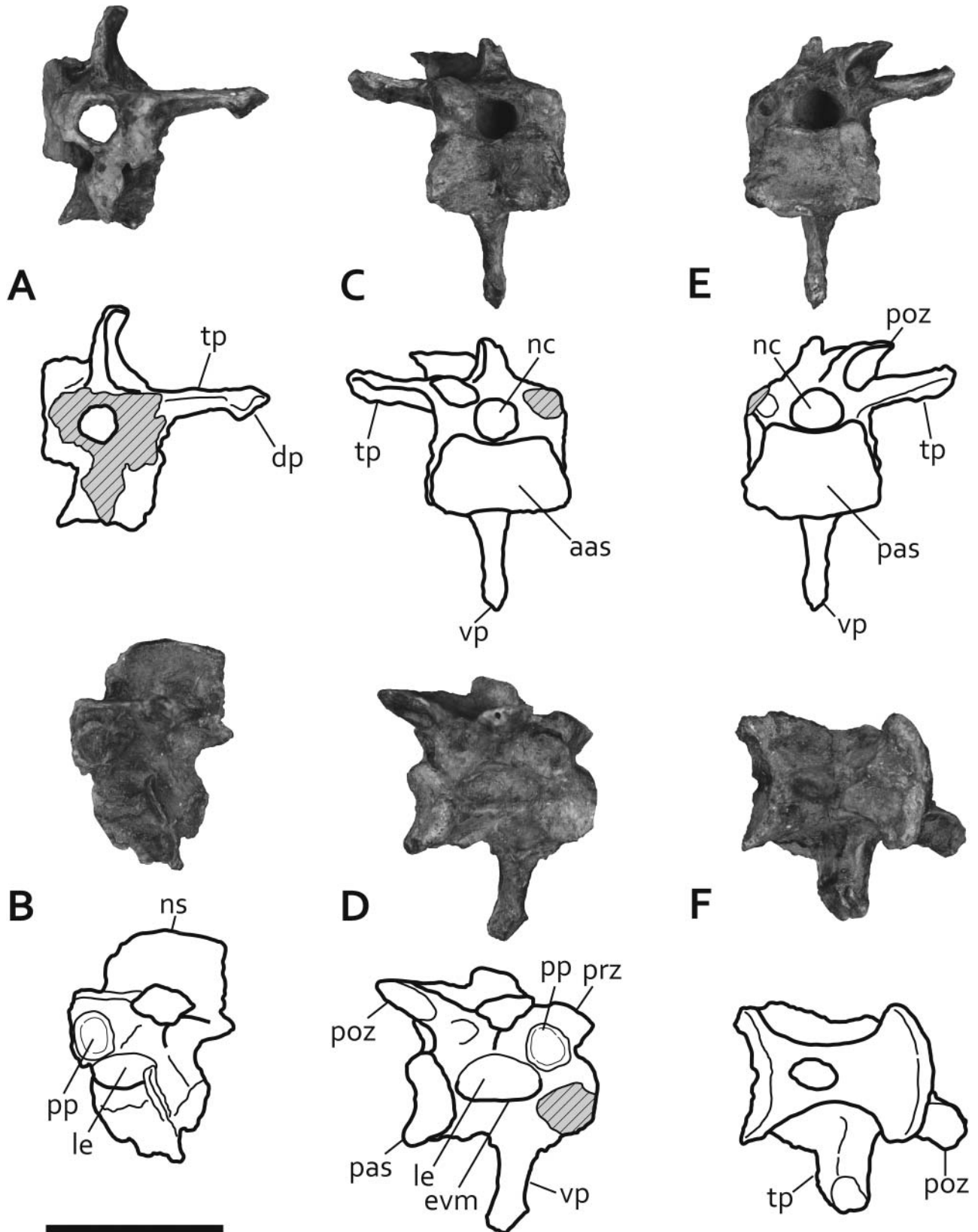


Figure 4. *Chupkaornis keraorum* gen. et sp. nov. (MCM.A773). Third thoracic vertebra in **A**, anterior; **B**, left lateral views. Fourth thoracic in **C**, anterior; **D**, right lateral; **E**, posterior; **F**, ventral views. Abbreviations: aas, anterior articular surface; dp, diapophysis; evm, edge of the ventral margin; le, lateral excavation; nc, neural canal; ns, neural spine; pas, posterior articular surface; poz, postzygapophysis; pp, parapophysis; prz, prezygapophysis; tp, transverse process; vp, ventral process. Scale bar = 2 cm.

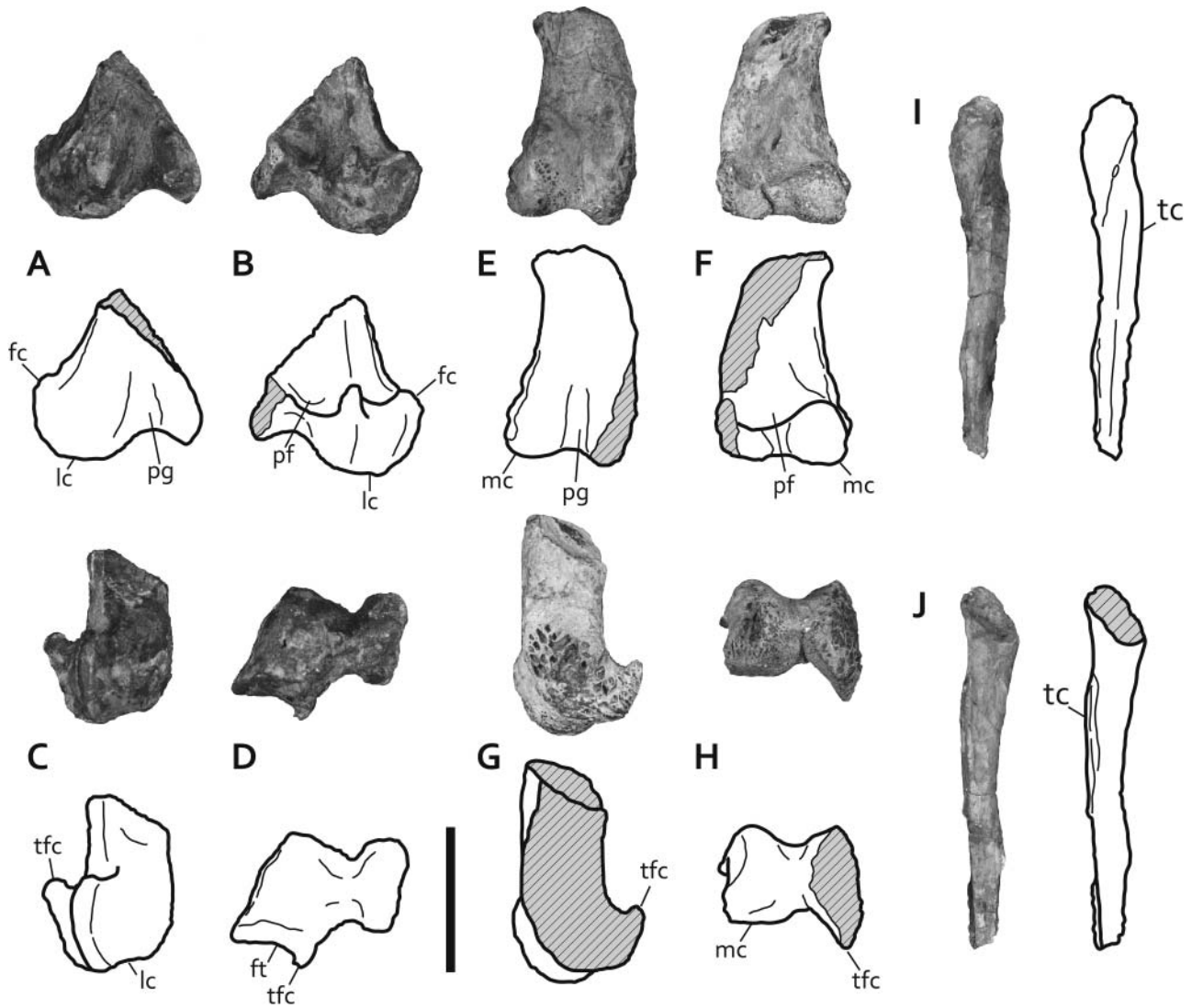


Figure 5. *Chupkaornis keraorum* gen. et sp. nov. (MCM.A773). Right femur in **A**, anterior; **B**, posterior; **C**, lateral; **D**, distal views. Left femur in **E**, anterior; **F**, posterior; **G**, lateral; **H**, distal views. Right fibula in **I**, anterior and **J**, posterior views. Abbreviations: fc, fibular condyle; ft, fibular trochlea; lc, lateral condyle; pf, popliteal fossa; pg, patellar groove; mc, medial condyle; tc, tibial crest; tfc, tibiofibular crest. Scale bar = 2 cm.

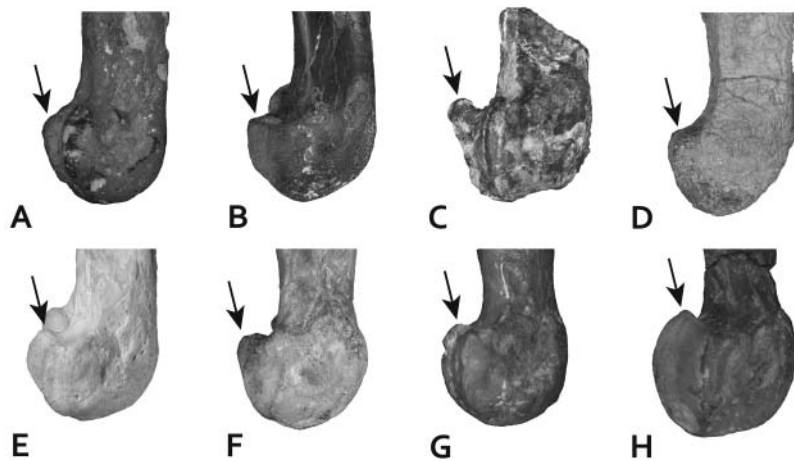


Figure 6. Comparisons of the distal end of right femur in lateral aspects in: **A**, *Enaliornis barretti* (NHMUK A163); **B**, *Pasquiaornis takei* (RSM P2077.10); **C**, *Chupkaornis keraorum* (MCM.A773); **D**, *Brodavis varneri* (SDSM 68430); **E**, *Baptornis advenus* (KUV P 2290); **F**, *Fumicollis hoffmani* (UNSM 20030); **G**, *Parahesperornis alexi* (KUV P 2287); **H**, *Hesperornis regalis* (YPM 1200). Arrows indicate the tibiofibular crest. Figures are not to scale.

vertebra with *Pasquiaornis tankei* (RSM P2989.23) and most Mesozoic birds (e.g. *Iteravis*, *Gansus* and *Ichthyornis*). However, the lateral sides of the thoracic vertebrae of the more derived hesperornithiforms (*Brodavis*, *Baptornis*, *Fumicollis*, *Parahesperornis* and *Hesperornis*) are depressed by fossae that are without a ventral margin. The ventral process is slender and is extended from the anterior part of the centrum. Its base is narrow and slender, unlike the wide and triangular ventral process of *Fumicollis* (UNSM 20030) and *Hesperornis* (YPM 1207). The anteroposterior length of the centrum of the fourth thoracic vertebra is approximately equal to that of *Fumicollis* (UNSM 20030) and is slightly larger than that of *Pasquiaornis tankei* (RSM P2989.23).

Hind limb. The distal ends of both the left and right femora (Fig. 5) are preserved. The lateral condyle of the left femur and the medial condyle of the right femur are missing. The size of the femur is similar to that of *Baptornis* (KUV P 2290) and *Fumicollis* (UNSM 20030) and slightly larger than that of *Pasquiaornis tankei* (RSM P2077.108). The proportions of the femur of *Chupkaornis* are

more massive and robust than those of *Enaliornis* and *Pasquiaornis*. In contrast, the femur of *Chupkaornis* is more slender than that of *Parahesperornis* and *Hesperornis*.

The fibular condyle is expanded laterally (Fig. 5A), as seen in the other hesperornithiforms and in extant foot-propelled diving bird taxa such as podicipediiforms (grebes) and gaviiformes (loons) (Cracraft 1982). The presence of a thick cortical area of the femoral cross section (cortical area/total periosteal area = 78%) supports the contention that *Chupkaornis* was adapted to a diving lifestyle (Habib & Ruff 2008). The lateral condyle is distally more extended than the medial condyle, which is the condition common to basal hesperornithiforms. The patellar groove is deep and narrow, unlike that of *Enaliornis*. The groove is uninterrupted and extends onto the distal intercondylar groove. These characters are also seen in *Enaliornis*, *Pasquiaornis*, *Brodavis*, *Baptornis* and *Fumicollis* (Tokaryk *et al.* 1997; J. E. Martin & Cordes-Person 2007; Bell & Chiappe 2015b). One of the most significant characters of *Chupkaornis* is the finger-like projected tibiofibular crest (Fig. 5D, H). This

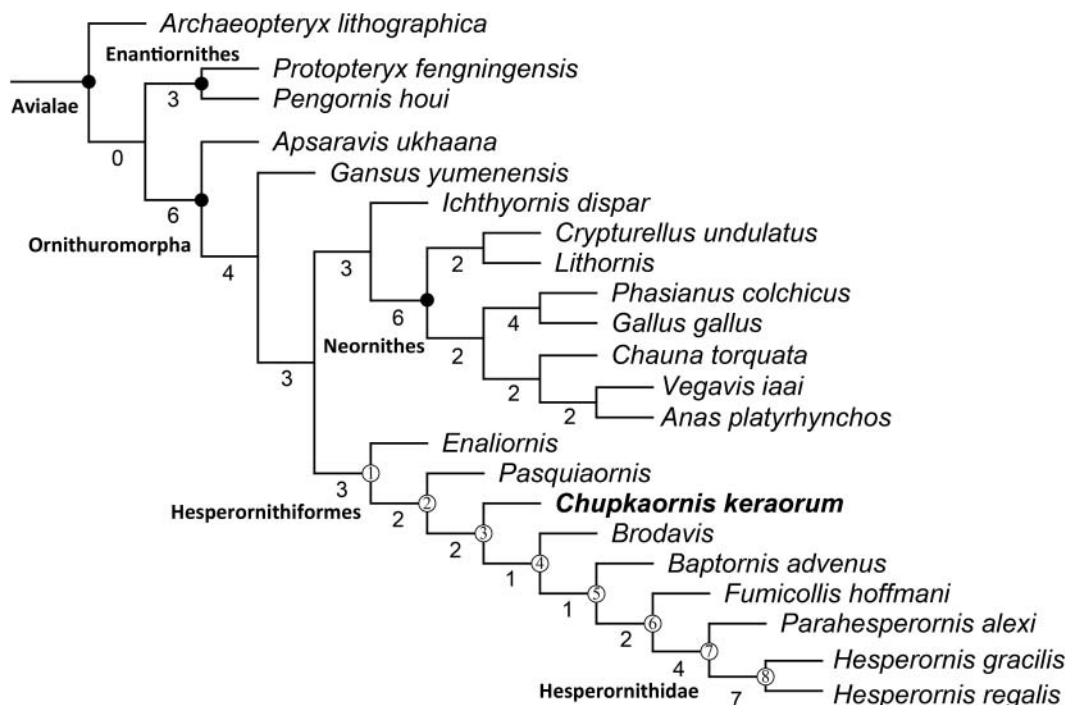


Figure 7. Cladogram of the most parsimonious tree (tree length: 410 steps, consistency index = 0.748, rendition index = 0.843) showing the hypothetical phylogenetic relationships of Mesozoic birds. Note that *Chupkaornis* is resolved as a basal member of the Hesperornithiformes. Bremer support values are labelled on the tree. Synapomorphies for each node: node 1 (30: 0 > 1, 154: 0 > 1, 155: 0 > 1, 165: 0 > 1, 214: 0 > 1, 228: 0 > 1, 230: 0 > 1, 233: 0 > 1); node 2 (150: 0 > 1, 158: 0 > 1, 205: 1 > 0); node 3 (30: 1 > 2, 167: 0 > 1); node 4 (33: 0 > 1); node 5 (228: 1 > 2); node 6 (170: 0 > 1, 189: 0 > 1, 214: 1 > 2, 221: 0 > 1, 234: 1 > 2); node 7 (126: 0 > 1, 133: 1 > 2, 134: 1 > 2, 150: 1 > 2, 154: 1 > 2, 156: 0 > 1, 157: 0 > 1, 162: 1 > 2, 163: 1 > 2, 164: 0 > 1, 171: 1 > 2, 172: 1 > 2, 174: 0 > 1, 175: 1 > 2, 176: 0 > 1, 177: 0 > 1, 180: 2 > 0, 181: 0 > 1, 183: 0 > 1, 184: 1 > 0, 185: 0 > 1, 196: 1 > 2, 198: 0 > 1, 212: 1 > 2, 216: 0 > 2, 219: 0 > 1, 229: 1 > 2, 230: 1 > 2, 231: 0 > 1, 232: 0 > 1, 233: 1 > 2, 235: 0 > 1, 236: 0 > 1, 237: 0 > 1, 238: 0 > 1, 239: 0 > 1); node 8 (165: 1 > 0, 168: 0 > 1, 169: 0 > 1, 173: 0 > 1, 199: 0 > 1, 208: 1 > 2, 214: 2 > 3). See Supplemental Appendix 2 for list of characters.

discrete feature of the tibiofibular crest differentiates *Chupkaornis* from other members of the hesperornithiforms (Fig. 6). The popliteal fossa on the posterior surface is deep and is separated by the transverse ridge that connects medial and lateral condyles. The fibular trochlea is transversely wider than those of *Pasquiaornis* (RSM P2077. 108) and *Fumicollis* (UNSM 20030). In distal view, the medial margin of the medial condyle is depressed as in *Baptornis*, *Brodavis*, *Fumicollis* and hesperornithids, a condition that is different from that of the other basal hesperornithiforms, *Enaliornis* and *Pasquiaornis*.

The middle part of the right fibula (Fig. 5I, J) is preserved. The midshaft diameter of the fibula of *Chupkaornis* is sub-equal to that of *Fumicollis hoffmani* (UNSM 20030) but is smaller than those of *Hesperornis regalis* (YPM 1200) and *Brodavis varneri* (SDSM 68430). The shaft has the articular surface to the fibular crest of the tibiotarsus on its posterior proximal surface (Fig. 5I). The posterior surface of the shaft is relatively flat.

Discussion

Phylogenetic analysis

Three previous panoptic phylogenetic studies used large data sets for Mesozoic birds (Chiappe 2002a: 169 characters and 24 taxa; Clarke *et al.* 2006: 205 characters and 25 taxa; M. 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 2002a; Clarke 2004; O'Connor *et al.*

2013) and 104 new characters. We adopted 67 characters from Bell & Chiappe (2015a) in the present analysis, based on direct observation of hesperornithiform specimens by one of us (TT).

The phylogenetic analysis based on the new data matrix produced a single most parsimonious tree with 410 steps (Fig. 7). In our study, *Chupkaornis keraorum* was recovered as a basal hesperornithiform.

Also, *Protopteryx fengningensis* plus *Pengornis houi* was identified as a monophyletic clade, the Enantiornithes, followed by the ornithuromorph birds *Apsaravis ukhaana* and *Gansus yumenensis*. In our analysis, *Ichthyornis* was united with the Neornithes in a monophyletic clade, as in the studies by Chiappe (2002a) and Clarke (2004), but unlike those of O'Connor *et al.* (2011) and Bell & Chiappe (2015a). Hesperornithiforms were identified as a monophyletic clade supported by eight synapomorphies (Fig. 7, node 1). The complete synapomorphy list of the most parsimonious tree can be found in Supplemental Appendix 6.

Within the Hesperornithiformes clade, *Enaliornis* was recovered as the basal-most taxon, and *Pasquiaornis*, *Chupkaornis keraorum*, *Brodavis*, *Baptornis advenus* and *Fumicollis hoffmani* were successive sister groups of the Hesperornithidae. *Paraesperornis alexi* is identified as a basal hesperornithid bird, followed by *Hesperornis*.

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. 7), in contrast to the recent phylogenetic study by Bell & Chiappe (2015a) that identified

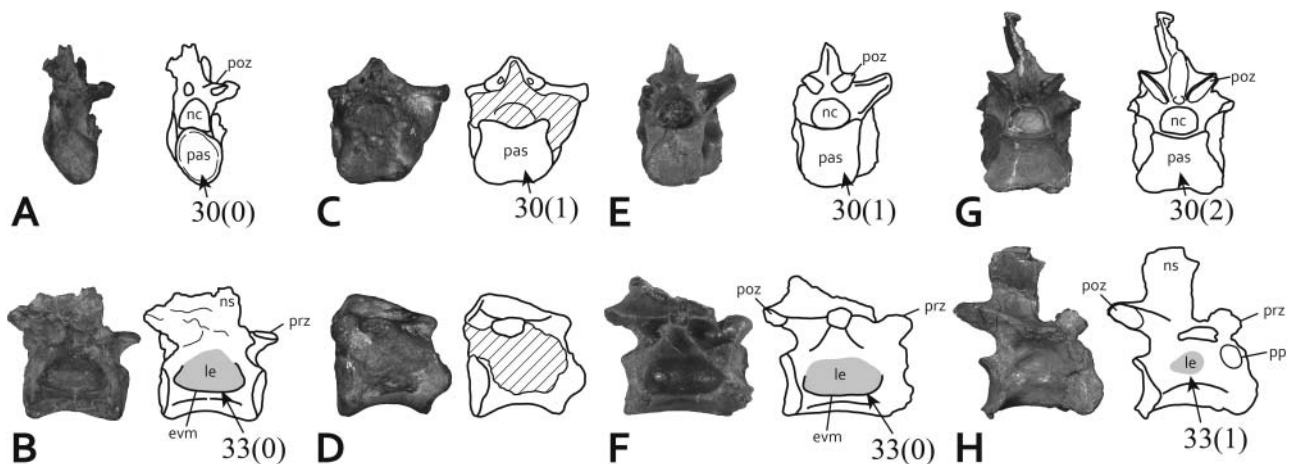


Figure 8. Comparisons of the thoracic vertebra in posterior (A, C, E, G) and right lateral (B, D, F, H) aspects in: **A, B**, *Ichthyornis dispar* (YPM 1732); **C, D**, *Enaliornis barretti* (CAMSM B55277); **E, F**, *Pasquiaornis tankei* (RSM P2989.23); **G, H**, *Paraesperornis alexi* (KUVV 2287). 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.

Pasquiaornis as the most basal Hesperornithiformes. Both *Enaliornis* and *Pasquiaornis* have long been recognized as primitive taxa within the Hesperornithiformes (Martin 1984; 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. Our morphological study of *Chupkaornis keraorum* provides an opportunity to reassess the phylogenetic relationships of basal hesperornithiform taxa including *Enaliornis* and *Pasquiaornis*.

The clade of *Pasquiaornis* and higher taxa (Fig. 7, node 2) is supported by three unambiguous synapomorphies of the hind limbs. One of these unambiguous synapomorphies is related to the degree of anterior development of the trochanteric crest of the femur (character 150). In *Enaliornis*, the trochanteric crest of the femur is significantly expanded anteriorly compared to the femoral head in proximal view (150:0, Fig. 10A), 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 the femoral head (150:1, Fig. 10E). Another synapomorphy is the condition between the femoral trochanter and head (character 158). In *Enaliornis*, the femoral trochanter and head are nearly continuous or separated by a shallow notch (158:0, Fig. 10B), a condition that is different from *Pasquiaornis* and higher taxa (158:1, Fig. 10F, I, L). The third synapomorphy is the absence of a plantarly projected hypotarsus of the tarsometatarsus (character 205). In *Enaliornis* (Fig. 12I), as well as in *Gansus yumenensis* (Fig. 12D) and *Ichthyornis dispar*, a well-defined hypotarsus without a distinct groove and crest is well developed on the plantar surface of the proximal end of the tarsometatarsus (205:1). In contrast, *Pasquiaornis* and the more derived hesperornithiform birds share a flat surface of the hypotarsus area (205:0, Fig. 12M, P, S).

Phylogenetic position of *Chupkaornis keraorum*

The present analysis recovered *Chupkaornis keraorum* as one of the basal hesperornithiforms, but more derived than *Enaliornis* and *Pasquiaornis*. The clade of *Chupkaornis* and the more derived taxa (Fig. 7, node 3) is supported by two unambiguous synapomorphies. One of the unambiguous synapomorphies is the presence of a heterocoelous articular surface of the thoracic vertebrae, characterized by articular surfaces which are strongly saddle shaped (30:2, Figs 4C, E, 8G). The heterocoelous articular surface is compressed dorsoventrally (Fig. 8G), which differs from the subrounded outline of the articular surfaces (e.g. amphicoelous or ophisthocoelous) as seen in *Gansus* and *Ichthyornis* (Fig. 8A). Previously, Galton & Martin

(2002a) 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* (CAMSM B55277; Fig. 8C) possesses a general heterocoelous outline, the articular surface is only weakly concave and almost flat, lacking the saddle-shaped articular surface, concave on one axis and convex on the other (Fig. 8D). As in *Enaliornis*, the articular surfaces of the thoracic vertebrae of *Pasquiaornis* are also compressed dorsoventrally (Fig. 8E), and have a more pronounced concavity. These features in *Enaliornis* and *Pasquiaornis* (30:1) are different from those in *Chupkaornis* and the more derived hesperornithiforms, which have true heterocoelous articular surfaces (30:2; Figs 4E, 8G). The other unambiguous synapomorphy is a depressed medial margin of the medial condyle of the femur (167:1; Figs 5D, 10J, M).

The clade of *Brodavis* and more derived taxa (Fig. 7, node 4) is supported by one unambiguous synapomorphy: the lateral excavations are depressed without the well-defined edge of the ventral margin (33:1, Fig. 8H). The lateral excavations are deep with a pronounced and sharply defined edge of the ventral margin in *Chupkaornis*, *Ichthyornis*, *Pasquiarornis* and most other Mesozoic birds. The edge of the ventral margin of the lateral excavation (Fig. 8B, F) is not seen in *Brodavis*, *Baptornis*, *Fumicollis* and hesperornithids.

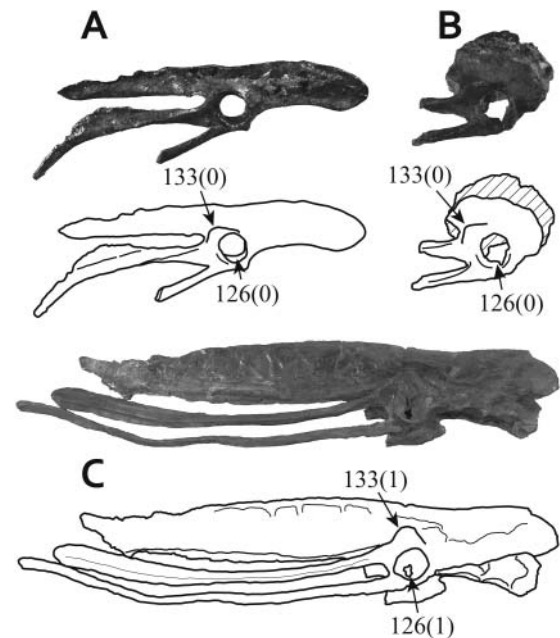


Figure 9. Comparisons of the pelvis in right lateral aspects in: **A**, *Gansus yumenensis* (CAGS-07-CM-009); **B**, *Pasquiaornis tankei* (RSM P.2997.62); **C**, *Hesperornis regalis* (UNSM 1212). Figures are not to scale.

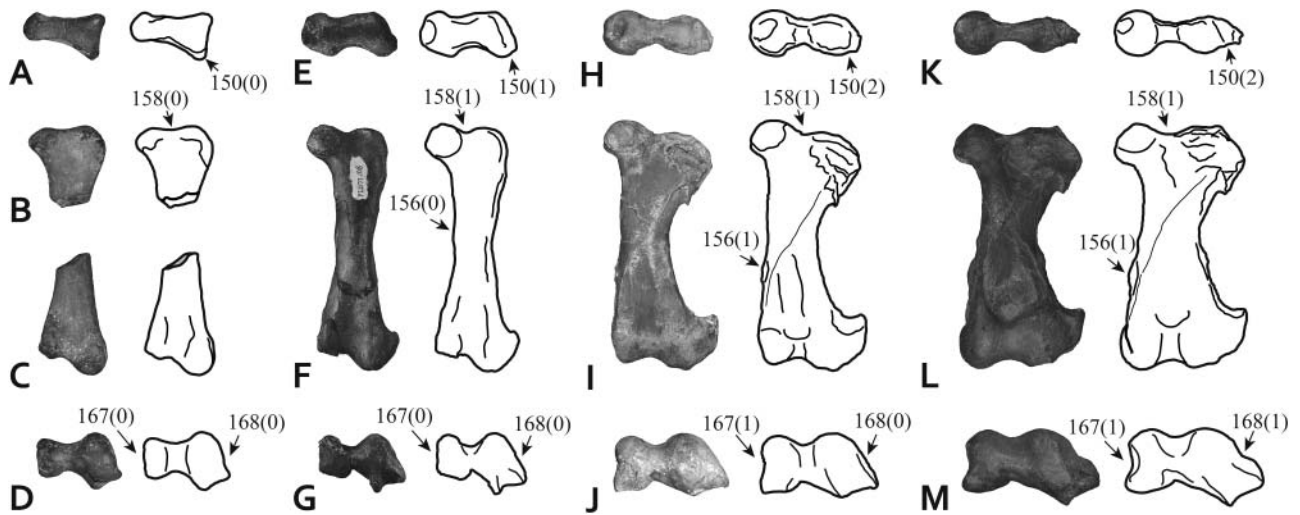


Figure 10. Comparisons of the right femur in proximal (A, E, H, K), anterior (B, C, F, I, L), and distal (D, G, J, M) aspects in: **A, B**, *Enaliornis* sp. (CAMSM B55289); **C, D**, *Enaliornis sedgwicki* (CAMSM B55295); **E, F, G**, *Pasquiaornis tankei* (RSM P.2077.108); **H, I, J**, *Parahesperornis alexi* (KUV P 2287); **K, L, M**, *Hesperornis regalis* (YPM 1200). Figures are not to scale.

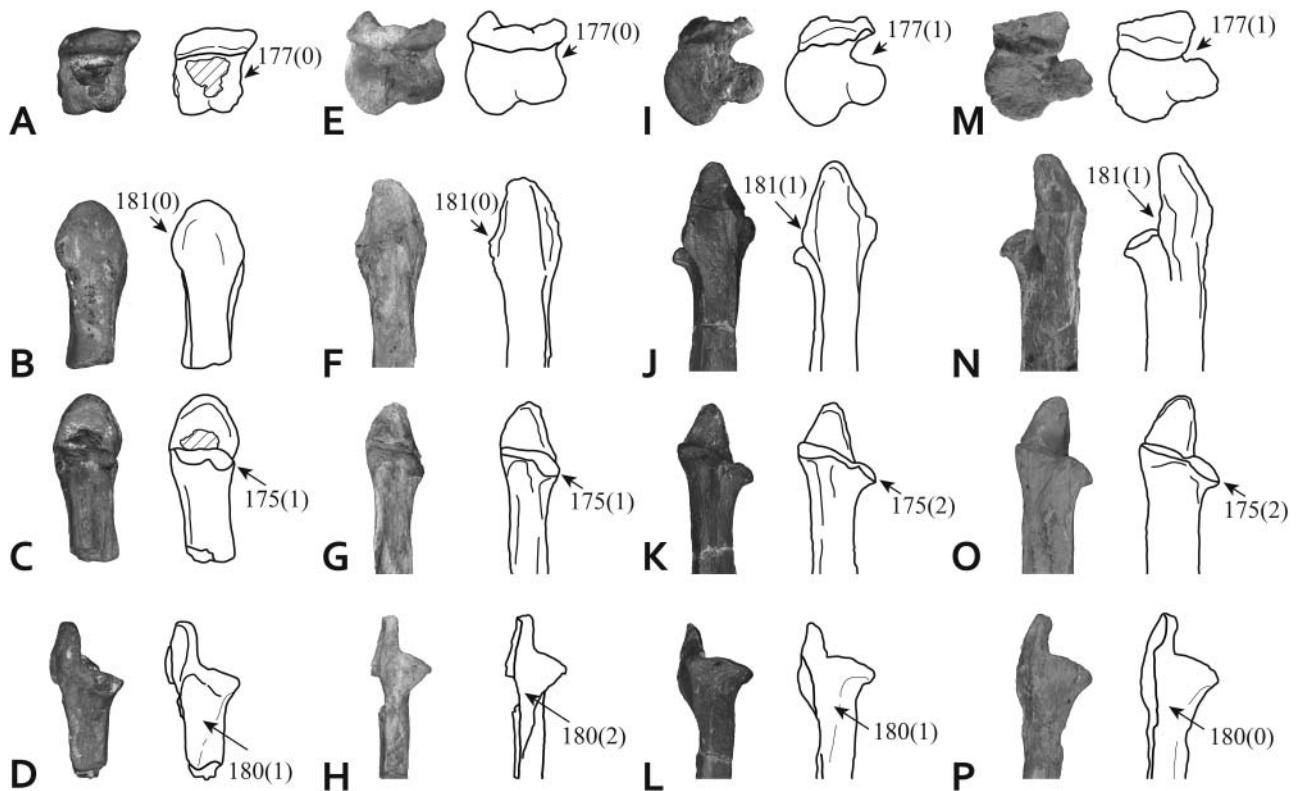


Figure 11. Comparisons of the left tibiotarsus in proximal (A, E, I, M), anterior (B, F, J, N), posterior (C, G, K, O), and medial (D, H, L, P) aspects in: **A, B, C, D**, *Enaliornis barretti* (NHMUK A477); **E, F, G, H**, *Fumicollis hoffmani* (UNSM 20030); **I, J, K, L**, *Parahesperornis alexi* (KUV P 2287); **M, N, O, P**, *Hesperornis regalis* (YPM 1200). Figures are not to scale.

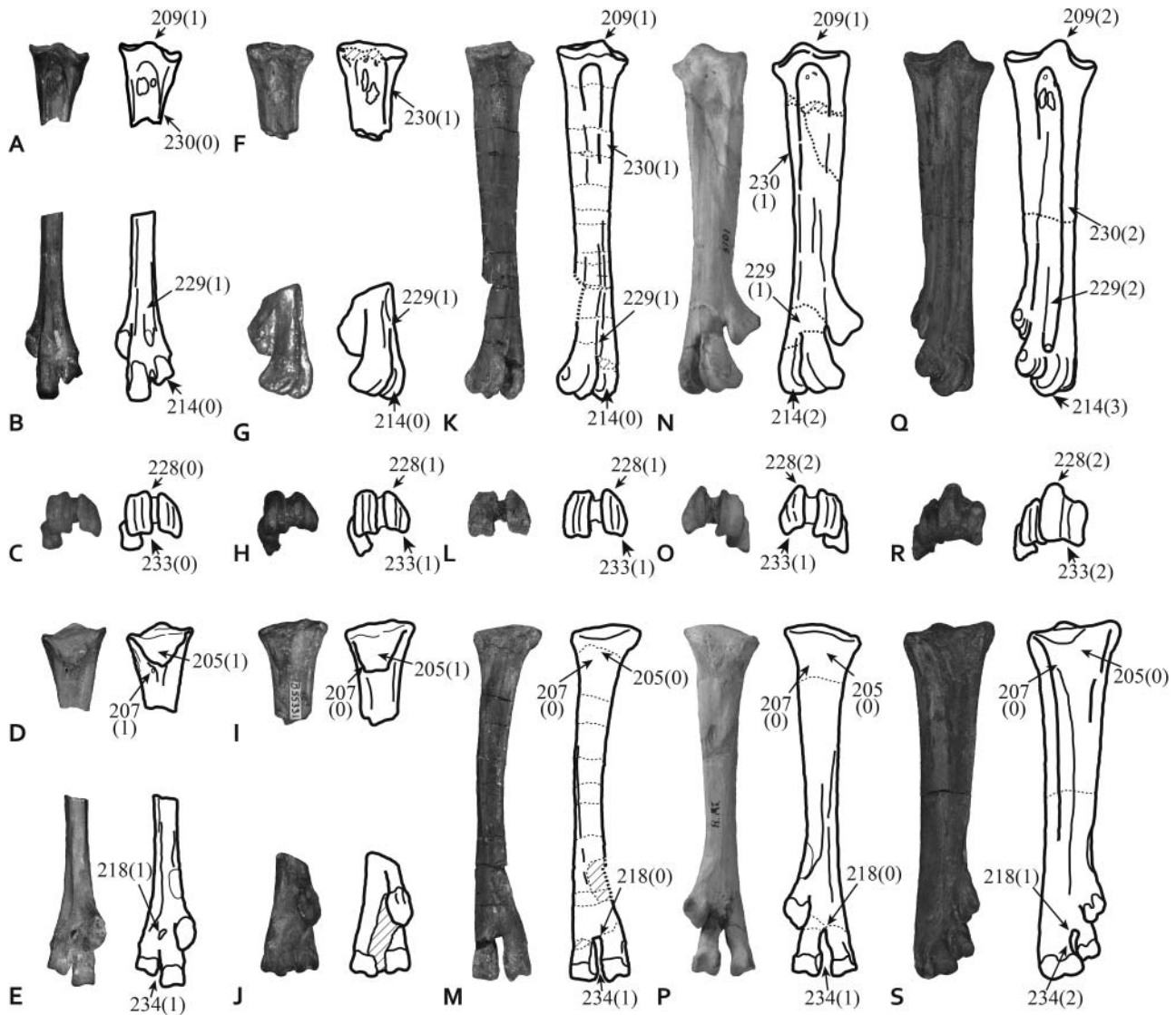


Figure 12. Comparisons of the tarsometatarsus in anterior (A, B, F, G, K, N, Q), posterior (D, E, I, J, M, P, S) and distal (C, H, L, O, R) aspects in: **A, B, C, D, E**, *Gansus yumenensis* (CAGS-04-CM-031); **F, I**, *Enaliornis barretti* (CAMSM B55331); **G, H, J**, *Enaliornis barretti* (NHMUK A477); **K, L, M**, *Pasquiaornis tankei* (RSM P2957.27); **N, O, P**, *Baptornis advenus* (AMNH 5101); **Q, R, S**, *Hesperornis regalis* (YPM 1200). Photo N courtesy of the American Museum of Natural History of New York; photos O and P courtesy of the Natural History Museum of Los Angeles County. Figures are not to scale.

Reassessment of the phylogenetic relationship of *Brodavis* and *Baptornis advenus*

O'Connor *et al.* (2011) and Bell & Chiappe (2015a) suggested that *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 than that of trochlear III (228:2, Fig. 12O, R), the dorsal edge of metatarsal trochlear IV of *Brodavis* and more basal hesperornithiforms, *Enaliornis* and

Pasquiaornis is positioned at about the same level as metatarsal trochlear III (228:1, Fig. 12H, L). This arrangement of the metatarsal trochleae seen in *Baptornis* and higher taxa is unique among all birds.

Morphology of *Funicollis hoffmani* and the Hesperornithidae

UNSM 20030 was originally described by L. D. Martin & Tate (1976) as *Baptornis advenus*, and later reassigned to *Funicollis hoffmani* by Bell & Chiappe (2015b). The present analysis shows that *Funicollis* is positioned as a

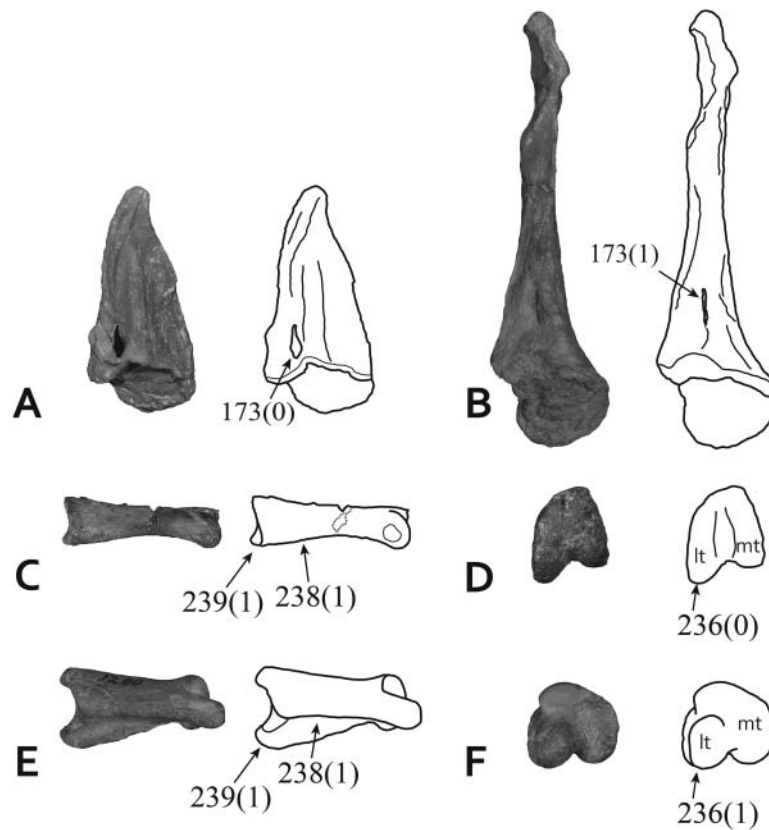


Figure 13. Comparisons of the right patella in medial (A, B), and the right first phalanx of the IVth digit in lateral (C, E) and distal (D, F) aspects in: **A**, *Parahesperornis alexi* (KUV P 2287); **B**, **E**, **F**, *Hesperornis regalis* (YPM 1200); **C**, **D**, *Pasquiaornis tankei* (RSM P.2997.68). Figures are not to scale.

sister taxon to the Hesperornithidae, corroborating the results of Bell & Chiappe (2015b). The clade of *Fumicolis* + Hesperornithidae (Fig. 7, node 6) is supported by five unambiguous synapomorphies: the lateral condyle of the femur constricts into a neck before widening at the shaft in lateral view (170:1); the medial condyle of the tibiotarsus is shorter than the lateral condyle in cranial view (189:1); the distal extent of the metatarsal trochlear IV is slightly farther than that of III (214:2); the proximal plantar margin of metatarsal II possesses a slight flange (221:1); and the intertrochlear incision between metatarsal trochlea III and IV is teardrop-shaped in plantar view (234:2; Fig. 12S).

The monophyly of the Hesperornithidae (Fig. 7, node 7) is supported by 36 unambiguous synapomorphies related to the pectoral girdle and hind limbs. In hesperornithid birds, the acetabular foramen of the pelvis is extremely reduced by ossification (126:1, Fig. 9C). The antitrochanter of hesperornithids is oriented dorsally (133:1, Fig. 9C), in contrast to that of other Mesozoic birds which are oriented dorsoposteriorly (133:0, Fig. 9A, B). The trochanteric crest and the fibular condyle of the femur are greatly expanded laterally (Fig. 10I, L), giving them a short and robust

appearance (171:2, 172:2). The tubercle for *muscular iliofemoralis* and *m. caudofemoralis* in the medial margin of the femoral shaft is well developed (156:1, Fig. 10I, L). The patella is compressed laterally and is highly elongated (174:1, Fig. 13A, B). These osteological changes indicate that the area of muscle attachment on the hind limb bone elements increased in hesperornithids and likely served for powerful foot-propelled diving behaviour. In the tibiotarsus, both medial and lateral cotylae of the proximal articular surface are strongly tilted laterally (175:2, Fig. 11K, O). 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, differing from that of non-hesperornithid hesperornithiforms (177:1, Fig. 11I, M). The groove likely reflects the development of the *m. tibialis cranialis* for powerful dorsal flexion of the intertarsal joint during the recovery stroke. The lateral margin of the lateral cnemial crest of the tibiotarsus is only slightly flared laterally in hesperornithids (181:1, Fig. 11J, 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

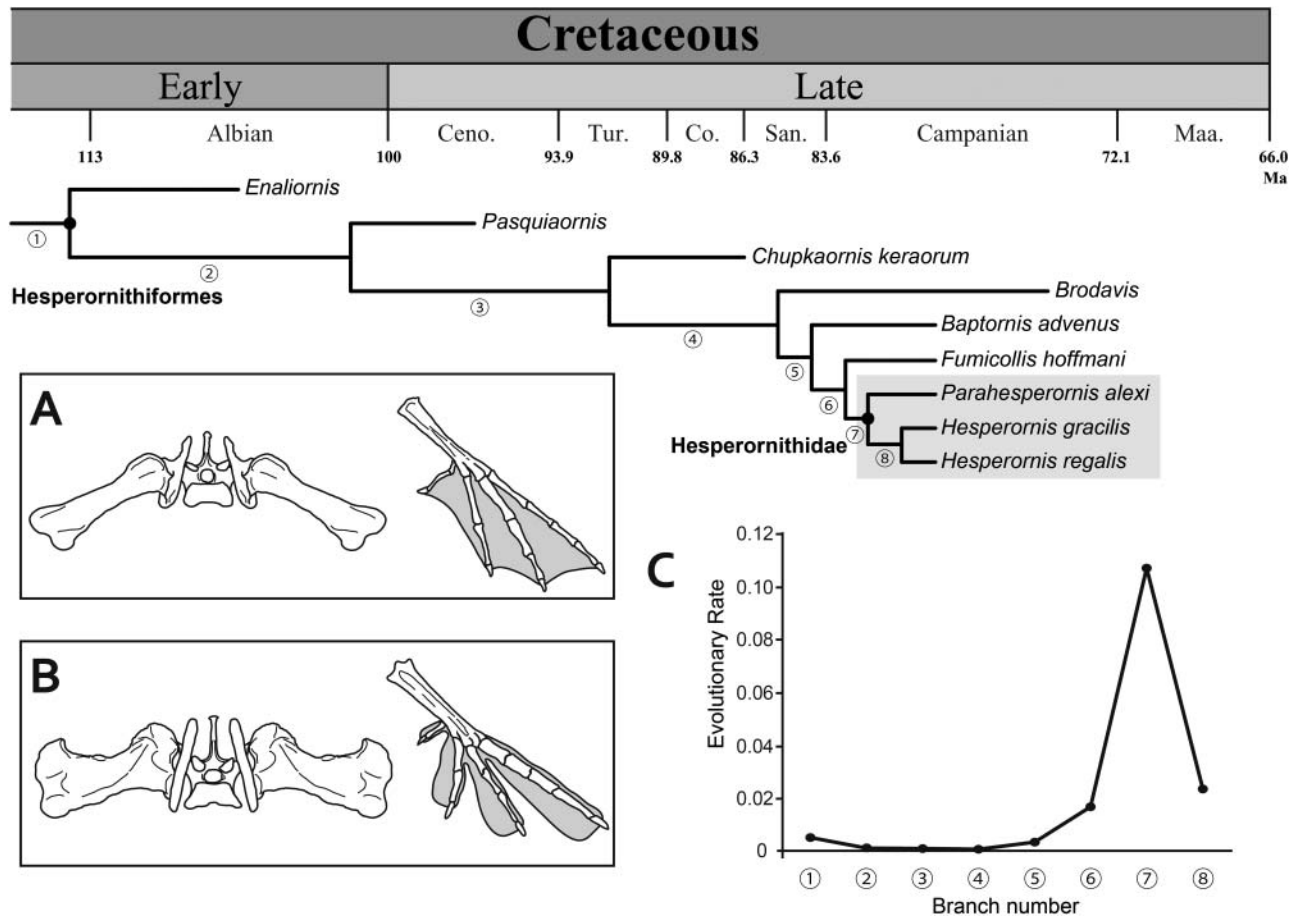


Figure 14. Time-scaled phylogeny of the Hesperornithiformes through the Cretaceous. **A**, anterior view of the pelvis of non-hesperornithid hesperornithiforms showing the position of the femora, and webbed feet; **B**, anterior view of hesperornithid bird showing the position of the femora, and suggested lobed feet. Labels at the branches in phylogenetic cladogram correspond to **C**, evolutionary rate value. Note that the evolutionary rate value at the base of Hesperornithidae (branch 7) is much higher.

cotyla completely in non-hesperornithid birds (181:0, Fig. 11B, F).

The clade of *Hesperornis regalis* + *H. gracilis* is supported by two unambiguous synapomorphies: a strongly concave lateral surface of the fibular condyle of the femur (168:1, Fig. 10M), unlike the smooth lateral surface of the fibular condyle in other taxa (168:0, Fig. 10D, G, J) in distal views, and the foramen for *m. ambiens* of the patella is located at around the centre in medial view (173:1, Fig. 13B).

Evolutionary rate and diving adaptation in Hesperornithiformes

The evolutionary rate (patristic dissimilarity/time duration of branch; Brusatte 2011) for each branch in the Hesperornithiformes (Fig. 14C) indicates a much higher evolutionary rate at the base of the Hesperornithidae compared to the remaining branches. The increased tempo of morphological evolution may be related to the change in

swimming style because of the foot-propelled diving adaptation exhibited within the Hesperornithidae.

Several synapomorphies, supporting the clade Hesperornithidae, are related to these foot-propelled diving specializations. The dorsally directed antitrochanter of the pelvis (Fig. 9C) allows the femora to elevate above the body level during the propulsive stroke for foot-propelled diving (Fig. 14B; Kurochkin & Vasiliev 1966; Zinoviev 2011). In hesperornithids, the first phalanx of the fourth digit is prominently developed (Fig. 13E). Its distal articular surface has unique structures such as the enlarged medial trochlea and the reduced, distally extended lateral trochlea that makes a rounded, peg-like projection (236:1, Fig. 13F). L. D. Martin & Tate (1976) suggested that this type of articular surface is highly specialized for toe-rotation as exhibited by the lobed-footed diving birds, the grebes (Podicipediiformes). In non-hesperornithid hesperornithiforms such as *Pasquiaornis* and *Baptornis*, the medial and lateral trochleae of the fourth toes are parallel and about the same size (Fig. 13D), permitting phalanx IV to move anteriorly and

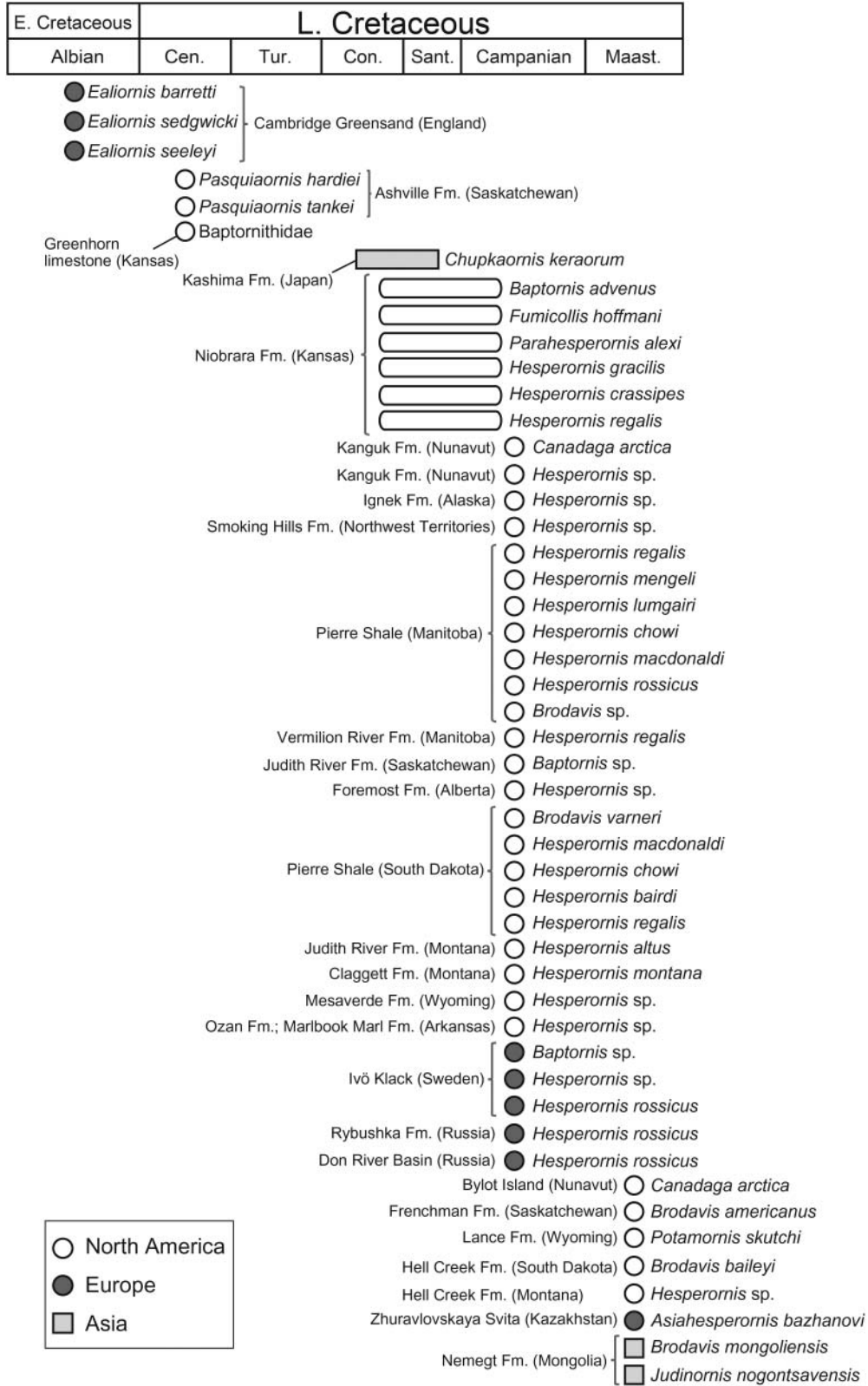


Figure 15. List of fossil occurrences of Hesperornithiformes. Open circles, solid circles and grey squares show North American, European and Asian taxa, respectively.

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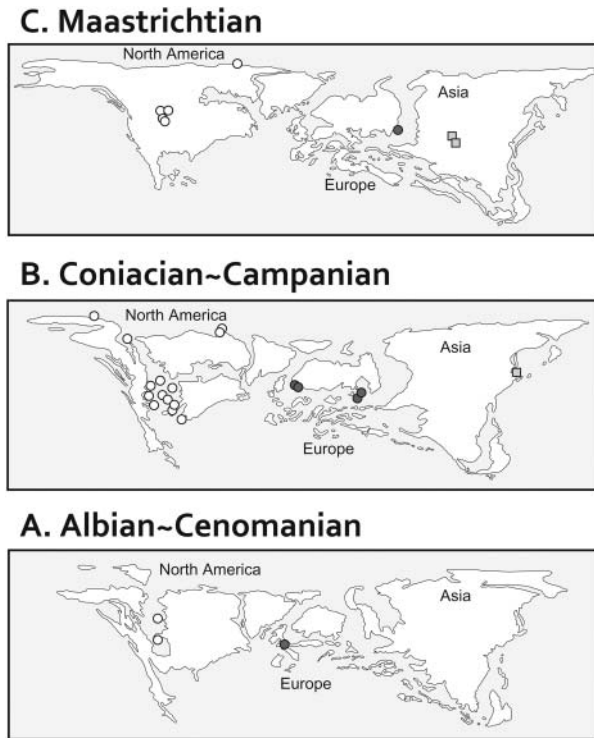


Figure 16. Palaeogeographical distribution of the Hesperornithiformes in **A**, Early Cretaceous Albian to Late Cretaceous Cenomanian; **B**, Coniacian to Campanian; **C**, Maastrichtian. Open circles, solid circles and grey squares show North American, European and Asian taxa, respectively. Maps are modified from Blakey (2009).

posteriorly as in the web-footed diving birds, the loons (Gaviiformes; Proctor & Lynch 1993).

Loons and grebes are representatives of extant foot-propelled diving birds that employ different fourth-toe kinematics during foot-propelled diving. While loons are a drag-based foot-propelled diver with webbed feet, grebes use lift-based propulsion with lobed feet (Johansson & Lindhe Norberg 2000; Thewissen & Taylor 2007). Johansson & Lindhe Norberg (2001) suggested that the lift-based paddling locomotion of grebes considerably increases the maximum swimming speed and energetic efficiency. Similarly, the character change in the fourth toe recovered in the present analysis is likely to be related to a morphological change from webbed feet (Fig. 14A; *Pasquiaornis* and *Baptornis*; L. D. Martin & Tate 1976; Sanchez 2010) to probable lobed feet (Fig. 14B; *Hesperornis*; Stolpe 1935; Zinoviev 2011), and this change in morphology reflects a change in locomotion that increased the maximum swimming speed and energy efficiency.

Distribution of Hesperornithiformes during the 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, these attributions remain controversial.

Neogaenornis wetzeli from the Maastrichtian of Chile was initially grouped with the hesperornithiforms (Lambrecht 1929, 1933; L. D. Martin & Tate 1976). However, Orson (1994) later redefined the holotype as a Cretaceous loon (Gaviidae). Kurochkin (1995) and Feduccia (1996) 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 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; Nesson & Prizemlin 1991; Martin & Varner 1992; Tokaryk & Harington 1992; Tokaryk *et al.* 1997; Malakhov & Ustinov 1998; Hill *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 Figs 15, 16).

Palaeobiogeographical implication of *Chupkaornis keraorum*

The oldest known hesperornithiform, *Enaliornis*, occurs only in the latest Albian Cambridge Greensand of England (Fig. 16A). 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 north-eastern Saskatchewan of Canada (Tokaryk *et al.* 1997; Cumbaa *et al.* 2006; Sanchez 2010). Another Cenomanian hesperornithiform, a baptornithid, has been reported from the Greenhorn Limestone of Kansas (Everhart & Bell 2009). During the Coniacian to the latest Campanian, hesperornithiforms more widely inhabited the Western Interior Seaway (WIS) of North America, including north of the Arctic Circle in Canada and Alaska (Fig. 16B). During the Maastrichtian, sea level dropped and the southern portion of the WIS disappeared. *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.* 2000), *Brodavis mongoliensis*, *B. americanus* and *B. baileyi* (L. D. 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 (Figs 15, 16B, C). Most of the hesperornithiforms that have been reported from WIS deposits in North America occur from the Late Cretaceous. In contrast, Asian hesperornithiforms are extremely rare (Figs 15, 16). In Asia, both previously known hesperornithiforms (*Judinornis* and *Brodavis mongoliensis*) are found within the non-marine deposits of the Maastrichtian Nemegt Formation.

The newly discovered taxon, *Chupkaornis keraorum*, is the first hesperornithiform specimen from the eastern margin marine deposit of the Eurasian continent, and is also the oldest hesperornithiform record (Coniacian to Santonian) from Asia. The discovery of *Chupkaornis* suggests that basal hesperornithiforms had dispersed to the eastern margin of Asia no later than Coniacian to Santonian.

Conclusions

A new hesperornithiform, *Chupkaornis keraorum* gen. et sp. nov. (MCM.A773) from the Late Cretaceous of Japan, is the first record of the group from the eastern margin of the Eurasian continent and the oldest record for this avian group from Asia. The new material is the best-preserved Asian hesperornithiform specimen recovered thus far, and provides new palaeobiogeographical insights for the broad taxonomic group as well as significant new anatomical data. *Chupkaornis keraorum* is diagnosed by a unique combination of characters from thoracic vertebrae and femur.

A phylogenetic analysis suggests that *C. keraorum* is a basal hesperornithiform. The new taxon is more derived than *Pasquiaornis* and more basal than *Brodavis*. The present analysis also suggests new phylogenetic relationships within the Hesperornithiformes; *Enaliornis* is the most basal hesperornithiform, and *Baptornis advenus* is a more derived taxon than *Brodavis*. The evolutionary rate calculation indicates that the rate of change is much higher within basal members of the Hesperornithidae compared to later branches. This rate change suggests that the most important morphological changes for highly foot-propelled diving adaptation are concentrated at the base of the Hesperornithidae.

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Supplemental data

Supplemental material for this article can be accessed here: <https://doi.org/10.1080/14772019.2017.1341960>.

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