A NEW SPECIMEN OF LARGE-BODIED BASAL ENANTIORNITHINE *BOHAIORNIS* FROM THE EARLY CRETACEOUS OF CHINA AND THE INFERENCE OF FEEDING ECOLOGY IN MESOZOIC BIRDS

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ABSTRACT—A new specimen of *Bohaiornis guoi* from the Jiufotang Formation, comprising a nearly complete skeleton, sheds light on enantiornithine morphological variation and ecological specialization. The new specimen was collected from near Lamadong Village in Liaoning Province, which is the same area where the sub-adult holotype specimen was reported. It provides new information on the cranial and pectoral girdle anatomy of the species, e.g., broad nasal, strikingly robust acromion, medially curved acrocoracoid process. In contrast to the holotype, the newly referred specimen has small rounded stones in the thoracic region that in other extinct taxa has been interpreted as direct evidence of diet. Direct evidence of diet is so far unknown in other Enantiornithes. Specifically the lack of "stomach stones" or gastroliths in enantiornithines despite their excellent fossil record has been proposed to be related to their insectivorous diet as well as to their arboreal ecology. We hypothesize that cranial morphology as well as the number and shape of the preserved stones in *Bohaiornis* may be most consistent with a raptorial ecology previously unknown for Enantiornithes and considered rare for Avialae. While rostrum shape has a strong relationship to feeding ecology in living birds, in basal avialan birds most diversity is in dental morphology, number, and distribution of the teeth.

INTRODUCTION

ENANTIORNITHES HAS been proposed to comprise the most significant radiation of Mesozoic birds in terms of species richness and ecological diversity. Although fossils relevant for understanding this radiation are globally distributed, Early Cretaceous Enantiornithes is best represented in the Yixian and Jiufotang Formations of northeast China. Prior to the discovery of abundant fossil birds from the Jehol Group over the past twenty years, the fossil record of Early Cretaceous Enantiornithes was relatively limited in number and geographic distribution (Chiappe and Walker, 2002). Most enantiornithine birds from the Jehol Group are from the Jiufotang Formation (e.g., *Boluochia*, *Cathayornis*, *Eocathayornis*, and *Longipteryx*; Zhou and Zhang, 2006a). By contrast, a much smaller number of enantiornithine species have been reported from the Yixian Formation (e.g., *Liaoningornis, Jibeinia, Vescornis, Eoenantiornis*, and *Longirostravis*; Zhou and Zhang, 2006a). Many of these Yixian taxa have also been resolved phylogenetically as basal within Enantiornithes (Chiappe and Walker, 2002; Zhou and Zhang, 2006a; Hu et al., 2012). Recovered as the basal-most enantiornithine, *Protopteryx* is known from the Dabeigou Formation in Fengning, northern Hebei Province (Zhang and Zhou, 2000). The exact correlation of the Dabeigou Formation is controversial, but it has been proposed to be lower than the Yixian Formation (Zhou, 2006; Wang and Ji, 2009). Another basal enantiornithine bird, *Shenqiornis*, with robust skull and teeth (Wang et al., 2010), is from a distinct unit (Qiaotou Formation) exposed in northern Hebei Province. The Qiaotou Formation has been proposed to be older than the Yixian Formation (Ji, 2004). *Sulcavis*, the recently described species similar to *Shenqiornis*, with distinct longitudinal grooves on the robust teeth (O'Connor et al., 2013) was reported from Yixian Formation of Lamadong Village in Liaoning Province. The array of derived Enantiornithes from the younger Jiufotang

Formation and its proposed equivalents (e.g., *Otogornis*, Yijinhuoluo Formation from Inner Mongolia; Hou, 1994) are small bodied (Chiappe and Walker, 2002). Morphological variation within these species include taxa with short (e.g., *Eocathayornis*, *Cathayornis*, and *Boluochia*; Zhou et al., 1992; Zhou, 1995; Zhou, 2002) and long (e.g., *Longipteryx*, *Rapaxavis*, and *Shanweiniao*; Zhang et al., 2001; Morschhauser et al., 2009; O'Connor et al., 2009) rostra. More recently, enantiornithine specimens were reported from localities near Lamadong Village (e.g., *Pengornis*, *Bohaiornis*, *Xiangornis*, and *Sulcavis*), with relatively larger size and notable anatomical differences from most other known enantiornithine birds (Zhou et al., 2008; Hu et al., 2011, 2012; O'Connor et al., 2013).

The holotype of *Bohaiornis guoi* was inferred to represent a sub-adult specimen and tentatively reported to be from Yixian Formation (Hu et al., 2011). The relatively short and robust snout and distinct dental morphology distinguishes this taxon from other species from the same region. In this paper, we provide a detailed description of a new and well-preserved adult specimen of *Bohaiornis* from the Early Cretaceous Jiufotang Formation near Lamadong Village (Jianchang County, western Liaoning Province; Fig. 1). As in the holotype, the referred specimen preserves a short robust skull similar to the basal enantiornithine *Pengornis* and the older *Shenqiornis*. The new specimen provides new information on the cranial and pectoral girdle anatomy of the species. The specimen also preserves a few stones in the thoracic region. The new specimen is proposed to be first enantiornithine specimen to preserve direct evidence of diet. Data on the relationship between dentition, and other evidence of diet in Mesozoic avialans is reviewed in order to shed light on the possible feeding ecology of *Bohaiornis*.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758

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FIGURE 1—Map of Liaoning Province, China, showing the locality near Lamadong Village in Jianchang County where specimen IVPP V17963, referred to *Bohaiornis guoi,* was recovered.

AVIALAE Gauthier, 1986 sensu Gauthier and deQuieroz, 2001
ORNITHOTHORACES Chiappe, 1995
ENANTIORNITHES Walker 1981 sensu Chiappe, 1991
BOHAIORNIS GUOI Hu et al., 2011
Figures 2–5

Type specimen.—A sub-adult specimen represented by a nearly complete skeleton, LPM B00167 (Liaoning Paleontology Museum, Shenyang Normal University). The holotype was interpreted as a sub-adult or young adult based on the incomplete fusion of the semilunate carpal with the metacarpals, the proximal tarsals with the tibia, and between the metatarsals (Hu et al., 2011).

Referred specimen.—IVPP V 17963 (IVPP-Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China) comprises a nearly-complete articulated skeleton, primarily exposed in ventral view. There is only slight disarticulation of the distal hind limbs (i.e., tarsometatarsi from tibiotarsi and digits). The distal left tibiotarsus and proximal left tarsometatarsus are not preserved. The referred specimen differs from the holotype in complete fusion of compound bones (e.g., carpals, tibia, metatarsals) and a slight increase in size, consistent with its interpretation as an adult individual.

Occurrence.—The referred specimen is from the Early Cretaceous Jiufotang Formation (He et al., 2004) near Lamadong Village, Jianchang County (Fig. 1), Liaoning Province, China. However, the holotype was tentatively reported to be from the Yixian Formation of the same region of Liaoning Province (Hu et al., 2011). Recent fieldwork confirmed the outcrops of fossil beds exposed in Lamadong Village mainly belong to the Jiufotang Formation (X. L. Wang, personal commun.). Therefore, we consider both the referred and the holotype specimen to be most likely from the same stratigraphic unit.

Diagnosis.—Emended: *Bohaiornis guoi* is differentiated from all other Mesozoic birds by the following combination of characters: a strap-like and faintly ventrally recurved jugal bar; robust teeth; slightly medially hooked acrocoracoid; a flat to sub-concave lateral margin of the coracoid with a small lateral process and slightly recurved acrocoracoid; scapular acromion developed as a rectangular process with a broadly expanded tip; sternal midline with a slightly developed T-shaped terminus

approximately equal in posterior extent to the lateral trabecula; the glenoid facet on the coracoid positioned at approximately the same level as acrocoracoid process. The morphology of the posterior sternal midline differs from taxa with a more notable distal expansion (e.g., *Liaoningornis*). Most other enantiornithines lack a T-shaped terminus (e.g., *Longipteryx* and *Eoenantiornis*). *Bohaiornis* also shows several character states with a restricted distribution in Avialae and Enantiornithes including a rostrum with reduced maxillary and dentary dentition as well as notable broad scleral ossicles and elongate, strongly recurved pedal unguals. The third pedal digit claw is distinct in its larger size but less recurved shape compared to other pedal claws.

IVPP V17963 shows the unique combination of characters described above. It is larger than all the other described Early Cretaceous enantiornithines with the exception of *Pengornis* (Zhou et al., 2008). Body size and limb proportions of the referred specimen are very close to the holotype. For example, the humerus is about 52 mm in the referred specimen, compared to 47 mm in that of the holotype specimen; the femur/tibia ratio is about 0.83 in the referred specimen, compared to 0.85 of the holotype specimen (Hu et al., 2011, table 1; Table 1). *Bohaiornis guoi* differs in morphology of the coracoid and sternum from another recently described enantiornithine bird from Hebei Province, *Shenqiornis* (Wang et al., 2010). For instance, *Bohaiornis* has a concave rather than a flat to convex lateral coracoid margin as seen in *Shenqiornis*; the posterior sternal midline is distally flared into a T-shape in *Bohaiornis* rather than unflared distally in *Shenqiornis*. Finally, *Bohaiornis* is easily differentiated from *Pengornis* by morphologies of the dentition, with few robust teeth present as opposed to abundant small low-crowned dentary teeth in *Pengornis*.

Description.—The skull is preserved in left lateral view. Rostrally, the premaxillae are fused. Slender frontal processes contact the nasals rather than the frontals (Fig. 3). The left nasal is displaced anteroventrally and is partially covered by the left premaxilla. The nasal is broad, with a long premaxillary process wrapping the posterior tip of the premaxillae process. The dorsal ramus of the 'T-shaped' lacrimal is inclined slightly anteriorly. The maxilla has a well-developed dorsal process, which contacts the nasal (Fig. 3). The long axis of the antorbital fenestra is slightly longer than that of the external nares. The jugal is fused with the quadratojugal and forms a rod-like bar, slightly deflected ventrally; this feature is also seen in the holotype specimen. The posterior end of the jugal bears a small dorsally deflected process, similar to *Archaeopteryx* and *Shenqiornis* (Mayr et al., 2005; Wang et al., 2010). In *Pengornis*, preservation does not allow assessment of this morphology (Zhou et al., 2008). No postorbital is observed in *Bohaiornis*, in contrast to the well-preserved postorbital in *Pengornis*, *Shenqiornis*, and *Sulcavis* (Zhou et al., 2008; O'Connor et al., 2013). The frontals are domed and are not fused with the parietals.

At least seven scleral ossicles are visible, almost filling the orbit. They are significantly broader than those preserved in other Mesozoic birds compared, for example, *Archaeopteryx* and *Yixianornis* (Mayr et al., 2005; Clarke et al., 2006). A relatively narrow internal diameter of the scleral ring, implied by relatively broader ossicles relative to orbit length, has been one variable correlated with a diurnal activity pattern (Schmitz, 2009).

Four unserrated teeth are present in the left premaxilla, and two in the left maxilla. (Figs. 3, 5.1). The outline of the roots of the two anterior premaxillary teeth are faintly visible and appear much deeper than crown height. Both the holotype and referred specimen show similar variation in teeth size. The premaxillary teeth are slightly larger than the maxillary teeth. Maxillary teeth are restricted to its anterior half and appear to have slightly broader roots than the premaxillary teeth.
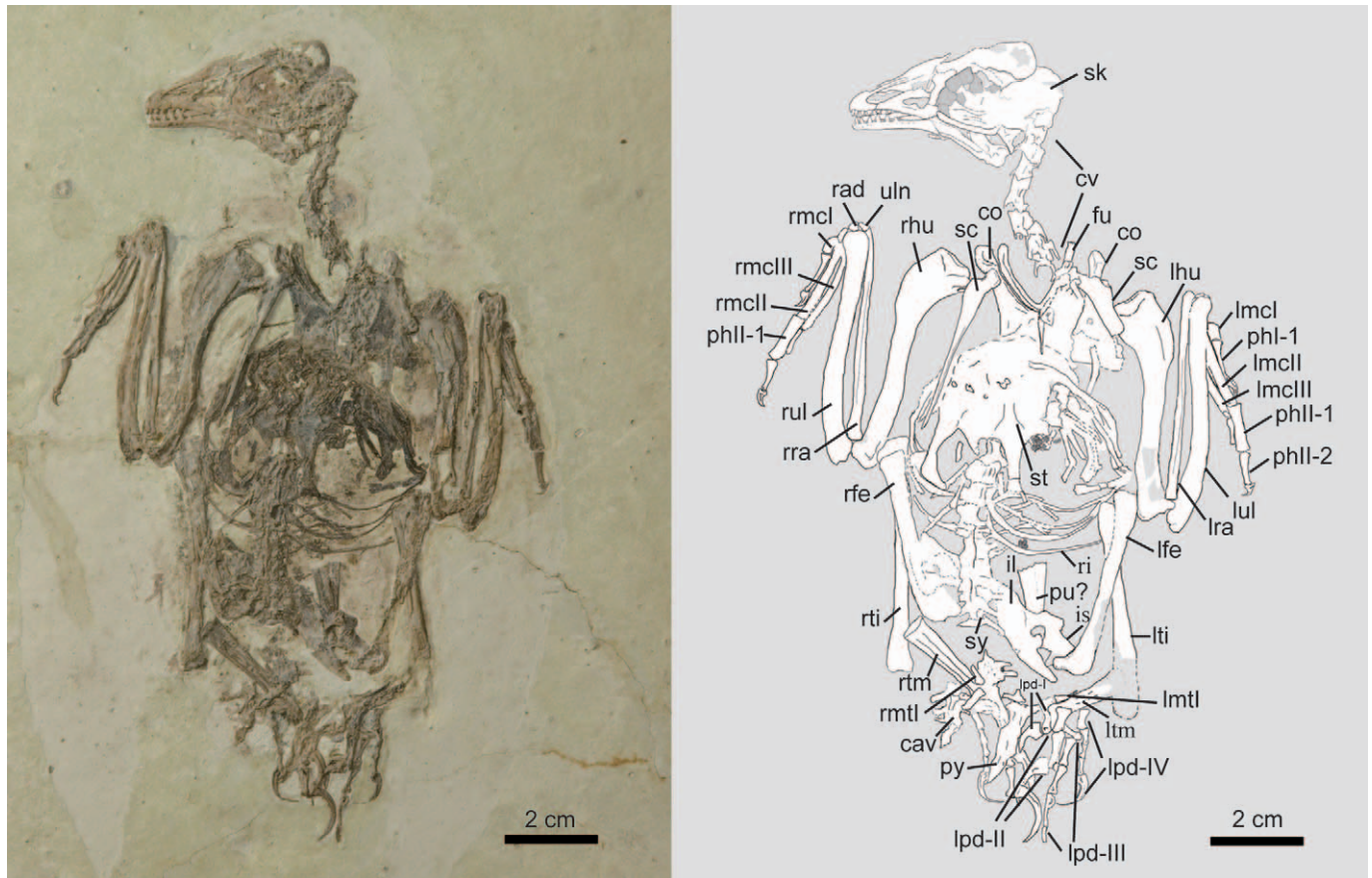
FIGURE *2*—Photograph and line drawing of the newly referred *Bohaiornis guoi* specimen (IVPP V17963). Anatomical abbreviations: ca=caudal vertebra; ce=cervical vertebra; co=coracoid; dI-1=the first phalanx of digit I; dII-1=the first phalanx of digit II; dII-2=the second phalanx of digit II; fe=femur; fu=furcula; g=gastroliths; ga=gastralia; hu=humerus; il=ilium; mcI–III=metacarpals I–III; mtI=metatarsal I; pd I–IV=pedal digits I–IV; pu? =pubis; py=pygostyle; r=radius; ra=radiale; ri=rib; sc=scapula; se=semilunate carpal; sk=skull; st=sternum; sy=synsacrum; ti=tibiotarsus; tmt=tarsometatarsus; tv=thoracic vertebra; u=ulna; ul=ulnare.

The dentary is straight and approximately half the length of the lower jaw. A line of small mental foramina are visible on its lateral surface (Fig. 3). The six dentary teeth are slightly recurved and bear weakly developed striations (Fig. 5.1). There is an apparent facet between the dentary and more posterior mandibular elements (Fig. 3), which may indicate the presence of a jointed intramandibular articulation common in enantiornithine birds (e.g., *Eoenantiornis*; Zhou et al., 2005), *Ichthyornis* and *Hesperornis* (Clarke, 2004) as well as in some non-avialan theropods (e.g., *Velociraptor*; Sues, 1977). The articular preserves a short retroarticular process and the lateral mandibular condyle (Fig. 3). The angular is slightly narrower than the surangular in lateral view.

The vertebral series is poorly preserved and partially disarticulated in the thoracic and caudal region. Seven cervical vertebrae are preserved in articulation. Three thoracic vertebrae are preserved in lateral view near the sternum. The centra of the thoracic vertebrae bear deep lateral excavations, as in other enantiornithines (Chiappe and Walker, 2002). The total number of either cervical or thoracic vertebrae is difficult to determine as both series are mostly obscured by other elements. Seven or eight fused sacral vertebrae form the synsacrum. The caudal vertebrae are disarticulated, and at least six can be identified. The pygostyle is similar to other enantiornithines (Fig. 2); it is relatively elongate, expanded at its base and tapering distally. Four sets of ribs are associated with the thoracic vertebrae and sternum. A set of five thin elements lying parallel to each other and ventral to the

ribs are interpreted as gastralia (Fig. 4). They seem to be slightly more robust than the gastralia in other avialans, for example *Cathayornis*, *Pengornis*, and *Yanornis* (Zhou et al., 2004, 2008; O'Connor and Dyke, 2010).

The sternum is exposed in dorsal view and is markedly wider than long (Figs. 2, 4). The ventral surface is flat. It has a pair of large lateral trabecula with expanded distal ends and a pair of shorter medial trabecula. A similar morphology is seen in most derived Enantiornithes. A distinct xiphoid process is not developed, and the sternal rib articulations are positioned just anterior to the divergence of the elongated lateral trabecula. There are minimally four processes with articulated sternal ribs (Fig. 4). The posterior extent of the lateral trabecula of the sternum is about the same as the posterior sternal midline, which is concave along its lateral margins and weakly flared into a T-shape at its distal terminus (Figs. 4, 5.3). The intermediate trabeculae are directed toward the sternal midline but are short and do not contact the midline to enclose a fenestra. The posterior terminus of the sternum is strongly T-shaped in *Liaoningornis* (Hou, 1997a) and *Eoalulavis* (Sanz et al., 1996), taxa which otherwise differ markedly in sternal morphology from *Bohaiornis*.

The left scapula is exposed in dorsolateral view and is much shorter in length than the humerus. The scapular blade is strongly mediolaterally compressed, and straight. The acromion is strikingly robust and about the same width as the proximal scapula; it is roughly rectangular and slightly expanded omally. The acromion appears most similar to that of an unnamed enantiornithine bird
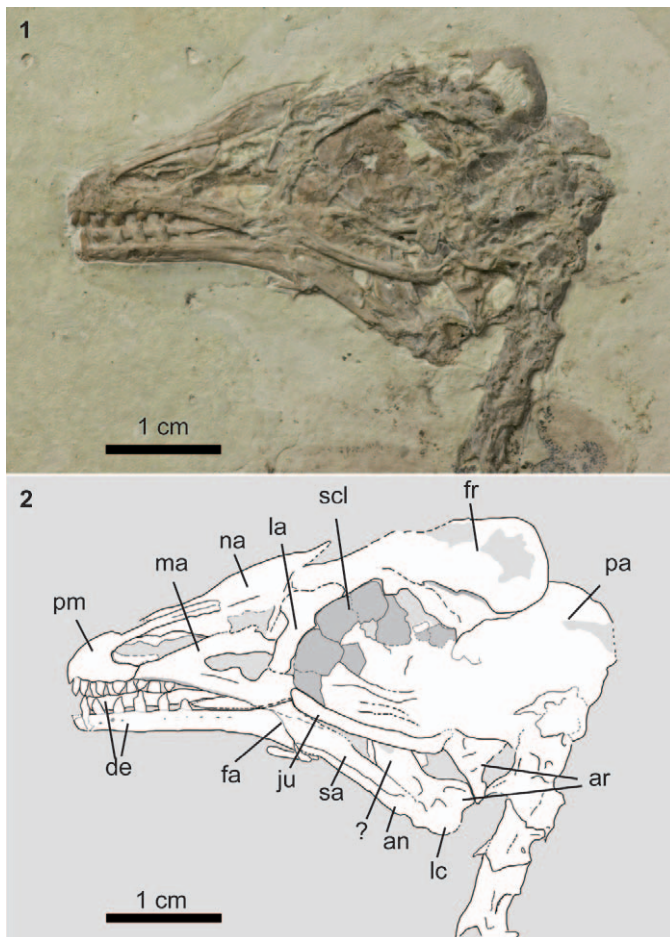
FIGURE 3—Skull of the referred *Bohaiornis guoi* specimen (IVPP V17963). *1*, photograph; *2*, line drawing. Anatomical abbreviations: an=angular; ar=articular; de=dentary; fa=facet; fr=frontal; ju=jugal; la=lacrimal; lc=lateral condyle; ma=maxilla; na=nasal; pa=parietal; pm=premaxilla; scl=scleral ossicles; sa=surangular.

described from Xiagou Formation (Early Cretaceous age and proposed to be slightly younger than Yixian or Jiufotang Formation; You et al., 2005; Lamanna et al., 2006) in Changma Basin, northwest China. The coracoids are preserved in dorsal view. Although the scapular articulation in the proximal part of the left coracoid is partially covered by the scapular acromion, the facet of coracoid visibly conformed as a prominent tubercle. The lateral margins of the coracoids are slightly concave, compared to the convex margin of more derived enantiornithine birds (e.g., *Cathayornis*). The distal lateral margin forms a convex expansion, similar to *Pengornis* (Figs. 2, 4). The dorsal surface of the coracoid is slightly concave. The acrocoracoid process is only weakly projected omally and seems to be slightly medially curved. The furcula is Y-shaped, and the hypocledium is approximately half the length of the furcular rami (Fig. 4). The angle between the two rami is about 65 degrees. The posterior surface of the furcular rami is laterally excavated, characteristic of Enantiornithes (e.g., Chiappe and Walker, 2002) while weak depressions are present in *Confuciusornis* (Chiappe et al., 1999) and other Mesozoic avialans (Zhou and Zhang, 2002, 2003b).

Both humeri are preserved in posterior view and slightly sigmoidal (Fig. 2). The humerus is approximately the same length as the ulna. The humeral head seems to be comparatively flat, differing from the globose-shaped humeral head in *Pengornis* and *Xiangornis* (Hu et al. 2012). The capital incisure appears shallow,

and the neighboring ventral tubercle is well-developed. The pneumotripital fossa is obscured by the scapula. The deltopectoral crest is projected further proximally than the humeral head. It is slightly narrower than the humeral shaft and extends approximately one-third the length of the humerus (Fig. 4). Distally, the sulcus m. scapulotricipitalis is visible on the left humerus.

The ulna is exposed in dorsal view and is slightly more than twice the width of the radius (Fig. 2). A deep longitudinal groove is present on the posteroventral surface of the radius, as in many other enantiornithines (e.g., *Neuquenornis*, *Rapaxavis*; Chiappe and Calvo, 1994; O'Connor et al., 2011a). The ulnare, radiale, and half of the semilunate carpal are covered by the distal ulna. The carpometacarpus appears to exhibit partial proximal fusion but not distal fusion, which is absent even in adult enantiornithines. Metacarpal I is short and bears a convex anterior margin. Metacarpal III is slightly curved and extends beyond the distal terminus of metacarpal II (Fig. 2). Phalanx I-1 is slim, slightly bowed, and articulates with a small recurved ungual. Phalanx II-1 has a long sub-rectangular shape and a slightly concave dorsal surface; phalanx II-2 is a little shorter and slender than II-1, followed by a small ungual (II-3) in articulation. A diminutive phalanx III-1 lies parallel to phalanx II-1.

The pelvic bones are poorly preserved and only those on the right side are visible. The left pelvic bones are crushed between the femur and the synsacrum; only a faint outline can be traced (Fig. 2). The ilium is relatively complete compared to the pubis and the ischium, of which only the proximal parts are preserved. The preacetabular ilium is expanded dorsoventrally, and is longer than the postacetabular portion. The postacetabular ilium is short, narrow and tapered distally. The antitrochanter is not strongly developed. Most of the dorsal process of the ischium is obscured by the right femoral head. As preserved, the dorsal process approaches the ventral margin of the ilium but does not contact it. Near the ilium, two broken rod-like, bony elements are interpreted as the pubes, with their distal portions covered by the ilium.

The bones of the hind limb are nearly complete (Fig. 2). The femur is straight and slightly shorter than the tibiotarsus. The trochanteric crest is weakly projected proximally. A patellar groove appears absent. The proximal tarsals are completely fused to the tibia. The distal medial condyle is slightly larger than the lateral one from the left tibiotarsus. Metatarsals II–IV appear fused with the distal tarsals. The width of metatarsals II–IV is similar, with metatarsal II just slightly wider than metatarsal IV (Fig. 2). Metatarsal II is slightly shorter than that of metatarsal IV, and metatarsal III is the longest. Metatarsal I is slender and has a J-shape similar to other enantiornithine birds (e.g., *Neuquenornis*; Chiappe and Calvo, 1994). A distinctive strongly developed plantar crest arises from approximately the midpoint of metatarsal II, extending approximately one-fifth its length.

The pedal digits are displaced in the left foot and are more articulated in the right side (Figs. 2, 5.2). In *Bohaiornis* all of the pedal unguals are very large and recurved, similar to *Sulcusavis*. The unguals are significantly larger than the penultimate phalanges. In digits II–IV, the penultimate phalanx is a little longer than the more proximal phalanges. The ungual of the hallux (digit I) and the digit II are relatively more robust in possessing a wider claw base. The ungual in digit III is the largest, but seems to be less recurved compared to the ungual in hallux or digit II, which is also clearly preserved in the holotype specimen.

Approximately 8–10 small stones are preserved in two clusters, near the posterior part of the sternum and between the thoracic ribs (Figs. 2, 4, 5.3, 5.4). They are relatively uniform in size (1–2 millimeters in diameter). There are approximately six close to the sternum, which are indurated, dark grey in color and very rounded
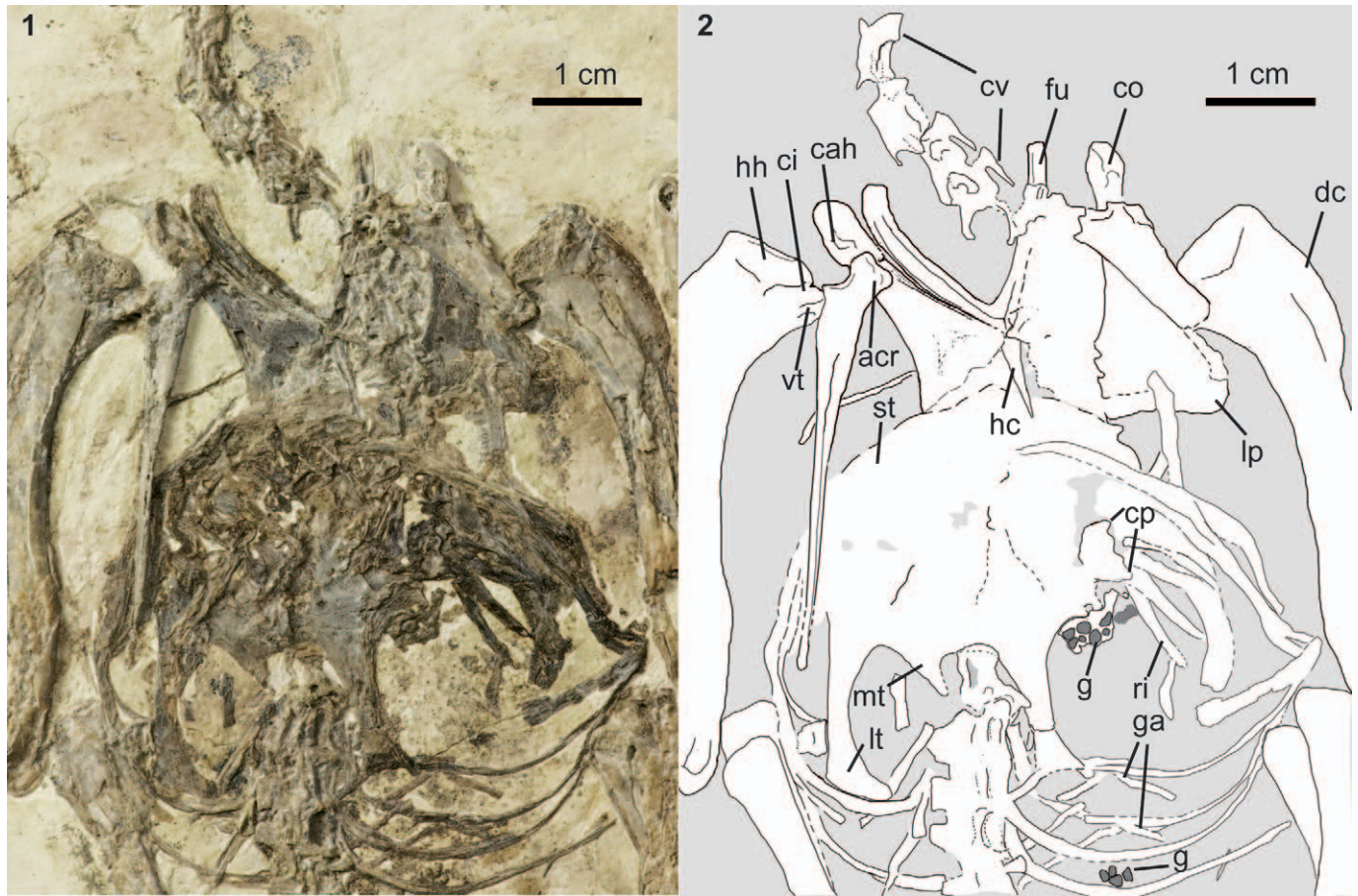
FIGURE 4—Pectoral girdle of the referred *Bohaiornis guoi* specimen (IVPP V17963). *1*, photograph; *2*, line drawing. Anatomical abbreviations: acr=acromion; ci=capital incisure; co=coracoid; ce=cervical vertebra; cp=costal process; dc=deltopectoral crest; fu=furcula; g=gastroliths; ga=gastralia; hc=hypocleidium; hh=humeral head; lt=lateral trabecula; mt=medial trabecula; ri=rib; st=sternum; vt=ventral tubercle.

(Fig. 5.3). Four slightly smaller stones are visible between two of the thoracic ribs. They are lighter grey in color and, as preserved, appear slightly more angular than the stones near the sternum (Fig. 5.4).

DISCUSSION

We reinvestigated the phylogenetic position of *Bohaiornis* using a dataset expanded and modified from that of Clarke et al. (2006) taking into account recent work on enantiornithine systematics (e.g., O'Connor et al., 2009). This dataset was revised by adding 16 additional characters (listed in online Supplemental file 1) to address morphologies present in these taxa and not encompassed by previous characters/character descriptions. A character (2) was modified from the combination of two characters (character 2 and 3) in the previous dataset. Taxonomic sampling was increased relative to Zhou et al. (2008) with the addition of four previously described basal enantiornithine birds, *Eoenantiornis* (Hou et al., 1999; Zhou et al. 2005), *Longirostravis* (Hou et al., 2004), *Longipteryx* (Zhang et al., 2001), and *Shenqiornis* (Wang et al., 2010) and two recently described ornithurines, *Longicrusavis* (O'Connor et al., 2010a) and *Jianchangornis* (Zhou et al., 2009). Thirty-six taxa were evaluated for a total of 220 morphological characters, 16 of which were newly added (see online Supplemental files 1 and 2). Heuristic searches were used given the size of the taxonomic sample. All analyses were performed using PAUP 4.0b10 (Swofford, 2003). Three thousand replicates of random stepwise addition (branch swapping: tree-bisection-reconnection) were performed holding only one tree at each step. Branches were collapsed to create soft polytomies if the minimum branch length was equal to zero. Five hundred bootstrap replicates with ten random stepwise addition heuristic searches per replicate were also performed with the same settings as in the primary analysis. Bootstrap support for those nodes recovered in greater than 50 percent of the 500 replicates performed and Bremer support values are reported to the right of the node to which they apply (Format, Bootstrap/Bremer). Bremer support values were calculated by iterative searches for suboptimal trees in PAUP 4.0b10 using the same heuristic searches as the primary analysis. Seven most parsimonious trees (MPTs) were recovered (L=567, CI=0.53, RI=0.80, RC=0.42; PIC only). In the strict consensus cladogram of resultant MPTs, *Protopteryx* was placed as the most basal enantiornithine bird, similar to the result from Zhou et al. (2008); *Longipteryx* and *Longirostravis* formed a clade consistent with previous analysis (O'Connor et al., 2009). *Bohaiornis* was placed within Enantiornithes in a basal polytomy consisting of *Eoenantiornis*, *Pengornis*, and *Shenqiornis,* the *Longirostravis*+*Longipteryx* clade and a clade including all sampled derived enantiornithines (Euenantiornithes; i.e., *Cathayornis*, *Concornis*, *Neuquenornis,* and *Gobipteryx*). Among these derived taxa, *Neuquenornis* and *Gobipteryx* formed a clade.

The new specimen increases our understanding of the complex pattern of body size variation and dentition in the
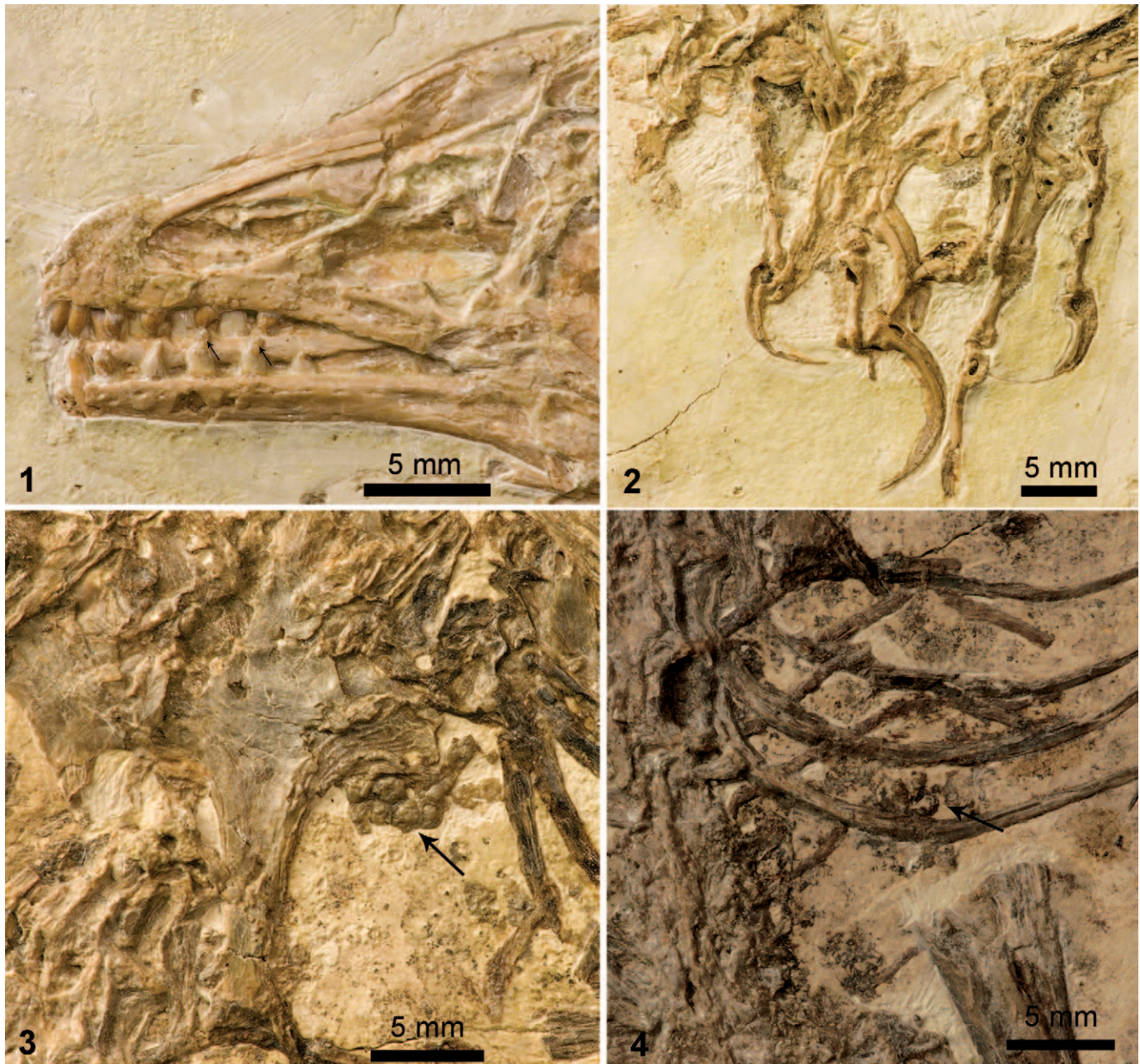
FIGURE 5—Anatomic details of the referred *Bohaiornis guoi* specimen (IVPP V17963). *1,* rostrum and dentition; *2,* recurved pedal unguals; *3*, *4,* thoracic region. Arrows indicate apparent areas of wear on the teeth in *1* as well as stones preserved near the posterior sternal margin in *3*, and between two thoracic ribs in *4*.

early evolution of Enantiornithes. While derived Early Cretaceous enantiornithines are typically small, taxa recovered close to the base of Enantiornithes from both the Yixian and Jiufotang Formations show considerable size variation. *Bohaiornis* is larger than all other enantiornithine specimens from the Jiufotang Formation except for the closely related basal forms *Pengornis* and *Xiangornis* (Zhou et al., 2008; Hu et al., 2012). It is also significantly larger than most species from the underlying Yixian Formation or older deposits, such as *Protopteryx* (Zhang and Zhou, 2000), *Paraprotopteryx* (Zheng et al., 2007), *Longirostravis* (Hou et al., 2004) and *Eoenantiornis* (Zhou et al., 2005), but only slightly larger than *Shenqiornis* (Wang et al., 2010). Both large- and small- bodied basal enantiornithines are present in the Yixian Formation, and proposed Yixian

equivalents or older geological units (e.g., Qiaotou Formation; Ji, 2004), and younger Jiufotang Formation. Strikingly, no Jehol or Jehol-equivalent enantiornithines placed in the clade of derived taxa "Euenantiornithes" (Fig. 6; Chiappe and Walker, 2002) are known to reach body sizes observed in some basal enantiornithine forms.

Dentition also shows complex variation in enantiornithine birds that is especially pronounced in basal forms. Basal enantiornithine teeth vary significantly in curvature, size, and root, with each species possessing a distinct suit of dental morphologies (O'Connor and Chiappe, 2011). From the dense, short-crowned and abundant teeth in *Pengornis*, the highly-recurved sparse anterior teeth of the Longipterygidae to the robust, distinctively-shaped and higher-crowned teeth of

TABLE *1*—Measurements (mm) of the new specimen referred to *Bohaiornis guoi* (IVPP V17963).

Skull length	47.1*
Skull height	25.5*
Orbit length	13.25*
Orbit height	11.1*
Antorbital length	8.1*
Antorbital height	3.5*
Synsacrum length	22.5†
Synsacrum maximum width	12.2†
Pygostyle length	19.2
Scapula length	36.7
Coracoid length	22.6* (right) 22.2 (left)
Coracoid distal width	10.75* (left)
Furcula length	23.6†
Furcula proximal width	16.0
Furcula, hypocleidium length	10.25†
Humerus length	51.95 (left)
Humerus, midshaft width	4.4 (right)
Ulna length	52.5 (left)
Ulna, midshaft width	4.0 (left)
Radius length	48.45 (left)
Radius, midshaft width	2.3 (left)
Carpometacarpus length	23.3* (left)
Metacarpal I	3.9 (left)
Metacarpal II length	19.45 (left)
Metacarpal III length	21.0* (left)
First phalanx of manual digit I length	19.0 (left)
First phalanx length of manual digit II	11.0 (right)
Second phalanx of manual digit II	7.25
Femur length	42.6 (right)
Tibiotarsus length	51.25 (right)
Tarsometatarsus length	22.7* (left)

* Estimated, † preserved length.

Bohaiornis, *Shenqiornis*, and *Sulcavis*, more variation is arguably seen in these basal enantiornithines than in Ornithurae or more basal avialans. *Bohaiornis* adds to this known diversity. In most enantiornithine birds, tooth reduction occurs mainly in the maxillae. For instance, the maxillary teeth in *Pengornis*, *Eoenantiornis*, *Shenqiornis*, and *Bohaiornis* are always restricted to the anterior portion of maxillae with differences in morphology and number (Zhou et al., 2005, 2008; Wang et al., 2010). They are completely lost in the Longipterygidae (e.g., *Longirostravis*, *Longipteryx* and others; O'Connor et al., 2009). By contrast, in ornithurine birds (Zhou and Zhang, 2001; Clarke, 2004; Clarke et al., 2006) a distinct pattern is seen; tooth reduction typically occurs in the anterior premaxillae. This pattern is distinct; anteriorly edentulous premaxillae are not known in Enantiornithes, and completely edentulous taxa are also more common in basal ornithurines (Norell and Clarke, 2001; Zhou and Zhang, 2005; Zhou and Zhang, 2006b) than in Enantiornithes. Furthermore, the only known edentulous enantiornithines lie within the derived Euenantiornithes clade (i.e., *Gobipteryx*; Chiappe and Walker, 2002). *Bohaiornis* adds to our understanding of known variation in dentition and presumably feeding ecology in enantiornithines, but inferences concerning its specific diet are more problematic.

Basal avialans, enantiornithine, and ornithurine birds proposed to eat seeds, fruits or other plant remains are highly varied in dentition and rostral morphology complicating proposed associations between morphology and diet (see summarization in Table 2). The basal avialan *Sapeornis*, known from specimens with crops filled with seeds (Zheng et al., 2011), has a short rostrum and large premaxillae teeth with reduced maxillary teeth and no dentary teeth (Zhou and Zhang, 2003b). *Jeholornis*, also known with large seeds in the gut region (Zhou and Zhang, 2002) has tiny maxillary and anterior dentary teeth with an edentulous premaxilla and posterior dentary (Zhou and Zhang, 2002, 2003a; O'Connor et al., 2012). By contrast, the ornithurine *Yanornis*, with one specimen with abundant

gastroliths, has an edentulous premaxillary tip but otherwise dense dentulous premaxilla, dentary and maxilla (Zhou et al., 2004). Another specimen of this taxon shows fish remains in the gut region and possible evidence of diet switching, which is common in living birds (Zhou et al., 2002, 2004). Other ornithurines, *Hongshanornis* and *Archaeorhynchus* are fully edentulous but proposed to be herbivorous based on the large number of gastroliths preserved in the abdominal area (Zhou and Zhang, 2006b; Zheng et al., 2011). *Pengornis* is the only enantiornithine proposed to have a herbivorous diet based on its unusual tightly-packed, low-crowned dentary teeth with apparent posterior wear facets (Zhou et al., 2008).

Proposed piscivorous taxa (i.e., *Confuciusornis*, *Longipteryx*, *Yanornis*, and *Jianchangornis*) also have diverse dentitions (see Table 2). Fish remains in the esophageal or thoracic region are known from only two Jehol specimens, one specimen of the edentulous basal avialan *Confuciusornis* (Dalsätt et al., 2006) and one of the ornithurine, *Yanornis*, with only an edentulous premaxilla tip and otherwise dense dentition (Zhou et al., 2002; see above). The basal ornithurine *Jianchangornis* also has abundant small and conical teeth and was proposed to be possibly piscivorous based on disarticulated fish remains surrounding the skeleton (Zhou et al., 2009). In Enantiornithes only part of Longipterygidae has been proposed to be piscivorous, deploying "kingfisher-like" fish capture with the tip of the rostrum (Zhang et al., 2001; O'Connor et al., 2010b). Kingfishers (Alcedines), however, have varied dietary preferences including insects, mammals and lizards as well as fish, and Longipterygidae taxa with similarly restricted anterior premaxillae and dentary dentitions and rostral morphologies were alternately proposed to be used in probing for invertebrates (Hou et al., 2004).

Occurrence of grit or gastroliths is not only associated with the dietary preferences in avian species but also relevant to their feeding ecology in Aves. Gastroliths or grit are generally found in gizzards of primarily herbivorous or granivorous birds, and only a few insectivorous birds (Gionfriddo and Best, 1996). Ground feeders tend to be more likely to accumulate large amount of gastroliths compared to aerial or arboreal feeders (Gionfriddo and Best, 1996). All reported Mesozoic birds and theropod relatives with the associated gastroliths have been proposed to be herbivorous, included basal ornithurines (e.g., *Yanornis* and *Archaeorhynchus*), the oviraptosaur *Caudipteryx*, and the ornithomimosaur *Shenzhousaurus* (Zhou et al., 2011). Although represented by hundreds of avialan specimens recovered from the Jehol Biota with proposed dietary preferences as seeds and insects, such as *Jeholornis*, *Confuciusornis*, and many enantiornithines, no obvious gastroliths accumulations are reported from these taxa so far. However, compared to the clusters of gastroliths that are preserved in basal ornithurines (i.e., *Archaeorynchus*, *Yanornis*, and *Hongshanornis*; Zhou et al., 2004; Zhou and Zhang, 2006b; Zheng et al., 2011), the stones in *Bohaiornis* are significantly less in number, and show less variation in size, shape and angularity. Individual gastroliths in *Yanornis* vary in diameter from less than 0.2 mm to 2.7mm and are subrounded as well as angular. These findings are consistent with recent experimental data that gizzard stones in herbivorous birds experienced fast abrasion, but no significant rounding or polish developed (Wings and Sander, 2007). Since the stones in *Bohaiornis* show quite different occurrence in number, shape, and color from other typical gastroliths from herbivorous and granivorous birds, the presence of a gastro-mill in *Bohaiornis* is not considered to be well supported.
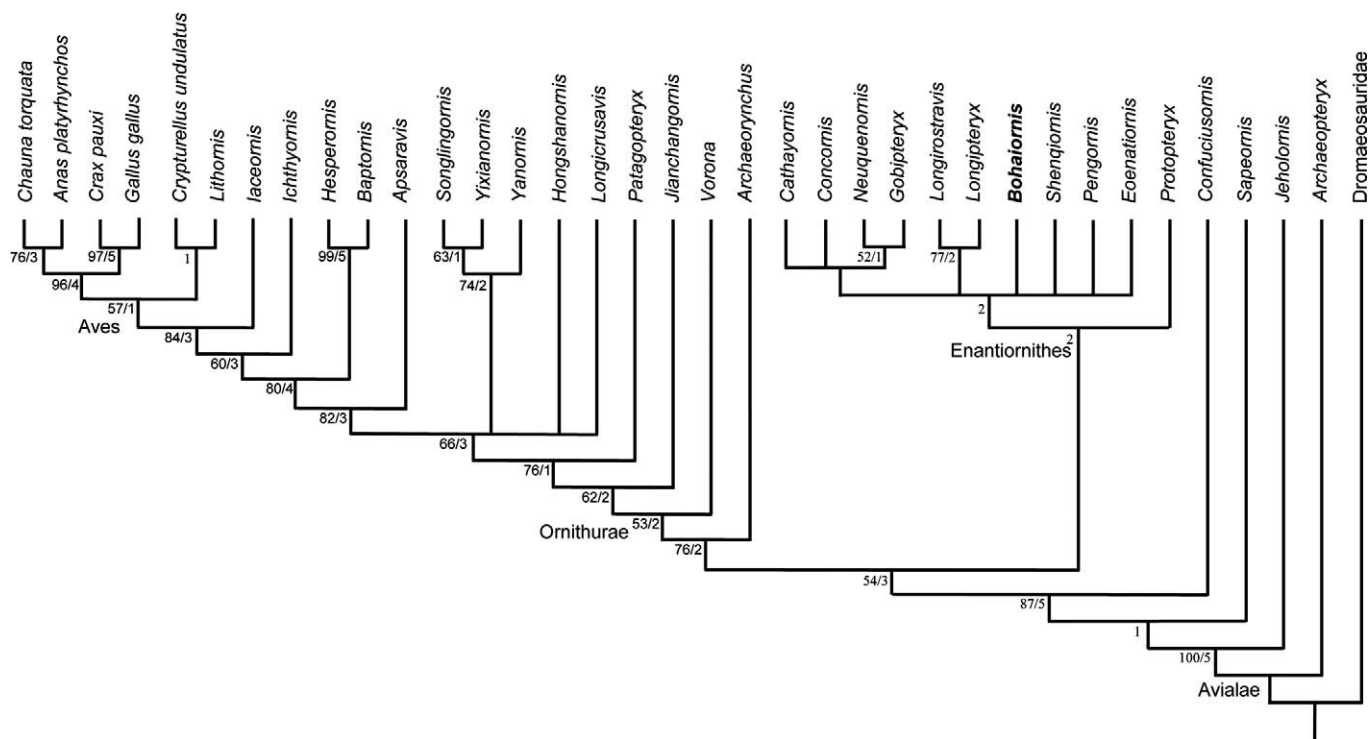
FIGURE 6—The phylogenetic placement of *Bohaiornis guoi* as a basal enantiornithine recovered in the strict consensus cladogram of seven most parsimonious trees (L=567, CI=0.53, RI=0.80, RC=0.42; PIC only) resulting from analysis of 220 (207 PIC) characters and 36 taxa.

Extant raptorial birds are known to regularly consume small numbers of very round stones (referred to as rangle; Albuquerque, 1982) that have been proposed to have a purging function in stomach (Wings, 2007). The morphology and smaller number of the stomach stones in *Bohaiornis* appear consistent with a feeding ecology similar to these predominantly carnivorous taxa. Other explanations for the presence of the stones such as accidental ingestion or ingestion for dietary supplementation (e.g., for salt or other minerals) are unsupported by other unambiguous anatomical data from the specimen. However, we cannot rule out these explanations. Accidental ingestion occurs in carnivorous taxa but is most common in ground feeding taxa (Wings, 2004). *Bohaiornis* has, for example, robust highly recurved claws and shows no other modifications consistent with such an ecology. Consumption of stones for their mineral content is generally, but not exclusively, associated with a low salt folivorous or frugivorous diet (e.g., parrots, tortoises). Soil and soft clays, unlike the preserved elements in *Bohaiornis*, are preferred for supplementation for obvious reasons (i.e., ease of absorption).

More recent discoveries of several enantiornithines (e.g., *Shenqiornis* and *Sulcavis*) with robust rostrum as well as teeth may imply similar dietary preferences for these taxa. The teeth in *Bohaiornis* are robust compared to most other enantiornithine birds (e.g., *Cathayornis*, *Protopteryx, Longipteryx,* and *Pengornis*) but are very similar to those present in *Shenqiornis* and *Sulcavis*, which were proposed to be adapted for hard food (e.g., insectivorous or durophagous) (Wang et al., 2010; O'Connor et al., 2013). Most enantiornithines have been inferred to be insectivorous or mixed feeding forms in part based on their small body-size and the forested Jehol environment (Zhou and Zhang, 2006a). Though with a relatively similar dentition and presumed diet, the presence of unusual stomach stones in *Bohaiornis*, which are rarely associated with insectivory in Aves (Potter, 1983), complicates this proposed inference.

CONCLUSIONS

Intriguingly, despite the array of proposed hypotheses concerning dentition, rostral morphology and diet, no Mesozoic avialans have previously or are currently hypothesized to comprise raptorial carnivorous taxa. A raptorial feeding ecology was inferred for the small enantiornithine bird, *Boluochia* (Zhou, 1995), in which the premaxilla was misinterpreted to be hooked due to poor preservation (O'Connor et al., 2010a). Proposed indicators of a raptorial ecology in *Boluochia* and *Sinornis* included strongly recurved pedal claws (Hou, 1997b; Zhou and Hou, 2002). However, claw morphology is generally similar to other Enantiornithes and *Confuciusornis* and is alternatively interpreted as related to perching and arboreal locomotion (Chiappe and Walker, 2002). Raptorial behavior is often inferred from non-avialan paravians (e.g., dromaeosaurids) rather than Avialae, some based on direct evidence of diet (O'Connor et al., 2011b). We suggest that although *Bohaiornis* could be the first raptorial avialan, overall this ecology may be extremely rare and possibly consistent with a competitive exclusion hypothesis of Mesozoic avialans from the latter ecology by non-avialan paravians. This hypothesis will be extremely difficult to test.

Extant birds exhibit an incredible variety of carnivores and carrion eaters, picivorous taxa, insectivores, mixed feeders, seed-specialists, folivores, frugivores and specialists on small invertebrates and an even greater variation in feeding ecology. Rostrum shape and foot morphology vary widely and have been related to major food resources utilized and feeding ecology (Storer, 1971; McLelland, 1979; Gill, 2007). While for some feeding ecologies and morphologies of raptorial birds such as eagles, hawks and falcons, owls and vultures with hooked bills and strong pedal unguals or talons (Storer, 1971), this

TABLE 2—Previously proposed specialized diet of Mesozoic birds from Jehol Group with the related supporting evidence.

Taxon	Specialized diet	Morphological evidence	References
Pengornis houi	herbivorous or soft food items	tightly-packed, low-crowned teeth	Zhou et al., 2008; O'Connor and Chiappe, 2011
Longipteryx chaoyangensis	piscivorous	highly-recurved sparse anterior teeth	Zhang and Zhou, 2001
Longirostravis hani	probing for invertebrates	long and slender bill with small recurved anterior teeth	Hou et al., 2004
Shenqiornis mengi	hard food (e.g., insectivorous or durophagous)	robust rostrum and teeth	Wang et al., 2010
Sulcavis geeorum	hard food (e.g., insectivorous or durophagous)	robust rostrum and teeth, enamel macrostructures	O'Connor et al., 2013
Sapeornis chaoyangensis	herbivorous (seeds)	short rostrum and large premaxillae teeth, gut content	Zhou and Zhang, 2003b; Zheng et al., 2011
Jeholornis prima	herbivorous (seeds)	edentulous premaxilla and posterior dentary, gut content	Zhou and Zhang, 2002
Confuciusornis sanctus	piscivorous	fully edentulous, gut content	Dalsätt et al., 2006
Yanornis martini	seasonal dietary switching (plant and fish)	gastroliths, edentulous premaxillary tip, gut content	Zhou et al., 2002, 2004
Jianchangornis microdonta	piscivorous	abundant small and conical teeth, fish remains surrounding the skeleton	Zhou et al., 2009
Hongshanornis longicresta	herbivorous (seeds)	fully edentulous, gastroliths, gut content	Zheng et al., 2011
Archaeorhynchus spathula	herbivorous	fully edentulous, gastroliths	Zhou and Zhang, 2006b

relationship may be relatively clear. For many other avian taxa, relationships between feeding morphologies and dietary preferences are more complicated or not yet studied in detail. For non-crown clade extinct birds it is arguably even more difficult to predict diet or feeding habit from skeletal evidence. Any relationships observed in crown birds may not hold for stem taxa. Further, stem taxa are non-analogous in the retention of plesiomorphic contacts and relative proportions of skull elements, and many taxa have lost teeth in crown Aves.

Dietary correlates of tooth loss in Avialae have been the topic of abundant speculation for individual taxa (e.g., Hou et al., 2004; Wang et al., 2010; O'Connor and Chiappe, 2011; Table 2) but there is little data to inform any potential relationship of this and other characters of bird (and other dinosaur) dentition. One recent quantitative study of proposed morphological correlates with other indicators of a herbivorous diet focused non-avialan theropod dinosaurs (Zanno and Makovicky, 2011). Associations between dental heterogeneity, reduction of teeth, and a herbivorous diet were recovered. A rigorous study of avialan dentition with dense taxonomic sampling expanding on the work of Zanno and Makovicky (2011) may provide important data to constrain inferences concerning the relationship between variation in diet and dentition. Plesiomorphic ontogenetic constraint on rostral shape (Bhullar et al., 2012) should also be taken into account. It may explain why diversity in dentition appears to exceed diversity in rostrum shape in early avialans.

ACCESSIBILITY OF SUPPLEMENTAL DATA

Supplemental data deposited in Dryad repository: http://dx.doi.org/10.5061/dryad.5fs6j.

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