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Novel evolution of a hyper-elongated tongue in a Cretaceous enantiornithine from China and the evolution of the hyolingual apparatus and feeding in birds

Zhiheng Li^{1,2} | Min Wang^{1,2} | Thomas A. Stidham^{1,2,3} | Zhonghe Zhou^{1,2,3} | Julia Clarke⁴

¹Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China

²CAS Center for Excellence in Life and Paleoenvironment, Beijing, China

³University of Chinese Academy of Sciences, Beijing, China

⁴Department of Geological Sciences, University of Texas at Austin, Austin, Texas, USA

Correspondence

Zhiheng Li, Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xizhimenwai Street, Beijing 100044, China.

Email: lizhiheng@ivpp.ac.cn

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Abstract

The globally distributed extinct clade Enantiornithes comprises the most diverse early radiation of birds in the Mesozoic with species exhibiting a wide range of body sizes, morphologies, and ecologies. The fossil of a new enantiornithine bird, *Brevirostruavis macrohyoideus* gen. et sp. nov., from the Lower Cretaceous Jiufotang Formation in Liaoning Province, northeastern China, preserves a few important skeletal features previously unknown among early stem and extant birds, including an extremely elongate bony hyoid element (only slightly shorter than the skull), combined with a short cranial rostrum. The long hyoid provides direct evidence for the evolution of specialized feeding in this extinct species, and appears similar to the highly mobile tongue that is mobilized by the paired epibranchials present in living hummingbirds, honeyeaters, and woodpeckers. The likely linkage between food acquisition and tongue protrusion might have been a key factor in the independent evolution of particularly elongate hyobranchials in early birds.

KEYWORDS

bony hyoid, Enantiornithes, feeding, Jehol Group

1 | INTRODUCTION

Enantiornithes are the most diverse clade of birds known in the Cretaceous, and they have a nearly global distribution (Chiappe & Walker, 2002; Wang & Zhou, 2017). While a large number of enantiornithine species have been recognized, the phylogenetic relationships among these taxa remain highly debated (O'Connor et al., 2009). Enantiornithine evolution spans much of the Cretaceous with their earliest records dating back to the late Early Cretaceous, and last fossils from near the end-Cretaceous mass extinction (O'Connor et al., 2011). Well-preserved skeletons of enantiornithines are known from Europe, North and South America, Africa, and Asia, in

particular fossil sites of the Early Cretaceous Jehol Biota exposed in Western Liaoning Province in China (Chiappe & Walker, 2002). These spectacular fossils have not only expanded our understanding of the morphological disparity within the clade, but they also provide direct evidence regarding their integument, ontogeny and growth, digestive and reproductive systems, and feeding ecology (Wang et al., 2016b; Zheng et al., 2013, 2018; Zhou, 2014). Features that consistently optimize as synapomorphies of the Enantiornithes include the extremely elongate hypocleidium on the furcula, a minor metacarpal that extends further distally than the major metacarpal, and a long coracoid with a convex lateral margin (Chiappe & Walker, 2002). While enantiornithines occupied a variety of habitats around

the world, most Jehol enantiornithines are considered to have been arboreal specialists living within a forest environment, interspersed with inland lakes (Zhou et al., 2003).

A coupled hyper-elongated hyolingual apparatus and beak occur in hummingbirds, honeyeaters, and woodpeckers in which their tongue and the elongated beak are both proportionally longer. Within crown birds, beak/rostrum length appears to be correlated in general with the length of the tongue. Other striking examples of this morphological association are revealed by the flat and wide beak and tongue apparatus in most filtering-feeding anatids (Li & Clarke, 2016). Here, we report a new enantiornithine fossil from the Early Cretaceous Jiufotang Formation (~120 Ma) in Liaoning Province, China. The new specimen reveals a few important skeletal features otherwise unknown among stem and extant birds, including an extremely elongate hyoid apparatus in combination with a short rostrum, variable cervical articulation, a cranio-lateral process of the sternum, and an asymmetric trochlea of metatarsal III. We trace the evolution of hyoid bony elements across Avialae, and hypothesize that the derived states of the hyolingual apparatus evolved independently among the stem bird lineages reflecting different patterns of morphology and function. While ornithurine birds (including all living species) have a tongue supported by separate elongate epibranchials, this new enantiornithine unexpectedly possesses a pair of extremely elongated ceratobranchials instead.

Within non-pygostylian theropods, there are a few taxa with unusual preservation of hyoid bones reported from time to time, including those of *Shuuvia*, *Citipati*, *Sciurumimus*, and *Carnotaurus* (Cerroni et al., 2020; Chiappe et al., 1998; Clark et al., 2002). Among these theropods, *Citipati* is a taxon with robust hyolingual bones that extend for more than half of the length of the skull. The robust hyoid elements might indicate that this beaked dinosaur evolved aspects of hyolingual feeding associated with a bird-like dietary adaptations for omnivory or herbivory (Zanno & Makovicky, 2010). The reported ossified basihyal of *Carnotaurus* is another example of derived hyolingual feeding as indication of its independent acquisition of the ossified midline element, as well as a pair of curved shaped ceratobranchial elements potentially used for food swallowing in late theropod evolution.

Re-evaluation of known enantiornithines suggests some other species (e.g., *Sulcavis geeorum*) have a similar long hyoid configuration (O'Connor et al., 2013). It appears that the independent evolution of the elongation of the hyoid apparatus through different pathways among different Early Cretaceous bird lineages as well suggests that novel feeding adaptations and homoplasy played a critical role in early avian hyolingual evolution.

2 | MATERIALS AND METHODS

In order to explore the phylogenetic relationship of IVPP V13266 (the holotype) with respect to other enantiornithines and early avialans, we performed phylogenetic analyses using a previously published data matrix (Wang et al., 2015). In addition to IVPP V13266, we added information from two recently described enantiornithine

taxa *Pterygornis dapingfangensis* and *Cruralispennia multidonta*, and the character scorings for these two taxa follows that of previous studies (Wang et al., 2017a, 2017b). The modified data set contains 61 taxa (58 Mesozoic bird species) and 262 morphological characters. Phylogenetic analyses were performed using the TNT software package (Goloboff et al., 2008) with the following settings: all characters were equally weighted; 33 characters were ordered as in a previous study (Wang et al., 2015); an unconstrained heuristic search with Wagner trees as the starting tree was performed; and 1000 replicates of random stepwise addition (branch swapping trees: tree-bisection-reconnection, TBR), with ten trees saved at each step; and branches were collapsed to create polytomies if the minimum branch length was zero. We calculated the absolute Bootstrap and the Bremer values as the supporting indices of the corresponding nodes. Bootstrap values were obtained after 1000 replicates in TNT using the default setting. Bremer values were calculated using the Bremer script embedded in the TNT program.

3 | SYSTEMATIC PALEONTOLOGY

Aves Linnaeus, 1758.

Enantiornithes Walker, 1981.

Brevirostruavis macrohyoideus gen. et sp. nov.

3.1 | Holotype

IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China) V13266 is a nearly complete skeleton preserved on a single slab (missing part of the humerus and the pelvic elements), with associated traces of preserved integument around the body (Figures 1–4).

3.2 | Etymology

The genus name refers to its short rostrum (and bird), and the specific epithet refers to the particularly long hyoid apparatus.

3.3 | Locality and horizon

Xiaotaizi Village, Jianchang County, Liaoning Province, China; Jiufotang Formation, Lower Cretaceous. Age approximately 120 Ma (He et al., 2004).

3.4 | Diagnosis

A medium-sized enantiornithine that is distinguished from all known enantiornithines based on the unique combination of the following features: a short and pointed skull rostrum lined with small

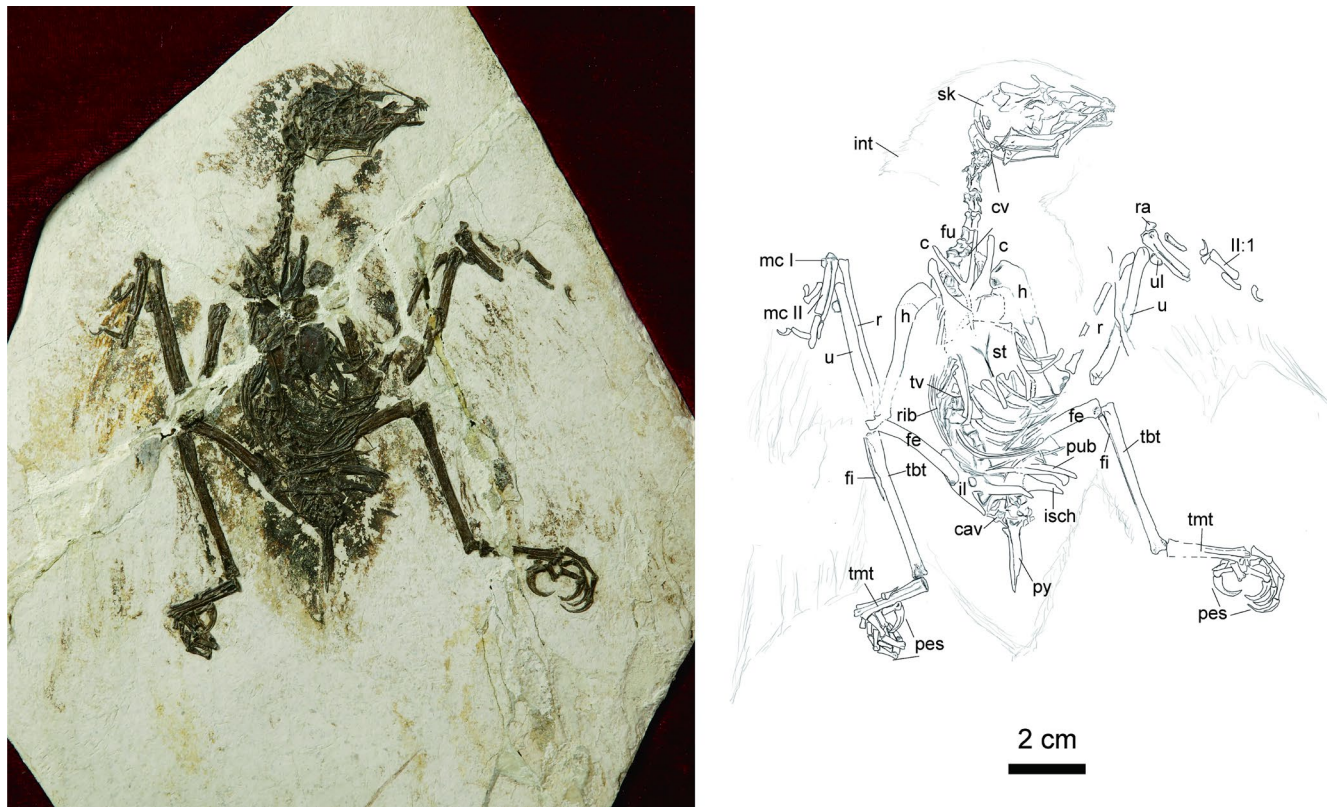


FIGURE 1 Photograph and line drawing of the body of the holotype specimen of *Brevirostruavis macrohoyoideus* (IVPP V13266).

Anatomical abbreviations: c, coracoid; cav, caudal vertebrae; cv, cervical; fe, femur; fi, fibula; fu, furcula; h, humerus; il, ilium; isch, ischium; int, integument; mc I, alular metacarpal; mc II, major metacarpal; pub, pubis; py, pygostyle; r, radius; ra, radiale; sk, skull; st, sternum; tbt, tibiotarsus; tv, thoracic vertebrae; tmt, tarsometatarsus; u, ulna; and ul, ulnare

peg-shaped teeth; a pair of extremely long ceratobranchials, only slightly shorter than the skull length (see Table 1); a sternum with well-extended cranio-lateral processes; lateral trabeculae of the sternum with expanded triangular processes at the caudal ends; elongate prezygapophyses of the cranial cervical vertebrae; postzygapophyseal facet of the axis is tear-drop shaped; third cervical vertebra with sub-rounded articular facet of the postzygapophyses; ischium bearing a pronounced proximodorsal process; distal tibiotarsus with a knob on its cranial surface; length ratio between the fibula and tibiotarsus approximately 0.7; tarsometatarsus about half of the length of the tibiotarsus; medial rim of metatarsal trochlea III larger than the lateral rim; and pedal digit-I more robust than other pedal digits.

4 | DESCRIPTION AND COMPARISONS

Except for part of humerus and tarsometatarsus, nearly all of the skeletal elements are well-preserved, but a halo of feather impressions are poorly preserved surrounding the body. The whole skeleton is exposed ventrally except for the skull. The skull of IVPP V13266 is preserved mainly in lateroventral view, and it has been heavily compressed (Figure 2). The short premaxillae are fused only rostrally (Figure 2: pm). The nasal processes of the premaxillae are long and slim. The wide pterygoid has a wedge-shaped rostral

margin (Figure 2). The jugal bar is dorsoventrally expanded, and it is deflected dorsally and narrows toward its caudal end, as in other enantiornithines like *Bohaiornis* (Li et al., 2014). The descending ramus of the right lacrimal is significantly longer (Figure 2: dr) and more robust than the dorsal ramus with its thin dorsal ridge. A tiny depression appears present in the center of the lacrimal. The nasal is morphologically similar to that of *Eoenantiornis*, with a pointed premaxillary process. A rounded square-shaped parietal is preserved caudal to the basicranium (Figure 2: pa). The left dentary is exposed in medial view, and has seven visible teeth. The rostral tip of the dentary seems to bend dorsally. There are four small teeth on each side of the premaxillae (Figure 2: to), and these teeth have a rounded crown and constricted base. Only three teeth are present in the right maxilla, and they are restricted to its rostral portion.

The frontals are fused to one another, and only part of the left parietal is visible because of the significantly crushed preservation. The quadrate body is very slender as in most other enantiornithines, but the otic head is distinctly inflated relative to the mediolateral diameter of the quadrate body. The mandibular process is greatly enlarged medially and laterally relative to the quadrate body, and the lateral mandibular condyle is wider than the medial. Though broken and largely covered, there appears to be at least a partial lateral crest on the quadrate as in *Longipteryx* (Stidham & O'Connor, 2021). Adjacent to the mandibles, a pair of dorsally curved hyoid apparatus

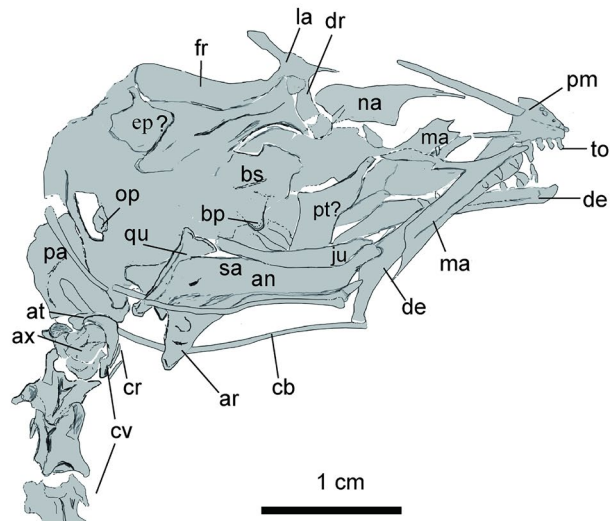


FIGURE 2 Photograph and line drawing of the skull of the holotype specimen of *Brevirostruavis macrohyoideus* (IVPP V13266). Anatomical abbreviations: an, angular; ar, articular; at, atlas; ax, axis; bp, basisphenoid process; bs, basisphenoid; cb, ceratobranchial; cr, cervical rib; cv, cervical; de, dentary; dr, descending ramus; ep?, ectopterygoid?; fr, frontal; la, lacrimal; ju, jugal; ma, maxillae; na, nasal; op, occipital process; pa, parietal; pm, premaxilla; pt?, pterygoid?; qu, quadrate; sa, surangular; and to, tooth

bones (Figure 2: cb) are markedly elongate with spatula-shaped caudal ends. The rostral ends of these ceratobranchials have concave surfaces, and are separated from one another. While the caudal portion of the ceratobranchials curve significantly dorsally, their more rostral portion appears to have been possibly concave ventrally. The distorted mediolateral width of the foramen magnum is twice that of its dorsoventral height.

Ten cervical vertebrae are preserved, including the atlas and axis preserved in articulation in ventral view (Figures 1 and 2). Only the dorsal portion of the atlas is preserved with a slender pointed lateral process. The axis is markedly wider than its length, and the odontoid process overlies the ventral corpus of the atlas (Figure 2). A low ventral ridge is present on the axis. The articular facet of the axis postzygapophyses are crescent shaped, differing from the rounded shape in the more caudal cervicals (Figures 2 and 3). The variation

in the shape of the articular facets between the second and more caudal postzygapophyses might be indicative of the evolution of an “S-shaped” curved neck evident among living birds (Kambic et al., 2017).

The prezygapophyses of the 3rd and 4th cervicals project cranially beyond the centra by a distance that is approximately half of the craniocaudal length of the respective centrum, a feature unknown in other enantiornithines. Moving caudally along the cervicals, the prezygapophyses become shorter and are subequal with the length of the postzygapophyses. The 4th to the 7th cervicals are longer than both the cranial and caudal ones in the neck (Figure 1). The ventral surfaces of the cervicals are keeled. Carotid processes are present on the 6th cervical, but the distribution of the processes among the other cervicals is obscured. Two short cervical ribs are displaced from the cervical axis (Figure 2). At least four paired long curved ribs

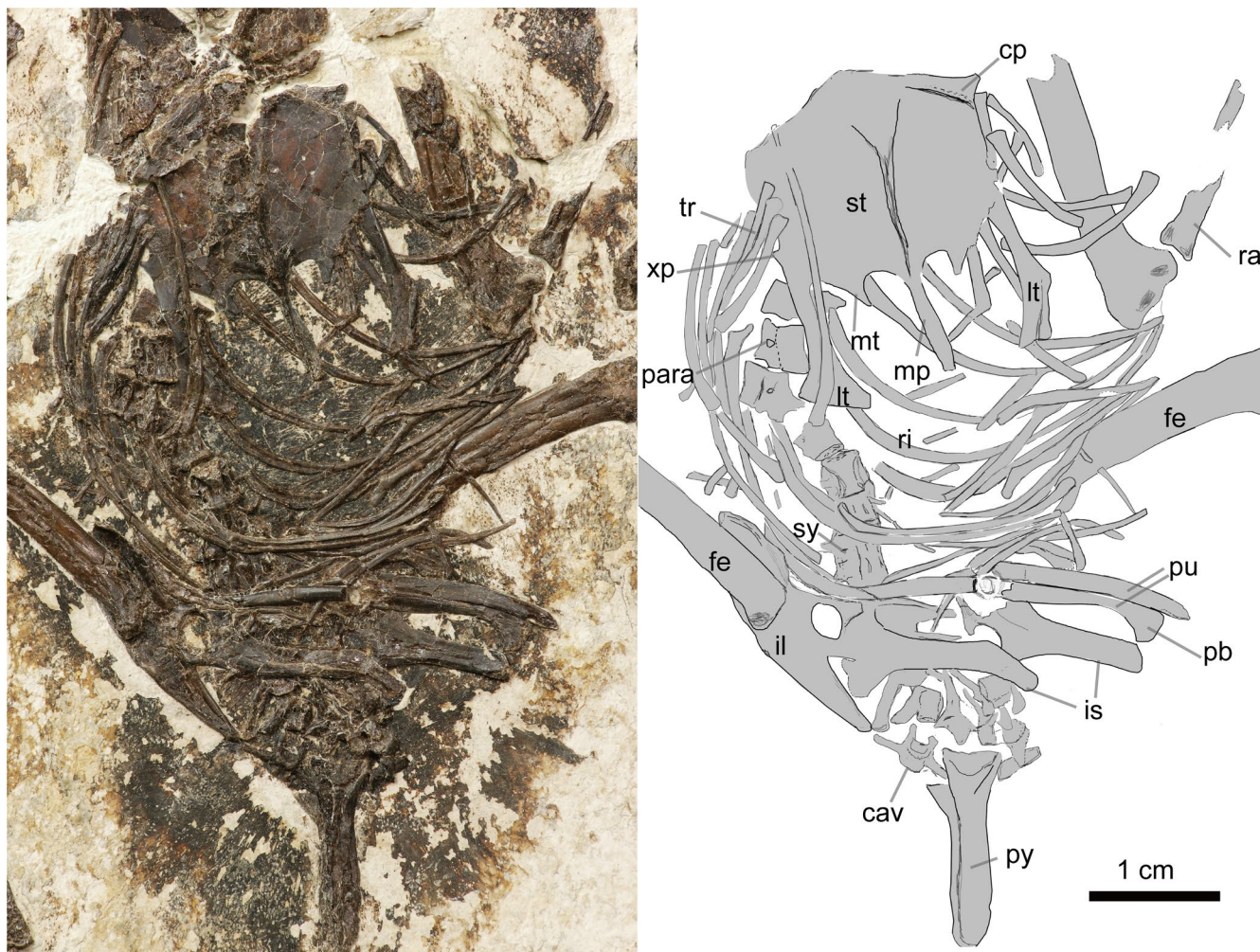


FIGURE 3 Photograph and line drawing of the sternum and pelvic girdle of the holotype of *Brevirostruavis macrohioideus* IVPP V13266. Anatomical abbreviations: cav, caudal vertebrate; cp, cranial lateral process; fe, femur; il, ilium; is, ischium; lt, lateral trabecula; mp, middle process; mt, medial trabecula; para, parapophysis; pb, pubic boot; pu, pubis; py, pygostyle; ra, radius; st, sternum; sy, symsacrum; tr, thoracic rib; and xp, xiphoid process

are associated with the lateral edge of the sternum. These sternal ribs are quite robust, bearing a medium depth on the shaft. A few gastralia are present.

Four caudal thoracic vertebrae are preserved cranial to the symsacrum (Figure 3). The parapophysis is centrally located on the lateral face of the centra, similar to the typical condition among Enantiornithes (Figure 3: para). The symsacrum is composed of about seven to eight vertebrae. Approximately five free caudal vertebrae are piled up together with markedly long transverse and ventral processes (Figure 3: cav). The long pygostyle has a pair of dorsal processes and a pointed caudal end.

The mediolateral width of the sternal plate is slightly longer than its craniocaudal length. The sternal keel is low, and diverges into two low ridges cranially, a feature only observed in enantiornithines (e.g., Martin 2011). Craniolateral processes project from the lateral edge of the sternum (Figure 3: cp) with a gentle slope transitioning between this process and the carinal sulcus. The craniolateral processes are rarely developed in Early Cretaceous enantiornithines with a few exceptions, including *Pteryornis* and *Concornis* (Wang et al., 2016a,

2017a; Zheng et al., 2012), and they have been proposed to form from ossification centers separate from the main sternal body.

Lateral and intermediate trabeculae are present on the caudal margin of the sternum (Figure 3). The lateral trabecula bears a large distal flare, and the intermediate one deflects toward the midline (Figure 3: lt). The sternal keel extends as far caudally as the lateral trabecula, similar to the condition in *Protopteryx* and *Cathayornis yandica* (Wang & Liu, 2016). The slim furcular rami form a sharp angle of approximately 45° (Figure 1: fu). The hypocleidium is less than half of the length of the ramus. The strut-like coracoids have a rounded, slightly raised acrocoracoid, and lack a procoracoid process. The lateral margin of coracoids appears to be straight or slightly concave (Figure 1). Only the proximal end of the scapula is exposed in medial view without any identifiable details (Figure 1).

The humerus preserved in ventral view, and has a narrow deltopectoral crest. The humeral head appears to be strip-like with a shallow transverse groove. The dorsal condyle is rounded, and more clearly defined than the ventral one. A small dorsal supracondyle is present. The ulna has a narrow m. brachialis scar proximally, and

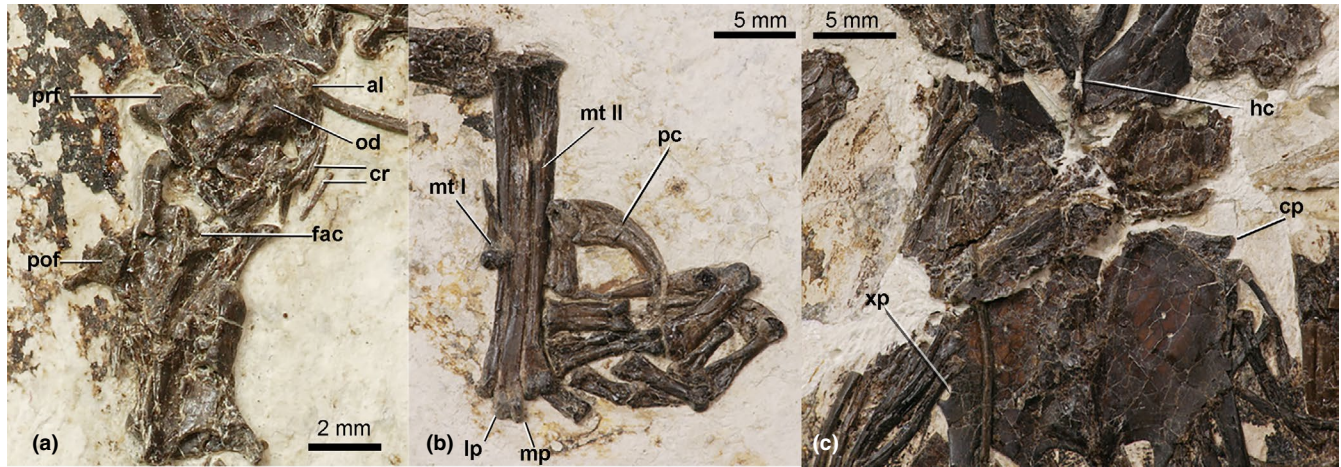


FIGURE 4 Photograph of cervical vertebrae (a), tarsometatarsus (b), and sternum (c) of the holotype of *Brevirostruavis macrohyoideus* (IVPP V13266) with features described in the text. Anatomical abbreviations: cr, cervical rib; cp, cranial lateral process; hc, hypocleidium; lp, lateral process; prt, facet of prezygapophysis; pof, facet of postzygapophysis; mt I, metatarsal I; mt II, metatarsal II; mp, medial process; od, odontoid process; pc, pedal claw; and xp, xiphoid process

the radial depression distally. The dorsal and the ventral rami of the ulnare are slightly differentiated, with the ventral one slightly larger. The semilunate carpal is fused with the proximal ends of the major and minor metacarpals. The carpometacarpi are preserved in ventral view and the infratrochlear fossa is visible. The alular metacarpal is short and partially fused with the major metacarpal. The proximal phalanx of the alular digit is short, less than half of the length of the major metacarpal. The minor metacarpal is slightly bowed and extends distally beyond that of the major metacarpal. The major and minor metacarpals have only a slim intermetacarpal space separating them. There are two small unguis associated with the first two manual digits. The forelimb is marginally longer than the hindlimb with a length ratio (humerus+ulna+carpometacarpus / femur+tibiotarsus+tarsometatarsus = ratio) of 1.05, similar to *Rapaxavis*, *Zhouornis*, and *Cathayornis* (Table 2 for measurements), and differing from other enantiornithines (Tables 1 and 2). The ilium, ischium, and pubis are not fused with one another around the acetabulum, and they are preserved in lateral view. The pre-acetabular portion of the ilium is longer and dorsoventrally wider than the caudal portion. There is a small crest on the cranial portion of the ilium. The proximo-dorsal process of the ischium is well projected (Figure 3), approaching, but not contacting, the ventral margin of the ilium. The pubis is rounded in cross-section proximally, lateromedially flattened distally, and flared at its distal end, forming a pubic boot (Figure 3: pb).

The right femur preserved in medial view is slightly bowed with the pit for the lig. capitis present on the medial surface of the femoral head. The periosteal surface of the distal femur appears to be rough, and the condyles are not well developed. The femur is 70% of the tibiotarsus length. The right and left tibiotarsi are preserved in cranial and caudal view, respectively (Figure 1). The medial condyle of the tibiotarsus is wider than the lateral one. The distal end of the tibiotarsus shaft is not significantly wider than the mid-shaft. The fibula is proportionally longer than many other enantiornithines. Although the distal end is missing, the preserved length of the left

fibula is more than 70% of that of the tibiotarsus. The tubercle for the insertion of the m. iliofibularis is caudolaterally directed. The popliteal tubercle is present on the proximal face of the tibiotarsus. The lateral cnemial crest and the fibular crest are present on the tibiotarsus. The distal tarsals are completely fused with the proximal metatarsals, forming a true tarsometatarsus in dorsal view. The tarsometatarsus is extremely short and measures only about half of the length of the tibiotarsus (Table 1). Metatarsals II-IV are fused with each other proximally, but not distally. Metatarsal II is slightly longer than metatarsal IV. Metatarsal trochlea III has a medial trochlear rim that extends further distally than the lateral rim (Figure 4: mp and lp). Metatarsal IV is slightly narrower than metatarsals II and III, a typical condition within Enantiornithes. The unguis phalanx of the middle pedal digit is the longest. The proximal two phalanges of pedal digit IV are much shorter than the distal ones. The size of the unguis claws is larger than most the proximal phalanges.

5 | DISCUSSION

IVPP V13266 can be referred to the Enantiornithes on basis of the presence of the following synapomorphies corroborated by our phylogenetic analysis: a "Y"-shaped furcula with a long hypocleidium, and minor metacarpal extending distal to the major metacarpal. The phylogenetic analysis produced 230 most parsimonious trees (MPTs) with a length of 1087 (Consistency index = 0.338, Retention index = 0.661). The strict consensus is poorly resolved, and most enantiornithines including *Brevirostruavis macrohyoideus* form a large polytomy with a few derived clades resolved (Figure 5A). The poorly resolved strict consensus tree results largely from unstable taxa that occupy different positions in the MPTs. In order to extract a consensus of phylogenetic information, we performed a reduced consensus analysis using TNT (Pol & Escapa, 2009). The ten most unstable taxa (*Elsornis*,

TABLE 1 Measurements of *Brevirostruavis macrohyoideus* (IVPP V 13266) in millimeters

Elements				
Skull length		40.0		
Ceratobranchials	Left	25.0	Right	28.4
Humerus length	Left	39.2		
Ulna length	Left	38.6		
Alular metacarpal	Left	2.6	Right	2.9
Metacarpal II	Left	15.0	Right	14.9
Metacarpal III	Left	17.7	Right	15.8
Phalanx I-1	Left	6.9	Right	6.6
Phalanx II-1	Left	9.6	Right	8.8
Phalanx II-2	Left	6.3	Right	5.5
Phalanx III-1	Left	4.6	Right	4.6
Manual Ungual	D-2	3.3	D-1	3.5
Sternum	Width	17.5	Midline length	25.3
Coracoid	Left	22.3 (estimated)		
Femur length	Left	28.3		
Tibiotarsus length	Left	40.0		
Fibula length			Right	29.3 (preserved)
Metatarsal I	Left	5.1		
Metatarsal II		18.8		
Metatarsal III		20.4		
Metatarsal IV		18.7		
Pygostyle length		19.8		
Pedal phalanx (left)	I-1	5.3		
	II-1	5.0		
	II-2	6.2		
	III-1	6.8		
	III-2	5.3		
	III-3	5.9		
	IV-1	2.6		
	IV-2	3.1		
Pedal Ungual (left)	D-1	8.3		
	D-2	7.7		
	D-3	8.4		
	D-4	6.8		

Gobipteryx, *Iberomesornis*, *Longirostravis*, *Rapaxavis*, *Shanweiniao*, *Vescornis*, *Qiliania*, *Fortunguavis*, and *Songlingornis*) were removed from the reduced consensus analysis, and the reduced consensus tree is relatively better resolved (Figure 5B). However, the interrelationships among the Enantiornithes are still obscured by a few polytomies, and *Brevirostruavis* falls into one of them (Figure 5B). A majority rule consensus tree was produced, and its topology is consistent with most recent studies in the composition of major groupings (O'Connor et al., 2009; Wang et al., 2017a, 2017b). In the majority rule consensus tree, *Eoalulavis*, *Vescornis*, *Cathayornis*, and

Brevirostruavis macrohyoideus are recovered as the successive outgroups to the *Neuquenornis* + *Concornis* clade. In comparison with other enantiornithines (e.g., *Cathayornis*), the new specimen has a proportionally shorter rostrum, reminiscent of, but more rounded than that of *Eoenantiornis* (Zhou & Zhang, 2003). In regards to postcranial features, *Brevirostruavis macrohyoideus* is different from *Eoenantiornis* in sternal morphology, including the extension of midline projection and the large craniolateral process. This process extends further dorsally in the new specimen than in most other taxa (Zheng et al., 2012). The relative width proportions of the

TABLE 2 Limb measurements of the *Brevirostruavis macrohoyoideus* with comparison of other avialans (Adopted from Zhang et al., 2013)

Taxa	H	U	Cmc	Fe	Tbt	Tmt	Forelimb/hindlimb
<i>Aberratiodontus wui</i> (LHV0001)	–	–	–	55.0	66.7	33.0	NA
<i>Boluochia zhengi</i> (IVPP 9770)	–	–	–	–	37.0	17.5	NA
<i>Brevirostruavis macrohoyoideus</i> (IVPP V13266)	39.2	38.6	15.0	28.3	40.0	20.4	1.05
<i>Cathayornis chabuensis</i> (BMNHC-Ph000110)	31.5	32.1	14.0	30.7	35.9	17.2	0.93
<i>Cathayornis yandica</i> (IVPP V9769)	33.0	34.0	18.0	28.0	34.0	21.0	1.02
<i>Dalingheornis liweii</i> (CNU VB2005001)	14.0	14.0	6.0	11.0	16.0	9.0	0.94
<i>Dapingfangornis sentisorhinus</i> (LPM00039)	22.0	27.0	11.0	23.0	29.0	16.0	0.88
<i>Eocathayornis walkeri</i> (IVPP 10916)	23.5	26.0	14.0	–	–	–	NA
<i>Eoenantiornis buhleri</i> (IVPP V11537)	29.5	31.0	12.0	26.5	31.0	22.3	0.91
<i>Longipteryx chaoyangensis</i> (IVPP V12325)	45.0	47.0	19.0	31.0	32.0	21.0	1.32
<i>Longirostravis hani</i> (IVPP11309)	24.4	25.5	–	20.0	25.5	14.0	NA
<i>Paraprotopteryx gracilis</i> (STM V001)	22.6	23.5	11.5	22.2	26.3	15.7	0.90
<i>Pengornis houi</i> (IVPP V15336)	64.3	70.7	34.3	48.0	50.4	26.5	1.36
<i>Protopteryx fengningensis</i> (IVPP11665)	27.5	27.9	14.7	22.6	29.1	16.5	1.03
<i>Rapaxavis pani</i> (DNHM 2522)	22.7	22.9	11.8	19.3	23.2	13.0	1.03
<i>Shanweinia cooperorum</i> (DNHM 1878/1/2)	22.4	23.4	–	17.6	22.5	11.8	NA
<i>Shenqiornis mengi</i> (DNHM 2950)	46.6	46.8	25.5	38.8	–	25.0	NA
<i>Sinornis santensis</i> (BVP 538)	24.0	–	10.8	–	26.4	14.6	NA
<i>Vescornis hebeiensis</i> (IVPP130722)	22.6	16.1	11.6	24.1	29.8	16.5	0.71
<i>Zhouornis hani</i> (CNU VB0903)	50.6	53.8	24.0	44.0	51.6	25.9	1.06

Anatomical abbreviations: H--humerus, U--ulna, Cmc--carpometacarpus, Tbt--tibiotarsus, and Tmt--tarsometatarsus. Institution abbreviations: DNHM--Dalian Natural History Museum, BMNHC/BVP--Beijing Museum of Natural History, China, CNU--Capital Normal University, and STM Shandong Tianyu Museum.

metatarsals (slightly narrower metatarsal IV in *Brevirostruavis*) differ from *Cathayornis* and *Boluochia*, in which the metatarsal IV is significantly narrower than the other metatarsals. IVPP V13266 is distinct in its smaller and less robust teeth, in comparison to *Bohaiornis* and other closely related taxa in Bohaiornithidae.

The known ecological diversity of the Enantiornithes is largely inferred on basis of variation in the shape of the rostrum and dental morphologies (Li et al., 2014, 2020). An inferred raptorial feeding ecology and fish consumption have been proposed for the long-rostrumed *Longipteryx* and *Changzuiornis* (Huang et al., 2016). A recent study of the quadrate in *Longipteryx* suggests potentially a stronger or quicker bite in that bird (Stidham & O'Connor, 2021). The long and delicate rostrum of *Longirostravis* has been hypothesized for filtering invertebrate and other nutrients from muddy sediments (Hou et al., 2004). In contrast, Bohaiornithidae is characterized by a stout rostrum (Li et al., 2014). This wide variety of rostral shapes among enantiornithines suggests that the combination of cranial characters and shapes may have facilitated the reduction of competition among these sympatric taxa, maximizing the exploitation of food resources. The spectrum of rostral variation can be analogous to the diversified beak forms among crown group birds (O'Connor et al., 2020) indicative of a high degree of ecological diversification among enantiornithines within the Cretaceous forested ecosystem (Zhou et al., 2003). For taxa with a similarly short rostrum, the Bohaiornithidae and Pengornithidae

are differentiated further by remarkable tooth morphologies. *Bohaiornis* has been hypothesized to use their robust teeth for crushing hard materials, while *Pengornis* might have used its blunt teeth for grinding (Zhou et al., 2008).

In addition to the rostrum and dental variation, *Brevirostruavis* adds significant new data related to the known diversity in feeding specializations present in enantiornithines and early diverging stem birds as a whole. The combination of a short rostrum paired with a hyper-elongated hyoid apparatus (i.e., ceratobranchial) is not known among early avialans. The significant elongation and distinct dorsal curvature of the ceratobranchials might have functioned similarly to the elongate epibranchials present in living birds, such as hummingbirds, woodpeckers, and honeyeaters (Paton & Collins, 1989). The elongate ceratobranchials in *Brevirostruavis* might have compensated for the absence of ossified epibranchials in early birds who required a long hyobranchial for food manipulation. Similar elongation of branchial elements appears to have evolved independently in *Jeholornis* and *Sulcavis* with their longer rostra (Figure 6). The long hyoid apparatus and associated tongue appendage (i.e. fleshy tongue and cartilaginous paraglossum) are known to be good indicators of dietary adaptations in crown birds (Erdoğan & Iwasaki, 2014). For instance, grazing-, filtering-feeding, and piscivorous anatids maintain different shapes of their fleshy and bony tongues, particularly related to their different feeding adaptation. The simplified and rudimentary shaped muscular tongue is present

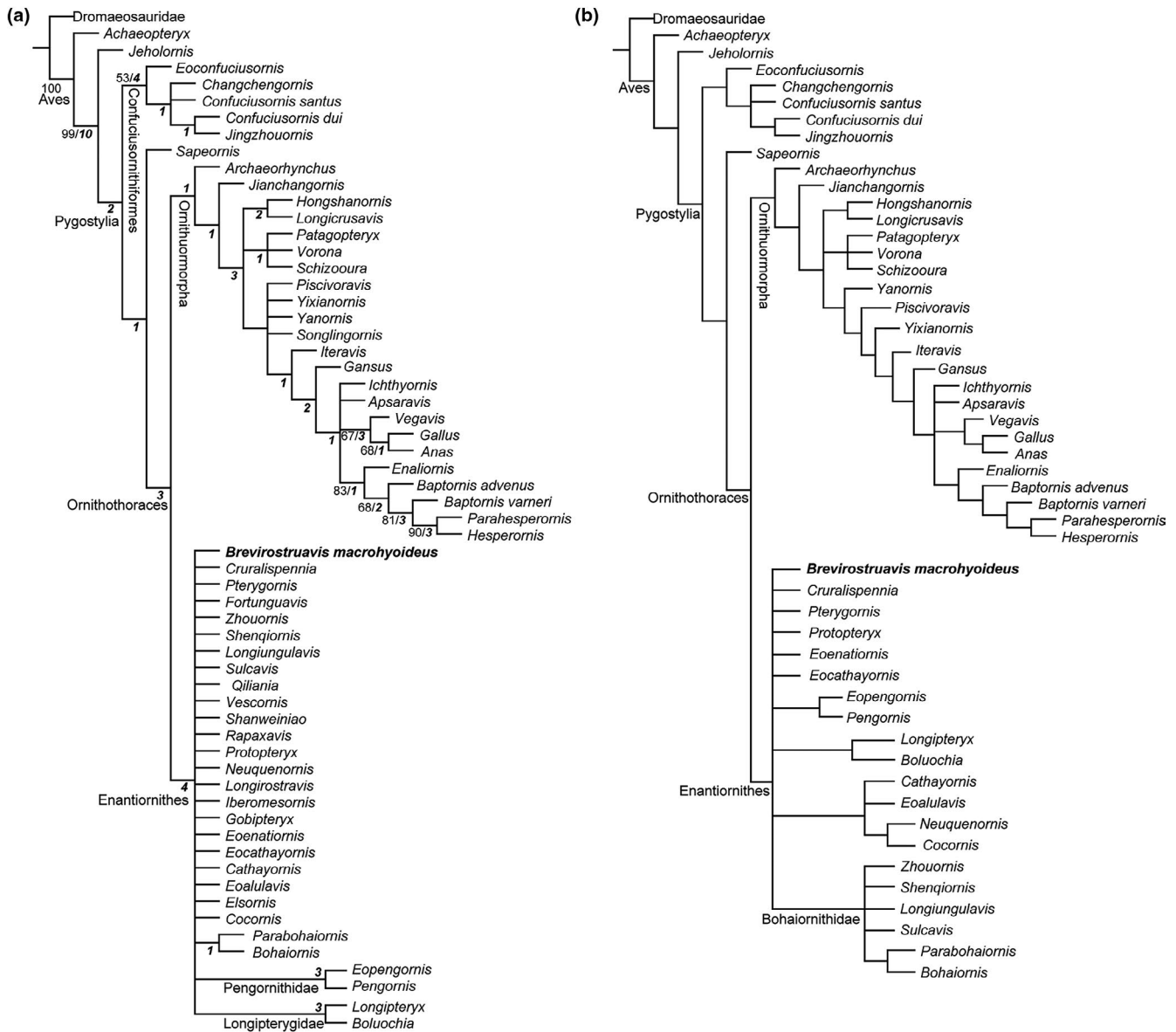


FIGURE 5 Phylogenetic position of *Brevirostruavis macrohyoideus* (IVPP V 13266) in Avialae. (a) Strict consensus tree from current phylogenetic analysis; (b) reduced consensus tree with ten most unstable taxa removed. The bootstrap and absolute Bremer support values are denoted in normal and bold italic fonts

in *Merganser* and other piscivorous ducks. By contrast, the muscular shape is strikingly different, being much wider and flattened, in grazing and filtering-feeding anatids (Erdoğan & Iwasaki, 2014; Li & Clarke, 2016).

The elaboration and ossification of different hyoid bony elements appeared early in avialan evolution as demonstrated by this Early Cretaceous indication of hyolinugal diversity. The mineralization (or ossification) of the basihyal is known in the pygostylian *Confuciusornis*, the ornithuromorph *Hongshanornis*, and even in the non-avialan *Microraptor* (Li et al., 2018). The ossified epibranchial and proposed mobile or protractible tongue evolved first in *Hongshanornis* (Li et al., 2018; Zhou & Zhang, 2005). The separate ossification center of the epibranchial represents a novel feature present in all living birds (Li et al., 2018). We propose that

the elongation of the hyoid apparatus evolved independently via different patterns in bird evolution (Figure 6). Within avialans, slightly longer ceratobranchials are present in *Jeholornis*, a seed-eating basal bird, and another enantiornithine (*Sulcvivis georum*). These taxa share relatively longer ceratobranchial elements with the new bird described here, and contrast with the states present in other more derived ornithuromorph birds. It is reasonable to hypothesize that the evolutionary pathway of hyolingual feeding in Mesozoic stem birds was achieved through the (initial) lengthening of the ceratobranchials in enantiornithines, and via the ossification of epibranchials in ornithuromorphs (including crown birds). The absence of cartilaginous epibranchials in the hyolingual apparatus in this enantiornithine is supported by the morphology of the caudal end of the ceratobranchials with a flattened tapered end that

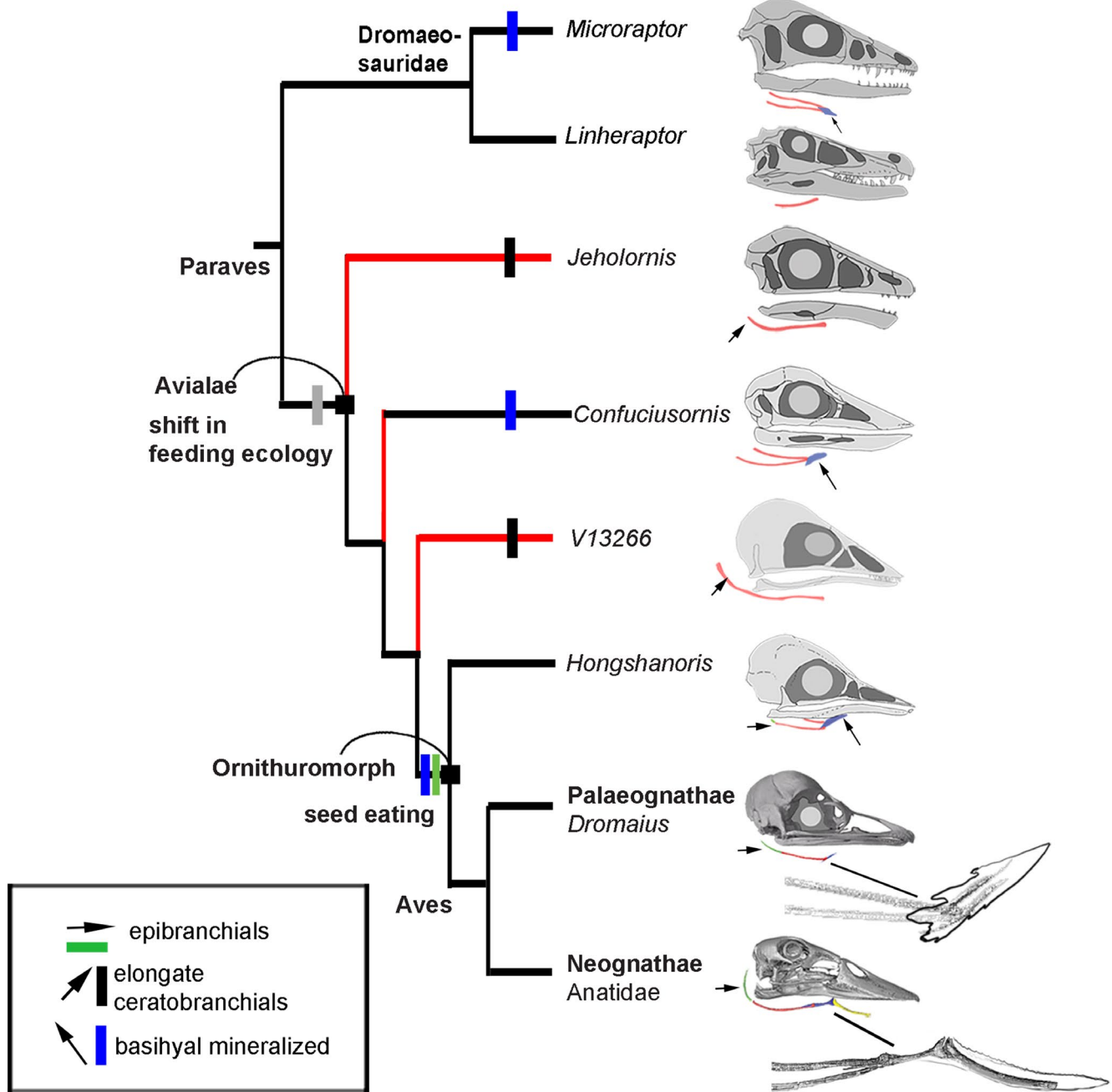


FIGURE 6 Proposed hyoid apparatus character evolution in birds including ceratobranchial elongation, mineralization of basihyale, and epibranchial evolution (modified from Li et al., 2018). The fleshy part of tongue is elaborated in extant taxa

differs significantly from the bulbous and rounded knob-like end which articulates with the epibranchial in living birds (Figure 6) and *Hongshanornis*.

Being absent in enantiornithines or more stem-ward avialans, the presence of an ossified epibranchial is optimized to have evolved among early diverging ornithuromorphs (Li et al., 2018). Dietary associated traits in enantiornithines and other Early Cretaceous stem birds (like the presence of a crop and gastroliths) are strongly indicative of a regime where herbivory and seed-eating played a key role in driving the early radiation of several lineages in Avialae

(Zanno & Makovicky, 2011). A major shift from carnivory in non-avian theropods to the herbivorous diet present among basal birds seems to drive cranial evolution leading to the origin of ornithurine birds, including all extant birds. The effective use of available food resources and the reduction in competition with other contemporary non-avian theropods and pterosaurs might have contributed to their major radiation in the Mesozoic. The elongation of the ceratobranchial bone in *Brevirostruavis* represents a novel evolutionary path that is unknown among extant birds and differs from their Mesozoic relatives. That elongation represents

a change in function, an increase in feeding efficiency, or an unknown specialization necessary to exploit certain food resources. In particular, this hyoid apparatus likely helped the bird to achieve protrusion of the tongue beyond the rostrum as a component of foraging and feeding.

The linkage between hyolingual feeding with the morphology of the rostrum and beak seems to be a synapomorphy of crown birds (Bongo-Tomlinson & Schwenk, 2000). However, such a close coupling or correlation between the hyoid and rostrum morphology might be derived from their functional coordination of the two components that is closely tied to feeding specialization, and thus, not linked to a particular clade. This novel linkage between the rostrum and hyolingual apparatus might be associated with the origin of avian cranial kinesis in ornithuromorph birds as well, and requires further testing.

It is interesting to note that enantiornithine birds likely lacked a kinetic skull as in crown birds, and even retained dinosaurian aspects to their skull and palate (Wang et al., 2021). Given that framework in enantiornithines along with the absence of epibranchials, the only evolutionary pathway open to them may have been to elongate the ceratobranchials as a functional mechanism to utilize or exploit available dietary resources. That difference also is indicated by the long ceratobranchials of *Brevirostruavis* contrasting strikingly with its abbreviated rostrum, suggesting an absence of the functional coordination between the rostrum and hyoid in early diverging avialans. Clearly, the combination of a short rostrum and a long tongue evolved in a relationship to obtain some dietary component, and that requirement may have necessitated extending the tongue beyond the rostrum as in some extant birds like woodpeckers. The ancient forests of northeastern China had abundant and various food resources, including diverse insects and even nutritious plant resources such as nectar and related reproductive structures (Ren et al., 2011) that could have been consumed by birds. The combination of a short rostrum and elongated tongue clearly increased the fitness of this enantiornithine bird, and allowed it to utilize a resource that other known birds did not.

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AUTHORS CONTRIBUTIONS

Z.L., Z.Z., and J.C. contributed to the design of the study, interpretation of results, and manuscript preparation. Z.L., M.W., and T.S. performed the data analyses. All authors contributed to the writing of the manuscript.

OPEN RESEARCH BADGES



This article has earned Open Data and Open Materials badges.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Zhiheng Li <https://orcid.org/0000-0002-6968-6982>

Thomas A. Stidham <https://orcid.org/0000-0003-4766-0041>

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