ORIGINAL ARTICLE

The Pleistocene Zhoukoudian 'Peking Man' site records the first Beijing (China) evidence of the Northern Raven (*Corvus corax*)

Thomas A. Stidham[1,2] · Jingmai K. O'Connor[3] · Zhiheng Li[1]

Abstract

Study of the holotype and only known material of the purportedly extinct corvid species '*Corvus fangshannus*' from the late Middle or Late Pleistocene locality 3 of the UNESCO Zhoukoudian 'Peking Man' site in Beijing, China, documents its identification instead as a member of the sedentary Northern Raven (*Corvus corax*) lineage. Shared features of the humerus including those consistent with species of *Corvus* (protruding ventral tubercle and rounded and not prominent bicipital crest) and a combination of features (including overall size and the presence of a concave ventral margin where the ventral supracondylar tubercle projects ventral to the diaphysis) help to support the allocation of this Pleistocene material to that particular species' lineage. Ravens do not occur historically within the Beijing Municipality, and this reidentified fossil is the first record from the area. When considered alongside a similar extralimital record based on a recently reported Middle Pleistocene raven skull from Liaoning Province, these fossils together may indicate that the Northern Raven's prehistoric geographic distribution in northeastern China encompassed a broader area south of its current distribution extending to ~40–41 degrees latitude. Changes to the raven's geographic distribution likely are linked to shifts between cooler and drier climates and warmer ones, along with their interactions with extinct non-analogous vertebrate communities of the Pleistocene. These ravens would have scavenged alongside hyenas, other large mammalian carnivores, and even early humans in northern China.

Keywords China · Fossil · Pleistocene · Raven · Zhoukoudian

Zusammenfassung

Die pleistozäne Fundstelle des „Peking-Menschen" aus Zhoukoud offenbart den ersten Nachweis des Kolkraben (*Corvus corax*) für Peking (China).

Untersuchung des Holotyps und des einzigen bekannten Materials der angeblich ausgestorbenen Rabenvogelart „*Corvus fangshannus*" aus der spätmittel- oder spätpleistozänen Fundstelle 3 der UNESCO Zhoukoudian Peking Man"-Stätte in Peking, China, belegt, dass es sich stattdessen um ein Mitglied der Abstammungslinie des residenten Kolkrabens (Corvus corax) handelt. Gemeinsame Merkmale des Oberarmknochens, einschließlich derjenigen, die mit Corvus-Arten übereinstimmen (hervorstehender ventraler Tuberkel und abgerundeter und nicht hervorstehender Bicipitalkamm), sowie eine Kombination von Merkmalen (einschließlich der Gesamtgröße und des Vorhandenseins eines konkaven ventralen Randes, an dem der ventrale suprakondyläre Tuberkel ventral in die Diaphyse hineinragt) unterstützen die Zuordnung dieses pleistozänen Materials zu dieser speziellen Abstammungslinie. Rabenvögel kommen im Stadtgebiet von Peking historisch nicht vor, und dieses neu identifizierte Fossil ist der erste Nachweis für dieses Gebiet. Zusammen mit einem ähnlichen Nachweis außerhalb der üblichen Verbreitung, der auf einem kürzlich gemeldeten mittelpleistozänen Rabenschädel aus der Provinz Liaoning beruht, könnten diese Fossilien darauf hindeuten, dass das prähistorische Verbreitungsgebiet des

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Kolkraben im Nordosten Chinas ein größeres Gebiet südlich seines heutigen Verbreitungsgebiets umfasste, das sich bis zum etwa zum 40.-41° nördlicher Breite erstreckte. Die Veränderungen in der geografischen Verbreitung der Raben stehen wahrscheinlich im Zusammenhang mit dem Wechsel zwischen kühleren und trockeneren und wärmeren Klimazonen sowie mit ihren Interaktionen mit ausgestorbenen, nicht verwandten Wirbeltiergemeinschaften des Pleistozäns. Diese Raben hätten an der Seite von Hyänen, anderen großen fleischfressenden Säugetieren und sogar frühen Menschen in Nordchina gejagt.

Introduction

Today, China hosts a diversity of at least 31 species of birds belonging to the Family Corvidae (crows, jays, magpies, and relatives) (MacKinnon and Philips 2000; Liu 2021), including the largest species of passeriform bird, the Northern Raven (*Corvus corax*). The Northern Raven is a largely sedentary and non-migratory bird, occupying mostly scavenger and predatory ecological roles across much of its Holarctic geographic range (Boarman and Heinrich 2020). This species is widespread across China today (MacKinnon and Philips 2000; Boarman and Heinrich 2020; Liu 2021) occurring across much of the Tibetan Plateau and Xinjiang Province in the west to the northeastern corner of Heilongjiang Province in the east (Fig. 1). Despite that wide distribution, the species' geographic range does not include areas east of the Tibetan Plateau in southeastern China and parts of central and northeastern China (Fig. 1), including the region of the Beijing Municipality (Zhao and Zhu 2021).

In contrast to Europe where a diversity of extinct crows and raven-sized taxa from the Pliocene and Pleistocene are recorded (including *C. pliocaenus*, *C. hungaricus*, and *C. harkanyensis*) along with fossils allocated to extant species (e.g., Mlíkovskỳ 2002; Bedetti and Pavia 2013; Pavia and Bedetti 2013; Kessler 2020; Núñez-Lahuerta et al. 2021), relatively few fossils attributed to the Family Corvidae are known from the Pleistocene of China. These include
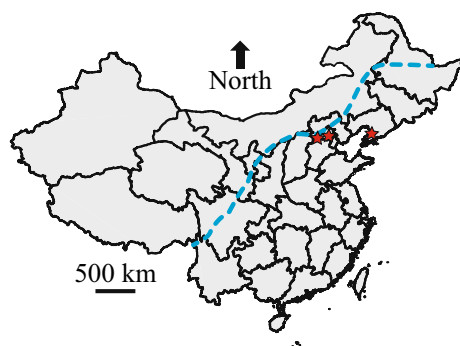
a tarsometatarsus from a large species of *Corvus* in the Nihewan Basin in Hebei Province (Wang et al. 2013) and several species including magpies and crows from the various cave localities of the UNESCO Zhoukoudian 'Peking Man' world heritage site in the municipality of Beijing (Hou 1993). A recent report of an extralimital record of a skull of a Northern Raven from near the city of Dalian in Liaoning Province of Northeastern China is the first definitive record of the species as a fossil in China (Fig. 1; Stidham et al. 2021). Furthermore, that record is south of the current geographic distribution of the species in China (Fig. 1; Stidham et al. 2021), and those authors suggested that other previously published fossils attributed to *Corvus* also may be that of the *C. corax* lineage. Those specimens include the holotype material of the extinct species '*C. fangshannus*' from Locality 3 of Zhoukoudian in Beijing (Hou 1993) and the large tarsometatarsus from the Nihewan Basin in western Hebei Province (Wang et al. 2013). Stidham and coauthors (2021) pointed out preliminary size and morphological features that suggest that those specimens could represent additional southern records of the Northern Raven in China. Further study (see below) documents the wider past geographic range in the Pleistocene of the Northern Raven across the area.

While the fossil record of (Pleistocene) mammals commonly is used to study the long-term impact of climate change on geographic distributions (e.g., Graham et al. 1996), the less abundant avian fossil record has not yet been leveraged in a similar manner or magnitude. Fossils of birds have been used to document ancient climate related intercontinental dispersals (Stidham and Eberle 2016; Stidham and Zelenkov 2017), and workers have reported extralimital records of Pleistocene birds (e.g., Brasso and Emslie 2006; Sagebiel 2010). However, no systematic study of fossil bird distributions has been conducted with respect to the question of geographic ranges and past climate change in the Quaternary.

There are some hurdles to accumulating and analyzing such data. For example, the taxonomic identification of fossil birds to lower taxonomic levels like genus and species can be fraught with issues because, unlike mammals with their readily diagnosable and commonly preserved teeth, Quaternary bird identification is limited mostly to isolated postcranial bones and their fragments. Ideally, researchers should utilize and present morphological synapomorphies

Fig. 1 Provincial map of mainland China. The southern edge of the geographic range of the Northern Raven *Corvus corax* is a blue dashed line. The fossil localities are red stars with the localities (from left to right) being Nihewan, Zhoukoudian, and Jinyuan Cave

to support the identification of individual bones using what is termed apomorphy-based identification (Bell et al. 2010), but the reality of avian skeletal evolution, with significant homoplasy, typically restricts identification to using a unique (derived) combination of traits. However, the work in circumscribing such derived taxonomically and phylogenetically useful osteological characters and their combinations applicable to identifying individual genera and species (in particular passeriforms) has really only begun (e.g., Stidham et al. 2015, 2021; Zelenkov et al. 2021) and is limited in part by the availability of complete skeletons of bird species (of both sexes) in museum collections and a robust phylogenetic framework of extant species. In addition, given that we know bird geographic ranges have and continue to change (Rushing et al. 2020, Stewart and Jacobi 2015), comparisons between modern and fossil or archeological material should encompass a broad range of geographic distributions and biodiversity, not limiting comparisons solely to current local or regional species (Bell et al. 2010). For example, the studies cited above with extralimital species (Brasso and Emslie 2006; Sagebiel 2010) list the Northern Raven in their faunas, but it is unknown whether the fossils were compared to the Chihuahuan Raven (*C. cryptoleucus*), which occurs today in Texas and New Mexico where those fossiliferous caves are located and has significant genetic mixture with North American populations of the Northern Raven (Kearns et al. 2018). Such limitations on comparisons (or lack of publication details of comparisons) can result in type I and II errors in identification of a specimen and incorrectly rejecting or accepting identification data despite known evolutionary and geographic range changes in bird taxa over time (Jirinec et al. 2021). In other words, identification should be based primarily on phenotypic character data, not geography. Naturally, everyone should avoid identifying specimens to taxonomic levels beyond the limits of the character data available in a fossil. Simple phenetic or 'matching' approaches utilizing overall osteological similarity among specimens also should be avoided since as evolutionary biologists, we need to examine and document evolutionary/phylogenetic lineages and their individual responses to climate change over time. Workers also should be aware of publications simply listing species present without supporting phylogenetic or morphological data (not just size measurements, as we know that body mass and shape changes in birds over changing climatic conditions and across geographic ranges; e.g., Stewart 2007; Jirinec et al. 2021), and of older publications that may use taxonomy not in line with current species delimitations. For example, the discovery that the traditionally recognized "Canada Goose" is paraphyletic, and has been split into the monophyletic Canada (*Branta canadensis*) and Cackling Goose (*Branta hutchinsii*) species (Ottenburghs et al. 2016), renders questionable all identifications of fossils attributed to *Branta canadensis* that were published previously. Despite

those hurdles, the fossil record of birds potentially offers a wealth of data about the past occurrences of birds under a variety of climatic and environmental conditions that can be leveraged for predictive climate-geography model testing and revision.

Materials and methods

All fossils presented here are housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) of the Chinese Academy of Sciences in Beijing, and modern comparative skeletons of the Northern Raven examined are maintained in the Field Museum of Natural History, Chicago, USA (FMNH). Osteological terminology follows that of Baumel and Witmer (1993) with English equivalents used.

Results

Systematic Paleontology.
Corvidae Vigors, 1825.
Corvus Linnaeus, 1758.
Corvus corax Linnaeus, 1758.

Junior synonym: *Corvus fangshannus* Hou (1982) from Locality 3 of Zhoukoudian, Beijing, China.

Newly referred fossil material: IVPP V6437 (holotype left humerus and left tibiotarsus of '*C. fangshannus*') from Locality 3 of Zhoukoudian, Beijing, China.

Description of the holotype material of '*C. fangshannus*'

We provide a description of the holotype material to help communicate the morphological features present that help to identify the specimen as a member of the *C. corax* group and because an extensive description has never been published for this material. The holotype consists of a left humerus and a left tibiotarsus that may or may not belong to the same individual. The humerus is mostly complete except for a few small missing chips of bone and small perforations on the deltopectoral crest, diaphysis, and on the distal end associated with a crack through the specimen (Fig. 2). The humerus has a total length of 86.9 mm, a distal dorsoventral width of 19.6 mm, and proximal dorsoventral width of 24.5 mm. The transverse ligament groove is a broad concave area rather than a narrow groove. Dorsal to it and adjacent (distal) to the humeral head and dorsal tubercle, the cranial surface also is concave and separate from the ventrally positioned groove. The humeral head does not form a lip or
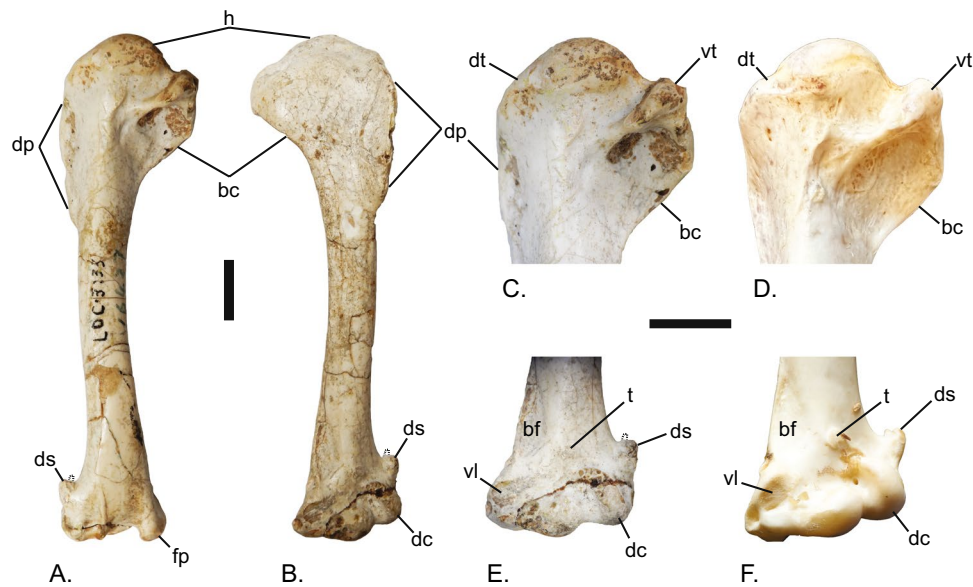
Fig. 2 Comparison of the fossil humerus IVPP 6437, newly referred to *Corvus corax* (holotype of '*Corvus fangshannus*'), with that from a modern *Corvus corax* FMNH 465346. Humerus IVPP 6437 in A. caudal view and B. cranial view. Proximal humerus of C. IVPP 6437 and D. FMNH 465346 in caudal view. Distal humerus of E. IVPP 6437 and F. FMNH 465346 in cranial view. Note the dashed line indicates one branch of the broken bifurcation of the dorsal supracondylar process. Scale bars equal 1 cm. Osteological abbreviations: *bc*—bicipital crest; *bf*—m. brachialis fossa; *dc*—dorsal condyle; *dp*—deltopectoral crest; *ds*—dorsal supracondylar process; *dt*—dorsal tubercle; *fp*—flexor process; *h*—humeral head; *t*—tubercle; *vl*—facet for the ventral collateral ligament; and *vt*—ventral tubercle

overhang over the capital incisure or humeral shaft. The long axis through the ventral tubercle is oblique to the humeral long axis with the proximal end ventral to the distal end. The bicipital crest and ventral rim of the pneumotricipital fossa are thickened. There is a single pneumatic opening within the single pneumotricipital fossa, and it is subcircular in outline positioned near the dorsal crus. The ventral wall of the pneumotricipital fossa is damaged and there may have been some much smaller pneumatic foramina or perforations within the fossa. The bicipital crest has an overall straight margin (cranial/caudal view) and smoothly curves into the diaphysis distally. The dorsal surface of the deltopectoral crest is concave, and the crest extends distal to the bicipital crest. The dorsal tubercle faces dorsoproximally and is positioned dorsal to the humeral head on the proximal surface of the bone.

The m. brachialis fossa is elongate and positioned along the ventral edge of the diaphysis (Fig. 2). It narrows to a point proximally. On the ventral face of the bone just distal to the m. brachialis fossa is a muscular origination pit for one of the pronator muscles, and that pit is just proximal to the facet for the ventral collateral ligament on the ventral supracondylar tubercle. That facet is subcircular in outline and is directed craniodistally. The ventral surface of the humerus adjacent to the ligament facet is slightly concave. There is a small tubercle located proximal to the notch between the dorsal and ventral condyles. The dorsal condyle is fractured and partially missing from a crack through the distal

end. The dorsal supracondylar process is large and projects proximally. The process is bifurcated with a large bulbous cranial branch and a more caudally positioned and smaller branch that has been broken away. There is a concave facet on the caudal face of the dorsal supracondylar process. The olecranon fossa is deeply inset with a concave area extending proximally into the distal face of the humerus dorsal to the dorsal condyle. There is a m. scapulotricipitalis fossa bounded dorsally by a broad convex area and ventrally by an elongate narrow ridge that extends proximally to near the level of the proximal tip of the dorsal supracondylar process. The flexor process is large, positioned caudal to the condyles, and has a large facet for muscle origination on its caudodistal face.

The left tibiotarsus is missing much of its proximal articular surface, adjacent cnemial crests, and the distal approximately half of both distal condyles (Fig. 3). Its preserved length is 100.0 mm with a distal width across the condyles of 10.9 mm. There are some missing fragments of bone associated with fractures in the diaphysis. In its current state, the distal end appears to be rotated relative to the proximal part with the condyles directed laterally (Fig. 3), and that condition contrasts with the drawing provided by Hou (1993, Fig. 71c). That rotation may suggest that the bone was reconstructed missing some of the shaft (and hence the bone was longer than its current state) because the remaining fragments appear to fit one another for the most part. The medial side of the proximal articular surface is preserved.

Fig. 3 Comparison of the fossil tibiotarsus IVPP 6437, newly referred to *Corvus corax* (holotype of '*Corvus fangshannus*') with that of a modern *Corvus corax* FMNH 465345. Tibiotarsus IVPP 6437 in **A**. cranial view and **B**. the distal end oriented to be in cranial view. Note the distal end is not aligned anatomically with the proximal end. Expanded cranial view of the distal end of **C**. IVPP 6437 and **D**. FMNH 465345. Scale bars equal 1 cm. Osteological abbreviations: *fc*—fibular crest; *fg*—m. fibularis groove; *lc*—lateral condyle; *lr*—lateral attachment of the extensor retinaculum; *mc*—medial condyle; and *mr*—medial attachment of the extensor retinaculum
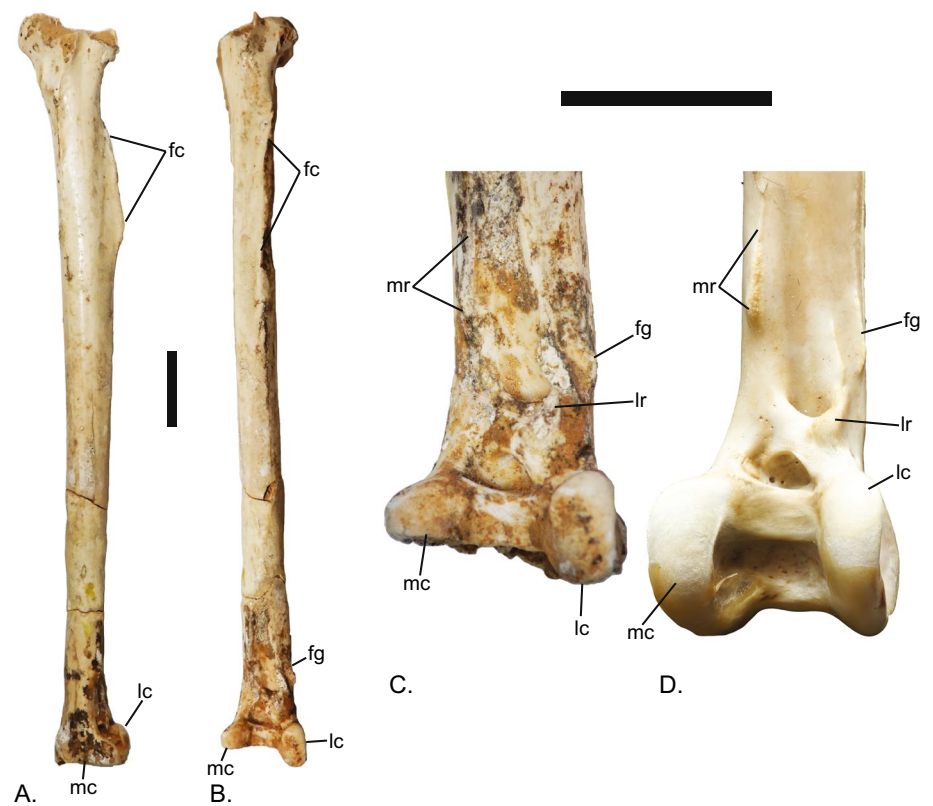
Only the bases of the cnemial crests are present, but the preserved portions show that they are proximodistally short. The fibular crest is prominent and thick with its distal end positioned slightly lateral to its proximal end. The thin crest or low ridge that extends distal from the cranial cnemial crest ends near the level of the proximodistal midpoint of the fibular crest.

The extensor sulcus is oriented somewhat oblique to the diaphysis with its proximal preserved end in the medial part of the shaft, ending at a fracture, and the more distal end at the supratendinal bridge located more laterally (Fig. 3). The elongate attachment for the medial side of the extensor retinaculum lies proximal to the level of the m. fibularis groove on the lateral side of the shaft. The length of the m. fibularis groove is about the same length as that of the supratendinal bridge. The groove's medial edge is formed by the lateral attachment site of the extensor retinaculum (which extends onto the supratendinal bridge), and it has a lateral flange of bone that extends laterally beyond the tibia's shaft. The distal opening of the extensor groove beyond the ossified bridge is directed distomedially. The lateral condyle extends proximal to the medial condyle and the intercondylar sulcus is a wide U-shape (distal view) with the deepest part located medial to its mediolateral midpoint. There is a small lateral epicondyle preserved. Most of the medial side of the medial condyle is missing. Only the proximal end of the articular surface for the tibial cartilage is present. The medial condyle appears to be positioned medial to the tibial shaft.

Diagnosis, identification, and comparisons

Hou's (1993: p. 284) diagnosis (in partially corrected English) states, "Big crow, it bigger than *C. macrorhynchos* and *C. torquatus*, but smaller than *C. pliocaenus*. Pneumal fossa of humerus large and shallow, divided fork of ectepicondylar prominence not clear. Tibiotarsus slender and long, intermuscular line is long." No description is provided in English. In Chinese, Hou (1993: p. 224–225) provides a diagnosis that is largely the same as the English one. In addition, Hou (1993) says in a Chinese description and comparison section that the pneumotricipital fossa is large and shallow, there is a deep capital incisure, the transverse ligament sulcus is large but shallow, the ectepicondylar (dorsal supracondylar) process is large, the olecranon fossa is big but shallow, the deltopectoral crest is large and rounded, the bicipital crest is small (without a clear sulcus), the total length of the humerus is 87 mm with a proximal width of 14 mm and distal maximum width of 21.2 mm, the condyles of tibiotarsus are not well developed, and the ossified supratendinal bridge is short allowing for referral to *Corvus*. Hou (1993) also states that the fossil shares with the European *C. pliocaenus* and *C. corax antecorax* the lack

of the development of a discrete visible boundary (origin) of the biceps muscle, and that the lateral condyle of the tibiotarsus is larger.

This Beijing material is larger than that of other fossil-based taxa from Europe such as *C. pliocaenus*, *C. hungaricus*, and *C. harkanyensis*. While Hou (1993) stated the size of the Zhoukoudian fossils as being smaller than *C. pliocaenus*, that appears incorrect. Though reportedly having a raven like morphology, fossil material referred to *C. pliocaenus* has been considered in the same size class as the extant *C. corone* (Bedetti and Pavia 2013; Pavia and Bedetti 2013), and therefore it is distinctly smaller than *C. corax*. The humeri referred to *C. pliocaenus* from Spain (Núñez-Lahuerta et al. 2021) are smaller than that from Beijing (length 78.3–71 mm and distal width 17.7–15.9 mm). In addition, the youngest specimens referred to *C. pliocaenus* are from the Middle Pleistocene (Bedetti and Pavia 2013), and this Beijing material likely is from the Late Pleistocene (Cheng et al. 1996) or late Middle Pleistocene (Jiangzuo et al. 2018).

This Chinese humerus has a distal dorsoventral width of 19.6 mm (measured in its currently preserved state), and that is clearly larger than extinct European taxa including *C. hungaricus* (13.5 mm) and *C. harkanyensis* (11.53 mm) (Kessler 2020). At the same time, that measurement is within the lower end of the size range for modern *C. corax* (24.2–19.3 mm; Tomek and Bochenski 2000). Furthermore, the distal tibiotarsus of *C. harkanyensis* is 5.60 mm (Kessler 2020), substantially more narrow than the 10.9 mm width in the Beijing specimen. In addition, the validity of these extinct European species is unclear with their fossils having been referred to extant species of *Corvus* as well (Mlikovskỳ 2002). While a French fossil assemblage was allocated originally to the extinct species *C. antecorax* (Mourer-Chauviré 1975), more recent work has considered these and other similarly referred fossils as representing an extinct subspecies of the Northern Raven (i.e. *C. corax antecorax*; Mourer-Chauviré 2004, Stewart 2007). The age of the Zhoukoudian fossils and their overall small size with respect to extant raven individuals is consistent with their potential allocation to *C. corax antecorax*, but we refrain from extending our efforts of taxonomic identification allocation below the species level.

The features presented in the diagnosis, description, and comparisons of Hou (1993) are inadequate to separate '*C. fangshannus*' as distinct from *C. corax*, or really any large extant corvid. Both the fossil and *C. corax* are larger than *C. macrorhynchos* and *C. torquatus* with a large singular pneumotricipital fossa. The statement about the subdivision of the dorsal supracondylar process being unclear is true, but the division in the supracondylar process is clearly present when viewed under a microscope where it can be seen that one division of the bifurcation has been broken away

(Fig. 2). It is unclear which intermuscular line is referred to in the tibiotarsus with more than one present, and the bone is long and slender in many taxa, not specifically one species of *Corvus* (see Tomek and Bochenski 2000).

Kessler (2020) lists several diagnostic features across the skeleton for the genus and species level for the Northern Raven. The holotype humerus of '*C. fangshannus*' exhibits the protruding ventral tubercle and rounded and not prominent bicipital crest attributed to species of *Corvus* (Kessler 2020). The holotype exhibits a concave ventral margin (cranial/caudal view) where the ventral supracondylar tubercle projects ventral to the diaphysis that is present in *C. corax*, but not other Eurasian species of *Corvus* (see Fig. 7 in Kessler 2020). The flexor process has a flattened, truncated morphology shared by *C. corax*, *C. monedula,* and *Pyrrhocorax pyrrhocorax* (Kessler 2020). It also has a rounded dorsal condyle and a two pronged dorsal supracondylar tubercle with unequal branches as in many corvids (Kessler 2020). The intercondylar sulcus of the tibiotarsus exhibits an asymmetrical U shape (distal view) consistent with *C. corax* and *Pyrrhocorax* (Kessler 2020), and prominent attachments for the extensor retinaculum present in multiple taxa including *C. corax*. The combination of traits found in the holotype humerus and tibiotarsus are consistent only with *C. corax* with the ventral projection of the ventral supracondylar tubercle as a potential autapomorphy of the species (shared with the fossil humerus). In addition, with a total length of 86.9 mm, a distal width of 19.6 mm, and proximal width of 24.5 mm, the holotype humerus is within the size range reported by Stewart (2007: length 108.84–84.96 mm; distal width of 26.42–20.12 mm, note his distal width was measured along an oblique non-dorsoventral direction) and Tomek and Bochenski (2000: length 101.6–88.4 mm; distal width 24.2–19.3 mm) though on the smaller side of the range. The length of the tibiotarsus is estimated to have been about 105 mm (100 mm preserved), and that length with a distal width of 10.9 mm similarly places the fossil at the small end of the size range of *C. corax* (Tomek and Bochenski 2000, Stewart 2007). Therefore, it appears that the morphology and size are consistent with living populations of *C. corax*, and no aspect of the morphology of the bones appears inconsistent with the placement in that species. In addition, no features of these fossil bones (size or morphology) appear unique warranting their recognition as a separate extinct species of *Corvus*.

Discussion

Today, Northern Ravens occupy the largely more arid regions of China from the high-altitude Tibetan Plateau to the deserts and grasslands of Inner Mongolia and Xinjiang Province (Fig. 1). The past occurrence of ravens along a

rough line of latitude (of approximately 40–41 degrees) from Dalian in Liaoning Province to the Beijing Municipality across a variety of ages in the Pleistocene likely indicates the southerly expansion of their preferred habitats and conditions during those mostly colder and drier times.

The ages of these northern China raven fossils differ. The skull from Liaoning Province (Stidham et al. 2021) is about ~450–580 ka (Middle Pleistocene), and the material from Zhoukoudian Locality 3 is younger and thought to be Late Pleistocene (Cheng et al. 1996) or late Middle Pleistocene (Jiangzuo et al. 2018). Given the known climatic fluctuations across the region related to the glacial and interglacial intervals throughout the Pleistocene and the resulting habitat shifts among forested and steppe/grassland habitats in the region, it is possible, if not likely, that the Northern Raven was not a resident in the Beijing and Dalian areas through the entire Pleistocene. However, the paleohabitat interpretations of Jinyuan Cave on Luotuo Hill in Liaoning Province (layer 2 where the fossil was recovered) is as being a dry, cold, shrubby grassland (Stidham et al. 2021). By contrast, the mammalian fauna of Locality 3 of Zhoukoudian indicates a relatively warmer climate and more forested habitat with taxa typically further south in China being present in the Beijing area (Cheng et al. 1996). Those habitat reconstructions suggest that ravens were in this region during both dry and colder glacial climates, as well as at least one warmer and wetter interglacial interval. The absence of the Northern Raven during the current warm interglacial (and its presence in a previous one) may have more to do with the loss of much of the region's mammalian megafauna at the end of the Pleistocene and interrelated changes in community structure, and their largely scavenging diet than simply a relationship with climate. Additional well-dated fossil material from the region is needed to address those questions. Furthermore, the smaller size of the fossils from the warmer interval and the larger Liaoning specimen from a colder interval might possibly relate to a climate-body size relationship like Bergman's Rule.

However as noted above, workers should utilize sound paleontological data, not simply faunal lists from older publications. With the increased accuracy of geochronological dating techniques for Quaternary fossil sites and materials over the last several decades, those historically older publications (and their fossils) also need to be reexamined with respect to current age estimates. In this case, these taxonomically revised fossils document a geographic range change that is not known from historic data, and thus, the recognition of this change in distribution in a large-sized, scavenging, sedentary bird species is important for examining the ongoing responses to climate change present among other non-migratory avian taxa. Furthermore, those Pleistocene ravens were components of a non-analogous terrestrial community that included other scavengers like extinct hyenas (and even hominins) with whom they likely competed for food resources. Interestingly, the co-occurrence of ravens and individuals of *Homo* at Zhoukoudian perhaps could extend the recent hypothesis of a Paleolithic interrelationship between humans and ravens (synanthropism) further back in time (and to Asia; Baumann et al. 2023). Additionally, the synonymization of '*C. fangshannus*' with *C. corax* lessens the magnitude of the extinction of birds at the end of the Pleistocene (Tyberg 2008), and this taxonomic revision reflects another important aspect of correctly placing fossils within phylogenetic lineages in terms of their impact on both macroevolutionary and extinction studies.

Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by TS, JO'C and ZL. The first draft of the manuscript was written by TS, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability All data related to this research are included within the article.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

References

Baumel JJ, Witmer L (1993) Osteologica. In: Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC (eds) Handbook of avian anatomy: Nomina Anatomica Avium, 2nd edn Cambridge, MA, Nuttall Ornithological Club, 23. pp 45–132

Baumann C, Hussain ST, Roblíčková M, Riede F, Mannino MA, Bocherens H (2023) Evidence for hunter-gatherer impacts on raven diet and ecology in the Gravettian of Southern Moravia. Nat Ecol Evol. https://doi.org/10.1038/s41559-023-02107-8

Bedetti C, Pavia M (2013) Early Pleistocene birds from Pirro Nord (Puglia, southern Italy). Palaeontographica, Abt. A: Palaeozool—Stratigr 298:31–53

Bell CJ, Gauthier JA, Bever GS (2010) Covert biases, circularity, and apomorphies: a critical look at the North American Quaternary Herpetofaunal Stability Hypothesis. Quatern Int 217:30–36. https://doi.org/10.1016/j.quaint.2009.08.009

Boarman WI, Heinrich B (2020) Common Raven (*Corvus corax*), version 1.0. In: Birds of the World. Billerman SM (eds). Cornell Lab of Ornithology, Ithaca. https://doi.org/10.2173/bow.comrav.01

Brasso RL, Emslie SD (2006) Two new late Pleistocene avifaunas from New Mexico. Condor 108:721–730

Cheng J, Tian M-Z, Cao B-X, Li L-Y (1996) The New Mammalian Fossils from Zhoukoudian (Choukoutien), Beijing, and their

Environmental Explanation. China University of Geosciences Press, Beijing (In Chinese with English abstract)

Graham RW, Lundelius EL Jr, Graham MA, SchroederEK TIIIRS, Anderson E, Barnosky AD, Burns JA, Churcher CS, Grayson DK, Guthrie RD, Harington CR, Jefferson GT, Martin LD, McDonald HG, Morlan RE, Semken HA Jr, Webb SD, Werdelin L, Wilson MC (1996) Spatial response of mammals to late quaternary environmental fluctuations. Science 272:1601–1606. https://doi.org/10.1126/science.272.5268.1601

Hou L (1982) Avian fossils in Zhoukoudian. Vertebrata PalAsiatica 20:366–368

Hou L (1993) Avian fossils of Pleistocene from Zhoukoudian. Memoirs of the Institute of Vertebrate Paleontology and Paleoanthropology Acadademia Sinica 19:165–297

Jiangzuo Q, Liu J, Wagner J, Dong W, Chen J (2018) Taxonomical revision of fossil Canis in Middle Pleistocene sites of Zhoukoudian, Beijing, China and a review of fossil records of Canis mosbachensis variabilis in China. Quatern Int 482:93–108

Jirinec VJ, Burner RC, Amaral BR, Bierregaard RO Jr, Fernández-Arellano G, Hernández-Palma A, Johnson EI, Powell LL, Rutt CL, Lovejoy TE, Wolfe JD, Stouffer PC (2021) Morphological consequences of climate change for resident birds in intact Amazonian rainforest. Sci Adv 7:1743. https://doi.org/10.1126/sciadv.abk1743

Kearns AM, Restani M, Szabo I, Schrøder-Nielsen A, Kim JA, Richardson HM, Marzluff JM, Fleischer RC, Johnsen A, Omland KE (2018) Genomic evidence of speciation reversal in ravens. Nat Commun 9:906. https://doi.org/10.1038/s41467-018-03294

Kessler J (2020) Evolution of corvids and their presence in the Neogene and the Quaternary in the Carpathian Basin. Ornis Hungarica 28:121–168

Liu Y (2021) The CNG Field Guide to the Birds of China. Chinese National Geography, Changsha. (in Chinese)

MacKinnon J, Phillips K (2000) A field guide to the birds of China. Oxford Press, Oxford

Mlikovskỳ J (2002) Cenozoic birds of the World. Part 1: Europe. Ninox Press, Praha

Mourer-Chauviré C (1975) Les Oiseaux Du Pléistocène Moyen et Supérieur de France. In: Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon, n. 64, 2 fasc.

Mourer-Chauviré C (2004) Les oiseaux du Pliocène supérieur de Saint-Vallier (Drôme, France). Geobios 37(supplement 1):S97–S114

Núñez-Lahuerta C, Galán J, Cuenca-Bescós G, Huguet R (2021) Birds from Sima del Elefante, Atapuerca, Spain: palaeoecological impications in the oldest human bearing levels of the Iberian Peninsula. Riv Ital Paleontol Stratigr 127:453–484

Ottenburghs J, Megens H-J, Kraus RHS, Madsen O, van Hooft P, van Wieren SE, Crooijmans RPMA, Ydenberg RC, Groenen MAM, Prins HHT (2016) A tree of geese: a phylogenomic perspective on the evolutionary history of True Geese. Mol Phylogenet Evol 101:303–313

Pavia M, Bedetti C (2013) Early Pleistocene fossil birds from Cava Sud, Soave (Verona, North-Eastern Italy). Proceedings of the 8th international meeting of the society of avian Paleontology and evolution. Naturhistorisches Museum Wien: 171–184

Rushing CS, Royle JA, Ziolkowski DJ Jr, Pardieck KL (2020) Migratory behavior and winter geography drive differential range shifts of eastern birds in response to recent climate change. Proc Natl Acad Sci 117(23):12897–12903. https://doi.org/10.1073/pnas.2000299117

Sagebiel JC (2010) Late Pleistocene fauna from Zesch Cave, Mason County, Texas. Quatern Int 217:159–174

Stewart JR (2007) The Evolutionary Study of Some Archaeologically Significant Avian Taxa in the Quaternary of the Western Palaearctic. Archaeopress, Oxford

Stewart JR, Jacobi RM (2015) The long term response of birds to climate change: new results from a cold stage avifauna in northern England. PloS One 10(5):e0122617. https://doi.org/10.1371/journal.pone.0122617

Stidham TA, Eberlee T (2016) The palaeobiology of high latitude birds from the early Eocene greenhouse of Ellesmere Island. Arctic Can Sci Rep 6(1–8):20912. https://doi.org/10.1038/srep20912

Stidham TA, Smith NA, Li Z (2021) A Pleistocene skull of the Common Raven (Aves, Corvidae) from Jinyuan Cave, Liaoning Province, China. Quatern Int 591:80–86

Stidham TA, Zelenkov N (2017) North American-Asian aquatic bird dispersal in the Miocene: evidence from a new species of diving duck (Anseriformes: Anatidae) from North America (Nevada) with affinities to Mongolian taxa. Alcheringa: An Australasian. J Palaeontol 41:222–230

Stidham TA, Wang X, Li Q, Ni X (2015) A shelduck coracoid (Aves: Anseriformes: *Tadorna*) from the arid early Pleistocene of the Qinghai-Tibetan Plateau, China. Palaeontologia Electronica 18.2.25A: 1–10

Tomek T, Bocheński ZM (2000) The Comparative Osteology of European Corvids (Aves: Corvidae), with a Key to the Identification of Their Skeletal Elements. Institute of Systematics and Evolution of Animals. Polish Academy of Sciences, Krakow

Tyberg T (2008) The late Pleistocene continental avian extinction—an evaluation of the fossil evidence. Oryctos 7:249–269

Wang M, O'Connor JK, Zhou Z (2013) The first fossil crow (*Corvus* sp. indet.) from the early Pleistocene Nihewan paleolithic sites in north China. J Archaeol Sci 40:1623–1628

Zelenkov N, Sayfulloev N, Shnaider SV (2021) Fossil birds from the Roof of the World: The first avian fauna from High Asia and its implications for late Quaternary environments in Eastern Pamir. PLoS ONE 16(10):e0259151. https://doi.org/10.1371/journal.pone.0259151

Zhao X, Zhu L (2021) Birds of Beijing. China Forestry Publishing House, Beijing