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The first fossil crow (*Corvus* sp. indet.) from the Early Pleistocene Nihewan Paleolithic sites in North China

Min Wang^{a,b,*}, Jingmai K. O'Connor^a, Zhonghe Zhou^a

^aKey Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China

^bGraduate University of Chinese Academy of Sciences, Beijing 100044, China

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ABSTRACT

We describe a three dimensional preserved right tarsometatarsus, representing the first fossil crow from the well-known Early Pleistocene Nihewan paleolithic sites in North China. The new specimen is distinguished from other known species of the genus *Corvus* by the combined morphological features, especially the peculiar hypotarsus. The phylogenetic significance of the arrangement of canals at the proximal hypotarsus in passerines is discussed. Although the fossil was too incomplete to warrant the erection of a new species of *Corvus*, it nonetheless increases the taxonomical diversity of the Nihewan fauna and improves our knowledge on Pleistocene birds in China. Finally the paleoenvironment of the Nihewan sites are discussed in terms of its faunal composition.

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1. Introduction

The Nihewan Basin preserves well-developed lacustrine and fluvial strata representing Pliocene to Pleistocene age deposits (Zhu et al., 2001, 2003; Deng et al., 2008), and is of importance for its paleolithic sites that provide information regarding early hominid evolution in East Asia (Xie, 2006; Xie et al., 2006; Zhu et al., 2007). This basin has also yielded numerous mammalian fossils, which form the Nihewan fauna (Teilhard de Chardin and Piveteau, 1930; Qiu, 2000; Zhang et al., 2003). To avoid confusion, the general conception of Nihewan fauna is followed in this paper, i.e., it refers to all the faunas found in the Nihewan Basin (nominally, Nihewan fauna *sensu lato*) and Nihewan fauna *sensu stricto* (or Classical Nihewan fauna) that refers to the Xiashagou fauna only (Zhu et al., 2007). Since the mammal fossils were first described by Teilhard de Chardin and Piveteau (1930), subsequent paleontological work has served not only to enrich the taxonomic diversity, but also revealed evolutionary patterns and allowed for comparison with contemporary faunas in Europe (Qiu, 2000). Although the Nihewan Fauna does provide important insights regarding the biostratigraphy and

paleontology of the basin, a precise geochronological framework for the fossil locality is still needed. Recent progress has been made and some mammalian faunas in the Nihewan Formation have been dated using magnetostratigraphy (in review by Zhu et al., 2003, 2007; Deng et al., 2008). Zhu et al. (2007) proposed that the temporal span of the Nihewan fauna is 1.2 Ma (2.0–0.8 Ma). However, several important faunas, such as the Xiashagou, Danangou and Dongyaozitou faunas, still lack precise datings (although chronological constraints for these faunas have been assumed based on faunal correlations), which undermines our understanding of the chronological sequence of the mammalian Fauna of the basin as a whole (Qiu, 2000; Zhu et al., 2007; Deng et al., 2008).

The majority of the Quaternary avian fossil records in China were discovered in mammalian fossil localities or archeological sites. However, only preliminary reports on these materials have been published, most of which were from the Zhoukoudian locality (Hou, 1993). The morphological gap between Quaternary fossils and extant birds is minimal, which to some extent dilutes interest in these fossils compared to the bizarre and primitive birds from the Mesozoic or Paleogene. However, comprehensive descriptions of these fossils will not only allow us to extract the temporal span of an extant taxon through definite fossil representatives, but also shed light on how ecological factors and avifaunas interact.

Here we describe a three dimensionally preserved fossil avian tarsometatarsus from the Shanshenmiaozui (SSMZ) Paleolithic site

* Corresponding author. Present address: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Xizhimenwai Street No. 142, Beijing 100044, China. Tel.: +86 6833701; fax: +86 10 68337001.

E-mail address: wangmin_nju@163.com (M. Wang).

in the Guantin village, Yangyuan, Hebei Province, China. Although only recently recognized, SSMZ has yielded a large number of exquisitely preserved mammalian skeletons (Wei, 2004; Tong et al., 2011). Both the SSMZ and Xiaochangliang (XCL) localities are on the south bank of the Sangganhe River, whereas the Nihewan Fauna *sensu stricto* is located on the north bank (Tong et al., 2011). Although no precise dating is available, based on correlation of their elevations, SSMZ is inferred to be slightly younger than the nearby XCL, which has a magnetic age of 1.36 Ma (Zhu et al., 2001; Tong et al., 2011).

2. Material and methods

Anatomical terminology follows Baumel and Witmer (1993). Measurements follow the instruction indicated in Fig. 129 of Tomek and Bochenski (2000).

2.1. Institutional abbreviations and comparative materials examined

BMNH, Beijing Museum of Natural History, *Corvus frugilegus* B108607; *Corvus monedula* B108618. IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, *Corvus splendens* IVPP V873, V1159, V1158; *Corvus macrorhynchos* IVPP V1902, V1139; *Corvus monedula* IVPP V1904; *Corvus frugilegus* IVPP V1903; *Corvus torquatus* IVPP V1148; *Corvus corone* IVPP V7073; *Pica pica* IVPP V1870; *Cyanopica cyana* IVPP V1871; *Cissa erythrorhyncha* IVPP V1725. NZMC, National Zoological Museum of China, *Corvus*

dauricus N894.10292; *Corvus monedula* N894.10227; *C. frugilegus* N893.16841, N893.11039. SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, *Corvus corax* SMF 7675. USNM, Smithsonian Institution National Museum of Natural History, United States, *Corvus corone* USNM 500782.

2.2. Systematic paleontology

Order Passeriformes Linnaeus, 1758
Family Corvidae Vigors, 1825
Genus *Corvus* Linnaeus, 1758
Corvus sp. indet. (Figs. 1 and 2)

Material. A nearly complete right tarsometatarsus slightly damaged near the mid-length on the lateral side, IVPP V18331 (Fig. 1).

Locality and horizon. Shanshenmiaozui, Yangyuan, Zhangjiakou, Hebei Province; Nihewan Formation; Early Pleistocene.

Description. Approximately the same size as *C. corax* (Common Raven), with the following unique combination of characters of the tarsometatarsus: (1) relatively large and robust; (2) block-like hypotarsus with four bony canals and two sulci; (3) and rectangular articular facet for tibiotarsus, the depth (without the hypotarsus) measuring less than half of the corresponding width.

2.3. Measurements

See Table 1.

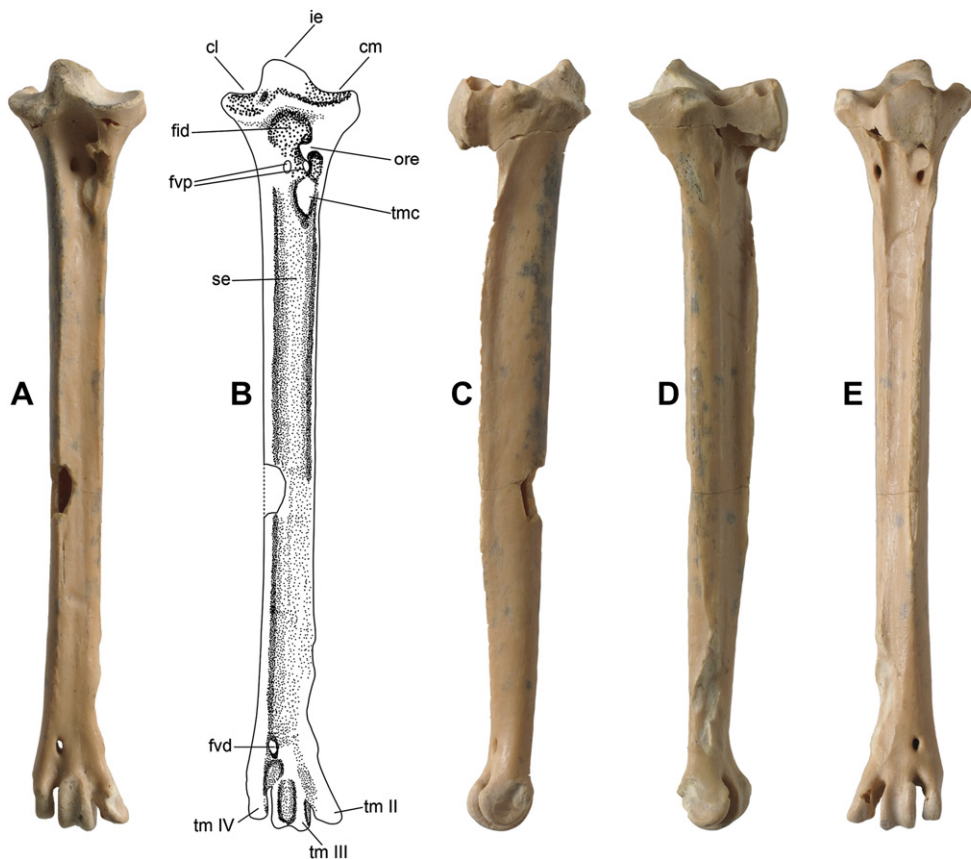


Fig. 1. (A) Dorsal view and (B) line drawing, (C) lateral, (D) medial and (E) plantar view of the right tarsometatarsus the material of *Corvus* sp., IVPP V18331. Abbreviations: cl, cotyla lateralis; cm, cotyla medialis; fid, fossa infracotyloides dorsalis; fvd, foramen vasculare distale; fvp, foramina vascularia proximalia; ie, intercotylar eminentia; ore, ossified retinaculum extensorium; tmc, tuberositas m. tib. cranialis; tm II–IV, trochlea metatarsi II–IV; se, sulcus extensorius. Scale bar is 10 mm.

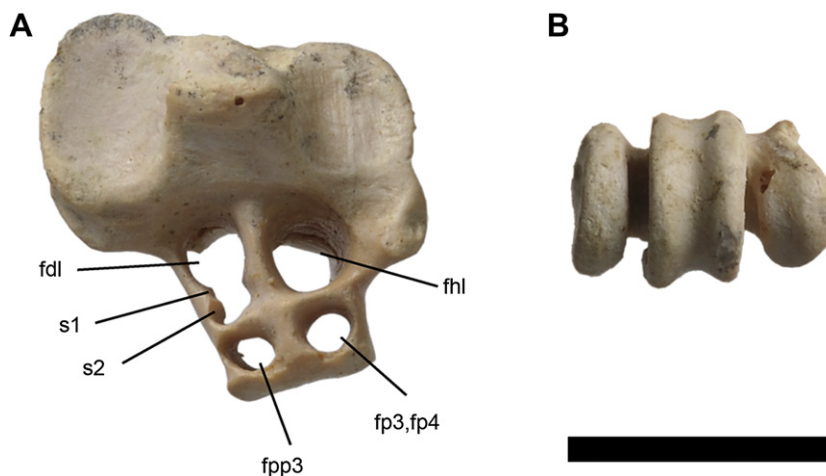


Fig. 2. (A) Proximal view of the hypotarsus and (B) distal view of the trochlea metatarsi II–IV of the material of *Corvus* sp., IVPP V18331. Abbreviations: fdl: the canal for the musculus flexor digitorum longus; fhl: the canal for the musculus flexor hallucis longus; fp3, fp4: canal for the musculus flexor perforatus digiti III and IV; fpp3: canal for the musculus flexor perforans et perforatus digiti II and the musculus flexor perforans et perforatus digiti II. Scale bar is 10 mm.

3. Description

The tarsometatarsus is typically *Corvus*-like in its overall morphology; it is straight, with minimal changes in medio-lateral width along the shaft, except for where the shaft narrows significantly just proximal to the fossa metatarsi I. Proximally the eminentia intercotylaris is high, abruptly dropping into the cotyla medialis and lateralis; the ventral side drops gently to the hypotarsus (Fig. 1A). In proximal view, if the facies dorsalis is considered as a horizontal plane and facing upward, the proximal end of the tarsometatarsus is twisted clockwise significantly, so that the dorsal margin is inclined laterally. The cotyla medialis is larger than the cotyla lateralis, and its dorsal rim projects more dorsally than that of the cotyla lateralis, so that the cotyla medialis is visible

dorsally as a triangular projection in medial view (Fig. 1C, D). The fossa infracotylaris dorsalis excavates the shaft deeply; the two foramina vascularia proximalia are on the same level, although the medial foramen is situated proximal to the lateral one in *C. corone*, *C. torquatus* and *C. splendens* (Fig. 3). The tuberositas m. tibialis cranialis is located distal to the medial foramen vasculare proximale. The retinaculum extensorium is ossified. The dorsal surface of the tarsometatarsus is excavated by a wide and shallow sulcus extensorius that shallows distally, vanishing near the foramen vasculare distale. The lateral margin has a greater dorsal projection than the medial margin.

In proximal view (Fig. 2A) the block-like hypotarsus is angled laterally. The hypotarsus possesses four fully enclosed bony canals. The medial lamina is nearly twice the length of the lateral lamina,

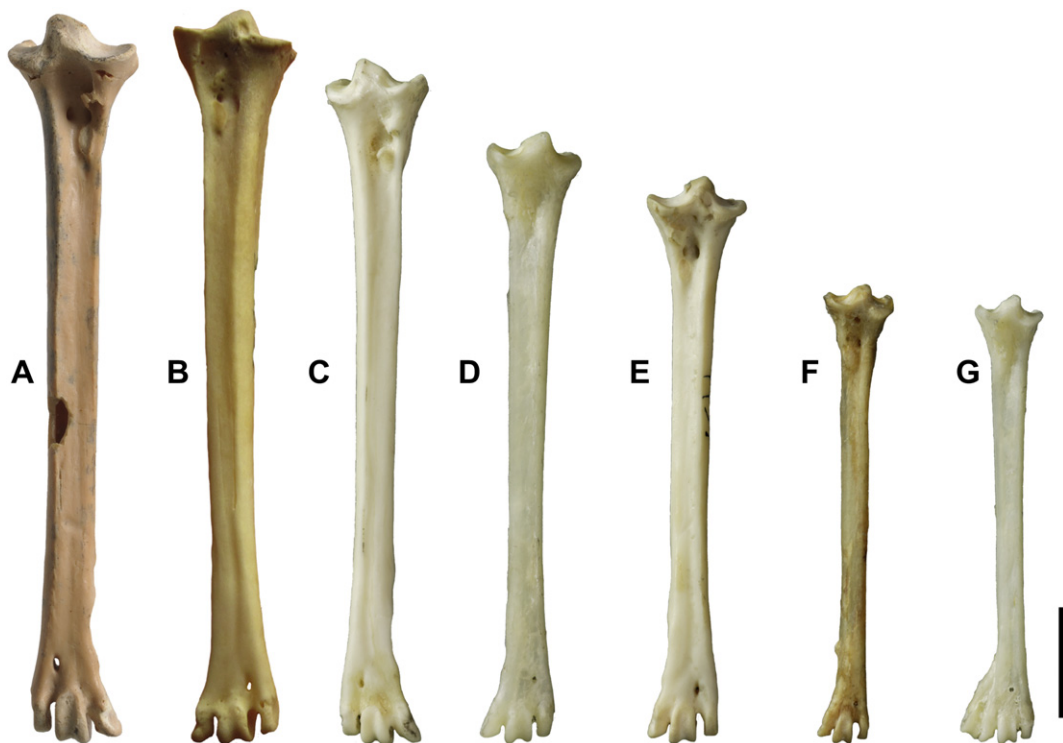


Fig. 3. Dorsal view of the tarsometatarsus of the six compared species of *Corvus* in: (A) *Corvus* sp., IVPP 18331; (B) *C. corone*, USNM 500782; (C) *C. torquatus*, IVPP V1148; (D) *C. frugilegus*, IVPP V1903; (E) *C. macrorhynchos*, IVPP V1139; (F) *C. splendens*, IVPP V873; (G) *C. monedula*, IVPP V1904. Scale bar is 10 mm.

which possesses a laterally projecting tubercle located at the conjunction between the hypotarsus and the tarsometatarsus. The plantar margin of the hypotarsus is angled with respect to the plantar margin of the tarsometatarsus so that in proximal view the hypotarsus appears angled laterally and the medioplantar corner projects furthest plantarly. The two cranial-most canals are much larger than the plantar two canals. The larger medial canal is pinched medially so that it is not round, like the other canals. The medial interior margin of the canal bears two small crests so that the medial margin is formed by three concavities, one large and two small; the lateral margin bears a single crest dividing it into two concave surfaces. The bony wall separating the medial and lateral canals is much thicker than the wall that separates the cranial and plantar canals (Fig. 2A). The two foramina vascularia proximalia are closer to each other in dorsal view than in plantar view (Fig. 1A, E). The crista plantaris lateralis is well developed, extending mediolaterally from the distal end of the hypotarsus for approximately two thirds the length of the tarsometatarsus; the crest decreases in plantar projection distally, giving the tarsometatarsus a triangular cross section. Similar well-developed crista plantaris lateralis only occurs in songbirds and cuckoos (Manegold et al., 2004). The crista plantaris medialis is weakly developed and rounded in plantar view (Fig. 1E).

Distally, the trochleae metatarsi II–IV are arranged in nearly the same plane (Figs. 1A and 2B). The trochleae metatarsi II and IV are medio-laterally compressed, much narrower than the trochlea metatarsi III, lacking an articular furrow. The trochlea metatarsi II is strongly curved medially, forming an angle of 39° with the longitudinal axis of the tarsometatarsus. The trochlea metatarsi III curves medially slightly, with a well-developed articular furrow on both the dorsal and plantar surfaces. The trochlea metatarsi IV is medio-laterally thinner than the trochlea metatarsi II and not curved.

4. Comparison and discussion

The cosmopolitan distributed crow (*Corvus*) contains more than 40 species (Zheng, 2002), and currently eight modern species are living in China (according to Fauna Sinica, 2012), i.e., *C. splendens*, *C. monedula*, *C. dauuricus*, *C. macrorhynchus*, *C. torquatus*, *C. frugilegus*, *C. corone*, and *C. corax* (Fig. 3). Three size classes of Pliocene to Pleistocene *Corvus* can be distinguished in Europe, i.e., the smaller size like *C. monedula*, the medial one like *C. frugilegus* and *C. corone*, and the larger one like *C. corax* (Mlíkovský,

2002). The large gap of size clearly separates the new Nihewan species from smaller species, like *C. splendens*, *C. monedula* and *C. dauuricus*, the tarsometatarsus lengths of which are less than 50 mm (Table 1). *C. frugilegus*, *C. corone* and *C. corax* are assigned as larger corvids in Tomek and Bochenski (2000), and IVPP V18331 is much larger than *C. frugilegus*, but resides in the range of *C. corone* and *C. corax* (see Table 16 in Tomek and Bochenski, 2000). Therefore, the comparisons of IVPP V18331 were only necessarily performed with the relatively large modern and fossil species of *Corvus*. In IVPP V18331, visible in dorsal aspect on the medial side of the shaft, a shallow fossa is present abutting the fossa metatarsi I, representing the narrowest portion of the shaft, a feature hardly observed in *C. corone* (USNM 500782) (Fig. 4). The groove in the plantar side of trochlea metatarsi III of IVPP V18331 is broad (Fig. 2B), but narrow in *C. torquatus* (IVPP V1148), *C. macrorhynchus* (IVPP V1902, V1139), and *C. corone* (see Fig. 127 in Tomek and Bochenski, 2000). The crista plantaris medialis of IVPP V18331, between the fossa metatarsi I and the mid-length of the shaft, is rounded in plantar view, but conversely sharp in *C. macrorhynchus* and *C. frugilegus* (see Fig. 128 in Tomek and Bochenski, 2000). In proximal view, the medial lamina of the hypotarsus is nearly vertical to the plantar margin of the tarsometatarsus, therefore forms a deep concavity on the medial side of the hypotarsus in IVPP V18331 (Fig. 2A). Conversely, the same concavity is more confluent in *C. corax* (Fig. 5G).

The fossil representatives of *Corvus* are mainly found in Europe and their phylogenetic relationships have not been solved yet (see the synonym lists of the fossil species by Mlíkovský, 2002, and also a different view by Mourer-Chauviré, 2004a). To date, two records have been documented from China (Ye, 1989; Hou, 1993), in which only two fossils preserved the tarsometatarsus, i.e., *C. monedula* IVPP V7071 and *C. corone* IVPP V7073. The known Pleistocene fossil species of *Corvus* are rarely larger than *C. corax* (Magish and Harris, 1976). Three species were assumed to be close to or synonymy as *C. corax antecorax* in Brodkorb's "Catalogue of fossil birds" (1978), of which the tarsometatarsus are comparable with *C. corax* in size (Magish and Harris, 1976; Shufeldt, 1892; Mourer-Chauviré, 2004b), i.e., *C. shufeldti* Sharpe, 1909 (new name for *C. annectens* Shufeldt, 1892, which was occupied by *C. annectens* Brüggeman, 1877), *C. antecorax* Mourer-Chauviré, 1975 and *C. neomexicanus* Magish and Harris, 1976. The abundant *C. corax antecorax* are assumed to be the subspecies of modern *C. corax* (Mourer-Chauviré, 2004b), and few morphological features separated it from *C. corax* but only the size (Personal communication with Mourer-Chauviré, 2012). IVPP V18331 differs from *C. corax antecorax* mainly in the proximal end by

Table 1
Measurements (in mm) of the tarsometatarsus lengths of IVPP V18331 and all the compared species of the genus *Corvus*. *Estimated length; L/R: Left/Right side. Measurements of *C. corone corone*, *C. corone cornix* and *C. corax* are from Tomek and Bochenski (2000).

Taxon	Collection number	Total length	Proximal width	Distal width
<i>C. splendens</i>	V1159/L V873/L V1158/L	39.9 (37.0–42.8)	5.2 (4.5–6.2)	4.3 (4.0–4.6)
<i>C. monedula</i>	V1904/R B108618/L N94.10227/R	43.3 (41.0–44.8)	6.8 (6.3–7.1)	5.0 (4.8–5.2)
<i>C. dauuricus</i>	N894.10292/R	45.0	7.1	5.3
<i>C. macrorhynchus</i>	V1902/L V1139/L	52.3 (52.0–52.5)	8.8 (8.3–9.3)	6.4 (6.3–6.5)
<i>C. frugilegus</i>	B108607/L N93.16841/L N93.11039/L V1903/L	55.0 (53.7–56.7)	8.3 (8.0–8.6)	6.3 (5.9–6.6)
<i>C. corone corone</i>		57.7 (51.2–61.2)	9.5 (9.0–10.3)	6.9 (6.5–7.4)
<i>C. corone cornix</i>		57.7 (51.9–64.3)	9.4 (8.5–10.4)	7.0 (6.3–7.5)
<i>C. torquatus</i>	V1148/L	63.8	9.5	7.3
<i>C. corax</i>		68.0 (64.4–72.3)	13.3 (11.8–15.5)	9.3 (8.5–10.2)
IVPP 18331	V18331/R	66.5	11.9	7.9

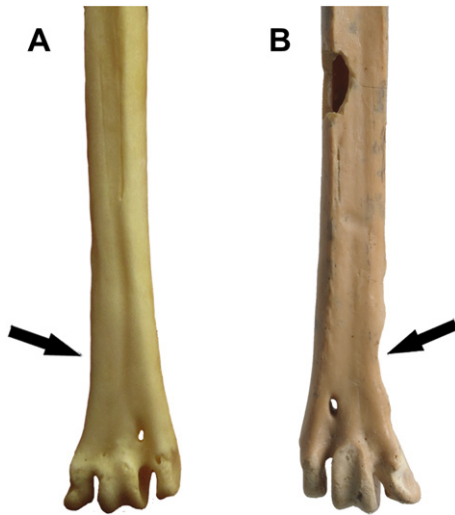


Fig. 4. Dorsal view of the distal ends of tarsometatarsus in: (A) *C. corone*, USNM 500782; (B) *C. sp.*, IVPP V18331. The black arrow in (B) indicates the concavity on the medial side of the tarsometatarsus, abutting the fossa metatarsi I, which is clearly absent in (A) *C. corone*. Scale bar is 10 mm.

the higher eminentia intercotylaris (see Figs. 3 and 18 in Mourer-Chauviré, 2004b) and the proportionally thinner proximal thickness of the shaft excluding the hypotarsus; Besides, four completely and one almost closed hypotarsus canals in *C. corax antecorax* is different from IVPP V18331 (Fig. 5H). Compared with *C. shufeldti*, IVPP V18331 is distinguished by that the proximal end is more medio-laterally extended, and the cotyla medialis is larger and more dorsal projecting (Fig. 5I). Besides, five canals are completely closed in *C. shufeldti* but only four in the former. The holotype of *C. neomexicanus* was a left femur, and no description or pictures about tarsometatarsus has been provided in the initial literature, but the measurement shows that the largest *C. neomexicanus* was considerably shorter than IVPP V18331 (see Table 1 in Magish and Harris, 1976).

Besides the aforementioned size and morphological differences, the peculiar hypotarsus morphology of IVPP V18331 clearly distinguishes it from all other known species of *Corvus*. The avian hypotarsus transmits the tendons of the flexor muscles of the toes,

and its structure is highly variable within Passeriformes. The larger medial and lateral canals of IVPP V18331 transmit the musculus flexor digitorum longus (fdl) and musculus flexor hallucis longus (fhl) respectively. The smaller superficial medial canal transmits the musculus flexor perforans et perforatus digiti III (fpp3), and the remaining canal transmits the musculus flexor perforatus digiti III (fp3) and IV (fp4). The two observed sulci on the plantar side of the medial canal probably conduct the musculus flexor perforatus digiti II (fp2) and the musculus flexor perforans et perforatus digiti II (fpp2) respectively, which are assumed to be merged with the larger canal for the fdl.

The morphology of the hypotarsus has proved to be informative in avian phylogenetic analyses (see Mayr and Clarke, 2003, character 103–106; Mayr, 2008; Mayr and Bertelli, 2011), and its variation and phylogenetic information for fossil and extant songbirds have been discussed in Manegold et al. (2004). The arrangement of canals in the hypotarsus varies among the Passeriformes and within the genus *Corvus* we examined. In *C. splendens* IVPP V873, the fp2 canal is not closed, but open dorsally to the canal for the fd1 (Fig. 5F); however, this canal is almost closed in *C. corone* USNM 500782 and *C. macrorhynchos* IVPP V1139 (Fig. 5A, B), and completely closed in *C. torquatus* IVPP V1148, *C. frugilegus* IVPP V1903, *C. monedula* IVPP V1904 and *C. corax* SMF 7675 (Fig. 5C, D, E, G), but it is uncertain which two canal were merged in the five canals of *C. shufeldti* and *C. corax antecorax* (Fig. 5H, I). In general, the two deep canals for the fhl and fd1 are larger than the others. The fp2 and fpp2 canals, which are aligned on the lateral side and intermediate between the fdl and fpp3 canals, are the smallest and their relative positions are highly variable: the canal for fp2 is on the dorsal side of the canal for fpp2 in *C. corone*, *C. macrorhynchos* and *C. torquatus* (Fig. 5A, B, E), but on the medial side in *C. monedula* and *C. corax* SMF 7675 (Fig. 5C, G). In *C. frugilegus* IVPP V1903, the fp2 canal is significantly wider medio-laterally, approaching the fpp3 canal in size, and surrounds the fpp2 canal dorsally and medially (Fig. 5D). In IVPP V18331, the two sulci (if closed, they would represent these two smallest canals) are arranged dorso-plantarly (Fig. 2A). Whether this variation in the hypotarsus is phylogenetically informative for *Corvus* cannot yet be determined, but merits consideration in future systematic research.

The large size and the combined characters presented on the tarsometatarsus of the new specimen exclusively indicate it belongs to a large *Corvus*, but do not justify its assignment to any of the

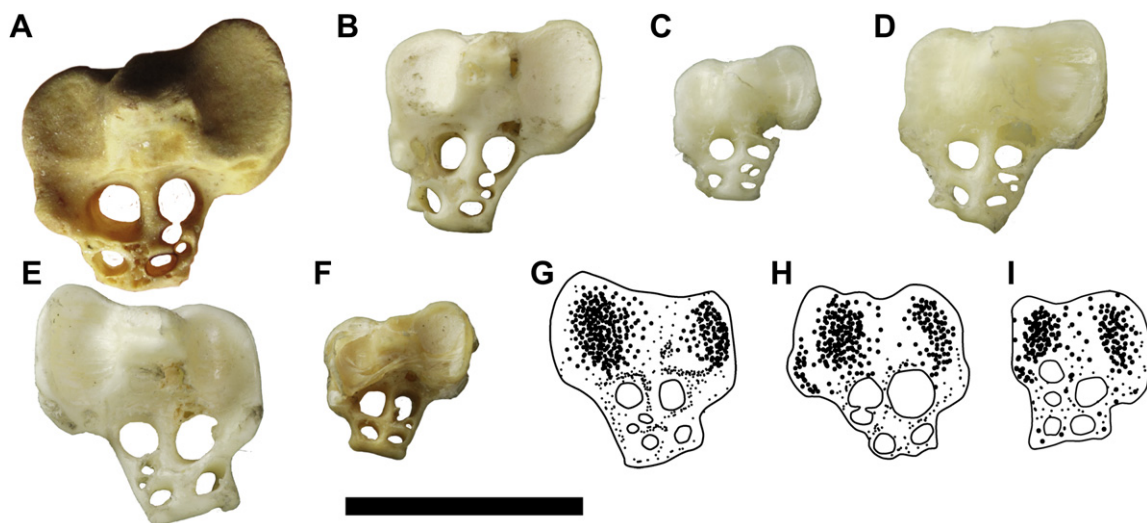


Fig. 5. Proximal view of the proximal ends of the tarsometatarsus of (A) *C. corone*, USNM 500782; (B) *C. macrorhynchos*, IVPP V1139; (C) *C. monedula*, IVPP V1904; (D) *C. frugilegus*, IVPP V1903; (E) *C. torquatus*, IVPP V1148; (F) *C. splendens*, IVPP V873. Scale bar is 10 mm; line drawing of (G) *C. corax*, SMF7576, (H) *C. corax antecorax* (based on the Fig. pl. 20.10 in Mourer-Chauviré, 1975), and (I) *C. shufeldti* (based on Fig. pl. XV.14 in Shufeldt, 1892), not to scale.

known extant or fossil species of this genus. Nevertheless, the material is too incomplete, and some morphological features aforementioned vary among inter- and intra-species level in *Corvus* (see Figs. 124–128 in Tomek and Bochenki, 2000). Besides, the structure of hypotarsus canal is not yet well understood and changes in both the arrangement and the degree of closeness complicate our understanding of the peculiar hypotarsus in this new material. Therefore, the erection of a new species for the Nihewan crow cannot be corroborated by the limited information at hand, and only more complete materials will shed light on its affinities.

5. Paleocology

Although no paleoclimate research has been performed in the SSMZ, this information can be obtained indirectly from the taxonomic composition and comparable faunas with paleoclimate data. At least fifteen species of fossil mammals are known from the SSMZ, many of which represent classical grassland occupants in arid conditions, such as *Equus sanmeniensis*, *Coelodonta antiquitatis nihowanensis*, *Gazella sinensis* and *Mammuthus trogontherii* (Tang, 1980; Tong et al., 2011). Palynological research has been conducted on the adjacent XCL Paleolithic sites such as the Dachangling (DCL) (Deng et al., 2006) and Feiliang (FL) sites (Li et al., 1996). Magnetic stratigraphy and sedimentation rates confirm that the DCL, located 170 m to the west of XCL (Pei, 2002), has a similar sedimentary history and age (1.36 Ma) (Zhu et al., 2007), suggesting that a similar environment was prevalent at both localities. Given these facts, it is reasonable to make environment-related inferences for XCL and the neighboring SSMZ based on the results obtained from the DCL. Zhu et al. (2007) reported that the pollen assemblages in DCL were dominated by herbaceous taxa (95.7%), in which xerophil plants took the slight majority. When the mammalian fauna and palynological research is taken into consideration, the evidence suggests that the SSMZ and the adjacent areas where IVPP V18331 was collected were open, arid grasslands during the Early Pleistocene, and such habitat is preferred by some modern *Corvus* species, e.g. *C. albus*, *C. rhipidurus* (Zheng, 2002; BirdLife International, 2012). Fragmentary bird fossils have been found in other Paleolithic sites in Nihewan basin, including the Maquangou, Queergou and Xujiayao sites, nearly all of which were assigned to *Struthio* sp. in the preliminary report of Xie (2006). Therefore, the discovery of this fossil crow increases the taxonomical diversity of this vertebrate fauna and also indicates the potential for research on smaller birds at the Shanshenmiaozui site.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jas.2012.10.026>.

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