Webbed foot of an Early Cretaceous ornithurine bird *Gansus* from China

中国早白垩世今鸟类甘肃鸟的蹼足化石

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Abstract: *Gansus yumenensis* is the first Mesozoic bird found in China. It was collected from the Xiagou Formation in northwestern Gansu, which is considered to be equivalent to the Early Cretaceous strata yielding the Jehol biota in western Liaoning. Based on some characters such as elongated phalanges and short claws with pointed flexor tubercles, *Gansus yumenensis* is regarded as the bird adapted to life in the aquatic environment. *Gansus yumenensis* was originally erected only based on a unique specimen of the left pes, and some specimens have been found for a further study recently. In this paper, a newly discovered complete hindlimb of *Gansus yumenensis* is described, which shows the clear webbed structures among the distal portions of pedal phalanges. It is the first direct evidence to show that *Gansus yumenensis* with well-developed foot-webs is really the oldest known bird specifically well-adapted to life in the aquatic environment in the world.

Key words: *Gansus yumenensis*; webbed foot; Early Cretaceous; Gansu Province

摘要: 玉门甘肃鸟(*Gansus yumenensis*)是中国发现的第一只中生代鸟类化石。该化石产自甘肃西北部下沟组,时代与辽宁西部产热河生物群的早白垩世地层的时代大体相当。该鸟类趾节拉长,很短的爪具有较尖锐的屈肌结节,因而被认为是一种适应于水生生活的鸟类。玉门甘肃鸟的建立最初仅依据一件左足标本,直到最近又发现了少量可供进一步研究的新标本。本文描述了一件新的玉门甘肃鸟的完整后肢化石,标本在远端趾节之间显示出清晰的蹼的构造。这为玉门甘肃鸟具有发育足蹼的观点提供了最直接的证据。玉门甘肃鸟也成为世界上已知最古老的适应于水生生活环境的鸟类。

关键词: 玉门甘肃鸟;蹼足;早白垩世;甘肃省
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Originally erected by Hou and Liu[1] in 1984, the ornithurine *Gansus yumenensis* is the first record of the Mesozoic bird in China. Although represented by the unique specimen of left pes (holotype, IVPP V6862), the characters such as elongated pedal phalanges and short claws with pointed flexor tubercles indicate this bird to be adapted to life in aquatic environments[1,2]. Here we report a newly discovered complete hindlimb of *Gansus yumenensis*, which

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shows the clear webbed structures among the distal portions of pedal phalanges. The new finding not only gives the first direct evidence for the presence of well-developed foot-webs in *Gansus yumenensis*, but also suggests that it was the oldest known bird specifically well-adapted to life in aquatic environments in the world indeed.

The new specimen (IG-04-CM-008) was unearthed from the Xiagou Formation in the Changma region of Yumen City, Gansu Province, northwestern China. The fossil-bearing beds mainly consist of the grayish green and yellowish gray sandstones, siltstones and shales, where the holotype of *Gansus yumenensis* was ever discovered[1]. The associated fossils are bivalves, gastropods, ostracods, conchostracans (*Eosestheria*, *Yanjiestheria*), insects (*Ephemeropsis*), fishes (*Lycoptera*, *Sinamia*), plants[3], and enantiornithine birds[4,5]. They can be grouped into the *Eosestheria-Ephemeropsis-Lycoptera* assemblage of the Jehol Biota of Early Cretaceous in western Liaoning and even East Asia[6,7].

1 Description

The specimen IG-04-CM-008 is well preserved as a nearly complete right hindlimb and a left foot (Fig. 1). It is roughly as same as the holotype of *Gansus yumenensis* in size according to the length of tarsometatarsus[1]. The femur is obviously curved with two prominent distal condyles. Although its proximal portion is not well exposed, the femur is believed to be less than half the length of the tibiotarsus. The right tibiotarsus is basically straight and about 54.0 mm in length. Distally, its lateral condyle is remarkably larger than the medial one.

The tarsometatarsus is nearly completely fused except its distal ends, and approximately 60% the length of tibiotarsus. The trochlea of metatarsal Ⅱ is considerably higher and more plantar than those of metatarsals Ⅲ and Ⅳ. The trochlea of metatarsal Ⅲ is the lowest. In dorsal view, the distal end of metatarsal Ⅲ is the widest, but metatarsal Ⅳ the narrowest among them. Moreover, the distal articular surface of metatarsal Ⅲ is ginglymoid, differing from the round-shaped ones of the others. Metatarsal Ⅰ is short, and its distal end is distinctly higher than the trochlea of metatarsal Ⅱ (Fig. 2).

The phalangeal formula is 2-3-4-5-x. The hallux is completely reversed. The phalanges are slender and elongated with relatively shallow collateral ligament fossae. The fourth digit is the longest of the four, and the first digit occupies only 30% the length of the fourth. Both the third and fourth digits are longer than the tarsometatarsus. The proximal phalanx of each digit is the longest (Table 1). All the unguals are comparatively short and slightly curved, possessing remarkably pointed flexor tubercles.

It is noteworthy that several patches of distinct nodule-like structures can be observed on the webs in the distal portions (i.e., penultimate and prepenultimate phalanges) of the three main digits (Figs. 2,3). The nodule-like structures are generally smooth, round-shaped and closely spaced. They are very tiny and about 0.29-0.33 mm in diameter. The finding of the specimen IG-04-CM-008 gives the convincing proof that *Gansus yumenensis* had webbed feet.

2 Discussion

The specimen described above can be definitely assigned to *Gansus yumenensis* based on its much higher trochlea of metatarsal Ⅱ, the nearly completely fused tarsometatarsus, the fourth pedal digit longer than the third one and both also longer than tarsometatarsus, short claws with pointed flexor tubercles[1,2]. Moreover, it enriches our knowledge about the anatomy and lifestyle of *Gansus yumenensis*[8].

The avian webbed foot has been thought to appear firstly in the Early Cretaceous (Aptian-Albian) owing to the recent discoveries of the bird footprints in South Korea[9]. Some groups of extant web-footed birds, such as Gavi-

Table 1 Bone lengths in feet of *Gansus yumenensis* (IC-04-CM-008)

	Left/mm	Right/mm
Metatarsal Ⅰ	4.52	4.40
Tarsometatarsus	32.04	31.55
Pedal digit Ⅰ	11.71	12.07
Phalanx Ⅰ-1	8.20	8.19
Phalanx Ⅰ-2 (claw)	3.51	3.88
Pedal digit Ⅱ	29.01	28.53
Phalanx Ⅱ-1	13.74	13.40
Phalanx Ⅱ-2	10.81	11.19
Phalanx Ⅱ-3 (claw)	4.46	3.94
Pedal digit Ⅲ	34.89	35.27
Phalanx Ⅲ-1	13.82	14.19
Phalanx Ⅲ-2	8.88	9.01
Phalanx Ⅲ-3	7.73	7.65
Phalanx Ⅲ-4 (claw)	4.46	4.42
Pedal digit Ⅳ	38.46	38.58
Phalanx Ⅳ-1	11.23	10.98
Phalanx Ⅳ-2	8.34	8.39
Phalanx Ⅳ-3	7.42	7.35
Phalanx Ⅳ-4	7.29	7.30
Phalanx Ⅳ-5 (claw)	4.18	4.56

Fig.1 Complete hindlimb of *Gansus yumenensis* (IG-04-CM-008) with foot-web impressions (Scale bar, 2 cm)

iformes, Procellariiformes, Pelecaniformes, Anseriformes, Charadriiformes and so forth, usually have a complete web. Similar web is also seen in Paleogene webbed foot, such as the Eocene *Presbyorniformipes* in Utah[10], and the Oligocene bird webbed footprints in Spain[11]. The Late Cretaceous avian webs were relatively less developed, as shown by the bird tracks *Uhangrichnus* and *Hwangsanipes* from South Korea[10]. Furthermore, the known avian webbed feet of Early Cretaceous were represented only by the footprints, and

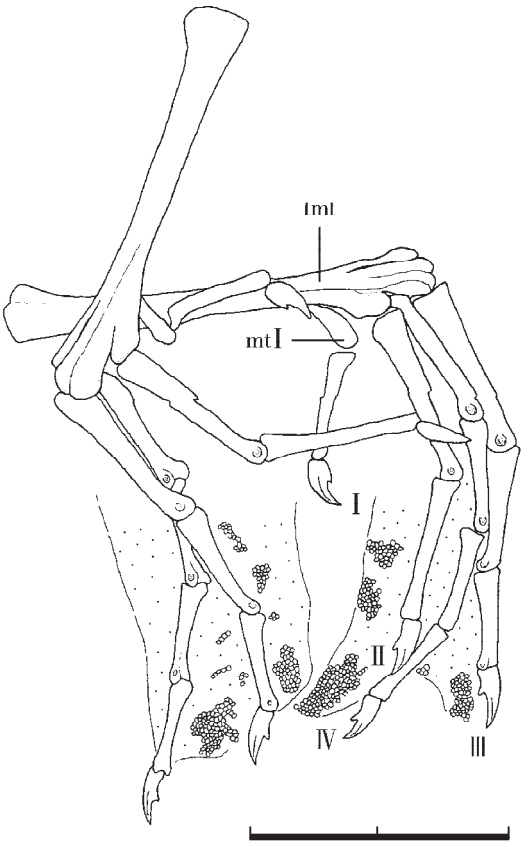

Fig.2 Line drawings of the feet of *Gansus yumenensis* (IG-04-CM-008), showing the webs with skin ornaments(Scale bar, 2 cm)
Abbreviations: mt Ⅰ, left metatarsal Ⅰ; tmt, left tarsometatarsus; Ⅰ-Ⅳ, left pedal digit Ⅰ-Ⅳ

Fig.3 Enlargement of the area labeled in Fig. 1, showing the detailed nodule-like structures of web in *Gansus yumenensis* (IG-04-CM-008)

their webs were generally semipalmate[9,10,12].

According to our study, the Early Cretaceous *Gansus yumenensis* possessed much more developed foot-webs as in most modern web-footed birds. This is the oldest record of the soft-tissue impression of avian foot-webs together with foot skeletons in the world. We are convinced that *Gansus yumenensis* was an Early Cretaceous wading or water bird adapted to life in aquatic environments, preying mainly on small fishes, shrimps, gastropods, conchostracans, insects and others. It seems that the web-footed birds in the Early Cretaceous had already been greatly diversified to adapt to different living environments on or around water. The new finding provides the direct evidence for our better understanding both the evolutions of avian foot-webs and the habit adaptation of early birds.

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