

On the horizon of *Protopteryx* and the early vertebrate fossil assemblages of the Jehol Biota

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***Protopteryx*, a monotypic fossil bird discovered from the Sichakou basin in Fengning, Hebei, is the most primitive enantiornithine currently known. The bird-bearing strata do not contain the index fossils of the Yixian Formation in western Liaoning; the fish and bird fossils have more primitive features than the related forms found in the Yixian Formation, and the conchostracans are those usually distributed in the Dabeigou and Dadianzi formations in northern Hebei. Besides, the *Protopteryx*-bearing strata underlie the deposits bearing the index fossils of the Yixian Formation in the neighboring basin. Thus, it could be confirmed that the horizon of *Protopteryx* should be lower than the Yixian Formation, and is approximately equivalent to the Dadianzi Formation in northern Hebei. This is the lowest horizon of the known fossil birds in China and Mesozoic enantiornithine birds in the world. Accompanying *Protopteryx*, there are other birds, acipenseriform fishes, salamanders, and mammals, which compose the *Peipiaosteus fengningensis*-*Protopteryx fengningensis* assemblage. This new assemblage traces the vertebrate evolution history of the Jehol Biota back to 130.7 Ma before. It is suggested that the demarcation of the Jehol Biota should be based on the large-scale tectonic-sedimentary cycles, and *Peipiaosteus*, instead of *Lycoptera*, could be taken as the vertebrate representative of the Jehol Biota.**

horizon of *Protopteryx*, early vertebrate fossil assemblages, Jehol Biota

Since 1992, various important clades of fossils have been discovered from the sedimentary intercalations of the Yixian Formation and the middle and lower parts of the Jiufotang Formation of the Jehol Group in western Liaoning. A vivid picture of the Jehol Biota, an early Cretaceous biota exquisitely preserved due to special geological environment, has been exposing itself to the world^[1–6].

However, because of the difference in tectonic belts and basin evolution, the stratigraphic sequence of the Jehol Group in western Liaoning is mostly lack of the strata corresponding to the Zhangjiakou Formation, Dabeigou Formation, and the lower part of the Dadianzi Formation of the Luanping Group in northern Hebei^[3]. Therefore, northern Hebei is a crucial area to trace the early history of the Jehol Biota.

In northern Hebei, the most extensively investigated is the Luanping basin, and the standard sections of the

Dabeigou and Dadianzi formations of the Luanping Group are located in this basin^[7,8]. Recently, great progress has been made on the stratigraphy and invertebrate paleontology of the Dabeigou and Dadianzi formations in the studies of the Jurassic-Cretaceous boundary, index fossils and stratotype sections, and the establishment of main stages as well^[9–12]. But except for fishes, only a few fragmentary vertebrate fossils of amphibians and dinosaurs have been found in this basin possibly because it is mainly a normal sedimentary basin.

During the 1990s, new forms of birds and acipenseriform fishes were also discovered from the Senjitu and Sichakou basins in Fengning, northern Hebei^[13–17].

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Fossils are abundant in these basins for the strata of the lower part of the Luanping Group, composed of extrusives, breccias and tuffs with intercalated sedimentary beds, are deposited as those of the Yixian Formation in western Liaoning. Since the mid 1990s, we have conducted a series of field investigations in the Senjitu and Sichakou basins, and carried out twice large-scale fossil excavations in the bird fossil-bearing sedimentary beds of the Sichakou basin in 2000 and 2007. Based on our work, it is found that the horizon of the bird fossil-bearing sedimentary beds in the Senjitu basin and that in the Sichakou basin are not the same; the former is corresponding to the Dawangzhangzi Bed of the Yixian Formation in Lingyuan, western Liaoning, and the latter is approximately equivalent to the Dadianzi Formation in Luanping, northern Hebei. With the clarification and confirmation of these two bird fossil-bearing horizons in the neighbouring basins of Senjitu and Sichakou, two early vertebrate fossil assemblages of the Jehol Biota could be established in northern Hebei, and the lower one, the *Peipiaosteus fengningensis*-*Protopteryx fengningensis* assemblage, is the earliest vertebrate fossil assemblage of the Jehol Biota up to now.

1 The horizon of *Protopteryx*

Protopteryx fengningensis, as the most primitive enantiornithine (opposite bird) to date^[17], is discovered from the Sichakou basin in Fengning County, northern Hebei Province (Figure 1).

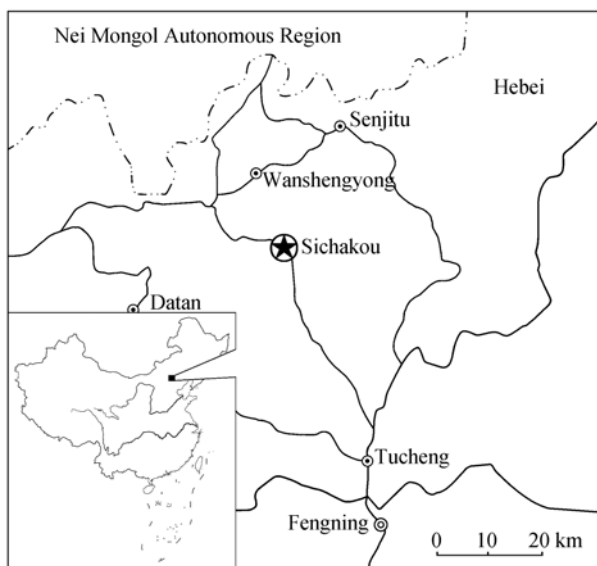


Figure 1 Sketch map of Sichakou in Fengning County, northern Hebei Province.

The Sichakou basin is situated at the conjunction of the Daxinganling-Taihangshan Tectonomagmatic Belt and the Inner Mongolian Earth Axis. Its evolution is evidently controlled by the tectonic stress field in NNE direction. During the period of bird-bearing deposition, the transmeridional width of the basin might be less than 10 km, while the meridional length could reach 30 km; the basin center is close to the south, and located in the vicinity of Hongqiangou-Jiechangou (Figure 2).

The Sichakou basin has not been properly investigated. From 1957, less than 20 preliminary surveys by local geological departments were briefly concerned with the regional geology and mineral resources in this basin, and special researches on stratigraphy and paleontology remain blank. Of the former works, the 1:200000 regional geological survey of Shanghuangqi by the Bureau of Geology of Hebei Province laid the foundation for divisions of the Late Mesozoic strata in this area. The other schemes afterwards are mostly identical only with minor differences (Table 1). Bi Ziwei and Yang Youshi provided some new understanding on the sedimentary sequence as well as the division and correlation of the Late Mesozoic strata in the Senjitu and Sichakou area after the 1:50000 regional geological surveys, whereas they were mainly based on the data of the Senjitu basin^[18].

The strata bearing *Protopteryx* and other fossil birds in the Sichakou basin consist of a sequence of fluvio-lacustrine deposits with abundant pyroclastics (Figure 2: K_1h^2). The upper part is composed of offwhite, isabel-line rhyolitic debris, crystal tuffs and brecciated tuffs, tuffaceous sandstones, siltstones interbedded with mudstones, and intercalated with multi-layers of shales; the lower part is composed of offwhite, ficelle tabular tuffaceous siltstones, silty mudstones, calcic mudstones interbedded with tuffs and bibliolites. This sequence of deposits practically measures 251.3 m thick in the Hongqiangou section and conformably or disconformably overlies the intermediate to basic volcanic rocks (Figure 2: K_1h^1). *Protopteryx* and other bird fossils are mostly yielded in interbedded shales in the lower part.

In early works, because of cursoriness in fossil collection and identification, and even some mistakes in them, as well as the difficulty in transverse correlation of volcanic sedimentary rocks, three representatives of the Jehol Biota (*Eosesthesia*, *Ephemeropsis trisetalis*, *Lycoptera*) were thought to exist in the bird-bearing deposits of the Sichakou basin. Consequently, the Sichakou

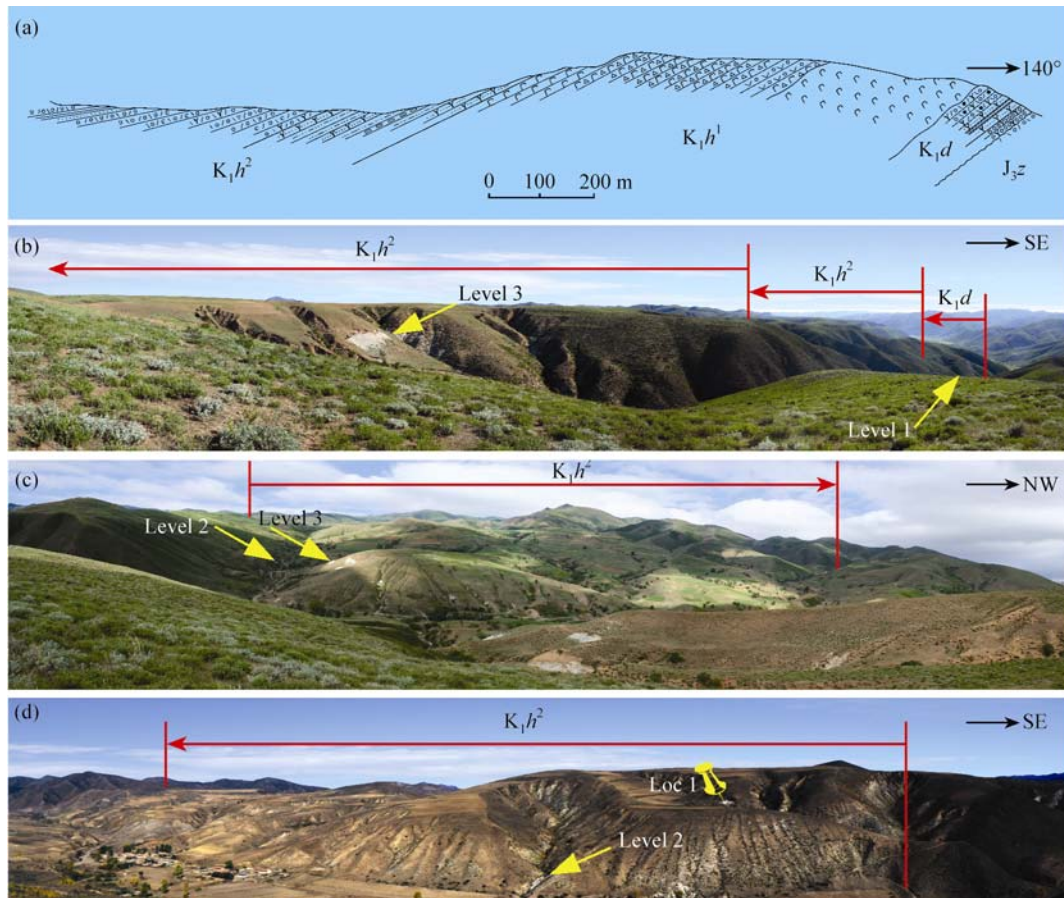


Figure 2 Sections of the Sichakou Sedimentary Member of the Early Cretaceous Huajiying Formation in the Sichakou basin, Fengning, Hebei. (a) Hongqiangou measured section (simplified from Bureau of Geology of Hebei Province, 1975: Figure II-14); (b) Xigoumen section, Youfang; (c) Jianchanggou section, Youfang; (d) Jiacaigou section. K_1h^2 , Sichakou Sedimentary Member of the Huajiying Formation; K_1h^1 , First Volcanic Member of the Huajiying Formation; K_1d , Dabeigou Formation; J_{3z} , Zhangjiakou Formation. Level 1, initial bed of the genus *Peipiaosteus*; Level 2, bed yielding *Protopteryx fengningensis*; Level 3, bed with abundant bird fossils; Loc 1, locality of *Protopteryx fengningensis*.

Table 1 Divisions of the Late Mesozoic strata in the Sichakou-Senjitu area of Fengning, Hebei

BGHP ^{a)} 1975		BGM RHP ^{b)} 1985		BGM RHP ^{c)} 1992		PRESENT				
Sichakou-Senjitu		Sichakou-Wanshengyong		Senjitu-Dahexi		Sichakou-Senjitu				
J_3	Qingshila Formation	K_1	Huajiying Formation	Qingshila Formation		K_1	Qingshila Formation			
	Jianchang Formation			Member III	Huajiying Formation		Xiadian Basalt-andesites	Huajiying Formation	5th Volcanic Member	
							Member II		Guohedao Sands	Guohedao Sedimentary Member
							Member I		Huojiagou Basalt-andesites	4th Volcanic Member
	Jingangshan Formation			Xiguayuan Formation	Nianzigou Sands		Nianzigou Sedimentary Member			
	Yixian Formation			Member II	Dabeigou Formation		Member II	Nanyingzi Basalt-andesites	Qiaotou Sands	3rd Volcanic Member
								Member I		
	Zhangjiakou Formation			J_3	Zhangjiakou Formation		J_3	Chapeng Formation		Dabeigou Formation
Member II		Member I	Sichakou Sedimentary Member							
Zhangjiakou Formation	J_3	Zhangjiakou Formation	J_3	Zhangjiakou Formation	J_3	Zhangjiakou Formation				

a) Bureau of Geology of Hebei Province, Report on the 1:200000 regional geological survey of Shanghuangqi, PRC, 1975. b) Bureau of Geology and Mineral Resources of Hebei Province, Report on the 1:50000 regional geological survey of Wanshengyong, PRC, 1985. c) Bureau of Geology and Mineral Resources of Hebei Province, Reports on the 1:50000 regional geological surveys of Senjitu and Dahexi, PRC, 1992.

fossil-bearing sedimentary beds were named “Jingangshan” or “Xiguayuan” formation, and no differentiation in transverse correlation was made with the bird-bearing deposits in the Senjitu basin, which results in the misunderstanding that the bird fossil-bearing sedimentary beds of these two neighbouring basins were equivalent in subsequent reports.

During the series of field investigations and twice large-scale excavations in the bird fossil-bearing sedimentary beds of the Sichakou basin, we had never found undoubted index fossils which are common in the bird fossil-bearing sedimentary beds of the Senjitu basin, such as *Lycoptera davidi* (Sauvage). In contrast, the acipenseriform fishes and birds discovered from the Sichakou basin show more primitive characters than the related forms from the Senjitu bird fossil-bearing sedimentary beds and their equivalents^[13–17]. This reveals that the bird fossil-bearing sedimentary beds of these two neighbouring basins should belong to deposits of different periods. Recently, a team from the Regional Geological and Mineral Resources Investigation Institute of Hebei Province also observed that the Sichakou bird fossil-bearing sedimentary beds underlie the Senjitu bird fossil-bearing sedimentary beds in field work (Kang Zilin et al., pers. comm.).

In addition to vertebrate fossils, the bird-bearing beds of the Sichakou basin also yield botanic and invertebrate fossils such as gastropods, bivalves, conchostracans, ostracods, insects, spiders, etc., of which the plant and insect fossils are relatively abundant. The invertebrate fossils we collected from the bird-bearing beds include: *Amplovalvata* sp., *Arguniella lingyuanensis* (Gu), *Sphaerium jeholense* (Grabau), *Asioestheria sandaogouensis* Wang, *A. nanyingpanensis* Wang, *Asioestheria* sp., *Yanshanina* cf. *xishunjingensis* Wang, *Yanshanina* sp., *Rhinocypris* sp., *Mongolianella* sp., *M. cf. palmosa* Mandelstam, *Yanshanina* ? sp. Among these preliminarily identified invertebrate fossils, the gastropods, bivalves, and ostracods are the common elements found both in the lower part of the Yixian Formation in western Liaoning and the Dadianzi Formation in northern Hebei; whereas the conchostracans are the forms usually occurred in the Dabeigou and Dadianzi formations in northern Hebei. Moreover, it is meaningful that there lack of both of the index invertebrate fossils of the Yixian Formation in western Liaoning and the Dabeigou Formation in northern Hebei, e.g. *Eosestheria*, *Cypridea*

of the Yixian Formation, and *Nestoria*, *Keratestheria*, *Luanpingella*, *Eoparacypris* of the Dabeigou Formation.

Furthermore, some fragmentary fish bones, abundant bivalves and a few conchostracans were discovered from the first sedimentary member (Figure 2: K_{1d}) overlying the acidic volcanics of the Zhangjiakou Formation in the Sichakou basin. The upper part of this sedimentary member consists of offwhite tuffs, tuffaceous sandstones and siltstones; the lower part consists of glaucous, ficelle tuffaceous siltstones, mudstones intercalated with paper shales, and the bottom contains conglomerates. This sequence of deposits practically measures 76.7 m thick in the Hongqiangou section. And the fossils mentioned above mostly occur in the lower mudstones and shales, which include: *Peipiaosteus* sp., *Arguniella* spp., *Abrestheria xishunjingensis* Wang, *A. cf. xishunjingensis* Wang, *A. cf. subovato* Wang, and *Abrestheria* sp. The fossils of the genus *Abrestheria* are widely distributed in the Dabeigou Formation and its equivalents in northern Hebei and southeastern Nei Mongol, and one species, *A. subovato*, can extend its highest occurrence to the lower part of the Dadianzi Formation in the Luanping basin.

Based on the above-mentioned fossil data and the contact relationships of strata, it could be confirmed that the horizon of the bird fossil-bearing sedimentary beds in the Sichakou basin is different from that in its neighbouring basin of Senjitu, and the former should underlie the latter; and that the bird fossil-bearing sedimentary beds and the first sedimentary member bearing *Peipiaosteus* and *Abrestheria* in the Sichakou basin are approximately equivalent respectively to the Dadianzi Formation and the Dabeigou Formation in the Luanping basin. Since it is still premature to rename formations in the Sichakou basin, the first sedimentary member remains its assignment by BGMRHP in 1985, and the bird fossil-bearing sedimentary beds, together with the underlying set of intermediate-basic volcanics, are assigned to the Huajiying Formation, as the second and the first member of this volcanic-sedimentary formation in the Sichakou and Senjitu area (Figure 2; Table 1).

2 The early vertebrate fossil assemblages of the Jehol Biota

From the bird fossil-bearing member in the Sichakou basin, the earliest discovered vertebrate fossils are *Peipiaosteus fengningensis* Bai and *Yanosteus longidorsalis* Jin et al.^[14]. During the excavations in 2000 and 2007,

lots of *Peipiaosteus* and *Yanosteus* were found from many beds in the lower part of this member. Among them, there are not a few big individuals, which indicates that the acipenseriform fishes were already flourishing at that time.

The bird fossils in the Sichakou basin were initially discovered in the late time of 1990s, and the first described is the famous enantiornithine bird, *Protopteryx fengningensis* Zhang et Zhou^[17]. Up to now, hundreds of bird fossils have been found from the bird fossil-bearing member in the Sichakou basin, of which there are some new forms remaining to be studied. Together with the abundant plant and insect fossils, it could be presumed that the terrestrial ecosystem in this area was also thriving.

Apart from fishes and birds, Hou Zhiqi, a local fossil amateur, once found a fossil salamander from the same horizon as *Protopteryx* on the south side of Jiecaigou in late 1990s. During the excavation in 2007, we also collected an almost complete mammalian mandible fossil. In the last decade, vertebrate fossils from the bird fossil-bearing member in the Sichakou basin had already included four major classes: fishes, amphibians, birds and mammals. And the left class, reptiles, could be expected along with in-depth work.

The first Mesozoic bird fossil from northern Hebei was discovered in the Senjitu basin, which is adjacent to the Sichakou basin (Figure 1). All known bird fossils in this basin were found from the sedimentary member along Qiaotou-Daluozigou (Qiaotou sedimentary member, Huajiying Formation in this paper). The described forms include: *Jibeinia luanhera* Hou and *Vescornis hebeiensis* Zhang et al. (= *Hebeiorins fengningensis* Yan (nom. nud.))^[15,16,19]. In addition, the same horizon also yielded a feathered dinosaur—*Jinfengopteryx elegans* Ji et al.^[20], which might belong to the family of Troodontidae^[21], and an eutriconodont mammal—*Yanoconodon allini* Luo et al.^[22] as well. The fish fossils from the Qiaotou sedimentary member of the Senjitu basin are much more diversified than those from the Sichakou sedimentary member. Besides the acipenseriform fishes of *Peipiaosteus* and *Yanosteus* found in the Sichakou Basin, there exist the paddlefish *Protosephurus* sp., and abundant teleosts of *Lycoptera davidi* (Sauvage) and *L. tokunagai*^[23].

Comparing the vertebrate fossils from the two different bird fossil-bearing members of the Sichakou and Senjitu basins, one can easily find the differences in

composition, diversity, as well as characteristic states of taxa between them. *Protopteryx* is the most primitive enantiornithine bird up to now. Enantiornithes, a significant monophyletic avian group in Mesozoic, is represented by many important forms both in the Yixian Formation and the Jiufotang Formation. The enantiornithes found from the Jiufotang Formation (e.g. *Cathayornis*, *Longipteryx*) are evidently more derived than those from the Yixian Formation (e.g. *Eoenantiornis*, *Liaoxiornis*). At present, there is no other kind of enantiornithe discovered from the horizon of *Protopteryx*, which reflects remarkable lower diversification in enantiornithes than that of the Yixian and Jiufotang formations. In addition, a new confuciusornithid bird from the Sichakou basin shows more primitive features compared with the birds of *Confuciusornis* from the Yixian Formation. Even though the acipenseriform fishes from the Sichakou and Senjitu basins are assigned into the same genera and species in the literature, they also reveals some characteristic differences along with the increase of specimens. For example, the fossils of *Peipiaosteus* from the Sichakou basin have a more compressed body-form and more developed dorsal caudal fulcra, which are plesiomorphic in peipiaosteid fishes. Moreover, between the fossil fishes from the two horizons there is a distinguished distinction that no undoubted fossils of *Lycoptera* have been found from the bird fossil-bearing member in the Sichakou basin. Therefore, the vertebrate fossils from the two different bird fossil-bearing members can be clearly divided into two assemblages: *Peipiaosteus fengningensis*-*Protopteryx fengningensis* assemblage in the Sichakou sedimentary member and *Lycoptera davidi*-*Jibeinia luanhera* assemblage in the Qiaotou sedimentary member. The age of the lower assemblage is about 130.7 Ma^[24], which is the earliest vertebrate fossil assemblage hitherto known in the Jehol Biota; and the age of the upper assemblage is not very clear yet by now.

In the Sichakou basin, fossils of *Peipiaosteus* initially occur in the first sedimentary member (Dabeigou Formation in this paper), which is the earliest horizon of vertebrate fossil records in this area. In the neighbouring Senjitu basin, *Peipiaosteus* is also known from the mid-lower part of the Dabeigou Formation in the Chengeng section. Furthermore, In the Luanping basin, salamander fossils begin to appear near the bottom of the Dabeigou Formation. All these clues indicate that there probably exists another vertebrate assemblage earlier

than the *Peipiaosteus fengningensis*-*Protopteryx fengningensis* assemblage.

Because of the intricacy and variety of volcanosedimentary rocks, it is rather difficult in stratigraphic correlations, especially among different regions. At present, the most immediate and effective method is still by means of fossil assemblages and closely related fossils of a monophyletic group. The two newly established early vertebrate assemblages in the Sichakou and Senjitu basins of Fengning, northern Hebei also provide basis for the stratigraphic correlation in different regions. For example, the *Lycoptera davidi*-*Jibeinia luanhera* assemblage is rather similar to the vertebrate fossil assemblage of the Dawangzhangzi Bed (=Daxinfangzi Bed) of the Yixian Formation in Lingyuan, western Liaoning, especially in terms of the known fishes, both have totally the same composition, which includes: *Peipiaosteus fengningensis* Bai, *Yanosteus longidorsalis* Jin et al., *Protopsephurus liui* Lu, *Lycoptera davidi* (Sauvage), *L. tokunagai* Saito^[14,23], and hence could be taken as one assemblage undoubtedly. Accordingly, it is reasonable to believe that the Qiaotou sedimentary member of the Huajiyi Formation in Fengning, northern Hebei is equivalent to the Dawangzhangzi Bed of the Yixian Formation in Lingyuan, western Liaoning (Figure 3). If this stratigraphic correlation between northern Hebei and western Liaoning is inerrant, the horizon of the Jianshangou Bed bearing the famous bird group of *Confuciusornis* (=Chaomidianzi or Sihetun Formation, etc.) in

Beipiao should be further confirmed. In former works, the Jianshangou Bed was mainly correlated with the Daxinfangzi Bed (now usually called Dawangzhangzi Bed) in Lingyuan, but it was also recognized as the lowest fossil-bearing sedimentary intercalation of the Yixian Formation in western Liaoning as well^[25]. The known fishes from the Jianshangou Bed include *Peipiaosteus pani* Liu et Zhou and *Lycoptera sinensis* Woodward. *Peipiaosteus pani* is evidently more derived than *P. fengningensis* in its relatively depressed body-form, and regressive dorsal caudal fulcra. *Lycoptera sinensis* was firstly discovered from the mid-upper part of the Laiyang Formation in the Laiyang basin of Shandong, and was once assigned to the genus *Asiatolepis* together with *Lycoptera muroii* (Takai), which was found from the Jingangshan Bed of the Yixian Formation^[14,23]. The bird group of *Confuciusornis* from the Jianshangou Bed is already considerably flourishing, and even includes the representative of ornithurine birds, *Liaoningornis longiditris* Hou. As for the known fossil fishes and birds, the horizon of the Jianshangou Bed in Beipiao should not be lower than the Dawangzhangzi Bed in Lingyuan, or possibly even higher.

3 The existing problems

Deposits containing the early elements of the Jehol Biota are widespread in Luanping, Fengning, Weichang of northern Hebei, and adjacent Chifeng and Duolun of Nei

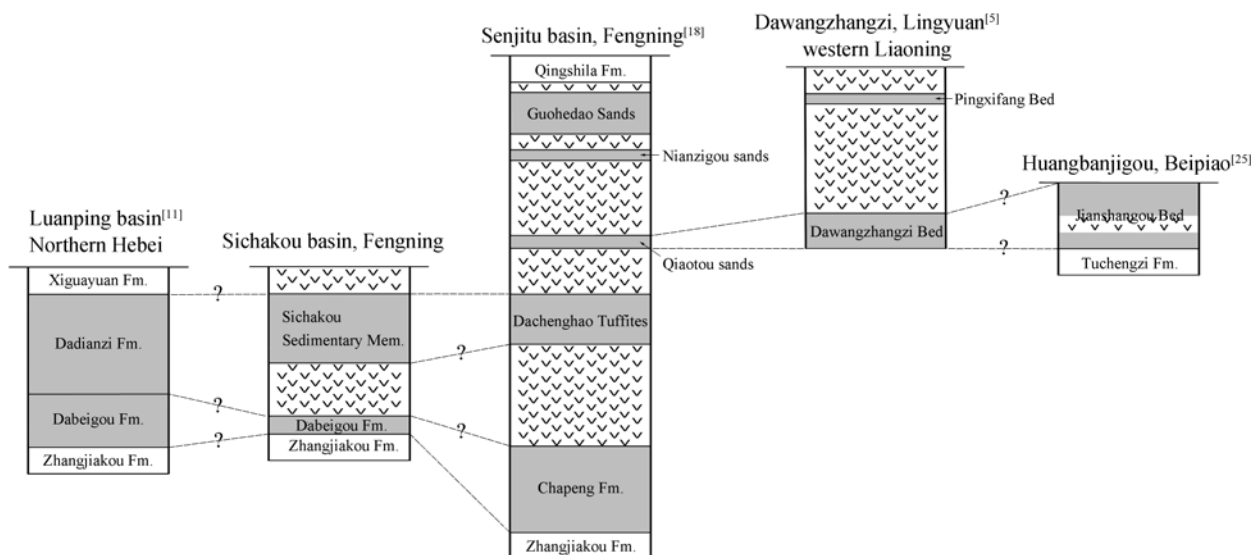


Figure 3 Correlation of the sedimentary beds bearing the fossils of the early vertebrate assemblages of the Jehol Biota in northern Hebei and western Liaoning.

Mongol Autonomous Region. These deposits have been assigned to different formations such as Dabeigou, Jingtangshan, Xiguayuan, Huajiying or Yixian, and await to be extensively investigated in the future.

Compared with the Senjitu basin^[5,18,26,27], the Sichakou basin needs much more work on basic geology. At present, the Sichakou bird fossil-bearing sedimentary member is still lack of index fossils, assemblages or zones of invertebrates, sporopollens and plants, which greatly influences the precise division and correlation of strata. Furthermore, the current Huajiying Formation in the Sichakou and Senjitu area comprises several sets of volcanic sedimentary deposits, and measures more than 4000 m in thickness, which could be analogous to a rock group (Figure 3), and also await to be checked up in further work.

Studies on the Jehol Biota have lasted over a century, but until now, the definition of this biota is still a controversial issue. Since Grabau named the Jehol Series in 1923, and the Jehol Fauna in 1928, their meaning has altered a few times. There was once a viewpoint that the biota included all fossils from the strata of four formations (Yixian, Jiufotang, Shahai, and Fuxin) in western Liaoning and their equivalents in a vast area^[28]. In recent years, a popular opinion is that the Jehol Biota is restricted to include the fossils from the Yixian and Jiufotang formations as well as their equivalent strata, that is, it is a biota represented by the three classic fossils: *Eoesteria*, *Lycoptera*, and *Ephemeropsis trisetalis*^[1,21]. After this view, fossils from the Dabeigou Formation and the lower part of the Dadianzi Formation are excluded from this biota because even though *Ephemeropsis trisetalis* occurs from the Dabeigou Formation, undoubtedly *Lycoptera* begins to appear until the top of the Dadianzi Formation. In fact, the fossils from these horizons, especially those from the Dadianzi Formation, have a close relationship with the Jehol Biota and represent the early evolution history of the biota. Therefore, it is suggested that the demarcation of the Jehol Biota had better depend upon the large-scale tectonic-sedimentary cycles. The upper boundary could be delimited by the commencing of the fan deltaic and lacustro-swampy coal-bearing deposits represented by the Shahai and Fuxin formations, and the lower boundary delimited by the ending of the eruptive-sedimentary cycle represented

by the acidic volcanics of the Zhangjiakou Formation. The Jehol biota should include all fossils of the cycle characterized by intermediate and basal volcanic-sedimentary deposits within the limits. Corresponding to this definition of the Jehol Biota, it is reasonable to substitute *Peipiaosteus* for *Lycoptera* as the vertebrate representative of the biota.

In recent years, substantial progress has been made in isotope dating of the horizons yielding significant fossils of the Jehol Biota in northern Hebei and western Liaoning. However, the Qiaotou sedimentary member of the Huajiying Formation and the Dawangzhangzi Bed of the Yixian Formation, which are pivotal in the stratigraphic correlation between northern Hebei and west Liaoning, still remain to be precisely dated for their known ages (122.1–126.9 Ma) are not widely accepted due to lack of accuracy^[3,6,29].

4 Conclusions

Protopteryx is the most primitive enantiornithine bird currently known, and its avian assemblage is evidently more primitive than that of the Yixian Formation. Based on the data of fossil fishes, birds, gastropods, bivalves, conchostracans, ostracods, as well as the contact relationships of strata, it could be confirmed that the horizon of *Protopteryx* should be lower than the Dawangzhangzi Bed of the Yixian Formation in Lingyuan, western Liaoning, and is approximately corresponding to the Dadianzi Formation in northern Hebei, which is the lowest horizon of the known fossil birds in China and Mesozoic enantiornithine birds in the world.

Accompanying *Protopteryx*, there are some other birds, abundant acipenseriform fishes, salamanders, as well as mammals, which compose the *Peipiaosteus fengningensis*-*Protopteryx fengningensis* assemblage. This is the earliest vertebrate fossil assemblage in the Jehol Biota, and traces the vertebrate evolution history of the biota back to 130.7 Ma before.

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