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Vertebrate diversity of the Jehol Biota as compared with other lagerstätten

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In the last twenty years, the extraordinary discoveries of vertebrate fossils from the Jehol Biota not only have important implications for studying the evolution of major Mesozoic vertebrate groups, their paleobiostratigraphy and paleoenvironmentology, but also provide critical evidence for understanding the biodiversity changes of the Early Cretaceous ecosystem. Currently, the Jehol Biota in a narrow sense (i.e., distribution limited to western Liaoning, northern Hebei, and southeastern Inner Mongolia) comprises a vertebrate assemblage of at least 121 genera and 142 species. Among them are 13 genera and 15 species of mammals, 33 genera and 39 species of birds, 30 genera and 35 species of dinosaurs, 17 genera and species of pterosaurs, 5 genera and species of squamates, 5 genera and 7 species of choristoderes, 2 genera and species of turtles, 8 genera and species of amphibians, 7 genera and 13 species of fishes as well as 1 genus and species of agnathan. All these known 121 genera are extinct forms, and only a small percentage of them (e.g., agnathans, some fishes and amphibians) can be referred to extant families. The Jehol vertebrate diversity already exceeds that of the contemporaneous lagerstätten such as Santana Fauna from Brazil and the Las Hoyas Fauna from Spain, and is nearly as great as that of the Jurassic Solnhofen Fauna and the Eocene Messel Fauna from Germany. Therefore, The Jehol Biota undoubtedly represents a world class lagerstätte in terms of both fossil preservation and vertebrate diversity. The success of the Jehol vertebrate diversity had a complex biological, geological, and paleoenvironmental background. Analysis of the habitat and diet of various vertebrate groups also indicates that the habitat and dietary differentiation had played a key role in the success of the taxonomic diversity of vertebrates of various ranks. Furthermore, the interactions among vertebrates, plants, and invertebrates as well as the competitions among various vertebrate groups and some key morphological innovations also contributed to the success of the Jehol vertebrate diversity.

Jehol Biota, Early Cretaceous, vertebrate, diversity, lagerstätten

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1 Introduction

The Jehol Biota represents a terrestrial and freshwater faunal and floral assemblage in the middle Early Cretaceous (131–120 Ma [1, 2]) that was mainly distributed in East Asia. It currently comprises invertebrates such as gastropods, bivalves, crustaceans (conchostracans, tadpole shrimps, ostracods, and shrimps), spiders and insects, vertebrates including agnathans, fishes (chondrichthyans, acipenseriforms, amiiformes and osteoglossomorphs), amphibians (anurans and urodeles), turtles, choristoderes, squamates, pterosaurs, dinosaurs (saurischians and ornithischians), birds (enantiornithines, ornithurines and more basal forms), and mammals (triconodonts, multituberculates, symmetrodonts, metatherians and eutherians), as well as algae, lichens, ferns, gym-

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nosperms and angiosperms. Abundant fossils, exceptional preservation, and the unique geological background of the region open a window into the evolution of various biological groups and the Early Cretaceous terrestrial ecosystem [3–5]. The Jehol Biota in a broad sense had a distribution in northern China, Mongolia, Kazakhstan, Siberia, Japan, and the Korea Peninsula, but in a narrow sense it only refers to the biota in northern Hebei, western Liaoning, and southeastern Inner Mongolia where the fossils are best preserved and represented.

In the 1860s, the French missionarier Père Armand David started to collect fish fossils in Lingyuan County of Chaoyang City, western Liaoning Province. In 1880 the French ichthyologist H. E. Sauvage studied these fossils, but misidentified them as a Tertiary fish and referred them to a new species of *Prolebias* (*P. davidi*), which was renamed *Lycoptera davidi* by the British ichthyologist A. S. Woodward in 1901. These earlier work marked the beginning of the scientific study of the Jehol Biota.

In the 1920s, the American geologist A. W. Grabau did some pioneering work on the Mesozoic stratigraphy and paleontology in western Liaoning, and for the first time proposed the name of "Jehol Fauna". In the 1930s and 1940s, the paleontological work in this region was done mainly by some Japanese paleontologists, and a number of well known reptilian fossils such as the lizard *Yabeinosaurus*, the choristodere *Monjurosuchus*, and the turtle *Manchurochelys* were described [6].

In the 1950s and 1960s, Chinese geologists and paleontologists conducted a comprehensive stratigraphic and paleontological survey of the region. In 1962, Z. W. Gu ushered in the concept of the "Jehol Group" and the "Jehol Biota". Liu and colleagues [7] published a systematic study of the fishes from the biota. Shortly after, another most common fish of the Jehol Biota, *Peipiaosteus pani*, a fossil acipenseriform, was reported [8].

In the 1970s and 1980s, many comprehensive papers or books were published on the biostratigraphy of the Jehol Group, but comparatively little progress was made on the study of the vertebrate fossils. This situation has dramatically changed since the 1990s with many important vertebrate fossils discovered and reported, and a new era in the study of Jehol vertebrate assemblages has begun. At present, the Jehol vertebrate diversity is already greater than any contemporaneous counterpart in other areas of the world.

Recently in the study of the Jehol Biota, significant progresses have been made not only in the origin of birds, their flight and feathers, and the early evolution of various important biological groups such as birds, mammals, pterosaurs, amphibians, insects and angiosperms [9–16], but also in the biostratigraphy, geochronology, paleomagnetism, and paleoenvironments [17–21]. These studies provided important clues to understanding the major features and mechanism of the Jehol vertebrate diversity.

It is noteworthy that the important vertebrate fossils from the late Mesozoic terrestrial deposits in northeastern China were from a long geological duration, ranging from the Middle Jurassic to the Middle Cretaceous, and belong to different biotae. For instance, the Middle and Late Jurassic Yanliao Biota (also known as the Daohugou Biota) is well known for producing many important groups of vertebrates such as primitive mammals, pterosaurs and feathered dinosaurs in addition to abundant insects and salamanders [22–25]. The Yanliao Biota bears some resemblance to the Early Cretaceous Biota; however, its fossil assemblage differs significantly from that of the latter. In addition, the Fuxin Biota represents a middle Cretaceous biota that is slightly younger than the Jehol Biota and also has a unique vertebrate assemblage. In this paper, we restrict our discussion of fossils from the Jehol Group (i.e., from bottom up, the Dabeigou Formation, Yixian Formation, and Jiufotang Formation), and the vertebrate taxa in the analysis of this paper only refer to those from the Jehol Biota in a narrow sense, i.e., only from northern Hebei, western Liaoning, and southeastern Inner Mongolia. Although some of the Jehol taxa are also known from other areas of northern China, such as Xinjiang, Gansu, middle and western parts of Inner Mongolia, Shaanxi, Jilin, and Shandong, they are not included in the statistics of this paper.

2 Analysis of the Jehol vertebrate diversity

Currently, the Jehol birds comprise 33 genera and 39 species, which constitute approximately one third of the known Mesozoic avian species globally, or about 40% if only the species published since 1990 are counted [26]. Chinese materials are represented mostly by complete skeletons and often with preservation of feathers, and thus the information they provide on the early avian evolution is greater than from other contemporaneous regions.

Most of the Jehol birds are recognized as arboreal forms. They demonstrated significant differentiations in morphology, size, flight, diet, and habitat, representing the first major radiation in avian evolutionary history.

The Jehol dinosaurs currently comprise 30 genera and 35 species. The number of dinosaur species in China is now greater than from any other countries (Hailu You, pers. comm.), and more than two thirds of them were described since 1990. The Jehol dinosaurs constitute about 20% of all dinosaur species from China, and both its species diversity and number of individuals exceed that of any other fauna.

Among the dinosaurs from the Jehol Biota, theropods are most diversified, comprising 21 genera and 24 species and constituting about two thirds of the total dinosaur diversity of the biota. The Jehol theropods represent nearly all major Cretaceous lineages, and many are feathered, characteristic of the appearance of many arboreal or herbivorous forms [27–30].

The Jehol pterosaurs comprise 17 genera and species, and can be referred to at least 10 families or superfamilies. All except one genus and species belong to the pterodactyloids, and the only exception represents a member of the short tailed rhamphorhynchoid family Anurognathidae. China now has the richest pterosaur fossil record largely due to the recent discoveries from the Jehol Biota. The Jehol pterosaur assemblage already exceeds that of the Late Jurassic Solnhofen in both abundance and the generic diversity. The Late Jurassic Solnhofen now only comprises 8 genera and approximately 16–19 species (Helmut Tischlinger, pers. comm.).

The Jehol pterosaur discovery has remarkably changed our view on the ecological niches of pterosaurs. Previous discoveries were mainly from the sea shores whereas the pterosaurs from the typical terrestrial or lake shore environments in the Early Cretaceous of northeastern China have expanded their distribution to more diverse areas [31–33].

Although about 300 genera of mammals are known from the Mesozoic globally, and the Jehol Biota only comprises 13 genera and 15 species, the information about early mammalian evolution as inferred from the Jehol mammals is extraordinary as they are almost all represented by complete skeletons while about 100 species of mammals from over 50 different localities in other areas are mostly fragmentary teeth or partial skeletons [26]. The Jehol mammals can be referred to five major groups of Mesozoic mammals: Triconodonta, Multituberculata, Symmetrodonta, Metatheria, and Eutheria. Among them, triconodonts, multituberculates, and symmetrodonts are all important Mesozoic mammalian groups, and the earliest members of the metatherians and eutherians represent the beginning of their later evolution and radiation [13, 34–36].

In addition to birds, dinosaurs, pterosaurs, and mammals, the Jehol fishes, amphibians, turtles, choristoderes, and squamates also demonstrated distinctive radiations.

The only known agnathan from the Jehol Biota is a lamprey genus and species that represents its earliest freshwater record worldwide [37]. Fishes comprise 4 orders (or higher ranks), 6 families, 7 genera and 13 species, as well as a few fishes of undetermined family or species. Among these fishes are a chondrichthyan (gen. et sp. undet.), acipenseriformes that comprise two families, three genera and four species, and amiiformes represented by one genus and species. Teleostei are most diversified, with two families, two genera and seven species belonging to osteoglossomorphs, and one genus and species of undetermined order and family.

The Jehol amphibians all belong to lissamphibians, including four genera and species of frogs and four genera and species of salamanders, as well an advanced frog belonging to a species of undetermined order and family [38]. These fossils represent the earliest radiation of lissamphibians in East Asia [39], which is characteristic of abundant individuals and marked species differentiation as well as the appearance of representatives of extant families such as the Discoglossidae [40, 41]. Although currently only one genus is referred to an extant family, seven genera have not yet been referred to any family. Some of them such as *Mesophryne* possibly belong to an extinct family [39, 42] while others such as *Liaoxitriton* and *Regalerpeton* seem to be closely related to the origin of some extant taxa [11, 14, 43].

The Jehol turtles currently comprise two genera and species belonging to an extinct family. Despite the abundance of individuals in some horizons, their taxonomic differentiation is less significant than other reptiles.

Choristoderes all belong to an extinct reptilian lineage, and are referred to three families, five genera and seven species. Among them, two genera and three species are referred to the Simoedosauridae, one genus and two species to the Hyphalosauridae, and two genera and species to the Monjurosuchidae. These aquatic or semi-aquatic animals represent the top level predator in the food web of Jehol lake ecosystem.

The squamates from the Jehol Biota comprise five genera and species of lizards, and none of them has been referred to a known family. Among them, two genera and species (*Yabeinosaurus tenuis* [44], *Liushusaurus acanthocaudata* [45]) are the relics of the Jurassic lineage from Laurasia, and one genus and species (*Xianglong zhaoi* [46]) belongs to Iguania, and the rest belong to Scleroglossa [14, 43, 47].

To sum up, the Jehol vertebrate assemblage now comprises 121 genera and 142 species. All of them are extinct genera and species. Most of them can only be referred to extinct families, with a few exceptions in agnathans, some fishes and amphibians which have been referred to extant families (Table 1, Figure 1). We estimate that the count of the Jehol genera and species will certainly increase with many new discoveries to be reported in the near future. We did not count the total number of families mainly because many published genera and species have not been referred to any familial category, and more morphological and taxonomic work of these materials is needed. The species number will also most likely increase with more detailed morphological and comparative studies of the known Jehol vertebrate fossils.

It is notable that we made a rough estimate of the number of at least 180 vertebrate species of the Jehol Biota in a broad sense, i.e., from Xinjiang, Gansu, middle and western parts of Inner Mongolia, Shaanxi, Jilin, and Shandong in addition to western Liaoning, northern Hebei and southwestern Inner Mongolia. This number does not include those outside of northern China due to incomplete data and the difficulty of precise stratigraphic correlations.

3 Dietary and habitat differentiation of the Jehol vertebrates

The Jehol vertebrate diversity is characterized not only by

Table 1 List of vertebrates of the Jehol Biota

Order or higher taxa	Family	Genus	Species
Agnatha: one order, one family, one genus and species			
Petromyzontiformes	Petromyzontidae	*Mesomyzon*	*M. mengae*
Pisces: four orders, 6 families, 7 genera and 13 species (one additional genus and species undetermined)			
Elasmobranchii	Hybodontoidea	indet.	indet.
Acipenseriformes	Peipiaosteidae	*Peipiaosteus*	*P. fengningensis*
			P. pani
		Yanosteus	*Y. longidorsalis*
	Polyodontidae	*Protopsephurus*	*P. liui*
Amiiformes	Sinamiidae	*Sinamia*	*S. zdanskyi*
Osteoglossomorpha	Lycopteridae	*Lycoptera*	*L. davidi*
			L. fuxinensis
			L. muroii
			L. sankeyushuensis
			L. sinensis
			L. tokunagai
	Kuyangichthyidae	*Jinanichthys*	*J. longicephalus*
Teleostei	indet.	*Longdeichthys*	*L. luojiaxiaensis*
Amphibia: two orders, 1 family and 8 genera and species (one additional genus and species undetermined)			
Anura	Discoglossidae	*Callobatrachus*	*C. sanyanensis*
	indet.	*Liaobatrachus*	*L. grabaui*
		Mesophryne	*M. beipiaoensis* (=*Dalianbatrachus mengi*)
		Yizhoubatrachus	*Y. macilentus*
		indet.	indet.
Urodela	indet.	*Laccotriton*	*L. subsolanus*
		Liaoxitriton	*L. zhongjiani*
		Regalerpeton	*R. weichangensis*
		Sinerpeton	*S. fengshanensis*
Chelonia: one order, one family, two genera and species			
Chelonia	Sinemydidae	*Ordosemys*	*O. liaoxiensis* (=*Manchurochelys liaoxiensis*)
		Manchurochelys	*M. manchoukuoensis* (type lost)
Choristodera: one order, 3 families, 5 genera and 7 species			
Choristodera	Simoedosauridae	*Ikechosaurus*	*I. gaoi*
			I. pijiagouensis
		Liaoxisaurus	*L. chaoyangensis*
	Hyphalosauridae	*Hyphalosaurus*	*H. lingyuanensis* (=*Sinohydrosaurus lingyuanensis*)
			H. baitaigouensis
	Monjurosuchidae	*Monjurosuchus*	*M. manchoukuoensis*
		Philydosaurus	*P. proseilus*
Squamata: one order, 5 genera and species			
Squamata	indet.	*Yabeinosaurus*	*Y. tenuis* (type lost) (?=*Jeholacerta formosa*)
	indet.	*Xianglong*	*X. zhaoi*
	indet.	*Dalinghosaurus*	*D. longidigitus*
	indet.	*Liaoningolacerta*	*L. brevirostra*, nomen dubium
	indet.	*Liushusaurus*	*L. acanthocaudata*
Pterosauria: one order, 10 families, 16 genera and species			
Pterosauria	Anurognathidae	*Dendrorhynchoides*	*D. curvidentatus*
	?Gallodactylidae	*Feilongus*	*F. youngi*
	Anhangueridae	*Liaoningopterus*	*L. gui*
	Pteranodontidae	*Chaoyangopterus*	*C. zhangi* (=*Jidapterus edentus*; =*Eopteranodon lii*; =*Eoazhdarcho liaoxianesis*)
	Pterodactylidae	*Eosipterus*	*E. yangi*
		Haopterus	*H. gracilis*
	Tapejaridae	*Sinopterus*	*S. dongi* (=*Huaxiapterus jii*; =*Sinopterus gui*)
	Ctenochasmatidae	*Cathayopterus*	*C. grabaui*
		Elanodactylus	*E. prolatus*
		Gegepterus	*G. changae*

(*To be continued on the next page*)

(*Continued*)

Order or higher taxa	Family	Genus	Species
Pterosauria	Dsungaripteroidea	*Nemicolopterus*	*N. crypticus*
	Istiodactylidae	*Nurhachius*	*N. ignaciobritoi*
		Hongshanopterus	*H. lacustrisi*
		Liaoxipterus	*L. brachyognathus*
		Istiodactylus	*I. sinensis*
	Ornithocheiridae	*Boreopterus*	*B. cuiae*
Ornithischia: one order, 3 families, 7 genera and 19 species			
Ornithischia	Heterodontosauridae	*Tianyulong*	*T. confuciusi*
	Ankylosauria Nodosauridae	*Liaoningosaurus*	*L．paradosxus*
	Neoceratopsia Psittacosauridae	*Psittacosaurus*	*P. lujiatunensis* *P. meileyingensis*
			P. mongoliensis
			P. gobiensis
		Hongshanosaurus	*H. houi*
	Neoceratopsia fam. indet.	*Liaoceratops*	*L. yanzigouensis*
	Ornithopoda fam. indet.	*Jeholosaurus*	*J. shangyuanensis*
	Iguanodontia fam. indet.	*Jinzhousaurus*	*J. yangi*
Saurischia: one order, 8 families, 23 genera and 25 species (one additional species indertermined)			
Saurischia	Titanosauroidea	*Euhelopus*	*E.* sp.
	Titanosauriformes	*Dongbeititan*	*D. dongi*
	Tyrannosauroidea	*Dilong*	*D. paradoxus*
		Raptorex	*R. kriegsteini*
		Sinotyrannus	*S. kazuoensis*
	Coelurosauria fam. indet.	*Protarchaeopteryx*	*P. robusta*
		Yixianosaurus	*Y. longimanus*
	Compsognathidae	*Sinosauropteryx*	*S. prima*
		Huaxiagnathus	*H. orientalis*
		Sinocalliopteryx	*S. gigas*
	Maniraptora Troodontidae	*Sinovenator* *Mei*	*S. changii* *M. long*
		Sinusonasus	*S. magnodens*
		Jinfengopteryx	*J. elegans*
	Dromaeosauridae	*Sinornithosaurus*	*S. haoiana*
			S. millenii
		Microraptor	*M. gui*
			M. zhaoianus
		Graciliraptor	*G. lujiatunensis*
		Tianyuraptor	*T. ostromi*
	Oviraptorsauria fam. indet.	*Incisivosaurus*	*I. gauthieri*
	Caudipteridae	*Caudipteryx*	*C. dongi* *C. zoui*
		Similicaudipteryx	*S. yixianensis*
	Therizinosauroidea	*Beipiaosaurus*	*B. inexpectus*
	Ornithomimosauria Ornithomimidae	*Shenzhousaurus*	*S. orientalis*
Aves: 13 orders, 14 families, 33 genera and 39 species			
Jeholornithiformes	Jeholornithidae	*Jeholornis*	*J. prima* (= *Shenzhouraptor sinensis*; = *Jixiangornis orientalis*)
Sapeornithiformes	Sapeornithidae	*Sapeornis*	*S. chaoyangensis*
			S. angustis
Confuciusornithiformes	Confuciusornithidae	*Eoconfuciusornis*	*E. zhengi*
		Confuciusornis	*C. sanctus*
			C. dui
			C. suni

(*To be continued on the next page*)

(*Continued*)

Order or higher taxa	Family	Genus	Species
Confuciusornithiformes	Confuciusornithidae	*Confuciusornis*	*C. chuonzhous*
			C. feducciai
		Changchengornis	*C. hengdaoziensis*
		Jinzhouornis	*J. yixianensis*
			J. zhangjiyingia
Order indet.	indet.	*Zhongjianornis*	*Z. yangi*
		Zhongornis	*Z. haoae*
Protopterygiformes	Protopterygidae	*Protopteryx*	*P. fengningensis*
Eoenantiornithiformes	Eoenantiornithidae	*Eoenantiornis*	*E. buhleri*
Longipterygithiformes	Longipterygithidae	*Longipteryx*	*L. chaoyangensis*
		Longirostravis	*L. hani*
		Rapaxavis	*R. pani*
		Shanweiniao	*S. cooperorum*
		Boluochia	*B. zhengi*
Cathayornithiformes	Cathayornithidae	*Eocathayornis*	*E. walkeri*
		Cathayornis	*Y. yandica* (*= Cathayornis caudatus; =Cathayornis aberransis; = Longchengornis sanyanensis; = Cuspirostrisornis houi; = Largirostrornis sexdentornis*)
		Sinornis	*S. santensis*
Liaoxiornithiformes	Liaoxiornithidae	*Liaoxiornis*	*L. delicatus* (*= Lingyuanornis parvus*)
Jibeiniaithiformes	Jibeiniaithidae	*Jibeinia*	*J. luanhera*
Enantiomithes	indet.	*Pengornis*	*P. houi*
		Vescornis	*V. hebeiensis*
		Paraprotopteryx	*P. gracilis*
		Shenqiornis	*S. mengi*
Liaoningornithiformes	Liaoningornithidae	*Liaoningornis*	*L. longidigitris*
Chaoyangornithiformes	Chaoyangornithidae	*Chaoyangia*	*C. beishanensis*
	Indet.	*Songlingornis*	*S. linghensis*
Yanornithiformes	Yanornithidae	*Yanornis*	*Y. martini* (*=Aberratiodontus wui*)
Yixianornithiformes	Yixianornithidae	*Yixianornis*	*Y. grabaui*
Ornithurae	Hongshanornithidae	*Hongshanornis*	*H. longicresta*
Order indet.	indet.	*Longicrusavis*	*L. houi*
Order indet.	indet.	*Archaeorhynchus*	*A. spathula*
Order indet.	indet.	*Jianchangornis*	*J. microdonta*
Mammalia: three orders, 5 families, 13 genera and 15 species			
Triconodonta	Gobiconodontidae	*Gobiconodon*	*G. zofiae*
		Meemannodon	*M. lujiatunensis*
	Repenomamidae	*Repenomamus*	*R. robustus*
			R. giganticus
	Jeholodentidae	*Jeholodens*	*J. jenkinsi*
		Yanoconodon	*Y. allini*
Multituberculata	Eobaataridae	*Sinobaatar*	*S. lingyuanensis*
Symmetrodonta	Spalacotheriidae	*Akidolestes*	*A. cifellii*
		Maotherium	*M. sinensis*
			M. asiaticus
		Zhangheotherium	*Z. quinquecuspidens*
Metatheria	indet.	*Sinodelphys*	*S. szalayi*
Eutheria	indet.	*Eomaia*	*E. scansoria*
		Acristatherium	*A. yanensis*
Mammalia	indet.	*Juchilestes*	*J. liaoningensis*

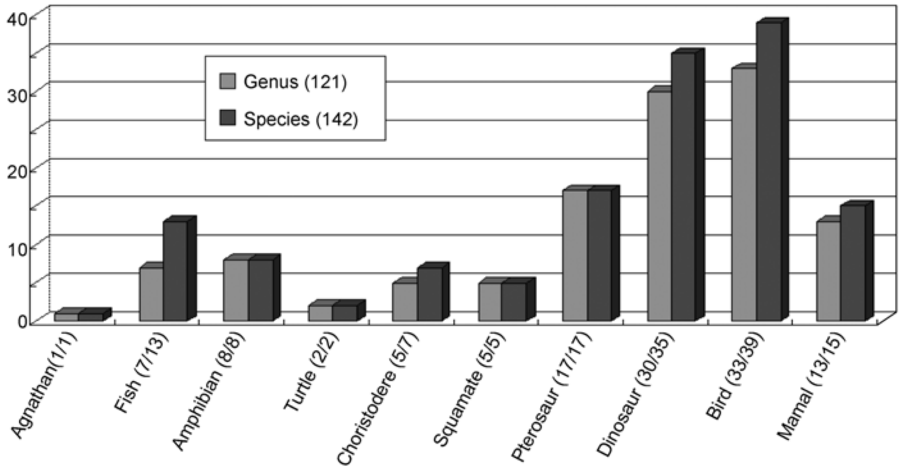

Figure 1 Comparison of the generic and specific numbers of major groups of the Jehol vertebrate assemblage. Numbers in the parenthesis after each taxon represent known genus and species.

the great taxonomic differentiation among various groups but also by the significant differentiation in their diets and habitats. Among the Jehol vertebrates, the agnathans, fishes, amphibians, turtles, and choristoderes were mostly dwelling in aquatic or semi-aquatic environments, constituting the top level of food web of the Jehol lake ecosystem. For instance, the lampreys were parasitical; the acipenseriforms were the largest fishes in the Jehol lakes, with some reaching over one meter long, and probably mainly filtering food items [48]. The teleosts were the most abundant fishes, and probably mostly carnivorous. Amphibians were all carnivorous, presumably mainly predating on insects or worms by living near the water. Turtles were also abundant and the known species had some aquatic features. Choristoderes represent extinct aquatic or semi-aquatic reptiles. Among them, *Monjurosuchus* lived a semi-aquatic life [49]; hyphalosaurids with a significantly elongated neck and tail were piscivorous and lived in the water. They currently comprise two species, one can be as long as one meter, and the other is smaller in size [50] and is represented by hundreds of individuals in fossil record. The third group of choristoderes is represented by *Ikechosaurus,* which is characterized by a large body size with elongated rostrum and believed to be as ferocious as crocodiles [51].

Unlike fishes and other aquatic or semi-aquatic vertebrates, the Jehol lizards were typical terrestrial forms. The newly discovered *Yabeinosaurus* material showed a robust body, in contrast to a previous view of slender body which is now recognized as a juvenile feature. Its habitat is comparable to some extant larger terrestrial lizards [44], and one newly discovered fossil actually preserved in its stomach some fish remains, suggesting at least some of them were piscivorous (Y. Wang, pers. observ.). The recently reported *Dalinghosaurus* possesses a hindlimb with scansorial adaptation [52]. *Xianglong* was probably a perching lizard and could glide with its unique membranes, representing a specialized clade of extinct lizards [46]. It seems that the forest environment had played a key role in the differentiation of the Jehol lizards.

The taxonomically diversified Jehol dinosaurs also demonstrate great differentiation in habitats. Although most dinosaurs were terrestrial animals, arboreal dinosaurs have been recognized (e.g., *Microraptor*), which not only significantly changed our view of the life of some theropods but also provided further evidence supporting the arboreal hypothesis on the origin of avian flight. The Jehol dinosaurs vary greatly in body size. For instance, among the smallest dinosaurs are the herbivorous *Psittacosaurs* and the carnivorous *Microraptor zhaoianus*, some of which are even smaller than the contemporaneous birds. The similar sized dromaeosaurid *Sinornithosaurus* was recently reported to have possessed venomous glands [53]. Tyrannosauroids from the Jehol Biota are larger, but still small compared to their Late Cretaceous relatives [29, 54, 55]. Together with compsognathids [56–58], tyrannosauroids constitute the most ferocious predators on the top level of the food web of the Jehol terrestrial ecosystem. The iguanosaurid *Jinzhousaurus* is gigantic with an estimated body length of 5–6 m. And the herbivorous titanosauriforms probably represent the largest animal in the Jehol Biota [59, 60].

The herbivorous ornithischian dinosaurs such as *Psittacosaurus* and *Jinzhousaurus* are also well represented in the Jehol Biota despite a lower diversity compared to saurischians. It is notable that among the theropods, some of them are raptatorial such as *Sinosauropteryx* that often preserved mammal or lizard remains in their stomach, whereas some other taxa are herbivorous and often preserved gizzard stones in the stomach, such as the oviraptorosaur *Caudipteryx* and the ornithomimosaurid *Shenzhousaurus* [61]. The oviraptorosaur *Incisivosaurus* even possessed a pair of incisor-like premaxillary teeth, suggesting a highly specialized herbivorous diet [62]. These discoveries have enriched our understanding of the dietary differentiation of theropods, and the presence of many herbivorous theropods also seems to be characteristic of the Jehol dinosaur assemblage.

As the first flying vertebrates, pterosaurs are mainly arboreal, as in the case of the Jehol pterosaurs. Although many of them were piscivorous, other dietary adaptations such as filtering or herbivory have also been recognized. For instance, *Sinopterus* is probably a seed eater (Z. Zhou, pers. observ.). The differentiation of the Jehol pterosaurs in body size is also significant and probably greater than that in birds, with the smallest (e.g., *Nemicolopterus*) as big as a swallow [33], and the largest (e.g., *Liaoningopterus*) with a wing span of about 5 m, definitely the giant of the sky at the time [32].

In extant birds, most species are arboreal. Arboreal forms were also predominant in early birds. In fact, the evolution of a reversed hallux and the possession of arboreal capability represent a major event in the evolution of birds and avian flight. Current study indicates that arboreal forms most likely represent the most primitive ecological types in avian history. Arboreal birds are dominant in the Jehol avian assemblage. Among the Jehol birds, the ornithurines are mainly terrestrial dwellers, but nearly all enantiornithines and more basal birds (e.g., *Jeholornis*, *Sapeornis* and *Confuciusornis*) are arboreal [63–65].

Due to limited preservation, our knowledge of the diets of the Jehol birds remains poor. Although it is generally presumed that most enantiornithines were probably insectivorous or feeding on other invertebrates, there is yet no direct evidence for this hypothesis. However, some other birds actually preserved direct evidence for their dietary preference. For instance, several specimens of *Jeholornis* and *Sapeornis* preserved seeds in their stomach, suggesting they were seed eaters [66]. Their dietary reconstruction was also consistent with analysis of their habitat and the morphological features of the jaws. Although a few *Confuciusornis* preserved piscivorous evidence, it is uncertain whether it mainly fed on fishes [67]; it might have as well been omnivorous. Among basal ornithurines, *Yanornis* and *Jianchangornis* were obviously piscivorous as several specimens preserved fish remains in their stomach [4, 68], and *Archaeorhynchus* was almost certainly herbivorous as several referred specimens preserved gizzard stones [69]. Some enantiornithines such as longipterygithids possess an elongated rostrum and teeth restricted to its rostral end, suggesting a probing diet [70, 71]. Although *Longipteryx* was presumed to be piscivorous, none of the Jehol enantiornithines preserved any direct fossil evidence of their diet [72]. Given the arboreal life of most enantiornithines, insects could well be their major food resources. It seems certain that dietary differentiation was significant in various lineages of birds in the Jehol Biota.

Most of the Jehol mammals probably fed mainly on insects or worms based on their dentitions. Multituberculates were omnivorous. *Repenomamus* was carnivorous as evidenced by the preservation of dinosaur remains in one of its specimens although it remains a mystery whether it was an active predator or scavenger [36, 73]. The Jehol mammals also show remarkable differentiation in body size. Although most of them, e.g., metatherians and eutherians, are small, some taxa such as *Repenomamus* already represent one of the largest mammals in the Mesozoic. Symmetrodonts such as *Zhangheotherium* were probably mainly terrestrial in life with a parasagittal posture [74]; however, the earliest known members of both metatherians and eutherians showed scansorial adaptation [35].

In sum, the Jehol vertebrate diversity is shown not only by its great taxonomic differentiations at generic or higher levels but also by its remarkable differentiations in diets and habitats. The dietary and habitat differentiations had undoubtedly played an important role in the evolution of the Jehol vertebrate diversity at various taxonomic ranks.

4 Mechanism for the evolution of the Jehol vertebrate diversity

The discoveries and studies of several major vertebrate groups of Jehol fossils are critical to our understanding of the evolution of the biodiversity of the Early Cretaceous terrestrial ecosystem. The great vertebrate diversity of the Jehol Biota must have had a complex paleoenvironmental and ecological background. In particular, among them are the unique paleoenvironmental, paleogeographic changes and the evolution of the lake ecosystems in East Asia in the late Mesozoic.

East and Central Asia were generally believed to be isolated from Europe during the Middle Jurassic and Early Cretaceous [75]; however, recent fossil discoveries seem to indicate that East and Central Asia were never completely separated, and by the middle and late Early Cretaceous when the Jehol Biota was most flourishing, the intercontinental biological changes were already frequent [75]. Even before the appearance of the Jehol Biota, in the Middle and Late Jurassic when the Yanliao Biota lived in an area similar to that of the Jehol Biota, there existed some faunal exchanges between East and Central Asia and Europe, e.g., mammals and pterosaurs [25].

The Jehol Biota not only contains some relics and regional fossil taxa [76, 77], but also comprise many taxa suggesting that the Jehol area was the cradle and evolutionary center for many biological groups [75], which was further supported by the study of the pterosaur assemblage of the Jehol Biota [31]. By the early Early Cretaceous with the disappearance of the paleogeographic barriers between Europe and Asia, many of the vertebrates that originated from Jehol spread to Europe and other continents, and during the same interval there also existed bilateral exchanges, which together account for the presence of many cosmopolitan elements in the Jehol Biota [5], such as dinosaurs (e.g., iguanodontids, dromaeosaurids, and ankylosauroids), birds (e.g., enantiornithines), pterosaurs (tapejarids and anhangurids), and mammals (e.g., multituberculates and gobiconodontids) [78, 79]. Obviously, the paleogeographic changes and the formation of the Eurasia continent in the Early Cretaceous had a significant impact on the origin and radiation of the Jehol vertebrates.

The East Asia had a complex and active tectonic background in the Early Cretaceous. For instance, the destruction of the North China Craton and the mantle thinning was probably the result of the active global tectonic activity (e.g., the subduction of the Pacific Plate, large scale volcanic eruptions, and the beginning of the Cretaceous Normal Superchron) [80]. In contrast to northeastern region of China, the western areas of China were much less affected. It was also proposed [20] that northeastern China was affected by several transgressions from the Pacific. During the Early Cretaceous, the global temperature was generally warm [81], which could have resulted in the flourishing of the flora. On the other hand, against this warm background, there probably also existed some short periods of cold temperature. A recent study of the oxygen isotopes from vertebrate teeth from Jehol and other areas suggests that at the time of the Yixian Formation, the average atmospheric temperature in East Asia was slightly lower than that of today (Romain Amiot, pers. comm.). Furthermore, seasonal climatic changes were probably present in the Early Cretaceous [4, 82]. Finally, the impact of the frequent volcanic eruptions in this region on the speciation rate and the turn-over of the paleoecosystems should not be ignored. Evidence of mass mortality of life due to volcanic eruptions has been well documented [83–85]. We estimate that the frequent volcanic eruptions must have played a key role in the pattern of the Jehol vertebrate radiation.

Undoubtedly, the diverse and abundant Jehol invertebrate assemblages, particularly the insect assemblage, as well as the Jehol flora have greatly contributed to the evolution of the Jehol vertebrate diversity as they were inseparable parts of the whole Jehol ecosystem. The invertebrates and plants in the middle or lower level of the food web provided not only food resources for the Jehol vertebrates but also the paleoenvironmental background for vertebrate diversification.

It seems that the insect radiation in the Early Cretaceous of northeastern China represents one of the greatest radiations in the evolutionary history of insects. Liu et al. [86, 87] showed that the insect assemblage in the Yixian Formation comprises about 16 orders, 95 families, 201 genera and 271 species. The lakes at this time were relatively deep and extensive, and the lacustrine ecosystem was relatively stable. The temperature was generally humid, warm, with seasonal arid or semiarid niches. Liu et al. [86, 87] also predicted the presence of high mountains nearby with an altitude of over 800 meters surrounded by lakes, swamps, and ponds, suitable for diverse animals and plants to thrive [87].

The Jehol Flora was dominated by gymnosperms and ferns, and the angiosperms were only slightly differentiated [88, 89]. There already exists evidence of the co-evolution between insects and angiosperms [90], and the aquatic adaptation of early angiosperms [91, 92]. The forests were vital to the evolution of various vertebrate groups as shown by the presence of a high percentage of arboreal and herbivorous forms in the vertebrate assemblages, such as birds, pterosaurs, dinosaurs, lizards, and mammals.

The Jehol fishes became important food source for many birds, pterosaurs, and aquatic reptiles. For instance, the terrestrial ornithurines *Yanornis* and *Jianchangornis* most likely were mainly piscivorous as fish remains were often preserved in their stomach [68]. The diet of the mainly arboreal confuciusornithids is still unclear although a few specimens actually preserved evidence of fish eating [67, 93]. Although the dietary evidence for Jehol pterosaurs is generally lacking, it is generally believed that most of them were piscivorous based on their jaw morphology [32]. Furthermore, some theropod dinosaurs (e.g., *Sinosauropteryx*) often preserved remains of lizards and mammals in the stomach.

It should be pointed out that the success of the Jehol vertebrate diversity is related to the evolution of each major vertebrate group. For instance, since its first appearance in the Late Jurassic, birds by the Early Cretaceous had possessed a number of important features relating to their flight such as a pygostyle, a well-developed wing, and the pectoral girdle and sternum nearly identical to that of modern birds. In pterosaur evolution, the Early Cretaceous assemblage was dominated by short-tailed pterodactyloids with several morphological innovations (e.g., elongated wing metacarpal and wing digit) beneficial to more powerful flight.

To sum up, the success of the Jehol vertebrate diversity had a complex geological and paleoenvironmental background; it was also closely related to both the interactions among vertebrates, invertebrates and plants in the Jehol ecosystem, and the appearance of many major morphological innovations of each vertebrate group.

5 Jehol vertebrate diversity as compared to that of other lagerstätten

The Jehol Biota in a narrow sense (i.e., distribution limited to western Liaoning, northern Hebei, and southeastern Inner Mongolia) currently comprises a vertebrate assemblage of 121 genera and 142 species (Figure 1, Table 1). The number of vertebrate species of the Jehol Biota in a broad sense, i.e., geographically including those from other areas of northern China (e.g., Xinjiang, Gansu, middle and western Inner Mongolia, Shaanxi, Jilin, Shandong), is estimated to be about 180. Currently, as many of the Jehol vertebrate genera have not been referred to a family or higher ranks, it is difficult to calculate and compare the Jehol vertebrate diversity at familial or higher level, and thus the faunal comparison in the paper is restricted to generic and species level. The Santana Fauna in Brazil is among the most famous terrestrial Early Cretaceous vertebrate faunae outside China. It is well known for preserving abundant and diverse fishes and pterosaurs. No mammal or bird skeleton has been reported so far [94]. It currently comprises about 30 fish species (Alexander Kellner, pers. comm.), which include chondrichthyans, actinopterygians, and sarcopterygians [94]; all four known dinosaurs are theropods [95], and there are two frogs and two crocodilians (Alexander Kellner, pers. comm.), as well as six turtles [96]. Besides fishes, pterosaurs are the most diverse vertebrate group among the Santana Fauna. Kellner and Campos [94] estimated the presence of about 14 species, and most are represented by incomplete individuals and belong to the families of Anhangueridae and Tapejaridae. It is notable that members of the two families have also been reported from the Jehol Biota. Sayão and Kellner [97] provided a list of the Santana pterosaurs that comprises 11 genera and 23 species. According to A. Kellner (pers. comm.), two more species can now be added to this list. Therefore, besides fishes and pterosaurs, the Santana vertebrate groups are generally not as diverse as the Jehol vertebrates at species level, and the Jehol pterosaurs are more diverse at familial level.

The Las Hoyas Fauna from the La Huérguina Formation (Upper Barremian) in Cuenca, Spain is another important Early Cretaceous terrestrial fauna, which is well known for its exceptional preservation of abundant animal imprints, ferns, cycads, conifers, insects, birds, fish, crocodilians, dinosaurs, amphibians, and lizards, over 200 nearly complete terrestrial vertebrate fossils in total (http://palaeo.gly.bris.ac.uk/Palaeofiles/Lagerstatten/Lashoyas/lasfauna.html). The Las Hoyas Fauna currently comprises three genera and species of birds, all belonging to enantiornithines [98]. Its fish assemblage is more diverse, comprising about 12 genera belonging to various higher ranks of taxa. Among the four known amphibian genera, the anuran *Eodiscoglossus* can be referred to the family Discoglossidae. One unnamed species can be referred to pipiforms. There are also two genera of urodeles, and one genus of albanerpetontids. The latter group has not been discovered from China, and is recently regarded to represent an extinct amphibian lineage other than frogs, salamanders, and caecilians. Lizard fossils comprise three genera and species. The best known dinosaur is the theropod *Pelecanimimus*, and there are also some fragmentary sauropods. The Las Hoyas vertebrate assemblage also comprises one species of turtle and four species of crocodilians [99].

Las Hoyas is only the best known locality of the La Huérguina Formation. Fossil-bearing deposits of this formation are also distributed in other areas such as Buenache and Uña. In addition to abundant fishes from these two localities, there are two other anurans and four lizard genera and species, as well as fragmentary materials of lepidosauromorphs and a few more turtles. Besides several fragmentary crocodilians, there are some crocodilomorphs referrable to at least three families. Fragmentary pterosaurs cannot be referred to any definite taxon now. Dinosaurs and mammals are best preserved in the Uña assemblage, including such dinosaurs as *Richardoestesia*, *Paronychodon*, dromaeosaurines, velociraptorines, and hypsilophodontids, and such mammals as *Crusafontia*, *Galveodon*, *Eobaartar*, and another multituberculate [99].

To add up the vertebrate taxa from the above-mentioned three localities, the Early Cretaceous La Huérguina Formation has yielded about 20 genera and species of fishes, 8 amphibians, 3 turtles, 8 lizards, 9 crocodilians or crocodilomorphs, 7 dinosaurs, 3 birds, and 4 mammals (Herculano Alvarenga, pers. comm.). Thus, the total estimate of the vertebrate species is probably no more than 70, approximately similar to that of the Santana Fauna, but significantly less than that of the Jehol Biota. The La Huérguina vertebrate assemblage lacks agnathans or choristoderes that were present in the Jehol Biota, but the Jehol assemblage lacks albanerpetontids and crocodilians.

The Late Jurassic Solnhofen Fauna was preserved in marine or lagoon deposits; however, many of the vertebrate fossils were from the continent. The Solnhofen fossils generally refer to those from the Solnhofen Lithographic Limestone (Solnhofen Formation, Lower Tithonian, hybonotum Zone); however, fossils from other Late Jurassic horizons slightly older or younger have often been referred to this fauna, such as the eighth example of *Archaeopteryx* that was from the slightly younger Moernsheim Formation (Helmut Tischlinger, pers. comm.). According to information provided by H. Tischlinger, due to controversy over the taxonomic treatment, the Solnhofen fish assemblage probably comprises about 74–90 genera and 107–130 species, there are 1 genus and 2–3 species of birds, 2 genera and species of dinosaurs, 8 genera and 16–19 species of pterosaurs, 7–9 genera and 8–10 species of crocodilians; 6 genera and 6–8 species of sphenodonts, 2–3 genera and 2–4 species of ichthyosaurs, 4 genera and species of squamates, and 7–9 genera and 8–10 species of turtles. Thus, the total estimate of the Solnhofen vertebrates is 111–132 genera and 155–190 species (Helmut Tischlinger, pers. comm.). Compared to the Jehol Biota, The Solnhofen fishes are more diverse and account for over half of the total vertebrate genera or species. Other vertebrate groups from Solnhofen, particular birds, are less diverse as compared with the Jehol Biota. The Solnhofen fauna comprises the marine ichthyosaurs, but lacks the terrestrial amphibians and mammals.

The Middle and Late Jurassic Yanliao Fauna represents another lagerstätte from the late Mesozoic of Northeast China. It is well known for its beautiful preservation of abundant insects and salamanders, as well as mammals, pterosaurs and feathered dinosaurs. The most famous locality is Daohugou in Ningcheng County, southeastern Inner

Mongolia; other major vertebrate localities also include Guancailiang in Jianpin County, Linlongta in Jianchang County and Wubaiding in Linyuan City, western Liaoning, and Gangou in Qinglong County, Hebei Province. Because most of these vertebrate discoveries have been made in recent years, and the scale of excavation is also smaller compared to that of the Jehol Biota, the Yanliao vertebrate assemblage currently only comprises 19 genera and species, as well as 3 unnamed species [25]. It comprises three genera and four species of mammals, four genera and species of dinosaurs, five genera and species of pterosaurs, one genus and species of lizards (two additional juvenile individuals probably represent two different genera and species), four genera and species of urodeles, one unnamed juvenile individual of anuran, and one genus and species of fish. No bird, choristodere or turtle has been reported from the Yanliao Biota. It is also notable that salamanders are most abundant among all the Yanliao vertebrates and are often represented by hundreds of completely articulated skeletons or impressions, showing a variety of ecomorphs and differentiation [100–103]. Overall, the vertebrate diversity of the Yanliao Biota is much lower than that of the Jehol Biota.

The study of the fossils from the Eocene Green River Formation in North America has a history of over 150 years, and approximately 60 vertebrate species have been reported (http://www.ucmp.berkeley.edu/tertiary/eoc/greenriver.html), including about 14 families, 19 genera and 26 species of fishes (http://www.manzanitalab.com/store.php/content/green-river-fish) and 11 species of reptiles, as well as many birds and mammals. It represents one of the most famous Cenozoic fossil lagerstätte, whereas the number of its total vertebrate species is fewer than half of the Jehol Biota.

The Eocene Messel shales in Germany have preserved many exceptional fossils, including avian feathers, mammalian hairs, skin impressions, stomach contents, etc. The fossil collecting history of Messel is also over one hundred years. Up to now, about 142 species of vertebrates have been known [104] (Gerald Mayr, pers. comm.), same as that of the Jehol vertebrate assemblage. The Messel vertebrate assemblage comprises 45 species of mammals, 52 species of birds referable to at least 23 families, 32 species of reptiles referable to 12 families (including 7 crocodiles, 20 squamates, and 5 turtles), 5 species of frogs and salamanders referable to 4 families, and 8 species of fishes referable to 6 families. Among this vertebrate composition, birds and mammals have the highest species diversity, and reptiles are second to them, well reflecting the successful radiation of birds and mammals in the early Cenozoic that had replaced the ecological niches left by extinct Mesozoic reptiles. On the contrary, the Jehol reptiles are most diverse, with birds being the second, and the diversity of mammals is much lower than birds. The diversity of fishes, amphibians, and turtles is similar in both biotae. On the other hand, the Messel Fauna is also rich in squamates and crocodiles whereas crocodilians have not yet been reported from the Jehol Fauna and choristoderes that probably shared a similar ecology are not found in the Messel.

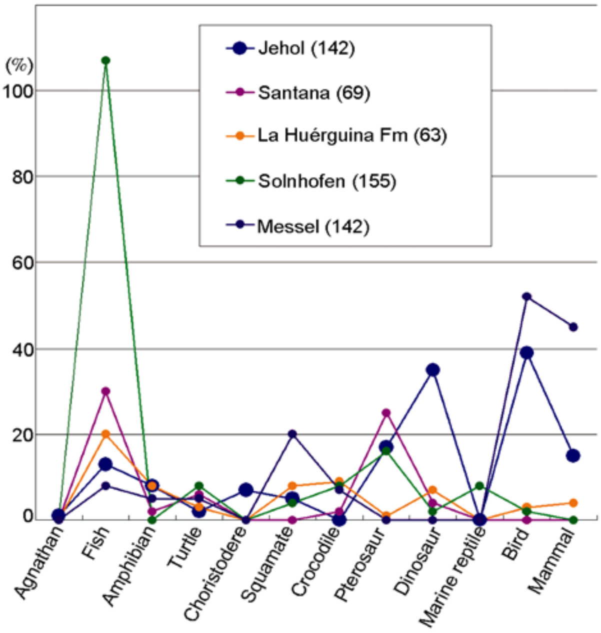

Figure 2 Comparison of the species diversity of the Jehol Biota with other lagerstätten over the world. Numbers in the parenthesis after each biota name represent the minimum count at species level.

From comparisons above, it seems clear that the Jehol vertebrate diversity exceeds those from other contemporary lagerstätten. It is undoubtedly among the best lagerstätten even compared to some most famous biotae such as the Late Jurassic Solnhofen or the Eocene Messel or Green River (Figure 2).

This comparison, however, is based on published taxa without considering the collecting history and other bias, thus it may not completely reflect the actual paleobiodiversity of each biota. For instance, the distribution and outcrops of the Yanliao Biota-bearing sediments are much less extensive compared to the Jehol Biota, and furthermore the scale of fossil collecting of the former is also much smaller. The collecting history of the Santana Fauna is long and also similar to that of the Jehol Biota in the fact that most of the vertebrate fossils were the result of commercial collectings. Finally, the duration of the Jehol Biota had lasted for at least 11 Ma, which is probably also longer than some other biotae, which might be part of the reason for a high vertebrate diversity.

Nevertheless, the Jehol Biota is undoubtedly now the best widow into the Early Cretaceous terrestrial ecosystem; it has preserved arguably the best evidence for studying the evolutionary history of major Mesozoic vertebrate groups [3, 105] as well as reconstructing their paleoecological history.

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