The Mesozoic Acipenseriformes in northeast China and adjacent areas

X Li1,2 and Y Chen1
1Key-Lab for Evolution of Past Life and Environment in Northeast Asia, Ministry of Education, 130026 Changchun, China
2Dinosaur Evolution Research Centre, College of Earth Sciences, Jilin University, Changchun 130061, China
lixiaobo@jlu.edu.cn

Abstract. The distribution of modern Acipenseriformes was restricted at the river and estuary system of the northern hemisphere, and their Mesozoic ancestor fossils had been discovered in east Asia. The northeast Asia is the key region for the early diversification and evolution of Acipenseriformes, because the extinct family †Peipiaosteidae should have appeared in western Liaoning of China since the Middle Jurassic, then occurred in the Middle-Late Jurassic of western Asia, and flourished in the northeast Asia during the Early Cretaceous. There were at least six species of Peipiaosteidae and an early form of Polyodontidae distributed in the Lower Cretaceous volcano-sedimentary strata in northeast China and adjacent areas including the Mongolia and Transbaikalia of Russia.

1. Introduction
The Acipenseriformes Berg 1940 is constituted by two living families of the Acipenseridae Bonaparte 1831 and Polyodontidae Bonaparte 1838 and the extinct fossil families of the †Chondrosteidae and †Peipiaosteidae Liu et Zhou 1965 [1-3]. The geographical distribution of modern Acipenseriformes (sturgeons and paddlefishes) is restricted at the river and estuary system of northern hemisphere, and the fossil taxa were mainly distributed in northeast Asia (Fig. 1) [4-6]. The fossils of the †Peipiaosteidae had been widely distributed in the Lower Cretaceous volcano-sedimentary strata in Yanliao area of China, Gobi of Mongolia, and Transbaikalia of Russia, and they were associated with the fossils of the famous Jehol Biota [7-9]. The phylogenetic analysis on †Peipiaosteidae indicated that they were sister group of the Acipenseridae [5]. The northeast Asia is the distribution range not only for the fossil taxa, but also for the modern Acipenseridae, and some modern Acipenseriformes in North America might have originated from Asia. Therefore, the northeast Asia became a key region for the early diversification and evolution of Acipenseriformes. The previous palaeontological works resulted that the members of †Peipiaosteidae should have appeared in northeast Asia, specifically in Western Liaoning since the Middle Jurassic, then they occurred in western Asia during the Middle to Late Jurassic, and recovered and flourished in northeast Asia during the Early Cretaceous, when the family diversified into at least 5 genus and 6 species [5]. A lot of fossil materials of †Peipiaosteidae are distributed in the Lower Cretaceous “Lycoptera Bed” of Mongolia, Transbaikalia of Russia, and Yanliao area and Greater Khingan Mountain of China. However, most of those materials have not been well studied, except those from the Yanliao area [5]. As a result, the taxonomy, biostratigraphy, and biogeography of the Mesozoic Acipenseriformes are still obscure at the broader scale.
2. Methods

The fossil records of the Mesozoic Acipenseriformes distributed in northeast China and adjacent areas were analysed at a broad scale. The phylogeny, evolution, and paleobiogeography of the extinct family †Peipiaosteidae were briefly discussed.

3. Results

The origin of the Acipenseriformes is still not clearly known, some fossils demonstrate that they derived from the paleozoic palaeonisciform groups. The Early Triassic fossil Acipenseriformes indicated that the clade might originate from the western China [10].

The western Liaoning became world famous since the 1990s because of a great number of important Mesozoic vertebrate fossils including feathered dinosaurs, early birds, and mammals discovered there during the past 30 years [7, 11]. The †Peipiaosteidae was erected based on materials from western Liaoning of China [12], where the Lower Cretaceous strata yield the fossils of the well-known Jehol Biota. During the early Cretaceous, the family diversified into at least 5 genus and 6 species, and they distributed in the “Lycoptera Bed” of Mongolia, Transbaikalia of Russia, Yanliao area of China, and northern Greater Khingan Mountain in China.

The phylogeny relationship of the †Peipiaosteidae could be divided into two sub-families of the †Stichopterinae and †Spherosteiniae [4]. The †Stichopterinae is constituted by four genera of Liaosteus, Yanosteus, Peipiaosteus, and Stichopterus. The †Spherosteiniae is constituted by Spherosteus. The Liaosteus is represented by only one species, the Liaosteus hongi, which yield from the Middle Jurassic Haifanggou Formation in Beipiao, western Liaoning of China [5, 13]. The Peipiaosteus fengningensis are distributed in the Dabeigou Formation in northern Hebei Province [5, 14]. The
fossils of *Peipiaosteus pani* were yield from the Yixian Formation in western Liaoning and correlated strata of adjacent areas. Several specimens of *Peipiaosteus* were exceptionally preserved with soft tissues of skin and muscles and toes (Fig. 2). The fossils of *Stichopterus* were discovered from the Lower Cretaceous strata in Transbaikalia and Mongolia [4, 5]. The *Yanosteus longidorsalis* were discovered from the Lower Cretaceous Yixian Formation in western Liaoning [15, 16]. However, some fragmented materials were discovered from the most northern area of China, at the southern side of the Amur river [9]. The *Protopsephurus liui* belongs to the Polyodontidae (Fig. 3), and they are distributed in the Jiufotang Formation in western Liaoning [5, 17, 18]. The *Protopsephurus* might be the largest fish within the Jehol Biota.

There are some problems on the relationships between *Peipiaosteus* and *Stichopterus*, because their morphological characteristics were very similar, which indicates that some species might be synonyms. The origin and biogeography of the Mesozoic Acipenseriformes in northeast Asia and their relationships to the living Acipenseriformes in North America are crucial for understanding the evolution of the Mesozoic freshwater fish. Therefore, more fossil sites should be investigated and excavated, and a composite database for paleobiogeographic research is needed.

**Figure 2.** A specimen of *Peipiaosteus pani* with impressions of soft tissues. Specimen is hosted in Paleontological Museum in National Park of Bird Fossils in Chaoyang, Liaoning Province, China.

**Figure 3.** A specimen of *Protopsephurus liui*. Specimen is hosted in Paleontological Museum in National Park of Bird Fossils in Chaoyang, Liaoning province, China.
4. Conclusion
The northeast Asia is the key region for understanding the early diversification and evolution of Acipenseriformes. The Mesozoic Acipenseriformes from east Asia represented by the extinct family †Peipiaosteidae appeared in western Liaoning of China since the Middle Jurassic, then occurred in the Middle-Late Jurassic of western Asia and flourished in the northeast Asia during the Early Cretaceous. There were at least six species of †Peipiaosteidae and an early form of Polyodontidae distributed in the Lower Cretaceous volcano-sedimentary strata in northeast China and adjacent areas including the Mongolia and Transbaikalia of Russia. The broader-scaled research works are urgently needed for the taxonomy, biostratigraphy, and biogeography of the Mesozoic Acipenseriformes.

Acknowledgements
This work is supported by the National Natural Science Foundation of China (grant No: 41688103) and the Key-Lab for Evolution of Past Life and Environment in Northeast Asia, Ministry of Education, China to Li Xiaobo.

References
[1] Bemis W E, Findeis E K and Grande L 1997 Environ. Biol. Fish. 48 25
[2] Findeis E K 1997 Environ. Biol. Fish. 47 73
[3] Hilton E J 2005 Environ. Biol. Fish. 72 135
[4] Bemis W E, Findeis E K and Grande L 1997 Environ. Biol. Fish. 48 25
[5] Jin F 1999 Palaeoworld 11 188
[6] Peng Z, Ludwig A, Wang D, Diogo R, Wei Q and He S 2007 Mol. Phylogenetics Evol. 42 854
[7] Zhou Z, Barrett P M and Hilton J 2003 Nature 421 807
[8] Chang M M and Miao D S 2004 Mesozoic Fishes 3 – Systematics, Paleoenvironments and Biodiversity Arratia G and Tintori A eds (München: Verlag Dr. F. Pfeil) pp. 555-563
[9] Li X, Zhang M and Wang Y 2011 Geol. J. 46 323
[10] Lu L, Zhang M and Wang Y 2011 Earth Sci. Front. 27 371
[11] Xu X, Zhou Z, Wang Y and Wang M 2020 Sci. China Earth Sci. 63 757
[12] Liu H T and Zhou J J 1965 Vertebrata PalAsiatica 9 237
[13] Lu L 1994 Fauna and Stratigraphy of the Jurassic-Cretaceous in Beijing and the Adjacent Areas Ren D, Lu L W, Guo Z G and Ji S A eds (Beijing: Beijing Seismological Press) pp. 121-140, 197-202
[14] Bai Y J 1983 Vertebrata PalAsiatica 21 341
[15] Jin F, Tian Y P, Yang Y S and Deng S Y 1995 Vertebrata PalAsiatica 33 1
[16] Hilton E J, Grande L and Jin F 2021 J. Paleontol. 95 170
[17] Lu L 1994 Vertebrata PalAsiatica 32 132
[18] Grande L, Jin F, Yabumoto Y and Bemis W 2002 J. Vertebr. Paleontol. 22 209