The most primitive lower tetrapod fauna in China

LI Jinling (李锦玲)

Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China (email: pljinling@263.net)

Received January 28, 2000

Abstract A comprehensive analysis of the fauna indicates that three vertebrate assemblage zones existed in the Upper Permian of China. Among them the Dashankou lower tetrapod fauna consisting mainly of therapsids is the most primitive and abundant one. It is more closely related to Zone II of Russia than to the *Eodicynodon* Assemblage Zone of South Africa. Zone II of Russia in the Late Permian played a role of bridge for the dispersal of tetrapods from North America to South Africa and China at that time.

Keywords: Yumen, Russia, South Africa, Late Permian, vertebrates.

The Dashankou locality of Late Permian tetrapods was discovered in Yumen, Gansu Province by Prof. Cheng Zhengwu. Large-scale excavations and study of the fossils began in the early of the 1990's. Since then, 6 papers[1—6] about the stratigraphy of the locality and the elements of the fauna, mainly on the anatomy and phylogeny of the animals have been published.

Up to now, 3 species from 3 genera of amphibians and 4 species from 4 genera of reptiles in the Dashankou fauna are reported. They are *Anakamacops petrolicus* Li et Cheng, 1999 (Dissorophidae, Temnospondyli); *Ingentidens corridoricus* Li et Cheng, 1999 and *Phratochronis qilianensis* Li et Cheng, 1999 (Chroniosuchidae, Anthracosauria); *Belebey vegrandis* Ivachnenko, 1973 (Bolosauridae, Captorhinomorpha); *Biseridens qilianicus* Li et Cheng, 1997 (Biseridensidae, Eotitanosuchia); *Stenocybus acidentatus* Cheng et Li, 1997 (Stenocybusidae, Dinocephalia); *Sinophonus yumenensis* Cheng et Ji, 1996 (Anteosauridae, Dinocephalia) (fig. 1). Considering the numerous individuals and unstudied specimens of reptiles, the fauna is composed principally of therapsids.

The present paper attempts, for the first time, to analyse and compare the members of the fauna with their equivalents from the other Late Permian vertebrate assemblages from China, Russia and South Africa, and to discuss the age of fossil-bearing beds and their correlations. The Dashankou vertebrate assemblage is not only the most abundant and primitive lower tetrapod fauna in China, but also a diverse one. The occurrence of 6 families 7 genera are not known in other Late Permian tetrapod faunas of China.

In China Late Permian vertebrates are also found in Xinjiang, Inner Mongolia, Shanxi and Henan. The Quanzijie-Guodikeng Formations of Xinjiang, Naobaogou Formation of Inner Mongolia, and Sunjiagou Formation of North China are considered as typical late Late Permian deposits, which are correlated with Zone IV of Russia and *Dicynodon* Assemblage Zone of South

Africa, for yielding chiefly dicynodonts in Quanzijie-Guodikeng Formations and Naobaogou Formation, and pareiasaurs in Sunjiagou Formation.

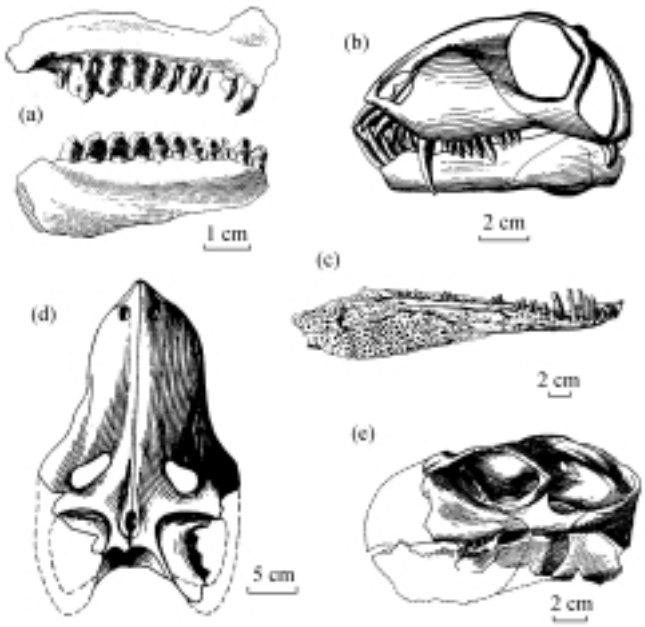

Fig. 1. (a) Upper and lower jaws of *Belebey vegrandis* (from Li and Cheng[1]); (b) reconstruction of skull of *Stenocybus acidentatus* (modified after Cheng and Li, 1999); (c) right ramus of lower jaws of *Ingentidens corridoricus* (from Li and Cheng[6]); (d) reconstuction of skull of *Sinophoneus yumenensis* (modified after Cheng and Ji[3]); (e) reconstruction of skull of *Biseridens qilianicus* (from Li and Cheng[5]).

The Jiyuan fauna consisting of 6 genera and 6 species belonging to bystrowianid, pareiasaur, dinocephalian, gorgonopsian and cynodont from Shangshihezi Formation (= Upper Shihezi Formation) of Jiyuan, Henan[7] was thought to be comparatively close to Dashankou fauna. However, 5 local genera and species out of 6 (*Honania complicidentata*, *Tsiyuania simplicidentata*, *Taihangshania imperfecta*, *Wangwusaurus tayuensis*, *Hwanghocynodon multidenspidus*) were considered invalid for the poor preservation of the specimens represented only by isolated teeth, vertebrae, or incomplete bones[8,9]. But the later researchers seem to hold unanimous views that there exist bystrowianid, pareiasaur, gorgonopsid and cynodont in the Jiyuan fauna except dinocephalian. Bystrowianids and cynodonts were found previously in the strata of Tatarian age of Russia and South Africa, pareiasaurs and gorgonopsids in the deposits of Ufimian-Tatarian age. So, as pointed out by Young[7], Jiyuan fauna may be comparable with *Endothiodon* Zone (=*Tropidostoma* Assemblage Zone[10]) of South Africa and Zone III of Russia.

Among the 6 families in Dashankou fauna, the Chroniosuchidae is commonly known in the strata of Tatarian age of Russia. The Dissorophidae, Bolosauridae and Anteosauridae appeared firstly in Carboniferous, Early Permian and Ufimian of Late Permian respectively, with the former two becoming extinct by Kazanian age, the Anteosauridae by Tatarian. The Biseridensidae in the Dashankou fauna is closely related to Eotitanosuchidae discovered in Zone I of Russia. The

Stenocybusidae are primitive representatives of dinocephalian extending from Ufimian to Tatarian. Through analyzing the existence age of the animals, it is reasonable to conclude that Dashankou fauna is older than Jiyuan fauna. The discosaurisid amphibian *Urumuqia* from Lucaogou Formation of Xinjiang may be of the same age as the Dashankou fauna. To sum up, there exist three vertebrate fossil-bearing beds in the Upper Permian of China as shown in table 1.

Table 1

Strata	Fauna	Fossil
Quanzijie-Goudikeng Fms., Naobaogou Fm., Sunjiagou Fm.		Dicynodontidae Pareiasauridae
Shangshihezi Fm.	Jiyuan Fauna	Pareiasauridae gorgonopsian cynodonts bystrowianid
Xidagou Fm.	Dashankou Fauna	Chroniosuchidae Dissorophidae Bolosauridae Biseridensidae Stenocybusidae Anteosauridae
?Lucaogou Fm.		Discosauriscidae

The most extensive Late Permian tetrapod records are known from the Karroo Basin of South Africa and Ural region of Russia. The successive assemblage zones in both regions have been recognized, but their correlations are still uncertain. Zone II of Russia was considered older than *Tapinocephalus* Zone of South Africa by Anderson and Cruickshank[11], and Cooper[12], but younger than *Tapinocephalus* Zone by Lucas[9]. In order to ascertain the correlations of Dashankou fauna with Zone II of Russia and *Eodicynodon* Assemblage Zone of South Africa, the tetrapod families occurred in the areas, which are based on the comprehensive reports of Olson and Chudinov[13] for Russia and Rubidge[10] for South Africa, are shown in table 2.

Table 2

	Eodicynodon AZ of South Africa	Zone II of Russia	Dashankou Fauna of China
Amphibia			
Archegosauridae		xxxxxxxxxxxx	
Dissorophidae		xxxxxxxxxxxx	xxxxxxxxxxxx
Melosauridae		----------	
Seymouriidae		xxxxxxxxxxxx	
Chroniosuchidae			----------
Lanthanosuchidae		----------	
Reptilia			
Captorhinidae		xxxxxxxxxxxx	
Nyctiphruretidae		----------	
Bolosauridae		xxxxxxxxxxxx	xxxxxxxxxxxx
Rhipaeosauridae		----------	
Mesenosauridae		----------	
Caseidae		xxxxxxxxxxxx	
Phthinosuchidae		----------	
Biseridensidae			----------
Phreatosuchidae		----------	
Deuterosauridae		----------	
Stenocybusidae			----------
Titanosuchidae	----------		
Anteosauridae	----------	----------	----------
Venjukoviidae		----------	
?Galechiridae	----------		
Eodicynodontidae	----------		
Pristerognathidae	----------		
Gorgonopsia Family indet.	----------		

Being new discoveries in the 1980's, both Dashankou fauna and *Eodicynodon* Assemblage Zone of South Africa are, so far, not as rich as Zone II of Russia in composition. Zone II of Russia includes 16 families, 6 of which, Archegosauridae, Dissorophidae, Seymouriidae, Captorhinidae, Bolosauridae and Caseidae, are Early Permian holdovers (according to Benton[14], and Milner[15]). The continuity of tetrapod families from Early Permian into Late Permian indicates the primitive nature inherited from Zone II. The other 8 families, Melosauridae, Lanthanosuchidae, Rhipacosauridae, Mesenosauridae, Phthinosuchidae, Phreatosuchidae, Deuterosauridae and Venjukoviidae, had very strict distributions, which are neither recorded in the later Zone III and Zone IV of Russia, nor in the other Upper Permian localities outside of Russia. The Nyctiphruretidae is the most primitive family of procolophonids, with its member, *Owenetta* recovered from the *Cisticephalus* Zone of South Africa. The Anteosauridae is the only family present in Russia, South Africa and China. *Syodon* from Russia and *Australosyodon* from South Africa are considered relatively primitive members of the Anteosauridae.

No amphibian is recorded in the *Eodicynodon* Assemblage Zone of South Africa, but 5 families of reptiles and one family indet (Titanosuchidae, Anteosauridae, Galechiridae, Eodicynodontidae, Pristerognathidae and a gorgonopsid). All of them have their first appearance in the Late Permian, and 4 families except Anteosauridae are endemic. The early representative of dicynodonts in the Assemblage Zone are Eodicynodontidae and Galechiridae, which are not as primitive as Venjukoviidae of Zone II of Russia. The Pristerognathidae includes the oldest therocephalian. The *Eodicynodon* Assemblage Zone of South Africa is of great significance due to yielding the oldest therocephalian, gorgonopsian, dicynodont, but its nature for having no Early Permian holdover seems to be more advanced than that of Zone II of Russia.

In Dashankou fauna, the Dissorophidae and Bolosauridae as in Zone II of Russia are holdovers from the Early Permian. Although Chroniosuchidae does not occur in Zone II, *Ingentidens* of Dashankou fauna is close to *Chroniosuchus* of Zone IV of Russia. The Biseridensidae is the only eotitanosuchid found outside of Russia, which is more advanced than Biarmosuchidae of Zone I and Phthinosuchidae of Zone II of Russia. The Stenocybusidae is the most primitive dinocephalian, and a sister group of all other dinocephlians. *Sinophoneus*, a member of Anteosauridae in Dashankou fauna is closely related to *Titanophoneus* of Zone II of Russia. Owing to bearing the Early Permian holdovers and relatives of eotitanosuchids and chroniosuchids, and bearing no advanced members of therapsids, dicynodont, gorgonopsian and therocephalian, the Dashankou fauna is more close to Zone II of Russia than to *Eodicynodon* Assemblage Zone of South Africa. The higher percentage of sharing families of the Dashankou fauna with Zone II of Russia than the *Eodicynodon* Assemblage Zone of South Africa seems to indicate the more similarities of the Chinese fauna to the former than to the latter, and implies that the exchange of lower terrapods between the Laurasia and Gondwana during the Late Permian, seems not to be very easy and smooth, although the Pangea provided the convenience of the dispersal of animals.

The conclusion of the above analysis is in agreement with the views of Anderson and Cruickshank[11], and Cooper[12]. When their papers were published, the *Tapinocephalus* Zone was the lowest tetrapod assemblage zone in South Africa, and the *Eodicynodon* Assemblage Zone had not been found. Since Zones I and II of Russia are placed lower than the *Tapinocephlus* Zone of South Africa as suggested by them, it is logical to correlate Zone II of Russia with the *Eodicynodon* Assemblage Zone or to place the former a little lower than the latter. The facts that the dominance of pareiasaurs, gorgonopsians, therocephlians and dicynodonts is in the *Pristerognathus* and *Tropidostoma* Assemblage Zones of South Africa[16,17] do not support their correlation with Zone II of Russia as suggested by Lucas[9]. The *Eodicynodon* Assemblage Zone may not be the oldest lower tetrapod zone of the Upper Permian.

Acknowledgements I would like to thank Dr. Mee-mann Chang for reading and correcting the manuscript, to Yang Mingwan and Liu Jun for making drawings. I am greatly indebted to the discoverer of Dashankou Locality, Prof. Cheng Zhengwu, and to all colleagues who participated in collecting, preparing and researching fossils. This work was supported by the National Natural Science Foundation of China (Grant No. 49672087).

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