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燕辽生物群脊椎动物的多样性及与其他生物群的对比分析*

刘　璠[1,2]　武　瑞[2]　韩凤禄[2**]

1 贵州大学, 资源与环境工程学院, 贵阳 550025;
2 中国地质大学(武汉), 地球科学学院, 武汉 430074

提要　燕辽生物群已发现脊椎动物 54 属 58 种, 包括鱼类、两栖类、爬行类、哺乳类等, 但其脊椎动物多样性及其成因机制还未有详细研究。本文对该生物群脊椎动物进行统计分析, 并与同时代的其他生物群脊椎动物类型进行对比, 这为认识燕辽生物群脊椎动物的多样性及其成因提供了重要的证据。早期代表道虎沟生物群与晚期代表玲珑塔生物群虽存在时代上的传承关系, 但生物组合特征明显不同。对比燕辽生物群与相近时代的新疆五彩湾动物群和四川大山铺恐龙动物群, 脊椎动物组合特征差异显著。燕辽生物群恐龙类群主要以小型兽脚类恐龙为主, 还包括一些小型鸟臀类恐龙。另外还具有非常丰富的翼龙和哺乳动物。脊椎动物生态多样性高, 适应飞行、树栖、水生、穴居等多种生活方式, 但是脊椎动物的类型与同时代的相近地区明显不同。翼龙、恐龙和哺乳动物等类群都展现出独特的生物组合特征。有证据表明该时期东亚地区与其他地区可能存在一定程度的地理隔离, 结合陆生脊椎动物组合特征推测燕辽生物群脊椎动物与外界可能存在一定的交流障碍。

关键词　燕辽生物群　燕山运动　脊椎动物　生物多样性　古环境

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Vertebrate diversity of the Yanliao Biota and comparison with other biotas

LIU Fan[1,2], WU Rui[2], HAN Feng-lu[2]

1 *School of Resources and Environmental Engineering*, *Guizhou University*, *Guiyang* 550025, *China*;
2 *School of Earth Sciences*, *China University of Geosciences*, *Wuhan* 430074, *China*

Abstract　A total of 54 genera and 58 species of vertebrates, including fishes, amphibians, reptiles and mammals, have been reported from the Yanliao Biota, but the diversity and formation mechanism of vertebrates have not been

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** 通讯作者: 韩凤禄, 研究员, e-mail: hanfl@cug.edu.cn

well-studied in detail based on biological analysis. Here, a statistical analysis of the vertebrates in the Yanliao Biota and a detailed comparison with other biotas of similar age are present, which provides significant evidence for the diversity of vertebrates and the formation of the Yanliao Biota. Although the early Daohugou Biota and the late Linglongta Biota are continuous in time, they show different characteristics of biological combination of vertebrates, respectively. Yanliao Biota including a large number of invertebrates and vertebrates and plant fossils is significantly different from other biotas of similar age, such as the Wucaiwan Fauna from Xinjiang and Dashanpu Dinosaur Fauna from Sichuan Basin. Dinosaurs from the Yanliao Biota only contain small theropods and some early ornithischians. But Yanliao Biota is very rich in pterosaurs and mammals. Vertebrates from the Yanliao Biota have high ecological diversity and a unique combination of taxa groups. Some evidence indicates that there may exist geographic isolation between East Asia and other regions during this period. Combined with the characteristics of terrestrial vertebrate assemblage, it can be inferred that there may have been some obstacles in the communication between vertebrates of the Yanliao Biota and the outside world.

Key words　Yanliao Biota, Yanshan Movement, vertebrates, biodiversity, paleoenvironment

1　前　言

燕辽生物群是由“燕辽昆虫群”(洪友崇, 1983)和“燕辽动物群”(任东等, 1995)逐步扩展形成的, 主要分布在中国东北、华北和内蒙古等地区。生物群的化石大多发现于中、晚侏罗世陆相地层中, 包括内蒙古宁城道虎沟、河北青龙县南石门的道虎沟化石层、辽宁凌源无白丁的九龙山组、河北青龙县木头凳、辽宁建昌玲珑塔和大西山的髫髻山组等(图 1)。燕辽生物群化石门类和数量极其丰富, 包含植物、昆虫、脊椎动物、双壳类、腹足类以及叶肢介等(沈炎彬等, 2003; 姜宝玉, 2006; 季强、袁崇喜, 2008; 黄迪颖, 2016; Ren, 2002; Gao and Shubin, 2003; Ji *et al*., 2006; Lian *et al*., 2021)。根据生物组合特征可分为燕辽生物群的早期和晚

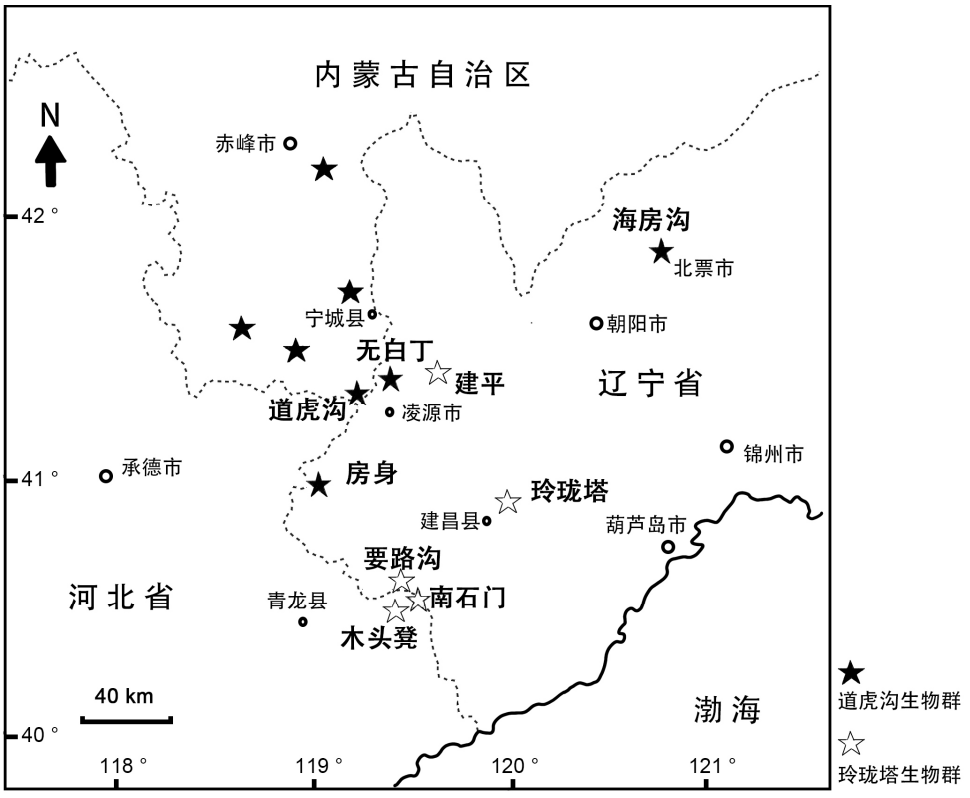

图 1　燕辽生物群脊椎动物主要化石点(据郭相奇, 2012 修改)

Fig. 1　Main vertebrates fossil sites of the Yanliao Biota (modified from Guo, 2012)

期阶段(黄迪颖, 2015; 韩凤禄等, 2016; Xu *et al*., 2016)。早期阶段是以燕辽划蝽—“滦平真叶肢介”—费尔干蚌—初螈为代表的道虎沟生物群, 晚期阶段是以柴达木叶肢介—额尔古纳蚌—古鳄为代表的玲珑塔生物群(黄迪颖, 2015)。二者在门类上既有传承, 又有很大差异(郭相奇, 2012)。20 世纪 90 年代以来, 燕辽生物群报道了大量脊椎动物化石, 不仅保存精美, 且类型独特(Gao and Shubin, 2003; Meng *et al*., 2006; Xu *et al*., 2009, 2015; Luo *et al*., 2011), 特别是带羽毛恐龙以及早期哺乳动物的大量发现, 极大的推动了有关鸟类起源以及早期哺乳动物演化的研究(Zhou and Wang, 2010; Sullivan *et al*., 2014; Xu *et al*., 2017)。前人对燕辽生物群生物组合特征的研究多注重于昆虫、叶肢介等无脊椎动物(黄迪颖, 2015; Liao *et al*., 2016), 虽然对脊椎动物的门类和属种有一定总结和归纳, 但并未详细分析脊椎动物各门类的生物组合特征(黄迪颖, 2015; 韩凤禄等, 2016; Xu *et al*., 2016)。Zhou 等(2017)对燕辽生物群的脊椎动物组合特征有一定的分析与讨论, 但仅与同地区时代较晚的热河生物群进行对比。郭相奇等(2012)注意到道虎沟和玲珑塔两个产地脊椎动物化石存在的差异, 不仅没有相同的种类, 且对应的类群也不能直接比较, 黄迪颖(2015)进一步推测两地之间可能存在交流障碍或两个化石层的时代并不完全相同。本文对道虎沟生物群和玲珑塔生物群的脊椎动物化石进行系统的总结与对比, 并且分别将两个生物群与其他同时代生物群进行对比, 讨论燕辽生物群的多样性及其形成机制, 这对于了解燕辽地区中生代晚期陆相生态系统和脊椎动物的演化有重要意义。

2 燕辽生物群的脊椎动物多样性

燕辽地区由于后期的构造运动以及人为因素, 地层出露情况较差。早期地层划分和命名一直难以统一(汪筱林等, 2000; 王原等, 2000; 季强、袁崇喜, 2002; 任东等, 2002; 张俊峰, 2002; 沈炎彬等, 2003; 黄迪颖等, 2015)。近年来高精度的同位素测年以及深入的地层对比工作为地层的厘定提供了重要证据(陈文等, 2004; Liu *et al*., 2012; Chang *et al*., 2009, 2013; 黄迪颖, 2019)。燕辽生物群由两部分组成。早期代表道虎沟生物群产自九龙山组或海房沟组, 晚期代表玲珑塔生物群则产自髫髻山组(黄迪颖, 2015; 2019)。燕辽生物群的多样性和特异性可能和古环境、古气候以及特异性埋藏有关(郑楠, 2010; 黄迪颖, 2015, 2016; Sun *et al*., 2008; Ren *et al*., 2010; Na *et al*., 2015; Xu *et al*., 2016), 但具体以哪种因素为主目前仍没有明确结论。

迄今, 燕辽生物群发现脊椎动物共计 54 属 58 种, 包括鱼类、两栖类、爬行类和哺乳类。鱼类、鳄形类、龟鳖类的发现很少; 未报道鸟类。早前报道的徐氏曙光鸟(*Aurornis xui*, Godefroit *et al*., 2013a)应为兽脚类恐龙(Brusatte *et al*., 2014)。两栖类仅报道有尾类, 某些属种还表现出捕食的选择性(Dong *et al*., 2012)。翼龙类以原始的喙嘴龙类为主, 也包括少数进步的翼手龙类以及处于过渡阶段的悟空翼龙类。恐龙仅发现小型肉食性兽脚类和小型的异齿龙类, 未报道大型植食性恐龙。其中赫氏近鸟龙(*Anchiornis huxleyi*, Xu *et al*., 2009)、郑氏晓廷龙(*Xiaotingia zhengi*, Xu *et al*., 2011)对于研究羽毛的起源和演化具有重要意义。哺乳动物特异性演化显著, 有适应辐射的表现, 尤其是具有飞行或滑翔能力的哺乳动物(Meng, 2006; Luo *et al*., 2017)。

截止目前, 燕辽生物群早期组合(道虎沟生物群)已发现的脊椎动物有鱼类 1 属 1 种, 两栖类 4 属 4 种, 有鳞类 3 种类型, 鳄形类一未定属种, 翼龙类 3 属 3 种, 兽脚类恐龙 4 属 4 种, 哺乳类 6 属 6 种(表 1)。晚期组合玲珑塔生物群已报道一鱼类未定种, 两栖类 3 属 3 种, 有鳞类 1 属 1 种, 龟鳖类 1 属 1 种, 翼龙类 12 属 14 种, 恐龙类 5 属 5 种, 哺乳类 9 属 11 种(表 2)。

3 燕辽生物群及对比

在中国与燕辽生物群相近时代还存在有三大著名的生物群(图 2)。一个是在中国西北地区新疆准噶尔盆地五彩湾地区, 发现有大量的恐龙以及其他脊椎动物化石(Andres *et al*., 2010; Choiniere *et al*., 2014; Han *et al*., 2015; Qin *et al*., 2019), 此

表 1　道虎沟生物群脊椎动物种类
Table 1　Vertebrates of the Daohugou Biota

道虎沟生物群			
分类位置	属种名称	产出层位	具体地点
	鱼类		
软骨硬鳞鱼类	洪氏辽鲟 *Liaosteus hongi* Lu, 1995	海房沟组	辽宁北票海房沟
	两栖类		
有尾类	天义初螈 *Chunerpeton tianyiensis* Gao and Shubin, 2003	九龙山组	内蒙古宁城道虎沟
	奇异热河螈 *Jeholotriton paradoxus* Wang, 2000	道虎沟化石层	内蒙古宁城道虎沟
	道虎沟辽西螈 *Liaoxitriton daohugouensis* Wang, 2004	道虎沟化石层	内蒙古宁城道虎沟
	中华胖螈 *Pangerpeton sinensis* Wang and Evans, 2006	九龙山组	辽宁凌源无白丁
	爬行类		
鳄形类	鳄形类属种未定 Crocodyliformes (Sullivan *et al*., 2015)	道虎沟化石层	内蒙古宁城道虎沟
有鳞类	杨氏矢部龙 *Yabeinosaurus youngi* Estes, 1983	九龙山组	辽宁凌源房身
	属种未定 Squamat A (Evans and Wang, 2007)	道虎沟化石层	内蒙古宁城道虎沟
	属种未定 Squamat B (Evans and Wang, 2009)	道虎沟化石层	内蒙古宁城道虎沟
翼龙类	宁城热河翼龙 *Jeholopterus ningchengensis* Wang *et al*., 2002	道虎沟化石层	内蒙古宁城道虎沟
	沃氏翼手喙龙 *Pterorhynchus wellnhoferi* Czerka and Ji, 2002	道虎沟化石层	内蒙古宁城道虎沟
	娇小道虎沟翼龙 *Daohugoupterus delicatus* Cheng *et al*., 2015	道虎沟化石层	内蒙古宁城道虎沟
兽脚类	道虎沟足羽龙 *Pedopenna daohugouensis* Xu and Zhang, 2005	道虎沟化石层	内蒙古宁城道虎沟
	胡氏耀龙 *Epidexipteryx hui* Zhang *et al*., 2008	道虎沟化石层	内蒙古宁城道虎沟
	宁城树栖龙 *Epidendrosaurus ningchengensis* Zhang *et al*., 2002	道虎沟化石层	内蒙古宁城道虎沟
	长臂浑元龙 *Ambopteryx longibrachium* Wang *et al*., 2019	海房沟组	辽宁凌源无白丁
	哺乳类		
三尖齿兽类	纤细辽兽 *Liaotherium gracile* Zhou *et al*., 1991	九龙山组	辽宁凌源房身
柱齿兽类	獭形狸尾兽 *Castorocauda lutrasimilis* Ji *et al*., 2006	九龙山组	内蒙古宁城道虎沟
	攀援灵巧柱齿兽 *Agilodocodon scansorius* Meng *et al*., 2015	九龙山组	内蒙古宁城道虎沟
翔兽类	远古翔兽 *Volaticotherium antiquus* Meng *et al*., 2006	道虎沟化石层	内蒙古宁城道虎沟
蜀兽类	粗壮假碾磨齿兽 *Pseudotribos robustus* Luo *et al*., 2007	九龙山组	内蒙古宁城道虎沟
小贼兽类	哺乳形巨齿兽 *Megaconus mammaliaformis* Zhou *et al*., 2013	道虎沟化石层	内蒙古宁城道虎沟

表 2　玲珑塔生物群脊椎动物种类
Table 2　Vertebrates of the Linglongta Biota

玲珑塔生物群			
分类位置	属种名称	产出层位	具体地点
	鱼类		
硬骨鱼类	古鳕类属种未定 Palaeoniscoidea (Duan *et al*., 2009)	髫髻山组	辽宁建昌玲珑塔
	两栖类		
有尾类	建平北燕螈 *Beiyanerpeton jianpingensis* Gao and Shubin, 2012	髫髻山组	辽宁建平棺材山
	大西山玲珑螈 *Linglongtriton daxishanensis* Jia and Gao, 2019	髫髻山组	辽宁建昌玲珑塔
	干沟青龙螈 *Qinglongtriton gangouensis* Jia and Gao, 2016	髫髻山组	河北省青龙干沟乡
	爬行类		
龟鳖类	新疆龟科未定种 *Annemys* sp. (Li *et al*., 2021)	髫髻山组	河北省青龙木头凳
有鳞类	谢氏红山蜥 *Hongshanxi xiei* Dong *et al*., 2019	髫髻山组	辽宁建平棺材山
翼龙类	李氏凤凰翼龙 *Fenghuangopterus lii* Lü *et al*., 2010	髫髻山组	辽宁建昌玲珑塔
	赵氏建昌翼龙 *Jianchangopterus zhaoianus* Lü and Bo, 2011	髫髻山组	辽宁建昌玲珑塔

续表

玲珑塔生物群			
分类位置	属种名称	产出层位	具体地点
翼龙类	强壮建昌颌翼龙 *Jianchangnathus robustus* Cheng *et al*., 2012	髫髻山组	辽宁建昌玲珑塔
	潘氏长城翼龙 *Changchengopterus pani* Lü, 2009	髫髻山组	河北省青龙木头凳
	李氏悟空翼龙 *Wukongopterus lii* Wang *et al*., 2009	髫髻山组	辽宁建昌玲珑塔
	中国鲲鹏翼龙 *Kunpengopterus sinensis* Wang *et al*., 2010	髫髻山组	辽宁建昌玲珑塔
	模块达尔文翼龙 *Darwinopterus modularis* Lü *et al*., 2010	髫髻山组	辽宁建昌玲珑塔
	玲珑塔达尔文翼龙 *Darwinopterus linglongtaensis* Wang *et al*., 2010	髫髻山组	辽宁建昌玲珑塔
	强齿达尔文翼龙 *Darwinopterus robustodens* Lü *et al*., 2011	髫髻山组	辽宁建昌玲珑塔
	玲珑塔古帆翼龙 *Archaeoistiodactylus linglongtaensis* Lü and Fucha, 2010	髫髻山组	辽宁建昌玲珑塔
	郭氏青龙翼龙 *Qinglongopterus guoi* Lü *et al*., 2012	髫髻山组	河北省青龙木头凳
	木头凳树翼龙 *Dendrorhynchoides mutoudengensis* Lü and Hone, 2012	髫髻山组	河北省青龙木头凳
	原始辽翼龙 *Liaodactylus primus* Zhou *et al*., 2017	髫髻山组	辽宁建昌大西山
	郑氏斗战翼龙 *Douzhanopterus zhengi* Wang *et al*., 2017	髫髻山组	辽宁建昌玲珑塔
兽脚类	赫氏近鸟龙 *Anchiornis huxleyi* Xu *et al*., 2009	髫髻山组	辽宁建昌要路沟
	郑氏晓廷龙 *Xiaotingia zhengi* Xu *et al*., 2011	髫髻山组	辽宁建昌玲珑塔
	短羽始中国羽龙 *Eosinopteryx brevipenna* Godefroit *et al*., 2013b	髫髻山组	辽宁建昌玲珑塔
	徐氏曙光鸟 *Aurornis xui* Godefroit *et al*., 2013a	髫髻山组	辽宁建昌要路沟
	奇翼龙 *Yi qi* Xu *et al*., 2015	髫髻山组	河北青龙县南石门
	哺乳类		
真兽类	中华侏罗兽 *Juramaia sinensis* Luo *et al*., 2011	髫髻山组	辽宁建昌玲珑塔
多瘤齿兽类	欧亚皱纹齿兽 *Rugosodon eurasiaticus* Yuan *et al*., 2013	髫髻山组	辽宁建昌大西山
柱齿兽类	短指挖掘柱齿兽 *Docofossor brachydactylus* Luo *et al*., 2015	髫髻山组	河北青龙县南石门
贼兽类	金氏树贼兽 *Arboroharamiya jenkinsi* Zheng *et al*., 2013	髫髻山组	河北省青龙木头凳
	阿霍氏树贼兽 *Arboroharamiya allinhopsoni* Han *et al*., 2017	髫髻山组	河北青龙县南石门
	陆氏神兽 *Shenshou lui* Bi *et al*., 2014	髫髻山组	辽宁建昌大西山
	玲珑仙兽 *Xianshou linglong* Bi *et al*., 2014	髫髻山组	辽宁建昌大西山
	宋氏仙兽 *Xianshou songae* Bi *et al*., 2014	髫髻山组	辽宁建昌大西山
	似叉骨祖翼兽 *Maiopatagium furculiferum* Meng *et al*., 2017	髫髻山组	辽宁建昌大西山
	双钵翔齿兽 *Vilevolodon diplomylos* Luo *et al*., 2017	髫髻山组	河北青龙县南石门
	济赞堂奇兽 *Qishou jizantang* Mao and Meng, 2019	髫髻山组	辽宁建昌大西山

处简称“五彩湾动物群”。另外两个是四川自贡大山铺著名的蜀龙动物群(中侏罗世)和马门溪龙动物群(晚侏罗世) (高玉辉等, 2004; 傅乾明等, 2005; 叶勇等, 2005; 彭光照, 2009)。这三个动物群脊椎动物化石非常丰富, 且研究历史较长, 适合与燕辽生物群脊椎动物进行对比研究。属种统计表明燕辽生物群中的脊椎动物类群相比于同时代其他地区的脊椎动物类群有很大的不同(图 3)。不仅体现在生物和生态多样性方面, 还有脊椎动物的特异性演化和趋同演化。

3.1 恐龙

道虎沟生物群目前报道的恐龙, 主要为营树栖的小型兽脚类恐龙, 并没有马门溪龙类、剑龙类等大型植食类群的报道(Zhang *et al*., 2002, 2008; Xu and Zhang, 2005)。在玲珑塔生物群的恐龙类群中, 还是以小型兽脚类恐龙为主, 包括赫氏近鸟龙、郑氏晓廷龙(Xu *et al*., 2011)等。两个动物群中鲜有蜥脚类及鸟臀类, 与中国及世界其他地区中、晚侏罗世恐龙类群显著区别(图 4)。蜀龙动物群以原始的蜥脚类恐龙为主, 体型开始变

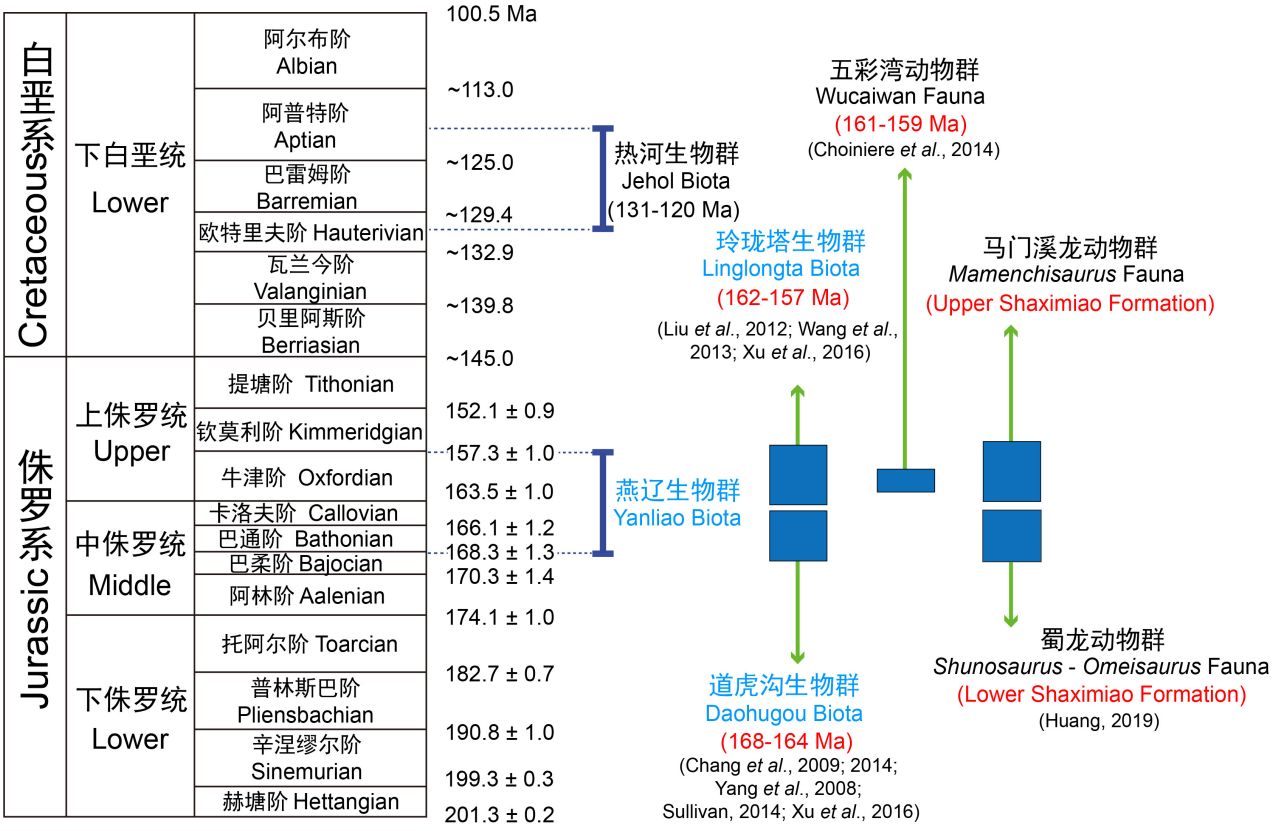

图 2　燕辽生物群与其他相近时代的生物群地层年代对比

Fig. 2　Stratigraphic correlation between the Yanliao Biota and other similar biotas

大; 兽脚类恐龙个体较小, 以肉食类为主; 鸟脚类和剑龙类都位于鸟臀类恐龙较基干的位置(彭光照, 1992; 高玉辉, 1993; 江山等, 2011)。马门溪龙动物群延续并进一步发展了蜀龙动的特点, 蜥脚类恐龙以体型巨大的较为进步的马门溪龙为主, 肉食性兽脚类恐龙向大型化发展(高玉辉, 1992)。其他类别的恐龙体型上也有所增大(张奕宏等, 1998; 叶勇等, 2001, 2005)。同为中、晚侏罗世著名的恐龙生物群, 新疆五彩湾动物群与燕辽生物群的恐龙类群也有很大差异。五彩湾动物群共计 16 属 16 种, 包括基干蜥脚类、大型兽脚类、剑龙类和角龙类, 也包括很多非常重要的中小型肉食类恐龙, 表现出典型的侏罗纪恐龙的组合特征(Xu *et al.*, 2006, 2009; Choiniere *et al.*, 2013; Han *et al.*, 2015; Qin *et al.*, 2019)。新疆和四川地区的生物群基本包括了中、晚侏罗世各个类群的恐龙(彭光照, 2009; Choiniere *et al.*, 2010, 2014)。

新疆五彩湾动物群、蜀龙动物群、马门溪龙动物群则整体与世界其他地区中、晚侏罗世的恐龙类群相似(例如美国的莫里森组化石群, Christiansen and Fariña, 2004; Harris and Dodson, 2004; Schwarz *et al.*, 2007; Woodruff and Foster, 2015), 是典型的中、晚侏罗世恐龙类群组合, 包括大型蜥脚类、大型兽脚类、小型兽脚类和一些中大型的鸟臀类恐龙, 燕辽生物群的恐龙组合则与之不同。这种脊椎动物组合的不同除了和古环境相关外, 还有可能和埋藏环境相关。如燕辽生物群的小型恐龙化石主要与其他水生脊椎动物一起发现在湖泊相页岩中。而新疆石树沟组为气候炎热半干旱的河湖相砂岩粉砂岩, 夹灰绿色泥岩沉积(Eberth, 2010)。石树沟组砂岩粉砂岩中保存有较多的大型但不关联的恐龙化石, 较为完整的小型恐龙化石多发现在泥岩当中(Choiniere *et al.*, 2010)。细密的沉积物有利于保存体型较小的古生物化石, 甚至软体构造, 也可以保存大型脊椎动物。如热河生物群在泥页岩、凝灰岩中也保存有大型恐龙化石, 包括杨氏锦州龙(*Jinzhousaurus yangi*, 汪筱林、徐星, 2001)和华丽羽王龙

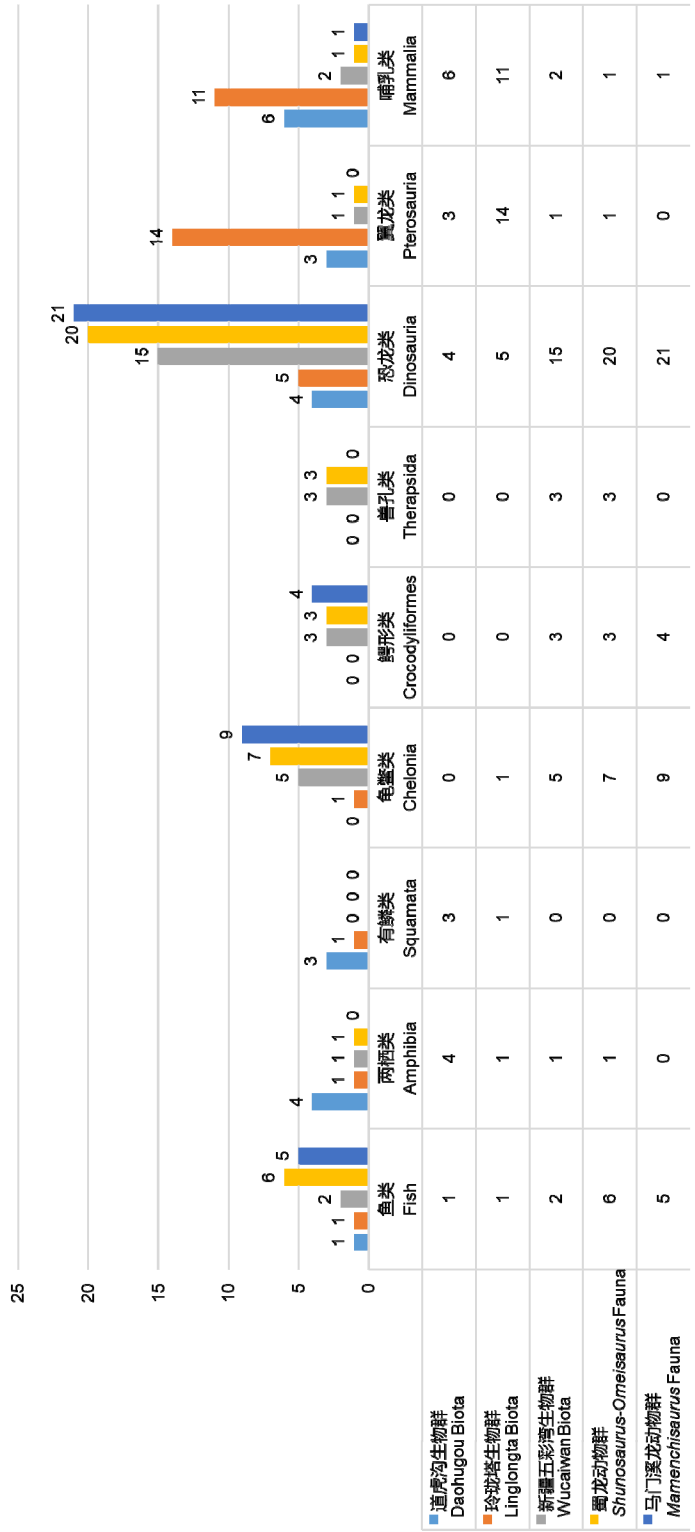

图 3 燕辽生物群与其他相近时代的生物群脊椎动物组合面貌对比图

Fig. 3 Comparison of the vertebrate assemblage between the Yanliao Biota and other similar biotas

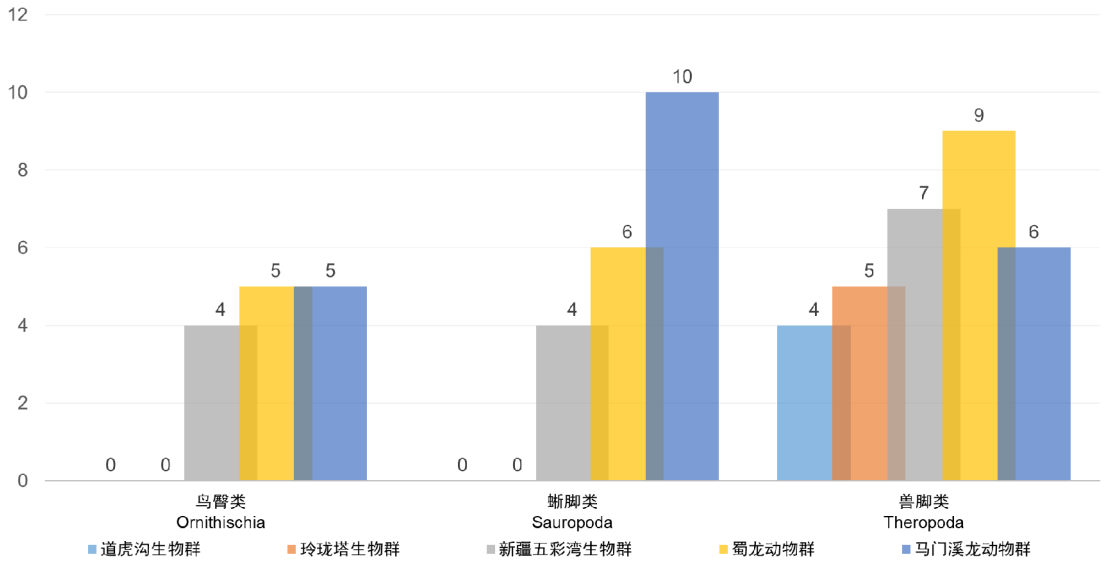

图 4　燕辽生物群和其他生物群恐龙类生物组合面貌对比图

Fig. 4　Comparison of the dinosaur assemblage of the Yanliao Biota and other biotas

(*Yutyrannus huali*, Xu *et al*., 2012)等。因此燕辽生物群未报道大型脊椎动物虽可能与特异性埋藏有关，但不是主要决定因素。

3.2　翼龙类

与恐龙情况不同，燕辽生物群翼龙类的多样性与分异度要远远高于中国国内其他同时代的生物群，共计 5 科 15 属 17 种。新疆五彩湾动物群仅包含喙嘴龙类五彩湾丝绸翼龙(*Sericipterus wucaiwanensis*, Andres *et al*., 2010) 1 属 1 种；四川蜀龙动物群中发现喙嘴龙类长头狭鼻翼龙(*Angustinaripterus longicephalus*, He *et al*., 1983) 1 属 1 种；四川马门溪龙动物群未报道翼龙类；而道虎沟生物群截至目前为止共发现翼龙类 3 属 3 种，包括原始的喙嘴龙类。而在玲珑塔生物群中，翼龙类的多样性与分异度显著增高，共计 12 属 14 种(图 5)，主要是处于过渡阶段的悟空翼龙类，形态特征介于原始的喙嘴龙类和较为进化的翼手龙类之间(汪筱林等，2016)，悟空翼龙类的化石发现证实了翼手龙类应该是某种喙嘴龙的后代的推论(Wellnhofer，1991)，为翼龙模块进化理论(演化机制)提供证据支持(吕君昌等，2010)。燕辽生物群的翼龙组合与国外地区其他侏罗纪翼龙组合存在相同点，例如中亚哈萨克斯坦 Karatau 生物群报道了蛙嘴翼龙科和掘颌翼龙科的翼龙。

值得注意的是，燕辽生物群在湖泊相页岩当中的翼龙类大多保存有精细的毛发与翼膜软组织印痕。化石证据显示这些翼龙躯体可能被毛发一样的丝状结构物所覆盖，称为“原始羽毛”，它的出现与飞行功能无关，具体原因还未明确(Kellner *et al*., 2010)。根据燕辽地区翼龙类与其他具有“飞行”能力的类群分析，推测“原始羽毛”很可能是为了保持体温(季强、袁崇喜，2002)。

3.3　哺乳类

燕辽生物群哺乳动物种类丰富，共计 15 属 17 种，包括三尖齿兽类、柱齿兽类、翔兽类、蜀兽类、真兽类和贼兽类，如中华侏罗兽(*Juramaia sinensis*, Luo *et al*., 2011)、欧亚皱纹齿兽(*Rugosodon eurasiaticus*, Yuan *et al*., 2013)、金氏树贼兽(*Arboroharamiya jenkinsi*, Zheng *et al*., 2013)、攀援灵巧柱齿兽(*Agilodocodon scansorius*, Meng *et al*., 2015)等，表明哺乳动物不仅多样性高，而且生态类型多样。而四川、新疆地区的动物群发现哺乳动物较少，仅以三尖齿兽类(Triconodontia)和柱齿兽类(Docodonta)为主，与

翼龙类 Pterosauria	道虎沟生物群 Daohugou Boita	玲珑塔生物群 Linglongta Boita	五彩湾动物群 Wucaiwan Fauna	蜀龙生物群 *Shunosaurus-Omeisaurus* Fauna	马门溪龙生物群 *Mamenchisaurus* Fauna
蛙嘴翼龙科 Anurognathidae	●	●	—	—	—
悟空翼龙科 Wukongopteridae	—	●●●●● ●●●●	—	—	—
掘颌翼龙科 Scaphognathidae	—	●	—	—	—
帆翼龙科 Istiodactylidae	—	●	—	—	—
喙嘴翼龙科 Rhamphorhynchidae	●●	●●	●	●	—

图 5 燕辽生物群和其他生物群翼龙类生物组合面貌对比图

Fig. 5 Comparison of the pterosaur assemblage of the Yanliao Biota and other biotas

燕辽生物群的哺乳动物相比, 在数量、种类、分异度上有明显差距。

3.4 其他类群

在两栖类方面, 道虎沟生物群发现了 4 属 4 种, 玲珑塔生物群 3 属 3 种, 新疆五彩湾动物群与蜀龙动物群各发现 1 属 1 种, 马门溪龙动物群未有报道。燕辽生物群的两栖类为有尾类, 包括捕食中华燕辽划蝽(*Yanliaocorixa chinensis*)的天义初螈(*Chunerpeton tianyiensis*, Gao and Shubin, 2003), 具有捕食选择性的奇异热河螈(*Jeholotriton paradoxus*, Wang, 2000), 以及最早的蝾螈亚目代表——建平北燕螈(*Beiyanerpeton jianpingensis*, Gao *et al*., 2012), 和大西山玲珑螈(*Linglongtriton daxishanensis*, Jia and Gao, 2019)等。

龟鳖类在燕辽生物群仅报道一未定种(Li *et al*., 2021), 但在新疆、四川地区龟鳖类分异度很高, 主要包括曲颈龟类、成渝龟类和蛇颈龟类(杨钟健、周明镇, 1953; 叶祥奎, 1986; 叶勇、皮孝忠, 1997; Tong *et al*., 2012; Brinkman *et al*., 2013)。鳄形类在道虎沟生物群中仅报道有一种基干鳄形类, 保存了完整骨骼与软组织(Sullivan *et al*., 2015; Zhou and Wang, 2017), 而在玲珑塔生物群至今未有报道。新疆五彩湾动物群已报道鳄形类 3 属 3 种, 蜀龙动物群有 3 属 3 种, 马门溪龙动物群有 3 属 4 种。这种类型的差异可能与古环境有关, 适应炎热环境的鳄形类在新疆、四川马门溪龙动物群数量多, 多样性较高(辛恒广, 2000; 钱利军等, 2012), 说明这些地区当时的古环境偏炎热, 而燕辽生物群则分布较少, 也说明了当时的古环境相对较寒冷一些 (黄迪颖, 2015; Tian *et al*., 2014, 2015), 可能不利于鳄形类的发展。

4 燕辽生物群的生态多样性

4.1 行为方式的多样性

早期哺乳动物的辐射演化显示了较高的生态分异。燕辽生物群的哺乳动物体型普遍较小, 但具有多种生态适应性, 包括陆生、游泳、树栖、穴居和滑翔等。獭形狸尾兽(*Castorocauda lutrasimili*, Ji *et al*., 2006)是已发现最早的半水生哺乳动物, 体型较大, 具有游泳能力, 可能主要捕食水中的鱼类等。中华侏罗兽(*Juramaia sinensis*)是已知最古老的真兽类(有胎盘类)哺乳动物, 其前肢和手部骨骼表现出攀爬特征(Luo *et al*., 2011)。阿霍氏树贼兽(*Arboroharamiya allinhopsoni*, Han *et al*., 2017)的化石保存了滑翔皮翼形态和毛发印痕的细节, 表明其攀援和在树丛间滑翔的行为方式。短指挖掘柱齿兽(*Docofossor brachydactylus*, Luo *et al*., 2015)是具有强大挖掘能力的穴居型食虫性原始哺乳动物。Bi 等(2014)报道的陆氏神兽(*Shenshou lui*)、玲珑仙兽(*Xianshou linglong*)、宋氏仙兽(*Xianshou songae*)具有典型的树栖动物的适应特征。

燕辽生物群还包含了一些从兽脚类恐龙到鸟类演化过渡类型(Zhou *et al*., 2017)。例如擅攀鸟龙科的奇翼龙(*Yi qi*)腕部具有独特的棒状结构用于支撑翼膜, 展现出恐龙的“飞行”行为(Xu *et al*., 2015)。近鸟龙科的郑氏晓廷龙(*Xiaotingia zhengi*, Xu *et al*., 2011)、短羽始中国羽龙(*Eosinopteryx brevipenna*, Godefroit *et al*., 2013b)和徐氏曙光鸟(*Aurornis xui*, Godefroit *et al*., 2013a), 表现出肢骨的特化并且有类似羽毛的结构发育, 但飞行能力较弱, 多以滑翔为主。翼龙、恐龙和哺乳动物行为方式的相似性表明在当时环境下具有飞行或者滑翔的功能是一种成功的演化方式(图 6)。

对比道虎沟生物群与玲珑塔生物群脊椎动物的行为方式, 可以发现后者具有飞行或者滑翔能力的动物比例大幅度增加(图 6)。翼龙类在该时期进一步辐射演化, 相比其他几个脊椎动物组合, 玲珑塔生物群中翼龙类多样性最高, 共计 13 属 15 种, 适应性演化显著, 发育“原始羽毛”和食性的变化。哺乳动物也演化出更多滑翔的类型, 比如阿霍氏树贼兽、似叉骨祖翼兽(*Maiopatagium furculiferum*, Meng *et al*., 2017)、双钵翔齿兽(*Vilevolodon diplomylos*, Luo *et al*., 2017)等。

●（种）	道虎沟生物群 Daohugou Boita	玲珑塔生物群 Linglongta Boita
飞行/滑翔	●●●●●●	●●●●●●●●●●● ●●●●●●●●●●●
树栖/攀援	●●●●	●●●●●
陆地	●●●●●	●●●●●
半水生/两栖	●●●●●	●
水生	●	●

图 6　道虎沟生物群和玲珑塔生物群脊椎动物的行为方式汇总对比

Fig. 6　Comparisons of sum of vertebrate behaviors between Daohugou and Linglongta biotas

4.2　取食方式的多样性

燕辽生物群脊椎动物食性也非常多样化。翼龙类食性的分异主要体现在头骨结构和牙齿形态的差异, 蛙嘴龙类的成员头骨短而宽, 是典型的以食昆虫为主的动物, 例如木头凳树翼龙(*Dendrorhynchoides mutoudengensis*, Lü and Hone, 2012)和宁城热河翼龙(*Jeholopterus ningchengensis*, Wang *et al*., 2002)。达尔文翼龙为肉食性种类, 具有尖锐而长的牙齿, 其骨骼结构又显示它很可能在空中掠食,捕食其他空中的小型脊椎动物(吕君昌, 2010, Zhou *et al*., 2017); 玲珑塔古帆翼龙(*Archaeoistiodactylus linglongtaensis*, Lü and FUCHA, 2010)其特殊的齿列咬合结构有利于在浅水中捕食鱼类。原始辽翼龙(*Liaodactylus primus*, Zhou *et al*., 2017)具有细长的喙部(占头骨长度的 54%), 有 128–136 颗锋利的牙齿, 喙尖牙齿较大且突出, 是迄今为止最早的滤食性翼龙。

燕辽生物群的水生有尾类还出现了明显的捕食选择性。奇异热河螈(*Jeholotriton paradoxus*, Wang, 2000)、天义初螈(*Chunerpeton tianyiensis*, Gao and Shubin, 2003)的胃中发现了残留的食物(Dong *et al*., 2012)。据此推断, 幼年的奇异热河螈多捕食较小个体的叶肢介, 而天义初螈以中华燕辽划蝽(*Yanliaocorixa chinensis*)为食, 且仅捕食成年或近成年的个体(Dong *et al*., 2012)。这表明捕食选择性不只体现在食物大小上, 还有对食物种类的选择。

哺乳动物牙齿形态多样, 显示了其食性的多样化和对环境的适应。中华侏罗兽的牙齿特征表明其为食虫类哺乳动物(Luo *et al*., 2011)。欧亚皱纹齿兽具有典型的多尖齿兽类的特征, 复杂多瘤的牙齿适于咀嚼植物(Yuan *et al*., 2013)。哺乳形巨齿兽(*Megaconusmam maliaformis*, Zhou *et al*., 2013)臼齿特化现象指示了在真正的哺乳动物冠群出现之前, 在哺乳形类动物中已经出现明显的植食性演化。远古翔兽(*Volaticotherium antiquus*, Meng *et al*., 2006)的牙齿结构比三尖齿兽更为进步, 尤其是在臼齿的功能性方面。

5 燕辽生物群的古环境分析

古生代以来, 燕辽地区就一直在侵蚀基准面之上接受风化剥蚀(黄迪颖, 2019)。华北中生代陆相环境中广泛的火山—岩浆造山活动导致了复杂多样的古地理, 可能为生物演化提供地理隔离, 进而加快生物的分化和演化(Zhou and Wang, 2017)。中侏罗世中期经过燕山运动序幕, 燕辽地区形成山间断陷盆地, 处于一个局部相对稳定的地质环境, 开始接受新的沉积, 发育全新的水系, 由最初的河流向湖泊缓慢过渡(黄迪颖, 2015; Davis *et al*., 2001; Liu *et al*., 2015), 逐渐建立了稳定的湖泊生态系统, 并形成了燕辽生物群的早期代表—道虎沟生物群。道虎沟化石层的中上部, 发现了大量脊椎动物, 且富集叶肢介(任东等, 2002; 张俊峰, 2002; 沈炎彬等, 2003; 柳永清等, 2004; 廖焕宇, 2017)。道虎沟生物群的叶肢介为 *Triglypta haifanggouensis* 和 *Triglypta pingquanensis* 两种(廖焕宇, 2017)。水生群落中还发现具有环境指示作用的昆虫辽蚊蝎蛉属(*Liaobittacus*, 任东, 1993), 以及多种喜温暖湿润的植物(张俊峰, 2002), 可以推测当时燕辽地区的气候比较温暖(Sun *et al*., 2008; Ren *et al*., 2010; Na *et al*., 2015)。树栖的兽脚类恐龙, 具有攀援或滑翔能力的哺乳动物, 以及丰富的翼龙类指示可能有丛林的存在。丰富的两栖类以及半水生哺乳动物獭形狸尾兽, 也可以反映出燕辽地区当时为温暖湿润的湖泊环境(Xu *et al*., 2016)。孢粉组合显示道虎沟生物群发育时期研究区的植被为以裸子植物松柏类针叶林为主(张前旗等, 2018)。这个时期的湖泊中并未发现鱼类化石, 水系与外界相对独立, 但水生群落中昆虫、鳃足类相当繁盛, 这些动物具有一定迁移能力, 且与外界保持了一定的生物交流(黄迪颖, 2015)。

随后湖泊逐渐萎缩, 九龙山组开始出现较多的黑色泥岩, 还有硅化木。燕山运动第一幕开始了新一轮的构造运动, 火山活动频繁, 生物群发生重大转折, 表现在难以逃逸的水生生物类群, 残余类型以种间变化为主, 迁移能力较强的飞行类群则快速辐射演化, 形成晚侏罗世的玲珑塔生物群(黄迪颖, 2015)。相对于道虎沟生物群较为单一的叶肢介组合面貌, 玲珑塔生物群展现出更高的多样性, 叶肢介类型属于 Triglpitdae 的一个晚期组合, 包括 *Triglypta* 的晚期分子, *Liaoxiestheria* 和 *Tianzhuestheria jianchangensis* 等类型(廖焕宇, 2017)。不同种叶肢介自化石层下部至顶部具有交替出现的特征, 这表明面对频繁的火山活动以及不稳定的水体环境, 多种叶肢介具有差异性适应特征。反复出现的薄石膏层证明早期的湖泊生态系统经历了多次干旱—湿润—干旱的反复变化(廖焕宇, 2017)。髫髻山组发现了大量的植物化石, 包括苏铁类、松柏类、似银杏以及苔藓植物(黄迪颖, 2015; Zhang *et al*., 2006; Jiang *et al*., 2008, 2012; Tian *et al*., 2014), 说明在玲珑塔生物群的早期阶段气候相对湿润, 形成了一套森林生态系统。对髫髻山组植物木化石(*Xenoxylon* and *Protaxodioxylon*)进一步的研究表明, 该地区为低温湿润的寒温带气候, 具有季节性变化, 冬季漫长寒冷, 夏季短促(Dromart *et al*., 2003; Liu *et al*., 2012; Wang *et al*., 2013; Tian *et al*., 2015)。Dromart 等(2003)根据海洋无脊椎动物迁移和同位素测温, 表明北半球在中、晚侏罗世(约 160 Ma)发生过一次显著的降温事件(中纬度较低地区 1–3 °C)。这一气候波动事件与髫髻山组沉积几乎发生在同一时期(Dromart *et al*., 2003; Tian *et al*., 2015)。

黄迪颖(2015, 2019)分析了燕山运动对燕辽生物群的影响, 认为中、晚侏罗世的燕辽地区并不是完全封闭的高原环境, 而是山间裂陷盆地, 但高山昆虫群落代表蛇蛉目昆虫的大量出现说明了高海拔山脉的存在(任东, 2003; Engel *et al*., 2008)。并且燕辽地区东、北面离海都不远, 形成了燕辽地区三面封闭的地理环境。频繁的火山活动造成了生物的逃逸和扩散, 最重要的扩散路径是由同纬度向西迁移(黄迪颖, 2015), 所以燕辽生物群与蒙古西南部的 SharTeg 生物群和哈萨克斯坦的 Karatau 生物群存在密切关系, 黄迪颖(2015)认为三者生物面貌十分相似, 气候条件相似, 可以归入广义的燕辽生物群。汪筱林等(2014)也认为 Karatau 生物群表现出与玲珑塔生物群相似的翼龙组合特征。但是对比脊椎动物的生物组合可以发现, SharTeg 生物群的龟鳖类、鳄类以及恐龙类明显与新疆、四川地区的动物群更为相似(Ponomarenko *et al*., 2014)。SharTeg 生物群中已报

道的龟鳖类都为新疆龟科(Xinjiangchelyidae) (Sukhanov, 2000; Sukhanov and Narmandakh, 2006); 鳄类分为两支, 一支包含水生类孙氏鳄属(*Sunosuchus*), 另一支形态学上与四川晚侏罗世较为原始的鳄类相似; 恐龙类主要为大型蜥脚类, 接近于四川的马门溪龙(Kurzanov *et al*., 2003); 哺乳类也与马门溪龙动物群的董氏蜀兽(*Shuotherium dongi*, Chow and Rich, 1982)相关(Ponomarenko *et al*., 2014)。Karatau 生物群也表现出与新疆、四川地区动物群的相似特征。

黄迪颖(2015)认为燕辽地区与中国新疆、蒙古国、哈萨克斯坦一带生物群的生存环境不存在大的海拔差异, 且生物交流广泛。但分析对比以上生物群的脊椎动物的组合特征来看, 中国西北邻区的脊椎动物类群与新疆、四川地区动物群较为相似, 却与东北地区的生物群存在明显差异。陆生脊椎动物组合和古地理研究显示, 在中侏罗世至白垩纪早期, 东亚地区可能与劳亚大陆的其他地区存在地理隔离(Russell, 1993; Upchurch, 1995; Upchurch *et al*., 2002)。在三叠纪至侏罗纪早期就出现了潜在的隔离机制, 包括东亚与西伯利亚之间的蒙古鄂霍次克海、欧洲与中亚之间的吐尔盖海以及连接东亚与其他劳亚大陆地区的准噶尔—塔里木—蒙古大陆桥的裂口(Russell, 1993; Upchurch, 1995)。到了侏罗纪时期, 燕辽盆地西北向已经发育形成了集宁—隆化断裂带、赤—巴彦鄂博断裂带、中亚造山带以及索伦缝合带(李振宏等, 2014)。晚侏罗世中国整个中东部进入了三面超级汇聚时期(西伯利亚板块、滨太平洋板块和印度板块) (董树文等, 2007, 2008), 华北克拉通的北缘和东缘发生了强烈的构造变形, 华北板块进而形成了盆—山一体化的构造格局(刘建忠等, 2004; 李三忠等, 2011; Li *et al*., 2012)。

将脊椎动物组合对比扩大至相邻地区较晚时代的热河生物群。可以发现, 燕辽生物群与热河生物群之间具有明显的时间间隔, 但二者在恐龙、翼龙类群具有一定的亲缘关系(Zhou and Wang, 2017)。有学者就此提出了一种推论, 即辽西及邻近地区是一个与世隔绝的“避难所”, 保存了较早时代留下的生物血统, 且有一定的演化发展(Luo, 1999)。这与东亚的恐龙类群在晚侏罗世至白垩纪早期与世界其他地区恐龙类群有很大差异的观察结果一致(Russell, 1993)。直到白垩纪早期, 热河生物群出现雷龙类、驰龙类和禽龙类, 辽西地区的地理隔离状态才得以结束(Barrett *et al*., 2002; Zhou *et al*., 2003)。

综上, 燕辽生物群与中国西北邻区的生物群存在部分交流, 但仅限于一些具有较强迁移能力的生物, 如一些昆虫、翼龙等。由此可以推测, 燕辽生物群与外界可能存在一定程度的地理隔离。除了具有长距离飞行能力的翼龙类存在一定的生物交流, 其余脊椎动物组合差异显著。地理环境可能限制了内部脊椎动物的对外扩散迁移, 也阻碍了外部大型脊椎动物对内的影响。

6 结　论

燕辽生物群已报道脊椎动物共计 54 属 58 种, 包括两栖类、爬行类、少量鸟类与鱼类, 以及丰富的哺乳类。翼龙类整体较为原始, 少有翼手龙类的发现; 恐龙仅发现小型肉食性兽脚类; 哺乳动物特异性演化显著。玲珑塔生物群和道虎沟生物群二者在演化上有一定的传承, 而玲珑塔生物群的翼龙类、哺乳类等方面展现出更高的生物多样性。燕辽生物群与同时代或相近时代的脊椎动物生物群进行对比, 包括新疆石树沟组生物群和四川沙溪庙组生物群等, 燕辽生物群在恐龙、翼龙和哺乳动物类群方面展现出独特的生物组合特征。燕辽生物群虽与中国西北邻区的生物群存在部分交流, 但仅限于一些具有较强迁移能力的生物, 如一些昆虫、翼龙等, 其他脊椎动物仍呈现独特的生物组合特征。结合古地理环境证据, 推测燕辽生物群与外界可能存在一定程度的地理隔离, 燕山运动造成区域内环境突变, 脊椎动物根据环境产生了适应性演化, 有利于燕辽生物群脊椎动物的多样性发展, 表现出与外界差异显著的脊椎动物组合特征。

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