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陕西水牛化石及中国化石水牛的地理分布和种系发生

薛祥煦[1] 李晓晨[1,2]

(1 西北大学地质系， 新生代地质与环境研究所 西安 710069)

(2 陕西师范大学生命科学学院 西安 710062)

摘要 描述并比较了在陕西大荔、咸阳发现的水牛化石，一为 *Bubalus teilhardi*，与周口店第一地点的相近；另一为 *B. youngi*，与河南孟县的相似。水牛化石在中国的分布至今仍集中在中一东部，南、北方都有，其栖息环境与现代水牛的基本一样，生活在温暖、湿润的环境中。用支序系统学方法分析了中国化石水牛的种系发生。

关键词 中国陕西，水牛化石，地理分布，种系发生

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根据记载，水牛(*Bubalus*)化石在中国的黑龙江、内蒙古、河北、山西、陕西、河南、山东、安徽、四川、台湾等地都有过发现。经 Hopwood、Boule、Teilhard de Chardin、杨钟健、Bohlin、高井冬二、Colbert et Hooijer、周明镇和徐余瑄、刘嘉龙和甄朔南等研究，共建立了9个种，分布在更新世中期到全新世的地层中。它们是：

Bubalus mephistopheles Hopwood, 1925; *B. wansijocki* Boule et Teilhard, 1928;
B. teilhardi Young, 1932; *B. brevicornis* Young, 1936;
B. tingi Bohlin, 1938; *B. bubalis* Linnaeus, 1758;
B. youngi Chow et Xu, 1957; *B. guzhensis* Liu et Zhen, 1981
B. triangulatus Liu et Zhen, 1981;

此外，陕西洛南早更新世晚期动物群中也产有水牛。

在本文之前，陕西水牛化石的报道只有两次：一次是发现于山阳九岔沟的一个右第二下臼齿(薛祥煦，1960)；另一次是发现于大荔甜水沟的一个第一或第二下臼齿(吴新智等，1979)，都只鉴定到属(*Bubalus* sp.)。

1996年及1998年，我们共收集到3个保存完好程度不等的水牛头骨化石：两个是本文第一作者及高级技师赵聚发在大荔收集到的；另一个是西安晚报记者黄卫平同志在咸阳七里铺工作时，得知该地出土了一个大化石，便设法转告本文第一作者，薛祥煦随即与黄卫平等赶到现场及标本存放地，经协商标本移交西北大学地质系保存并研究。研究表明，大荔的水牛化石为德氏水牛 *Bubalus teilhardi*；咸阳的水牛化石为杨氏水牛 *B. youngi*。

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1　陕西水牛化石记述

德氏水牛 *Bubalus teilhardi* Young, 1932

(图版 I, 2、3)

材料　两个不完整的头骨及双角。一个保留眼眶后缘之后的头骨，脑颅顶部及枕部保存相当完整，左角大部分保留，右角远端一段缺失，西北大学古脊椎动物化石编号：NWUV 1239；另一个仅保留少量额骨，但有近乎完整的右角及左角近端一段，NWUV 1240。

化石产地　陕西大荔解放村，后河村海龙沟。

时代　中更新世中期(或稍早)。

标本记述　标本最显著的特征是：角心横断面呈锐角三角形，枕部显著后凸。

头骨　中等大小。二眶后缘间的额骨窄而平，无明显的瘤突。二角基部间的额骨窄而稍凹陷。顶骨较 *B. youngi* 长大，强烈前倾。枕骨区比其他各种相对低而宽。顶—枕骨不在同一平面上，二者呈一小钝角相交，在角后显著后凸，角心后缘与枕嵴间距较大。枕嵴发育中等，枕嵴之下枕骨上部的肌肉附着窝远没有 *B. youngi* 的深大。枕髁及乳突保存得非常完好，后者粗壮，微弯。

角心　二角从头骨上侧角向两侧后上方伸出，和额骨上缘一起构成宽"V"形弧，角心远端稍有扭曲。角心与头矢状面呈 45°夹角。角心的三个面，即上面、下面及前面都很平，甚至有程度不同的下凹，三个面彼此间相连的交角都呈锐角且有明显的棱嵴，使角的横切面呈锐角三角形，仅在角远端一段，其后下角变得较圆。

头及角的主要特征、测量与对比见表 1、2。

比较与讨论　大荔水牛标本枕部显著后凸，两角靠后，与 *B. youngi* 和 *B. wansijocki* 等的特征明显不同，而与 *B. brevicornis*、*B. teilhardi* 和 *B. mephistopheles* 相似。但角的形状及量度又明显不同于 *B. brevicornis* 和 *B. mephistopheles* 的，后二种角的共同特征是短而粗，而大荔标本明显比这两种水牛的角心细长。大荔标本两角水平后伸，构成较窄的新月形，或宽"V"形，角的前面平直、上面稍凹，角心基部横切面呈锐角三角形，头骨顶部和枕部在角后显著后凸等特征几乎和 *B. teilhardi* 的一样，故将其归属德氏水牛 *B. teilhardi*。

杨氏水牛 *Bubalus youngi* Chow et Xu, 1957

(图版 I, 1)

材料　一个带有左右角的头骨。眼眶前大部分骨骼及枕嵴两则缘、茎乳突皆破损，但有几乎完好的一对角心及左上臼齿。标本编号：NWUV 1241。

化石产地　陕西咸阳七里铺。

时代　晚更新世晚期。

标本记述　该标本最醒目的特征是：个体硕大，角心特别粗壮长大，向侧后方向伸展，二角与额骨上缘构成一宽阔新月形。

头骨　个体很大。鼻—额骨接缝呈尖角向后的"V"型，鼻骨显著隆起，鼻骨两侧凹下呈浅沟。上颌骨前端两侧各有一隆起的面结节。额骨前部宽，二眼眶间及二眶上孔前的额

骨面光平，该区在矢状线处隆起，向两外侧倾斜，与眶上孔连成一浅沟。眶上孔大而深，其开口向前延伸至额骨末端。两眼较向前，眼眶大而圆。与 *B. brevicornis* 相似，额骨在二角基部之间呈缓弧形隆起，骨面粗糙，有瘤突。顶骨平，在枕嵴上稍向后倾斜。枕区宽大，枕骨在角后不突出。枕嵴强大，中间有椎骨切迹。枕嵴与角心后缘之间的距离很小。颧弓后段板状，其外缘稍向上倾斜。颞孔后端较窄。

角心　除右角尖约 30mm 长受损外，保存非常完好，粗壮长大。前视，两角心从基部较平地向两侧伸出不远，即向后外略向上弯曲，二角心与额骨一起连成一宽阔的新月形。

总体看来，角心横切面为一等腰三角形。角心前面最窄且平直，为该等腰三角形的底，上面和下面的宽度相近，上面宽平，下面外拱呈弧形。角心近端二分之一段的前面与下面相交呈一较粗的棱嵴；前面与上面的交角稍小于直角，交线非常明显；上面与下面的交角约为 60°。角心远端二分之一段的横断面近圆形，仅后侧角为圆缓的锐角。这些特征与 *B. youngi* 的很接近。角心基部表面粗糙，有许多瘤状突起，其他部分布满粗的纵纹和纤孔。

头骨及角的主要特征及测量与对比见表 1、2。

牙齿　仅保留有右 M1～3，其大小测量如下 (mm)：

	M1	M2	M3
长 (L.)	29	34	36.8
宽 (W.) 前	29	28.5	27.5
后	28.7	27	23.6

M1 近方形，磨蚀中等，前叶冠面平，后叶起伏不平。前尖、后尖呈长椭圆形，原尖方圆形，次尖中部收缩。前、后窝窄，呈宽 U 型。底柱较短。外壁上的前后肋发育好，等粗，前、中、后附柱较 M2、M3 的弱，但较直而收紧。

M2 长大于宽，冠面起伏不平，前尖、后尖短椭圆形。原尖、次尖中部都有明显收缩而呈向外侧开口的花篮形。前、后窝的内侧壁中部也有收缩。底柱较 M1 的长。前肋较后肋粗大，三个附柱都较发育。

M3 的特征与 M2 的相似，只因磨蚀较轻，前尖、后尖呈近圆形，原尖、次尖都较 M2 的短，比 M1 的更短，前肋虽较后肋小，但较粗，附柱发育情况与 M2 的相近。釉质层厚 1～1.5mm，有较厚的白垩质层包裹。

比较与讨论　从角的特征看，咸阳水牛标本角心粗大，呈宽阔新月形，角心近基部横断面呈等腰三角形，这些特征均与 *B. youngi* 十分相似，而与 *B. brevicornis* 和 *B. mephistopheles* 的不同，后二者的角心短粗；也与 *B. teilhardi* 的不同，后者的角心近基部横切面呈锐角三角形，棱角尖锐，且两角与矢状面的夹角为 45°。咸阳标本与 *B. wansijocki* 的差别也很明显，后者角心向上伸出，角心近端横切面为等边三角形，两角与额骨构成的新月形较小以及角心远端迅速变细。

从头骨看，咸阳标本枕部不后凸，很容易与 *B. brevicornis*、*B. teilhardi* 和 *B. mephistopheles* 区分开，而与 *B. youngi* 和 *B. wansijocki* 的相近。咸阳标本枕嵴发育，具明显的椎骨切迹也与 *B. teilhardi* 等种的不同。咸阳标本顶骨平直且向后稍倾斜与 *B. teilhardi* 不同，而与 *B. brevicornis* 相近。

总之，从角心指数、角的大小、二角所构成的新月形形态及枕骨不后凸等特征看，咸阳

表1 陕西大荔、咸阳水牛化石的测量与对比

Table 1 Measurements of fossil *Bubalus* from Dali and Xianyang, Shaanxi and comparison with others (mm)

种 Species / 性状 Character	*Bubalus* from Dali	*B.* from Xianyang	*B. teilhardi*	*B. youngi*	*B. brevicornis*	*B. tingi*	*B. wansijochi*	*B. mephist-opheles*	*B. guzhensis*	*B. trian-gulatus*	*B. buba-lus*
角基部前面宽 Breadth of the anterior face of the horn core at the base	99～97.7	130	85	120	79	62	95	74	105	100	55
角基部上面宽 Breadth of the superior face of the horn core at the base	135～148		105	200	162	87	220	108	200	170	86
角基部下面宽 Breadth of the posterior face of the horn core at the base	121～147	166	130	260	142	87	220	103	185	160	85
角基部周长 Length of the circumference at the base	360～423	500	340	520	405	257	535	300	485		236
角凸侧全长 Length of the horn core along the convex border	545～565	670	550	650	412	305+? 115	595或550	282	560	470	300
角凹侧全长 Length of the horn core along the concave border	440～510	600	470	600	350		480	225	491		240
角心指数 Horn core index	24.5～26.0	26.9	19.09	30.8	39.5		40	38.3	35.7	36.0	28.6
二角尖间距 Distance from tip to tip	1010	1000	840?	1120	665	501*	805	430	950		560
角基间最大宽(前) Maximum breadth between the horn cores at the base (from anterior)	114～115	178	100	182	93		110*	145	181		175
角基间最小宽(后) Minimum breadth between the horn cores at the base (from posterior)	80	86.5	99	85	42		50*	93			140
眶间额骨宽 Breadth of the frontal between the superior border of the orbits	210	170	210		230	220(?)	185*	255	170	120	167
眶后头骨宽 Breadth of the skull at the postorbital constriction		224	180		160			155			165
颞孔后端间宽 Minimum distance between the posterior ends of the temporal fossae	120	136	85		88			79			
眶上孔间距 Distance between the supra-orbital foramina	86	94	95		77	91*	90*	85			97
枕壁最大宽 Maximum breadth of the occipital wall	230		200	247	250		230*	248			170
枕壁最大高 Maximum height of the occipital wall	125	162	136*	130*	150*		130*	124*			80
眶后缘—角基最小距离 Minimum distance between the orbits and the horn core at the base	61	62	49		55			58			42
角后缘—枕嵴间距 Distance between the occipital crista and the posterior line of the horn cores	80	38	93	65	70			78			53
二枕髁外侧间距 Maximum breadth between the occipital condyles (from outside)	120	136	115		112*						97
顶骨区宽 Maximum breadth of the parietal	109	122	116*								105
顶骨区长 Length of the parietal	97	51	94*								100
资料来源 Source of data	作者 Author	作者 Author	Young, 1932	Chow et Xu, 1957	Young, 1936	Bohlin, 1937	Boule et Teilhard 1928	Hopwood, 1925	Liu et Zhen, 1981	Liu et Zhen, 1981	IVPP 73

注：角心指数=(基部上面宽/凸侧长)×100 Horn core index=(Breadth of the superior face/ Length along the convex border)×100; * 测图From figures.

表2　中国水牛化石的主要特征与对比

Table 2　Comparison of the main characters of *Bubalus* in China

种名 / 特征	*B. teilhardi*	*B. youngi*	*B. brevicornis*	*B. tingi*	*B. wansijocki*	*B. mephis-topheles*	*B. guzhensis*	*B. triangulatus*	*B. bubalis*	*B. bubalus*
角心粗细及伸展方向	角较细长，伸向后方，尖端有扭曲与矢状面呈45°角	很粗壮，长大。向两侧伸出，尖端向后上斜伸	很短，中等粗壮，向后外斜伸，缓缓内弯	角细小，强烈向后伸，近乎直，仅微弯	短但很粗壮，向上斜伸	较短，较细，向后伸，稍内弯	角长大，向后外伸	短而宽，水平伸，等腰三角形	向两侧平伸，稍向上弯	角心细小向后侧平伸
二角相连形态	较窄新月形	宽阔新月形	较宽新月形	二角近直角相交	较窄新月形	窄新月形	宽新月形	新月形	宽新月形	宽新月形
角心横断面形态	前-下面直角相交，到尖端为等边三角形	近端大半段为等腰三角形，近角尖为椭圆形	等腰三角形，近角尖切面为半圆形	角基部三个角的棱都尖锐，近角尖，侧棱变圆	近基部为粗大等边三角形，近角尖很快变细	各段皆为等边三角形，边棱都锐利。角的上面与上齿列平行	角上面与上齿面平行		不是正三角形	扁三角形
额　骨	窄，在角基间稍凹，在眶间窄平	角基间微隆，眶间微凹下	在角基间微隆起，在眶上孔间微凹		稍下凹	在角基间稍凹下，在眶间凹下强烈	角间额骨稍凹下		凸起	角间额拱起，眶间额凹下
顶　骨	在角的后方明显后突		顶部在枕嵴上缓倾						顶骨前倾	长15mm
枕嵴及枕区	“V”形，枕骨向后突出中等强度	枕部在角后不甚突出	枕部在角心之后明显突出，枕嵴发育中等有椎迹	后突显著	枕部不后突	枕壁宽而粗壮，副枕突粗，枕部在角后强烈突出	枕区在角下平，不后突，枕嵴中等强	不后突，平		枕区不后突，枕峰弱，但有椎迹
资料来源	Young, 1932	Chow et Xu, 1957	Young, 1936	Bohlin, 1937	Boule et Teilhard 1928	Hopwood, 1925	Liu et Zhen, 1981	Liu et Zhen, 1981	Colbert *et al.*, 1953	测IVPP 73
时代	Q_2	Q_3	Q_3	Q_3	Q_3	Q_4	Q_2～Q_3	Q_2～Q_3	Q_2～Q_4	现代

标本与 *B. youngi* 非常相似。至于咸阳标本两角基部间额骨区不凹陷、枕壁上部不隆起等特征,可以看作是 *B. youngi* 的个体差异。

2　中国化石水牛的地理分析

现生水牛是一类热带、亚热带常见的动物,我国现生水牛均属沼泽型,分布在亚热带、热带气候炎热、潮湿的环境(中国水牛协作组,1984;郑丕留,1985)。至今,中国的水牛化石有 9 个种,分布在我国东部,北从黑龙江南达广西,西起四川东抵台湾海峡。和当年杨钟健、周明镇等研究的相比,主要是在此范围内增加了一些分布点(图 1)。9 个化石水牛种的地理分布与现生水牛的并不完全一致。其中 *B. wansijocki* 分布较广,它较多地发现于黑龙江、吉林等省,在内蒙萨拉乌苏、辽宁南部的古龙山,甚至更南的江苏丹徒都有发现。王氏水牛在吉、黑两省区甚至辽宁南部都与猛玛象、披毛犀等共生,是晚更新世该地区猛玛象—披毛犀动物群的一个成员。猛玛象—披毛犀动物群是一个被公认的干冷冻土苔原地带的动物群,较稳定地分布在大约 45°N 以北地区,只有在气候更冷的盛冰期,它们有机会向南扩散到辽南,甚至更南达山东半岛(董为等,1996)。这样看来,与猛玛象—披毛犀共生的王氏水牛或许可以说也是一种能耐冷干环境条件的动物。但在几乎与古龙山处于同一纬度、位置偏西的萨拉乌苏地区,王氏水牛却与古菱齿象—披毛犀动物群共生,该动物群中没有猛玛象。猛玛象与古菱齿象是两类分类位置不同、生态环境不同的动物,前者是寒冷、干燥、冻土苔原地区的象,浑身长有长毛;后者主要分布在华北、西北、华南甚至更南的地区,是一类温热、湿润环境的象。至今尚未见猛玛象与古菱齿象

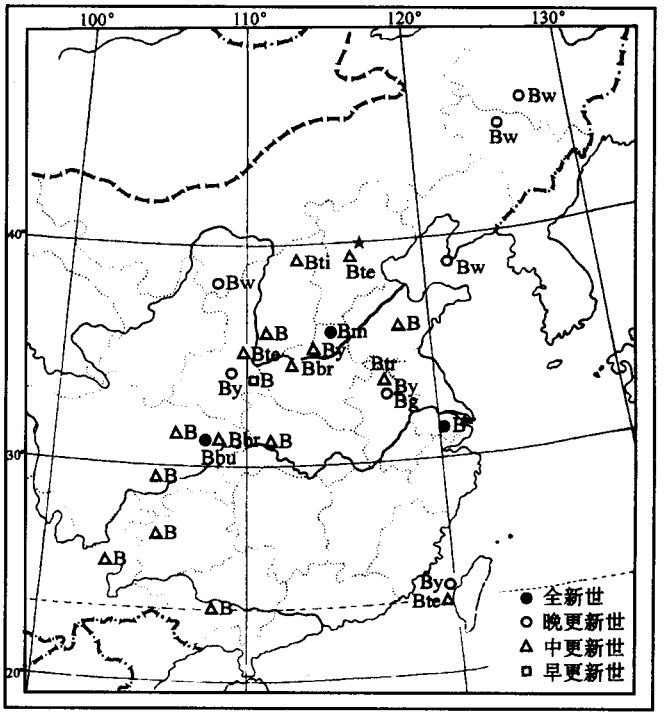

图1　中国第四纪各种化石水牛的分布地点
(依周明镇等,1957,有新补充)

Bm–*Bubalus mephistopheles*; Bw–*B. wansijocki*; Bte–*B. teilhardi*; Bbr–*B. brervicornis*; Bti–*B. tingi*; Bbu–*B. bubalis*; By–*B. youngi*; Bg–*B. guzhensis*; Btr–*B. triangulatus*. B–*Bubalus* sp.

Fig.1　Sketch map showing geographical distribution of fossil localities of Chinese bubaline bovids: square, Early Pleistocene; triangle, Middle Pleistocene; circle, Upper Pleistocene; black, Holocene (after Chow et Xu 1957, with addition of new data)

共生的记载。对王氏水牛既与猛玛象共生，又与古菱齿象共生这一事实，可能会有不同的解释。可认为王氏水牛就是一类像猛玛象那样，适应东北冷干环境的动物；也可认为王氏水牛是一类适应能力较强的动物。短角水牛在华南、华北都有分布。另一类有较多分布点的水牛化石是 *B. teilhardi*，它最初发现于周口店第一地点的第 7、8 层，与肿骨大角鹿等共生。之后，在台湾海峡水底打捞到许多较为完好的标本，其时代被认为是更新世晚期（何传坤等，1996）。如本文所述在陕西大荔也有所发现。根据化石特点及共生化石，德氏水牛的时代放在中更新世中期（或稍早）是合适的，台湾海峡标本的时代值得进一步斟酌，其生活的气候环境应是温暖、湿润，周围还有一些水体。

杨氏水牛最初发现于河南孟县上河村，没有化石层岩性及共生化石的资料。在陕西，杨氏水牛出土于渭河二级阶地的砂砾石层中，与之共存的化石有披毛犀、古菱齿象等，经 ^{14}C 测定化石层的年龄约为 20kaB.P.，孢粉分析认为当时为比较冷干的草原环境，在其南侧秦岭山麓可能还有一些稀树生长。孢粉分析的环境有可能反映的是大型动物致死和被埋藏时的环境，因为从几类主要大化石看，它们生活时的气候环境似乎应是比较温湿的丛林或森林环境。

其他的水牛化石，有的更接近现代，有的材料和发现地点有限，本文不作分析。

由上所述，水牛化石在我国的分布至今仍集中在中—东部，南、北方都有，其结构和生态特点基本上和现代水牛一样，是一类温暖、湿润环境的喜水动物。它反映了温湿、有水体存在的气候环境。

3 中国水牛化石的演变

杨钟健、周明镇和徐余瑄等先后对中国水牛化石的进化作过研究并作出进化图，刘嘉龙、甄朔南也对水牛的部分化石种之间的演化关系作了初探，为后人的研究奠定了很好的基础。本文用支序系统学方法就中国化石水牛的种系发生问题作分析，共选取 18 项具有种系发生意义的性状，以第四纪出现最早与水牛属同一亚科的丽牛（*Leptobos*）作为外类群，来确定性状的极性，祖征记为（0），衍征记为（1）。所选 18 项性状及其极性如下：

1. 枕部：后凸（0）；不后凸（1）
2. 枕骨：低而宽（其宽 / 高约小于 1.7）（0）；窄而高（其宽 / 高大于 1.7）（1）
3. 枕嵴：强大（0）；中等（1）
4. 枕嵴椎骨切迹：不存在（0）；存在（1）
5. 顶骨：短（小于 60mm）（0）；长（大于 60mm）（1）
6. 额骨眶间区：宽（0）；窄（1）
7. 角基间额骨区：凹陷（0）；平坦或隆起（1）
8. 角后缘至枕嵴间距：大（0）；小（1）
9. 眶后缘至角基间距：大（0）；小（1）
10. 眶上孔间距：大于 90mm（0）；小于 90mm（1）
11. 两眼位置：位于两侧（0）；较向前（1）
12. 角基周长：大于 400mm（0）；小于或等于 400mm（1）
13. 角心伸展：较后（0）；较前（1）
14. 角基间最大宽：大于 120mm（0）；小于 120mm（1）
15. 角心近基部横切面：圆或近圆形（0）；三角形（1）
16. 角心形状：细长（0）；短粗或粗大（1）
17. 角心与头骨矢状面之间的夹角：小（0）；大（1）
18. 角心指数：大（0）；小（1）

其矩阵如下：

种 Species	性状 Character																	
Leptobos	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?
B. teilhardi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
B. tingi	0	?	?	?	?	0	?	?	?	?	?	1	0	?	1	0	0	1
B. brevicornis	0	0	1	1	1	0	1	1	1	1	0	0	0	1	1	1	1	0
B. youngi	1	1	0	1	0	1	1	1	0	1	1	0	1	0	1	1	1	0
B. wansijocki	1	1	0	?	?	1	0	?	?	1	?	0	0	1	1	1	0	0
B. mephistopheles	1	0	1	1	1	0	0	0	1	1	1	1	0	0	1	1	1	0
B. guzhensis	1	?	1	?	?	1	0	?	?	?	1	0	1	0	1	1	?	0
B. triangulatus	1	?	1	?	?	1	?	?	?	?	1	?	1	?	1	1	?	0
B. bubalis	?	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1
B. bubalus	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1

用 PAUP 程序(3.1.1 版)对矩阵进行处理，得一严格合意支序图(图 2)。支序图表明，*B. teilhardi* 和 *B. tingi* 的系统关系不确定，可能与 *B. tingi* 的不确定性状太多有关。在全部 18 个性状中，*B. teilhardi* 仅有 1 项衍征，说明了该种比较原始，这与它所处地质时代较早(更新世中期)相一致。自 *B. teilhardi*、*B. tingi* 之后，依次分化出的是 *B. brevicornis*、*B. mephistopheles* 和 *B. wansijocki*。*B. guzhensis*、*B. triangulatus*、*B. youngi*、*B. bubalus* 及 *B. bubalis* 位于同一节点上，支持该节点的共近裔性状包括性状 1、6、11、13。这五个种之间除 *B. bubalus* 和 *B. bubalis* 互为姊妹群外，系统关系不确定，它们与 *B. wansijocki* 组成一对姊妹群，共同拥有性状 1、6。本文支序分析结果与周明镇和徐余瑄(1957)研究中国水牛演化后所得结论有相似之处，如本文支序图中 *B. teilhardi* 和 *B. tingi* 之间的系统关系以及它们与其他种之间的系统关系并不否定周明镇和徐余瑄所得出的相应结论。*B. mephistopheles* 和 *B. brevicornis* 的关系与本文的也有相似之处。但差别也是显而易见的。周明镇、徐余瑄认为，*B. youngi* 与 *B. wansijocki* 有较近的系统关系，而后者似直接起源于 *B. brevicornis*，但本文的分析结果并不支持这一结论。支序图表明，*B. youngi* 与 *B. bubalus* 的系统关系要比 *B. youngi* 与 *B. wansijocki* 之间的系统关系更相近一些。

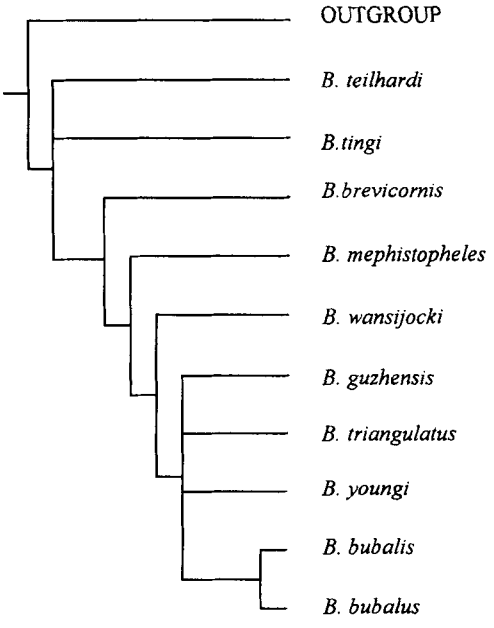

图2　中国化石水牛支序图(Length=31, CI=0.581, RC=0.471)

Fig.2　Cladogram showing possible phylogenetic relationship of fossil bubaline bovids from China

致谢 本文的支序图作图先后得到朱敏研究员及张江永博士的帮助；邸世祥教授及赵聚发高级技师参与了野外工作，王晓鸣博士修改英文稿，作者在此向他们致以衷心的感谢。

FOSSIL *BUBALUS* FROM SHAANXI, DIS TRIBUTION AND PHYLOGENY OF FOSSIL *BUBALUS* IN CHINA

XUE Xiang-Xu[1] LI Xiao-Chen[1,2]

(1 *Department of Geology, Institute of Cenozoic Geology and Environment, Northwest University* Xi'an 710069)

(2 *College of Life Sciences, Shaanxi Normal University* Xi'an 710062)

Key words Shaanxi, fossil *Bubalus*, geographic distribution, phylogeny

Summary

Nine species of fossil *Bubalus*, ranging from the Middle Pleistocene to Holocene, were found from Heilongjiang, Nei Mongol, Hebei, Shanxi, Shaanxi, Henan, Shandong, Sichuan, Anhui and Taiwan in China. They are:

Bubalus bubalis Linnaeus, 1758
B. mephistopheles Hopwood, 1925
B. wansijocki Boule et Teilhard, 1928
B. teilhardi Young, 1932
B. brevicornis Young, 1936
B. tingi Bohlin, 1938
B. youngi Chow et Xu, 1957
B. guzhensis Liu et Zhen, 1981
B. triangulatus Liu et Zhen, 1981

There are only two reports about the fossil *Bubalus* in Shaanxi before this article. One is a right m2 discovered from Shanyang (Xue, 1960), and the other is a m1 or m2 from Dali (Wu *et al.*, 1979). Three skulls of fossil *Bubalus* were collected by the senior author of this paper in 1996 and 1998. Two of them are from Dali and belong to *B. teilhardi*; one is from Xianyang and belongs to *B. youngi*. Besides description of these specimens, this paper will deal with the phylogeny and geographic distribution of this genus in China.

1 Description of fossil *Bubalus* from Shaanxi

Bubalus teilhardi Young, 1932

(pl.I, 2～3)

Materials Two incomplete horn cores with the back part of skulls behind the orbits (NWUV 1239, 1240).

Localities and horizon Jiefangcun and Houhecun, Dali County, Shaanxi; Middle Pleistocene.

Description The skull is medium-sized. Similar to the specimens of Zhoukoudian, the frontal area between the orbits is narrow and flat with very smooth surface, and

narrow and slightly concave between the horn cores at the base. Because of the close position of the horn cores to the orbits, the postorbital constriction is deep and narrow. The supraorbital foramina are large. The temporal fossae are rather narrow, extending far back to the parietal area. The parietal area above a strong to moderately arched supraoccipital crest slopes gently towards the horn cores. The occipital area is lower and broader than those of other species. It is not on the same plane as the parietal area, but forms an obtuse angle. The supraoccipital fossa is much shallower than that in *B. youngi*. The occipital condyle and mastoid process are well preserved. The latter is strong and slightly curved.

The horn cores are at about 45° from the sagittal plane of the skull and extend backward and upward, forming a slightly narrow crescent curve together with the frontal. Three surfaces, the upper, lower and anterior, of the horn cores are quite flat, even slightly concave. Thus the angles between each adjacent surfaces are rather acute with a sharp ridge. The cross section of the horn cores is an acute triangle. Further distally, the ridge between the upper and the posterior faces diminishes and the core becomes almost isosceles in section even round at the distal end.

The major features, measurements and comparison of the skull and horn cores are presented in Table 1 and Table 2.

Comparison and discussion The characteristics of Dali specimens, such as the backward projecting occipital and the backward directed horn cores, are similar to *B. brevicornis*, *B. teilhardi* and *B. mephistopheles*, but obviously different from *B. youngi* and *B. wansijocki*. On the other hand, the specimens of *Bubalus* from Dali are also distinguished from *B. brevicornis* and *B. mephistopheles* in having longer and slimmer horn cores which are directed backward at 45° from the sagittal plane and form a narrower crescent outline with the frontal bone. Apart from these, the very flat anterior face of the core, perpendicular to the slightly concave upper face, and the very sharp ridges of the horn cores, are also the prominent features, which are absent from known species of *Bubalus*. Thus the Dali specimens of Chinese buffalo can be included in *B. teilhardi*.

Bubalus youngi Chow et Xu, 1957

(pl.I, 1)

Material A pair of complete horn cores with a large part of skull and left upper molars (NWUV 1241).

Locality and horizon Qilipu, Xianyang, Shaanxi, Upper Pleistocene.

Description The skull represents a very large-sized buffalo. The naso-frontal suture is V-shaped with the angle pointing backward. Both nasals have a shallow groove, the right and left sides bulging markedly. There is a faciale tuber on each side of the anterior end of the maxilla. The frontal is wide at its anterior part, flat and smooth between the two orbits and before the supraorbital foramina but convex

around the sagittal suture, and convex with a rough surface between the base of the horn cores. The supraorbital foramina are big and deep with the opening extending forward to the end of the frontal. The orbits are big, round and set slightly forward. Similar to *B. brevicornis*, the frontal is convex between the horn cores at the base with a rough surface and many small tubercles between the horn cores at the base. The parietal area is flat, slightly sloping backward along the supra-occipital crest. The occipital area is wide and does not project backward behind the horn cores. The occipital crest is very close to the posterior border of the horn cores, and very strong with a conspicuous vertebra incision at the middle. The posterior part of the zygomatic arch is plate-like and slopes slightly upward. The temporal fossae are rather narrow at its posterior part.

The horn cores are preserved very well except the distal end (about 30cm long) of the right one was damaged. They are enormously large and strong, extending laterally, backwards and slightly upwards soon after extending horizontally outwards for some distance from their base. They form a wide crescent shape together with the frontal of the cranium when viewed from above. The cross sections of the horn cores are roughly in the form of an isosceles triangle. Its anterior surface is flat and the narrowest, and constitutes the base of the isosceles triangle-section. The upper surface is also flat, with the same width as the lower one, while the latter is convex. The ridge between the upper and the lower surfaces at the proximal part of the horn cores is strong with an angle of 56°. Gradually to the distal half of the horn cores, the cross sections become round. The surface of the basal part of the horn cores is rather rough with many tubercles, while the rest are full of longitudinal rough stripes and small holes.

Left upper M1～3 are preserved. They are also large and stout, and their crown surface are raising and falling except the anterior lobe of M1. M1 is almost square. Paracone and metacone are oval with narrow and projecting outer surfaces, which form strong ribs. Protocone is rounded quadrate in shape; the middle part of hypocone is compressed. The anterior and posterior fossae are narrow U-shaped. The paracone, metacone and metastyle are all weaker than those of M2 and M3. The length of M2 is greater than its width. Its paracone and metacone are short oval-shaped. The protocone and hypocone are clearly compressed at the middle part. The interior walls of the fossae are compressed at the central part. The anterior rib is stronger than the posterior one. All the styles are well developed. M3 is similar to M2, its paracone and metacone being somewhat rounded because of light wear, while its protocone and hypocone are shorter than those in M1 and M2. The ribs are strong, but the anterior one is slender than the posterior one.

Comparison and discussion The very big and strong horn cores, the wide crescentic curve of both cores with frontal, the isosceles triangle section of the horn

cores and the non-projecting occipital area are the prominent features of the buffalo specimen from Xianyang. They are very similar to those of *B. youngi* but obviously different from *B. brevicornis*, *B. mephistopheles* and *B. teilhardi*. The horn cores are smaller and shorter in *B. brevicornis* and *B. mephistopheles*. The cross section of the basal part of the horn cores of *B. teilhardi* presents an acute triangle. The *Bubalus* from Xianyang is also distinguished from *B. wansijocki* by the equilateral triangle of the cross section at the proximal part of the horn cores and extending slightly upward, forming a less crescent outline of the latter.

2 Geographical distribution of fossil *Bubalus* in China

More than nine species of fossil *Bubalus* have been described from China at present. They distribute mainly in the eastern part of China, from Heilongjiang in the North to Guangxi in the south, from Sichuan in the southwest to Taiwan Strait in the southeast. Among these species, *B. wansijocki* has an extensive distribution, such as, Guxiantun, Yushu and Yanjiagang in Heilongjiang and Jilin, Gulongshan in southern Liaoning. *B. wansijocki* from Shandong co-occurs with *Mammuthus primigenius*, and *B. wansijocki* from Salawusu of Nei Mongol co-occurs with *Palaeoloxodon*. *Mammuthus* and *Palaeoloxodon* are quite different elephants. The former with long hair is one of the chief members of the tundra fauna, while the latter lived in the warmer and moister environment of southern part of north China and south China, or even more south. According to the general characters of *Bubalus*, the fact that *B. wansijocki* coexisted with different kinds of elephants could be explained as follows: *B. wansijocki* was a sort of animal living in the warm and moist conditions, they walked or migrated northward to Heilongjiang during the warmer interglacial time, then died over there when the colder glacial was coming; or *B. wansijocki* was a sort of buffalo adapted to both warm and cold conditions.

Another species from several localities is *B. teilhardi* discovered first from the Loc. 1 of Zhoukoudian and studied by C. C. Young, then collected from Taiwan Strait and also Dali of Shaanxi in this paper. *B. youngi* was found from Shanghecun, Mengxian, Henan without information about the fossil-bearing bed and the coexisted species. The specimen from Xianyang is from the layer of 20KaB. P. dated by ^{14}C method and in association with *Coelodonta antiquitatis* and *Palaeoloxodon*, etc.

3 Phylogeny of the *Bubalus*

The phylogeny of fossil *Bubalus* was first studied by C. C. Young, and M. Z. Chow and others. Liu and Zhen also did a primary study on the evolutionary relationship among some species. Here we try to do the same work by the cladistic analysis. 18 characters are selected for the phylogenetic analysis. *Leptobus*, the earliest bovid appeared from the Early Quaternary was selected as the outgroup. The

symplesiomorphies are coded as (0); the synapomorphies as (1); the question marks represent uncertain character. The 18 characters and their polarities are as below:

1. Occipital area: projecting backward (0); flat (1)
2. Shape of occipital bone: low and wide (width / height < 1.7)(0);narrow and high (1)
3. Occipital crest: strong (0); weak or medium (1)
4. Vertebra incision on occipital crest: absent (0); present (1)
5. Parietal: short (less than 60mm)(0); long(more than 60mm)(1)
6. Frontal part between orbits: broad (0); narrow (1)
7. Frontal part between the base of horn cores: concave (0); flat or convex (1)
8. Distance between the posterior border of horn cores and occipital crest: long (0); short (1)
9. Distance between the posterior border of orbit, and the base of horn cores: long (0); short (1)
10. Distance between the supraorbital foramina: longer than 90mm (0); shorter than 90mm (1)
11. Position of orbits: facing laterally (0); facing somewhat forward (1)
12. Circumference of horn cores at the base: larger than 400mm (0); smaller than or equal to 400mm (1)
13. Direction of horn cores: backward (0); only slightly backward (1)
14. Maximum breadth between the base of horn cores: wider than 120mm (0); less than 120mm (1)
15. Cross section of the horn cores near the base: round or approximately round (0); triangular (1)
16. Shape of horn cores: slender and long (0); thick and short or bulky (1)
17. Angle between horn cores and the sagittal plane of the skull: small (0); big (1)
18. Index of horn cores: big (0); small (1)

Based on the features mentioned above, we obtained a character data matrix, and further gained a strict consensus cladogram after the data matrix was calculated with the program PAUP (version 3.1.1). The cladogram demonstrates that the phylogenetic relation between *B. teilhardi* and *B. tingi* is uncertain, probably partly because of too many uncertain characters in *B. tingi*. Of all 18 characters, only two apomorphies appeared in *B. teilhardi*, implying that it is rather primitive and is consistent with its old age (Middle Pleistocene). The species that successively evolved from the genus after *B. teilhardi* and *B. tingi* are *B. brevicornis*, *B. mephistopheles* and *B. wansijocki*. *B. guzhensis*, *B. triangulatus*, *B. youngi*, *B. bubalus* and *B. bubalis* are located at the same node based on synapomorphies 1,6,11 and 13. The phylogenetic relations among these five species are uncertain except that *B. bubalus* and *B. bubalis* are a sister group. They and *B. wansijocki* are a sister group based on synapomorphies 1 and 6. The result of the present analysis shares some similarities with the view from Chow and Xu (1957). For instance, the phylogenetic relation between *B. teilhardi* and *B. tingi* in this article does not negate the corresponding conclusion raised by Chow and Xu. The systematic relationship between *B. mephistopheles* and *B. brevicornis* proposed by Chow and Xu is also similar to the one in this article. However, the present analysis does not support the view held by Chow and Xu that there is a rather close relationship between *B. youngi* and *B. wansijocki*, and the latter evolved

directly from *B. brevicornis*. The cladogram indicates that *B. youngi* shares a closer relationship with *B. bubalus* rather than with *B. wansijocki*.

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图版 I 说明 (Explanations of Plate I)

1. 杨氏水牛 *Bubalus youngi*

完整双角及眶后头骨 (complete two horn cores and the skull behind the orbits), NWUV 1241

1a. 前视 (anterior view), ×0.08; 1b. 腹视 (ventral view), ×0.075; 1c. 后视 (posterior view), ×0.1; 1d. 左侧视 (lateral view from left-side), ×0.1; 1e. 左 M1～3，冠面视 (crown view), ×0.5

2、3. 德氏水牛 *Bubalus teilhardi*

不完整双角及眶后头骨 (incomplete two horn cores and the skull behind the orbits), NWUV 1239

2a. 前视 (anterior view), ×0.1; 2b. 后视 (posterior view), ×0.1; 2c. 左侧视 (lateral view from left-side), ×0.15

近完整的左角、不完整的右角及受压的眶后头骨 (a complete left, incomplete right horn core and the crushed skull) NWUV 1240，3a. 前视 (anterior view), ×0.1; 3b. 后视 (posterior view), ×0.1


3a
3b
2b
2a
2c
1d
1e
1c
1b
1a