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黑犀(奇蹄目,犀科)化石在中国的首次发现[1)]

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摘要： 黑犀(*Diceros* 属)的惟一现生代表 *D. bicornis* 生活在非洲。该属在新近纪时期曾广泛分布于希腊、土耳其和伊朗等地区,但从未在东亚地区发现过。新种甘肃黑犀(*Diceros gansuensis* sp. nov.)是该属在中国和东亚的首次发现。化石采自甘肃临夏盆地晚中新世柳树组中部。新种以尺寸较小、头型短、枕顶高耸、枕面窄而高、枕嵴无中沟、副枕突短小、下颌上升支距m3较近、前臼齿较小、DP1无后脊、P2原脊孤立、P2和P3后脊细窄而区别于东地中海地区的 *Diceros neumayri*。*D. neumayri* 的分类位置一直是一个争论的焦点,曾在黑犀(*Diceros* 属)和白犀(*Ceratotherium* 属)之间反复变更。研究显示,甘肃黑犀和 *D. neumayri* 的一系列共同的原始特征表明它们与更进步的白犀有明显的区别,应该归入黑犀属。

关键词： 甘肃临夏盆地,晚中新世,柳树组,犀科

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黑犀(*Diceros* 属)是犀科的4个现生属之一,现仅存一种(*D. bicornis*),生活在非洲。根据 Prothero and Schoch (1989)的分类方案,现生的黑犀与白犀(*Ceratotherium simum*)共同组成双角犀亚族(Dicerotina),而现生的另一种两角犀牛苏门犀(*Dicerorhinus sumatrensis*)则属于额鼻角犀亚族(Dicerorhinina)。在新近纪时期,黑犀曾分布于欧洲东部和亚洲西部,在希腊、土耳其和伊朗等东地中海地区的一些晚中新世地点都有其化石发现。然而,黑犀的化石以前从未在包括中国在内的东亚地区发现过。2005年8月我们在检查甘肃省和政古动物化石博物馆新采集的哺乳动物化石标本时,发现其中有两具保存得相当完好的黑犀头骨,且都带有下颌骨。标本采自临夏盆地内的广河县阿力麻土乡后山村,层位为晚中新世柳树组红粘土沉积的中部(邓涛等,2004,图5)。2006年,和政博物馆又在后山地点的同一层位采集到黑犀的两具头骨和一具下颌骨标本,同时还征集了一具产自临夏盆地,但地点不详的幼年黑犀头骨标本。这些化石在临夏盆地的发现对于了解黑犀化石的形态特征和分类地位,以及这类动物在地质历史时期的地理分布和进化过程都具有重要的意义。

LX为中国科学院古脊椎动物与古人类研究所野外地点编号。HMV为甘肃和政古动物化石博物馆标本编号。解剖术语依据 Sisson(1953),测量方法依据 Guérin(1980)。

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奇蹄目 Perissodactyla Owen, 1848

犀科 Rhinocerotidae Owen, 1845

真犀亚科 Rhinocerotinae Owen, 1845

黑犀属 *Diceros* Gray, 1867

甘肃黑犀(新种) *Diceros gansuensis* sp. nov.

(图 1-5;表 1-4)

正型标本　HMV 1421,一头骨带下颌,左侧鼻骨和枕骨顶部缺失(图 1、5B、5C)。

其他材料　HMV 1442,一老年头骨带下颌,下颌联合部前端缺失;HMV 1443,一青年头骨,DP4 刚刚脱落,M3 刚刚萌出(图 3B);HMV 1446,一相当完整的头骨,仅前颌骨末端缺失(图 2、4C、5A);HMV 1447,一幼年头骨带 DP1-DP4,M2 刚刚萌出,枕部右侧缺失(图 3A、4B);HMV 1448,一下颌骨,冠状突和左侧髁状突缺失(图 4A)。

名称来源　以产地甘肃命名。

地点和层位　甘肃省广河县阿力麻土乡后山(LX0008;地理坐标:35°29′00.6″N, 103°28′28.0″E),晚中新世柳树组中部。HMV 1447 的地点和层位不详。

特征　一种中等个体的黑犀,体型与现生的非洲黑犀接近。短头型,前颌骨退缩而无齿。鼻切迹底部约在 P3/P4 界线水平。头骨顶面凹陷,枕顶高耸。枕面垂直,窄而高,最大宽度在底部,枕嵴轻微中凹。副枕突短小,基结节及其纵嵴发育。下颌联合部窄,水平支厚实,上升支垂直而薄,与 m3 之间距离近。前臼齿相对较小,小刺微弱,无反前刺,DP1 无后脊,P2 原脊孤立,P2 和 P3 后脊细窄。

描述　头骨中等大小,鼻骨末端至枕嵴的平均长度为 591 mm,与现生的非洲黑犀(平均 567 mm,据 Guérin, 1980, table 2, 下同)接近,远小于现生的非洲白犀(平均 797 mm)。短头型,鼻骨末端至枕嵴长度与颧弓最大宽度的比值(头长指数)平均为 0.55。作为对比,非洲黑犀的头长指数平均为 0.58,非洲白犀平均为 0.43。Antoine(2002:92)将头长指数小于 0.5 定义为长头型,大于 0.5 为短头型。

鼻骨短而宽大,两侧强烈下垂;边缘圆滑,非常厚实,厚度为 30 ~ 36 mm;前部强烈向下倾斜,末梢宽圆而粗糙,具中沟;鼻骨腹面强烈凹陷,中央为尖端向后的三角形隆起区,两侧沟宽深。鼻骨愈合,具有一条中沟代表骨缝的位置;中沟宽深,底部窄,向后延伸至角座一半处。整个鼻骨游离部分被巨大的角座占据,HMV 1446 的鼻角角座长 164 mm、宽 144 mm;角座中央被窄菱形的不突起的微弱粗糙面分割,两侧为半月形的强烈粗糙隆起面。在幼年个体(HMV 1447)中没有任何鼻角存在的痕迹,而在刚萌出 M3 的青年个体(HMV 1443)中鼻角角座已显著发育。在幼年和青年个体中可以观察到鼻骨与额骨的骨缝,在单侧呈宽的 S 形,额骨鼻突窄而尖锐,强烈向前突伸。在幼年个体中可以观察到鼻骨不与泪骨接触。

前颌骨退缩,正型的前颌骨保存最好,在 DP1 之前的长度约 60 mm,没有门齿存在的任何迹象。前颌骨窄而薄,中部的上下宽度为 30 ~ 35 mm,下缘的内外厚度为 10 ~ 16 mm,与上颌骨呈平滑的过渡。鼻切迹呈宽大的 U 型,底部在 P3 中部至 P3/P4 界线水平;在 P2 前的高度为 61 ~ 67 mm,幼年个体的鼻切迹相对较窄。眶下孔大,椭圆型,高

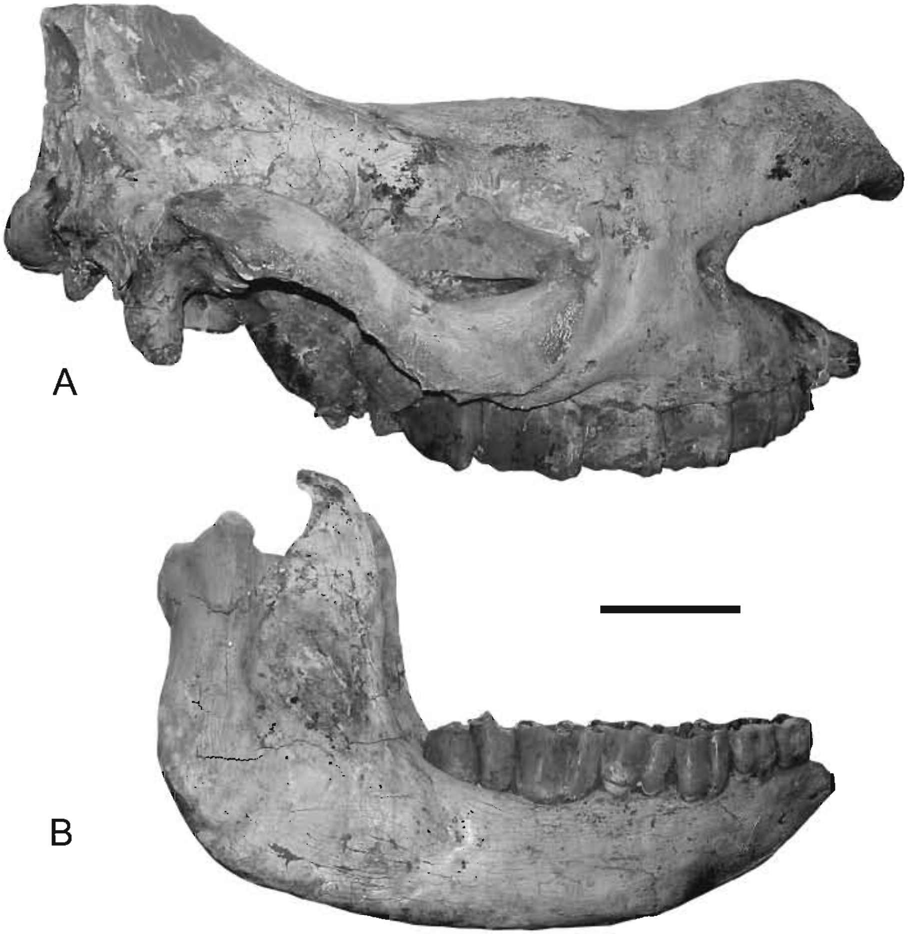

图 1　甘肃黑犀(新种)正型,HMV 1421,侧视

Fig. 1　Holotype of *Diceros gansuensis* sp. nov., HMV 1421, lateral view

A. 头骨 Skull; B. 下颌骨 mandible; 比例尺 scale bar = 10 cm

35 mm,长 25 mm,位于 P3/P4 界线至 P4 前部水平,位置接近鼻切迹底部,相距约 15 mm;开口向下,有时具宽浅的前导沟,后部具圆形压迹。

上颌骨表面平坦,在眶前具轻微凹陷的宽沟,自前上方向后下方倾斜。泪骨在面部的长度约 50 mm。HMV 1446 的眶前大约在泪骨与上颌骨骨缝的位置有凹陷面,凹陷面底部粗糙、后部有几个不规则的小滋养孔。眼眶位置低,不突出,其前缘在 M2 中部水平,其下缘面向外上方。泪结节粗糙而发达,强烈向侧面突出,但有时两侧的发育程度并不一致。眶上结节发达而粗糙,前后向延伸,具深的前、后切迹。额骨和颧骨都无眶后突。

颧弓在成年个体中较薄而窄,在中部内外厚约 10 mm,在后部上下宽约 35 mm;在幼年个体中较厚而宽,在中部厚约 15 mm,在后部宽约 50 mm。颧弓的后部位置低,向两侧扩张,后缘与颞嵴连贯;腹缘粗糙,具有纵向的隆嵴。

头骨顶面鼻骨后部和顶骨前部凹陷,在额骨的额角角座处轻微隆起,枕顶高耸。额骨

图2　甘肃黑犀(新种)头骨,HMV 1446

Fig. 2　Skull of *Diceros gansuensis* sp. nov., HMV 1446

A. 侧视 lateral view; B. 顶视 dorsal view; 比例尺 scale bar = 10 cm

纵向隆凸,向两侧倾斜,头骨顶面最宽处位于眶上结节之间。额角角座巨大,呈正菱形,HMV 1446 的角座宽度为188 mm。在幼年个体和青年个体中,额角都不存在。脑颅宽大,外壁陡立。顶嵴弱,中间为宽阔的平面。

枕面垂直,即与基枕面呈90°夹角;轮廓呈高而窄的梯型,底部最宽。枕嵴顶视呈宽浅的凹陷,中央有发达的结节,枕嵴侧缘前倾。头背大直肌窝深,轮廓呈三角形,颈结节较弱。中嵴弱,其顶端有一个发达的瘤状结节;侧嵴发达,宽大而圆隆;外嵴微弱,其下端末梢有一个强烈突起的球状结节。枕大孔圆形,其上缘与枕髁上缘约在同一水平。

副枕突呈三棱锥形,末梢尖锐,直或轻微后倾;在成年个体中较弱,但在幼年个体中却

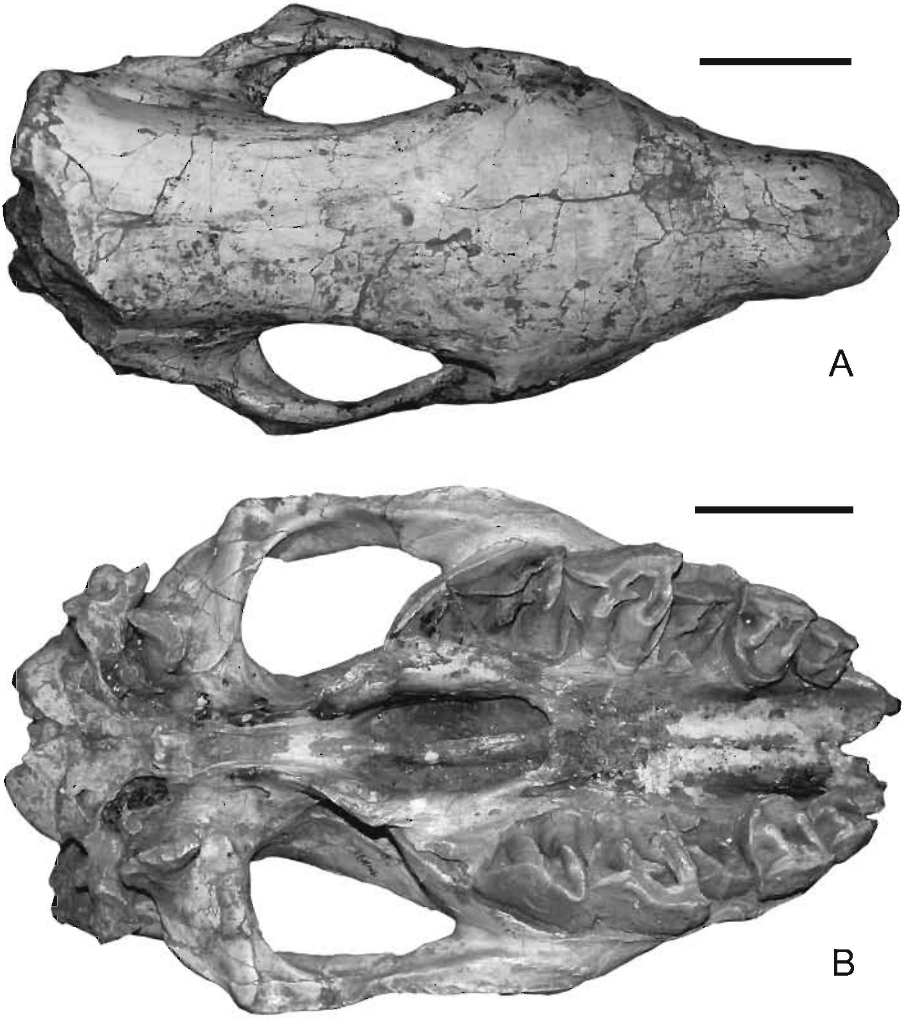

图 3　甘肃黑犀(新种)未成年头骨

Fig. 3　Juvenile and young skulls of *Diceros gansuensis* sp. nov.

A. HMV 1447,幼年 juvenile,顶视 dorsal view;B. HMV 1443,青年 young,腹视 ventral view;

比例尺 scale bars ＝10 cm

相当发达。鼓后突与副枕突在基部愈合。鼓后突薄,前倾,不向两侧扩展,其末端不超过关节后突中部。在大多数成年个体中鼓后突与关节后突愈合而形成假外耳道,但在幼年和青年个体中都不愈合。作为假外耳道上缘的颞嵴直而前倾。关节后突发达,轻微向前弯曲,并向前内方向倾斜,侧面具有强壮的纵嵴;内外薄而前后长,HMV 1446 的关节后突厚 13 mm,长 45 mm。

基枕骨后部宽阔而隆凸,中央呈三角形纵向突起;基枕骨与基蝶骨交角约 120°。基结节发达,中央有横向隆嵴,后部两侧为圆形粗糙面,其矢状嵴窄而高。翼骨夹谷宽深;犁骨前部宽圆,后部薄锐,与腭面相距较远。颞窝前缘在 M3 水平;颞髁轻微隆凸,髁后关节面

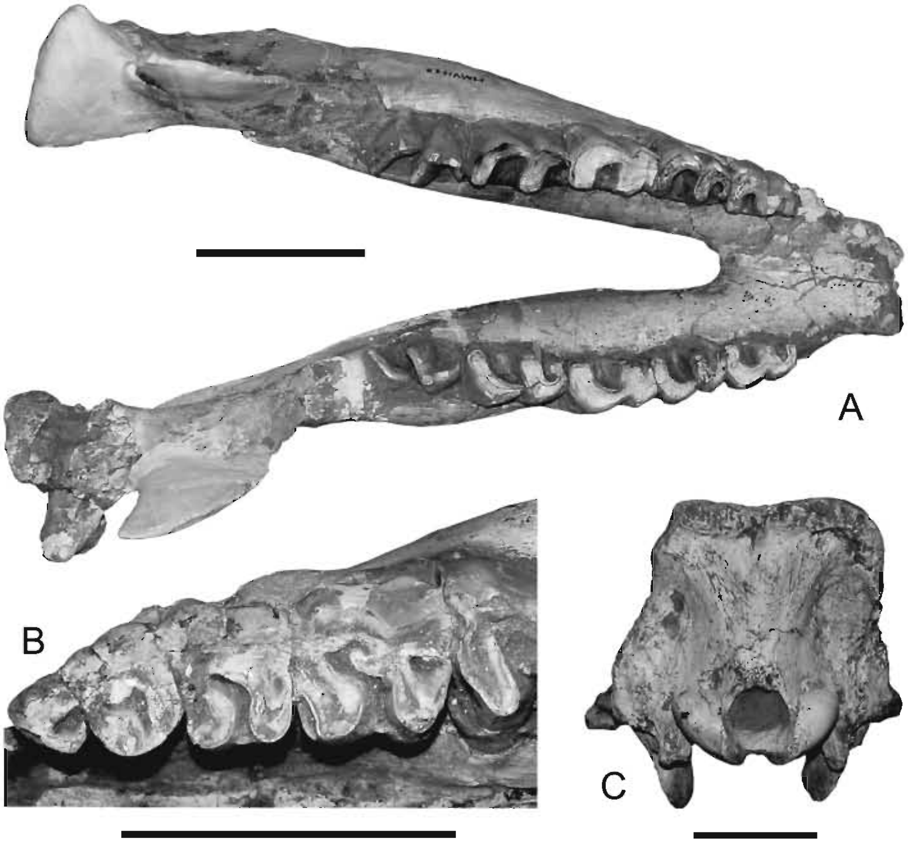

图4 甘肃黑犀(新种)头骨、下颌骨和乳齿列

Fig. 4 Skull, mandible and milk tooth row of *Diceros gansuensis* sp. nov.

A. HMV 1448,下颌骨 mandible,冠面视 occlusal view;B. HMV 1447,左上乳前臼齿列 left upper milk tooth row,冠面视 occlusal view;C. HMV 1446,头骨 skull,枕面视 occipital view;比例尺 scale bars = 10 cm

呈三角形,宽阔而光滑。硬腭微凹,其后缘呈 U 形,底部位置在 M2 中线水平。内鼻孔中等宽度,60 ~ 70 mm。成年个体的硬腭较窄,无中嵴,仅后端有一个微弱的结节;在幼年个体中硬腭却相当宽阔,且具有显著的中嵴。腭管前孔位于 M2 水平,腭管后孔大而圆,直径 15 mm,开口向后。

下颌联合部上翘,前端转为平伸,后缘在 p3 后部或 p4 前部水平。联合部窄,两侧缘平行,宽度 74 mm。齿槽间隙长度大于 64 mm,齿槽缘薄锐。联合部舌面凹陷;唇面平坦,具两个小的滋养孔。颏孔小而窄长,位于 p2/p3 界线水平,有时分裂成前、后两个。

下颌水平支下缘弧形弯曲,后半部较平。水平支低,非常厚实,中段厚度为 55 ~ 75 mm。血管切迹微弱;下颌角圆,边缘粗糙,厚约 35 mm。上升支垂直,内、外表面呈宽大的深凹陷,以致上升支的中央部分非常薄。冠状突相当发达,向后弯曲;薄,厚度仅 4.5 mm,外侧凹陷,内侧隆凸。髁状突细长,向两侧强烈扩展,外宽内窄,两侧具宽圆的隆嵴。髁状突后沟在内侧宽深,向外逐渐消失,具有强壮而圆隆的后嵴。

表 1　甘肃黑犀(新种)头骨测量

Table 1　Measurements of skulls of *Diceros gansuensis* sp. nov.　　(mm)

Measures	HMV 1421	HMV 1442	HMV 1443	HMV 1446	HMV 1447
1 Premaxillary tip - occipital condyle	~627	—	>550	>601	>556.5
2 Nasal tip - occipital condyle	649	561.5	559	645	586.5
3 Nasal tip - occipital crest	—	522.3	569.5	613	570
4 Depth of nasal notch	170.5	158	155.5	177	139.5
5 Minimal width of braincase	82	122.2	121	118.5	126
6 Postorbital process - occipital crest	—	279.5	326	337.5	318
7 Supraorbital tuberosity - occipital crest	—	313	342	369	331.5
8 Lacrimal tubercle - occipital crest	—	346.5	386	396.5	365
9 Nasal notch - orbit	142	118.4	108.5	132	111.6
13 M3 - occipital condyle	285	271	—	315	—
14 Nasal tip - orbit	307	263	248	297	249
15 Width of occipital crest	—	220	197	202	182
16 Width between mastoid processes	218	235.5	246	246	~200
17 Minimal width between parietal crests	39	47	63	62.5	95
18 Width between postorbital processes	—	224.3	214	252	191.5
19 Width between supraorbital tubercles	—	~258	268	262	224.5
20 Width between lacrimal tubercles	244	263	274	254	~215
21 Maximal width between zygomatic arches	292.5	352	326.5	322	287
22 Width of nasal base	—	178.5	156	147.2	147
23 Height of occipital face	—	139	122.3	142.5	~127
25 Height of skull in front of P2	224	192.5	213	217.4	201.5
26 Height of skull in front of M1	219	218	225	243	195.5
27 Height of skull in front of M3	219	227	208	243	—
28 Width of palate in front of P2	33	45.3	61	42	84.3
29 Width of palate in front of M1	50	63.4	89.5	67	95
30 Width of palate in front of M3	53	85	105	70	—
31 Width of foramen magnum	49	50.5	54	52.5	52
32 Width between occipital condyles	114	128	130	132.3	~140

乳上前臼齿的原尖和次尖不收缩,大小相近,舌缘圆;外壁轻微起伏,无前尖肋,前附尖弱;无反前刺和小刺;无内、外齿带,仅 DP3 和 DP4 中谷口有齿带痕迹。DP1 的原脊形成弧形内壁,无后脊,中谷与后谷连通,向后开口。DP2 有齿桥封闭中谷。DP3 和 DP4 的原尖与次尖分离,中谷口开放。DP2 无后谷,DP3 和 DP4 后谷小而封闭。DP2 和 DP3 的后脊平伸,DP4 的后倾。DP2 的牙齿内壁圆,DP3 和 DP4 的内壁中部收缩。DP1-DP3 无前刺,DP4 前刺发达。在成年个体中 DP1 较少存在,本文描述的材料中仅正型具有,其冠面轮廓呈膨大的圆三角形,双根。HMV 1447 的乳齿测量(长 × 宽 × 高,单位:mm):DP1 = 21.5 × 25 × 13.3,DP2 = 31 × 45.5 × 8,DP3 = 40 × 46 × 18.5,DP4 = 48 × 48.5 × 19。

上颊齿列轻微弧形弯曲并向前收敛,上前臼齿列(P2-P4)与上臼齿列的长度之比为 0.74。齿冠较高,未磨蚀的臼齿高度超过 70 mm。上颊齿无外齿带,外壁具白垩质覆盖。无反前刺和中窝。前附尖发达而尖锐,强烈突伸。

表 2 甘肃黑犀(新种)下颌骨测量

Table 2 Measurements of mandibles of *Diceros gansuensis* sp. nov. (mm)

	Measures	HMV 1421	HMV 1442	HMV 1448
1	Length	—	~465	~531
2	Posterior border of symphysis - ascending ramus	393	384	~437
3	Height of horizontal ramus in front of p3	69.5	50	69
4	Height of horizontal ramus in front of p4	74.5	62.5	75
5	Height of horizontal ramus in front of m1	83.5	82	88
6	Height of horizontal ramus in front of m2	94.5	87	88
7	Height of horizontal ramus in front of m3	94	93.5	84
8	Height of horizontal ramus behind m3	114	99	95
9	Distance between horizontal rami in front of m1	68	79	101
10	Distance between horizontal rami in front of m3	77	98	105
11	Length of symphysis	—	~100	~120
13	Antero-posterior diameter of ascending ramus	145	141	>156
14	Transverse diameter of condyle	115	117	—
15	Height at condyle	233	223	—
16	Height at coronoid process	296	265	—

上前臼齿的内齿带发达而连续,后端上升,止于次尖中部;后谷小,磨蚀后封闭;牙齿内壁圆;原尖不收缩,舌缘圆;小刺微弱;次尖舌缘具尖锐突起(HMV 1446)。P2 的次尖强烈膨大,原尖与次尖接触而将中谷封闭,但未愈合;原脊孤立,不与外脊相连,后脊强烈收缩;外壁轻度起伏,前尖肋微弱;前刺细小,有分叉现象。P3 的原尖与次尖分离,后脊收缩;外壁轻微波状起伏,前尖肋微弱;前刺细小,分叉或成两枚。P4 的原尖与次尖分离,后脊不收缩;外壁波状起伏,无前尖肋;内壁强烈弧形弯曲,具内沟;前刺显著。

上臼齿无小刺,前刺发达而粗壮,直向前伸;前齿带宽厚,无内齿带,仅 M1 中谷口有一个齿柱;外壁波状起伏,前尖肋发达。M1 的原尖舌缘平,原尖前部轻微收缩,次尖不收缩;后脊短,后附尖长,后尖褶显著;后齿带弱,后谷小,接近封闭。M2 的原尖舌缘圆,原尖、次尖不收缩;后附尖长,后尖褶宽深,后脊短;后齿带弱,后谷宽大。M3 的冠面轮廓呈三角形;原尖不收缩,舌缘圆;原脊后倾,前刺发达,几乎伸达原脊;内壁中央收缩;无后齿带。

下前臼齿列(p2-p4)与下臼齿列的长度之比为 0.71。下颊齿的前叶呈直角,下前脊发达,宽大,深达唇侧;外沟为窄而深的 V 形,p3 向基部变浅,其余的不变浅;无内、外齿带,仅 p3 后谷口有一枚齿柱。下前臼齿的后谷入口呈宽的 U 形。p2 的下前脊宽大,达 8 mm,末梢截平;下前尖弱,内侧轻微收缩。下臼齿的下次脊后倾。

比较与讨论 上述材料的双角犀属性很清楚,与其他的双角犀成员具有很多相同的性状(Prothero et al., 1986; Heissig, 1989; Cerdeño, 1995; Antoine, 2002; Geraads, 2005)。从头骨、下颌骨和牙齿的特点看,临夏标本与黑犀(*Diceros*)最为接近。它们之间的共同特征是:1)头骨为短头型;2)具有半球状的鼻角角座和宽大的额角角座;3)鼻骨前部显著缩短;4)眼眶下缘面向外上方;5)枕面垂直,枕嵴与枕髁在同一水平;6)头骨顶面凹陷,枕顶高耸;7)下颌上升支垂直;8)上臼齿的前尖肋发达。在双角犀类的成员中,临夏标本虽然有不少特征与白犀(*Ceratotherium*)接近,但它们不会是同一种双角犀。白犀的

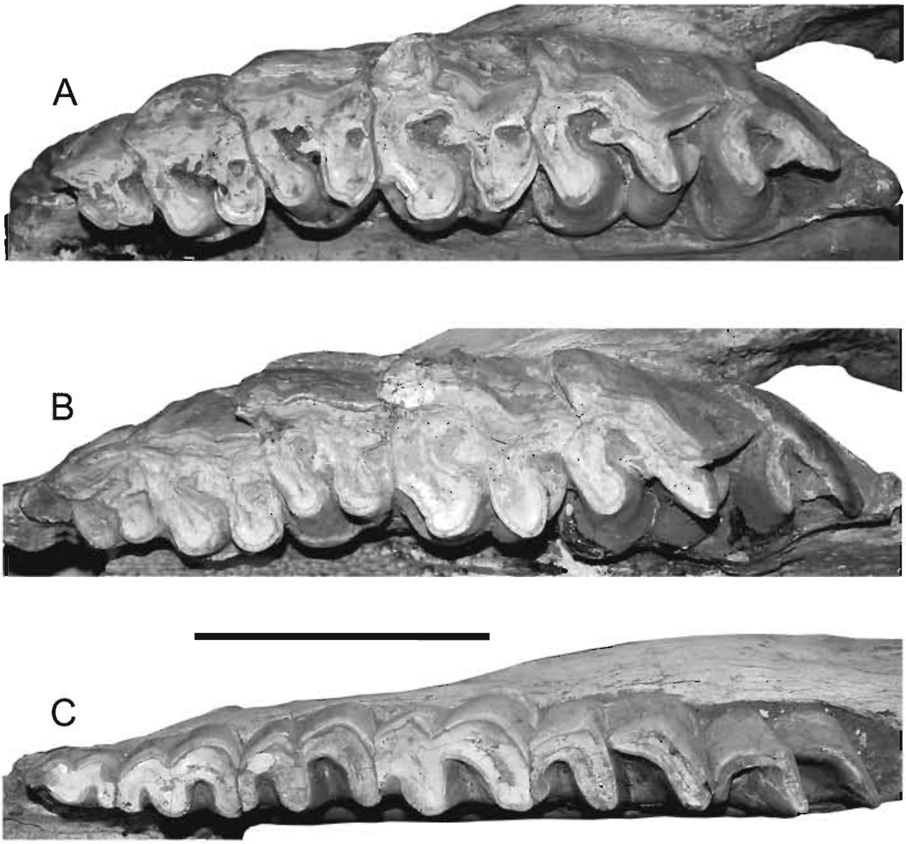

图 5　甘肃黑犀(新种)颊齿列冠面

Fig. 5　Occlusal view of cheek teeth of *Diceros gansuensis* sp. nov.

A–B. 左上颊齿列 left upper cheek teeth, A. HMV 1446, B. HMV 1421; C. 右下颊齿列 right lower cheek teeth, HMV 1421; 比例尺 scale bar = 10 cm

头骨为长头型,头骨顶面平缓或轻微凹陷,枕顶低;鼻切迹浅,底部在 P2/P3 界线附近;眼眶与鼻切迹之间距离远;枕面强烈后倾,枕嵴向后远超过枕髁水平;枕嵴中央呈深的 V 形凹陷;关节后突和副枕突细弱,鼓后突前伸程度低,未形成封闭的假外耳道;上升支强烈后倾而厚实,其前缘与 m3 之间的距离宽阔;上颊齿原脊和后脊强烈向后弯曲,小刺发达并形成中窝;上臼齿无前尖肋,m3 的下次脊接近纵向后伸。*Ceratotherium* 的特征,尤其是颊齿特征,显示它是一种相当特化的双角犀,不同于有不少原始性状的临夏标本。但临夏标本也不会是双角犀中已知最原始的类型 *Paradiceros*。*Paradiceros* 的鼻切迹相当浅,其底部在 P2 水平,关节后突与鼓后突分离,颊齿低冠,原尖收缩,反前刺突出,M3 近似四边形,DP2 具有中附尖(Hooijer, 1968; Guérin, 1976)。

双角犀类的化石记录相当复杂,除已绝灭的非洲中中新世的 *Paradiceros* 以外,现生的两个属 *Diceros* 和 *Ceratotherium* 都有化石代表。然而,古生物学家对于两个属在化石记录中的含义和使用有很大的分歧。为了弄清这些分歧,我们对与本文材料密切相关的欧亚

大陆双角犀类化石的研究历史作一简单回顾。

表 3 甘肃黑犀(新种)上颊齿测量(长×宽×高)

Table 3 Measurements of upper cheek teeth of *Diceros gansuensis* sp. nov. (L×W×H) (mm)

Measures	HMV 1421	HMV 1442	HMV 1443	HMV 1446
DP1	19×19×5	—	—	—
P2	39×40×34	35×40.6×27	38×41×53	36.5×37.2×31.4
P3	48×57.5×43.5	39.8×63.2×26.6	47.5×59×52	42.4×58.2×41.7
P4	54.6×66×48	43.5×70.3×22.6	—	50.5×64.5×52
M1	67.5×71.4×53.6	51.3×67.2×15	67.7×78.4×68	59.1×69.6×42.3
M2	73.5×71×65	62×75×28	70.6×73×70.5	65.6×75.3×55
M3	67.6×62.5×61	67×67×39.5	—	63.8×69.3×60.3

表 4 甘肃黑犀(新种)下颊齿测量(长×宽×高)

Table 4 Measurements of lower cheek teeth of *Diceros gansuensis* sp. nov. (L×W×H) (mm)

Measures	HMV 1421	HMV 1442	HMV 1448
p2	31×22×34.2	32×19×31.4	—
p3	43.4×29.8×35.4	41×29.2×27.8	43.5×32×32.5
p4	43.2×38.6×44	43.2×34.2×30	44.2×35.7×39.6
m1	54.2×38.5×43.7	42×39.6×16.2	53×39×42
m2	60.4×39×50.5	52×41.6×23	59.5×40×40
m3	61×38.4×54	54×35.5×30.3	63.2×33.8×51

Wagner(1848, pl. X, fig. 3, 4)以收藏于慕尼黑古生物博物馆中的一件Pikermi晚中新世的破碎幼年下颌骨为正型建立了一个新种*Rhinoceros pachygnathus*。Gaudry(1862–1867)描述了巴黎博物馆收藏的更多Pikermi的*R. pachygnathus*,这些材料明显具有双角犀类的特点:前部牙齿退化;鼻骨末端非常宽阔而厚实,额角位置也显著加厚;颧弓细弱;下颌角圆,从髁状突到下颌角发育强壮的隆嵴。Gaudry已经指出它与非洲黑犀的相似性,也接近于非洲白犀。不过,Ringström(1924)辨明Gaudry(1862–1867, pl. XXVIII, fig. 1, 2)描述的*R. pachygnathus*材料中单独的下颌骨实际上属于*Dicerorhinus orientalis* (= *pikermiensis*)。

Osborn(1900)研究了巴黎和伦敦博物馆的标本后认为,*R. pachygnathus*的头骨与非洲白犀相似,其鼻骨下倾的程度比非洲黑犀弱。与此同时,Osborn根据维也纳自然历史博物馆中采自Pikermi或Maragha的一具错误地标注为*Rhinoceros schleiermacheri*的雄性头骨建立了一个新种*Atelodus neumayri*。这个头骨与*R. pachygnathus*的相似性状包括:巨大的额角和鼻角角座,假外耳道封闭,颧弓细弱,下颌骨下缘隆凸。Osborn认为*A. neumayri*不同于*R. pachygnathus*的性状是:臼齿延长,趋于高冠,外侧有白垩质覆盖;前臼齿完全臼齿化;P3–M1有发达的后窝和次附尖褶;无反前刺(反前刺应位于前刺舌侧),但有一个发达的位于前刺唇侧的刺状结构(可称为反小刺,antecrista)几乎与强壮的前刺相连,接近形成一个特别的中窝(Osborn, 1900, fig. 16)。他认为这个从对角方向连接原脊和后脊的特别构造在披毛犀中也能观察到,由此提出*A. neumayri*与披毛犀的关系比与*R. pachygnathus*的关系更近。Osborn将一系列种都归入*Atelodus*属,包括非洲黑犀(*A. bicornis*)、非洲白犀(*A. simum*)、披毛犀(*A. antiquitatis*)、梅氏犀(*A. merckii*),以及*A. neumayri*和*A.*

pachygnathus,并将它们都置于 Atelodinae 亚科,其共同特点是门齿极度退化或缺失(这个亚科和属的拉丁文就是这个含义)。

Osborn 建立的新种 *Atelodus neumayri* 很难进行讨论,因为它缺乏描述,仅有一段简短的鉴定特征和一枚左 M2 的插图,却没有正型头骨的图像,造成对于这个种的头骨特征的认识模糊。因此,Weber(1904)在描述 Samos 的犀科化石时有一个保存非常好的 *Rhinoceros pachygnathus* 头骨,但他却完全没有对比 Osborn 的这个种。另一方面,Mecquenem(1908)认为 Osborn 描述的这个头骨应该属于 *Chilotherium persiae*,并认为 Osborn 错误地拼接上了一个 *Iranotherium morgani* 的鼻骨。Ringström(1924)明确地将 Pikermi 的犀牛称为 *Diceros pachygnathus*,并指出它与现生的 *D. bicornis* 关系最近。他同时认为 *D. pachygnatus* 的分布只限于欧洲东南部到小亚细亚,在 Maragha 没有这个种。Arambourg and Piveteau(1929)报道了在希腊萨洛尼卡附近的 Vathylakkos 发现的 *D. pachygnathus*,并认为这个种的分布范围从西欧(德国的 Eppelsheim)直到中国。Kretzoi(1942)的结论是 *D. pachygnathus* 既不同于 *D. bicornis*,又不同于 *Ceratotherium simum*,它的牙齿结构比现生的 *D. bicornis* 更原始,因此提议建立一个新属 *Pliodiceros*。不过,并没有人采用 Kretzoi 的观点。根据 Dietrich(1945)的意见,Pomel(1885)建立 *Atelodus* 属的原始材料已被修订为 *Dicerorhinus* 属,但 *Atelodus neumayri* 并不是 *Dicerorhinus* 属的成员,而应该被更名为 *Diceros neumayri*。Dietrich 还否定了 Eppelsheim 存在 *D. pachygnathus* 的看法,认为这个种只分布于Pikermi,可能还有 Vathylakkos 和 Samos。

Thenius(1955)重新研究了保存在维也纳博物馆地质古生物部的 *Atelodus neumayri* 的正型标本,以及有关的 *Diceros pachygnathus* 材料。他首先考订 Osborn 指定的这件头骨正型标本确实是出自 Maragha,而非 Pikermi。正型标本显著破损,尤其是缺失枕部,但拼接的鼻骨被认为是可靠的(Thenius, 1955, fig. 1.1),头骨特点明显指示它与现代的黑犀和白犀一样,都是双角犀类的成员。Thenius 证明 Osborn 所描述的反小刺的重要特征只不过是个体变异,在正型头骨的右 M2 上这个构造就不明显,仅有 2 mm 的突起。因此,Osborn 提出的这个最重要的鉴定特征并不合适。Thenius(1955)指出,Weber(1904)描述的 Samos的完整 *Rhinoceros* (= *Diceros*) *pachygnathus* 头骨能够为这种犀牛提供足够的信息,而 Maragha 的头骨表现的特征与 Samos 的高度一致,因此它们应该是同一个种 *Diceros pachygnathus*。另一方面,由于 Samos 和 Maragha 的头骨比 Pikermi 和 Vathylakkos 的更特化,也更进步,因此他建议分为两个亚种:东部亚种为 *Diceros pachygnathus neumayri*,西部亚种为 *D. p. pachygnathus*。

Heissig(1975)发现 Wagner(1848)建立新种 *Rhinoceros pachygnathus* 的幼年下颌骨正型实际上属于 *Rhinoceros schleiermacheri*,后者被 Schlosser(1921)修订为 *Dicerorhinus orientalis*,又被 Kretzoi(1942)归入 *Stephanorhinus* 属。因此,Heissig 认为 *Dicerorhinus orientalis* 应该被更名为 *Stephanorhinus pachygnathus*,而 Pikermi 动物群中真正的 *Rhinoceros pachygnathus* 应该是根据 Maragha 的头骨材料建立的 *Diceros neumayri*。此后,在 Heissig(1989)和 Prothero et al.(1989)的论述中,这个种都被称为 *D. neumayri*。

然而,Geraads(1988)认为 Pikermi 以及其他东地中海地区的 *D. neumayri* 虽然明显与现代非洲的双角犀类有密切的亲缘关系,但并非与 *Diceros* 属特别接近。奇怪的是,他并

没有说出什么具体的理由，就将这个种置入 *Ceratotherium* 属，而成为 *Ceratotherium neumayri*。他同时给出了 *C. neumayri* 的鉴定特征，却仅包括几个相对于 *C. simum* 的近祖性状：鼻骨前端圆、枕部后伸较弱、M3 三角形、颧弓简单、DP2 后谷退缩，其实这些特征明显也是 *Diceros* 属所具有的。他也提出另一个选择，为 *C. neumayri* 创建一个新属，而这只不过是重复 Kretzoi（1942）的观点。此后，*C. neumayri* 这一名称被一些研究者采用（Kaya, 1994; Heissig, 1996, 1999; Bonis and Koufos, 1999; Fortelius et al., 2003; Giaourtsakis, 2003; Antoine and Saraç, 2005）。然而，Geraads（2005）给出的 *Ceratotherium* 的一系列鉴定特征依然不得要领，几乎都是 *Diceros* 所具有的，包括：具鼻角和额角；鼻骨圆而短，不与泪骨接触；眼眶下缘外倾；眶后突微弱；枕嵴宽阔；前颌骨强烈退缩；上、下门齿退化或消失；前尖肋微弱；反前刺缺失。仅仅是前尖肋微弱这个特征可以在臼齿上与 *Diceros* 较强的前尖肋相区别。他认为 *C. neumayri* 是现代非洲白犀和黑犀的共同祖先，*Diceros* 属由 *Ceratotherium* 属进化而来（Geraads, 2005:458）。

Thenius（1955）早就指出以现代白犀为代表的 *Ceratotherium* 属在双角犀类中已相当特化。它与 *Diceros* 最大的区别在于：头骨长，顶面平；眼眶更靠后，约在 M2/M3 水平；枕部低，枕面后倾，枕嵴强烈后伸而超过枕髁水平；关节后突和副枕突细弱，二者之间距离较近；下颌上升支后倾；原脊、后脊强烈后倾；中谷和后谷磨蚀后易于封闭；小刺强壮，与前刺愈合形成发达的中窝；m3 下次脊强烈后倾。这些特征在非洲上新世至更新世的化石种类，如 *Ceratotherium mauritanicum* 上可以见到（Geraads, 2005）。*Diceros neumayri* 并不具有这些特征，而是与 *Diceros* 的性质一致，因此应该将其保留在 *Diceros* 属内。

最近 Antoine and Saraç（2005）记述了在土耳其安纳托尼亚中部 Turolian 中期Akkaşdağı 地点发现的犀科化石，他们描述为 *Ceratotherium neumayri* 的化石在这个地点最常见，包括一具保存相当完整的头骨。与其他东地中海地区的类似化石相比，Akkaşdağı地点的标本明显更进步一些，已经具有了一些 *Ceratotherium* 的特征，特别是枕部后倾的程度，已经超过枕髁水平。然而，对比现生的白犀和黑犀，Akkaşdağı犀牛的特点仍然具有典型的 *Diceros* 性质，因此，它应该是 *Diceros neumayri* 中最进步的一个亚种，或者是 *Diceros* 属内一个最进步的新种。

到目前为止，*Diceros neumayri* 已发现于东地中海地区的多个地点，其中以 Pikermi、Samos、Akkaşdağı和 Maragha 的材料最好。比较这些材料，可以发现 *D. neumayri* 与 *D. gansuensis* 之间的差别十分明显：1）*D. neumayri* 的头骨较大。*D. gansuensis* 的头骨大小与Samos的 *D. neumayri* 头骨相近，但明显小于 Maragha 和 Pikermi 的头骨，更远小于 Akkaşdağı的头骨，Akkaşdağı头骨的大小已落在现代白犀的变化范围之内（Antoine and Saraç, 2005, table 1）。2）*D. neumayri* 的头型比 *D. gansuensis* 更长。在本文描述的 *D. gansuensis* 材料中，有 3 件头骨可以计算头长指数，其中 HMV 1442 的指数达到 0.67，但这件标本在头骨中部因挤压而有折断的痕迹，因此纵向的长度不准确。HMV 1443 和 1446 的头骨保存完整并处于正常状态，其头长指数分别为0.57 和0.53。Pikermi 的 *D. neumayri* 头骨（Gaudry, 1862-1867, pl. XXVII）的头长指数为 0.41（从图上计算），Samos 的头骨（Weber, 1904, pl. XIV, fig. 1, 3）头长指数为 0.45（从图上计算），Akkaşdağı的头长指数为 0.46（Antoine and Saraç, 2005），它们都明显小于 *D. gansuensis*，表明后者的头骨要短得多。

3)Samos和 Akkaşdağı的 *D. neumayri* 头骨枕部抬升较弱,仅 Pikermi 头骨的枕部抬升程度与 *D. gansuensis* 接近。4)*D. neumayri* 的枕面宽低,枕嵴顶视具有发达的中沟,在Akkaşdağı的头骨上尤其显著,呈深的 V 形;而 *D. gansuensis* 的枕面窄高,枕嵴不发育中沟,仅有微弱而宽浅的凹陷。5)Samos 的 *D. neumayri* 头骨具有粗壮长大的副枕突;而 *D. gansuensis* 的副枕突细弱短小,在这一点上 Akkaşdağı的头骨与 *D. gansuensis* 相似。6)Pikermi 的 *D. neumayri* 下颌上升支前缘与 m3 之间有非常远的距离;而 *D. gansuensis* 的下颌上升支距 m3 相当近,在这一点上 Samos 的下颌骨与 *D. gansuensis* 相似(Thenius, 1955)。7)*D. neumayri* 的前臼齿相对较大,P2-P4 与臼齿列的长度之比超过 0.8,在 Samos 标本中甚至达到0.91(Weber, 1904, pl. XV, fig. 1,从图上计算),而 *D. gansuensis* 的比值仅为0.74。8)*D. neumayri* 的 DP1 后脊正常发育,DP2 存在中附尖,而 *D. gansuensis* 的 DP1 无后脊,DP2 不发育中附尖。9)Akkaşdağı的 *D. neumayri* 上前臼齿具有发达的小刺,与前刺相当接近,几乎形成中窝;*D. gansuensis* 上前臼齿的小刺弱小,在这个特征上其他地点的 *D. neumayri* 都与 *D. gansuensis* 相似。10)*D. neumayri* 的 P2 原脊与外脊相连;而 *D. gansuensis* 的 P2 原脊孤立,不与外脊相连,在这一点上 Maragha 的 *D. neumayri* 与 *D. gansuensis* 一致(Thenius, 1955, fig. 6)。11)*D. neumayri* 的 P2 和 P3 后脊相对较宽;*D. gansuensis* 的 P2 和 P3 后脊非常细窄,在这一点上 Akkaşdağı的 *D. neumayri* 与 *D. gansuensis* 相似。

Arambourg(1959)描述了阿尔及利亚 Bou Hanifia 地点 Vallesian 期的一个新种 *Dicerorhinus primaevus*。Geraads(1986)认为这个种相当原始,齿冠低,前臼齿具有发达的内齿带,与中中新世的 *Paradiceros* 接近,显然是双角犀类的成员,而非额鼻角犀。此后,Heissig(1989,1999)正式采用了 *Diceros primaevus* 的名称,并认为它是 *D. neumayri* 的祖先。Geraads(2005)根据头骨和乳齿列的性状,确认 *D. primaevus* 代表了 *D. neumayri* 这一支系的早期成员。*D. primaevus* 具有一些与 *D. gansuensis* 相似的独特性状,如它们的 DP1 都不发育后脊,DP2 和 DP3 的后脊与外脊结合部宽大等(Arambourg, 1959, fig. 20)。但 *D. primaevus* 与 *D. gansuensis* 也有明显的差异,前者的体型要小得多,其臼齿具有发达的内齿带和显著的原尖前收缩沟(Arambourg, 1959, fig. 21)。

Geraads(2005)将 Hooijer and Patterson(1972)根据肯尼亚 Kanapoi 上新世一个破碎头骨创建的 *Ceratotherium praecox* 修订为 *Diceros praecox*,其前移的眼眶、凹陷的头骨顶面、垂直的枕面、后伸较弱的枕嵴、发达的基枕部矢状嵴显示这个修订是正确的,它应该是 *Diceros* 属的成员。*D. praecox* 具有一些与 *D. gansuensis* 相似的独特性状,如它们的 DP2 都不发育中附尖且缺失后谷(Geraads, 2005, fig. 7)。但 *D. praecox* 能清楚地与 *D. gansuensis* 相区别,前者的鼻切迹底部位于 P2 后部水平,眼眶前缘位于 M1 水平,枕面下部不宽于上部;前臼齿不发育小刺,后谷宽大,磨蚀后也不封闭;P2 原脊与外脊连接;乳上前臼齿的小刺和前刺发达,几乎连接形成中窝;DP1 的后脊存在。这些特征显示 *D. praecox* 比 *D. gansuensis* 更进步,是 *D. bicornis* 的直接祖先(Geraads, 2005)。

Guérin(1966)描述的突尼斯晚中新世 Turolian 期的 *Diceros douariensis* 的惟一材料只是一件破碎的头骨,它被认为可能是 *D. neumayri* 的同物异名(Geraads, 2005)。Tsiskarishvili(1987)描述的高加索地区晚中新世 Vallesian 期的 *Diceros gabuniae* 被认为不过是代表了 *D. neumayri* 的地区性变异(Giaourtsakis, 2003)。Guérin(2000)描述的纳米比亚中中

新世的 *Diceros australis* 只有一枚第三掌骨,其性质很难判断。

D. gansuensis 与现生的非洲黑犀 *D. bicornis* 之间也存在显著的区别,后者的头骨更短;鼻骨相对更宽,鼻角角座的粗糙程度较低;鼻切迹较浅,底部位于 P2/P3 界线水平;眼眶前缘更靠前,位于 M1 中线水平;颧弓上的眶后突发达;枕面宽低,近方形,项结节弱,副枕突细长;下颌联合部后缘在 p3 中线水平,颏孔大;水平支厚度较小;上升支宽度较窄,外表面凹陷区域相对较小。

由于化石材料的稀少和破碎,人们对双角犀类的早期进化历史还知之甚少。目前已知最早的双角犀代表是发现于肯尼亚 Fort Ternan 和摩洛哥 Beni Mallal 中中新世晚期地层中的 *Paradiceros mukirii*,它具有相当原始的性状(Hooijer, 1968; Guérin, 1976)。在非洲大陆,阿尔及利亚晚中新世早期的 *Diceros primaevus* 与 *Paradiceros* 非常相似,它们之间可能有比较密切的关系。接下来是突尼斯晚中新世晚期的 *Diceros douariensis* (= *D. neumayri*),然后是在东非发现的早上新世的 *Diceros praecox*,至早更新世在东非出现了非洲黑犀(*Diceros bicornis*)的最早化石记录(Hooijer and Patterson, 1972; Geraads, 2005)。

在欧亚大陆,Heissig(1989:414)提到在安纳托尼亚和希腊 Chios 岛的中中新世地层中有一些双角犀类的早期材料,具有前部缩短的鼻骨和侧向倾斜的眼眶下缘,缺失有功能意义的门齿,其头骨与 *Diceros* 相似,但下颌骨相似于 *Ceratotherium*。然而,对这些标本并没有进一步的描述,所以它们的真正性质并不能确定(Giaourtsakis, 2003)。因此,在东地中海地区广泛分布的 *D. neumayri* 此前是双角犀类在欧亚大陆惟一确切的代表,其时代主要是晚中新世晚期,即 Turolian 期(Geraads, 1988; Heissig, 1989, 1996; Geraads and Koufos, 1990; Antoine and Saraç, 2005)。此次在中国发现的 *D. gansuensis* 生活于晚中新世早期,这与它比 *D. neumayri* 更原始的特点吻合。

Geraads(1988, 2005)错误地将 *D. neumayri* 归入 *Ceratotherium* 属,并且认为从白犀(*Ceratotherium*)分化出黑犀(*Diceros*),由此引起明显的进化矛盾。首先,黑犀有一系列比白犀更原始的性状,如垂直的枕部、宽浅凹陷的枕嵴、垂直的下颌上升支、微弱的小刺、显著的前尖肋等。其次,白犀是典型的以草本植物为食的动物(grazer),现代的非洲黑犀是典型的以灌木枝叶为食的动物(browser),从食草者向食叶者的进化与在有蹄类中发现的普遍规律恰好背道而驰(Jernvall and Fortelius, 2002)。

D. gansuensis 的材料采自临夏盆地晚中新世柳树组的红粘土中,这套沉积物的来源与风积作用有关(弓虎军等,2005)。化石产出地点后山及附近相同层位中发现的丰富三趾马动物群化石包括小臭鼬(*Promephitis parvus*)、中华副美洲獾(*Parataxidea sinensis*)、翁氏鬣形兽(*Hyaenictitherium wongii*)、巨鬣狗(*Dinocrocuta gigantea*)、保德四棱齿象(*Tetralophodon exoletus*)、贾氏三趾马(*Hipparion chiai*)、渭河三趾马(*H. weihoense*)、和政无鼻角犀(*Acerorhinus hezhengensis*)、维氏大唇犀(*Chilotherium wimani*)、伊朗犀(*Iranotherium morgani*)、新罗斯祖鹿(*Cervavitus novorossiae*)、后麂(*Metacervulus* sp.)、萨摩麟(*Samotherium* sp.)、河南兽(*Honanotherium schlosseri*)、和政羊(*Hezhengia bohlini*)、羚羊(*Gazella* sp.)和中新羚(*Miotragocerus* sp.)等(Deng, 2006),这些动物都是温带草原的类型。中国北方在晚中新世时期正处于一个草原广布、气候干燥的时期(梁忠、邓涛,2005),很显然,*D. gansuensis* 也是温带草原的栖居者。*D. gansuensis* 发育有垂直的枕面,根据这一结构特征的

意义(Zeuner, 1934),指示甘肃黑犀与它的现生后裔非洲黑犀一样,以草原地带的灌木枝叶为食。

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FIRST DISCOVERY OF *DICEROS* (PERISSODACTYLA, RHINOCEROTIDAE) IN CHINA

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Key words　Linxia Basin, Gansu Province; Late Miocene; Liushu Formation; Rhinocerotidae

Summary

The African black rhino, *Diceros bicornis*, once widespread across Africa has suffered a massive reduction in both numbers and range during the 20th century, but its origin and phylogenetic relationship remain debated. Here we report a primitive black rhino from the early Late Miocene of the Linxia Basin in Gansu, China. The new species, *Diceros gansuensis*, has a brachycephalic skull, a bulbous nasal horn boss followed by a frontal one, anteriorly shortened nasals, a laterally inclined lower border of orbit, a vertical occipital surface, a strongly concave cranial dorsal profile, a very high occiput, and a marked paracone fold.

Order Perissodactyla Owen, 1848

Family Rhinocerotidae Owen, 1845

Subfamily Rhinocerotinae Owen, 1845

Genus *Diceros* Gray, 1867

Diceros gansuensis sp. nov.

(Figs. 1-5; Tables 1-4)

Holotype　HMV 1421 (in collections of Hezheng Paleozoological Museum, Gansu, China), a skull and mandible without the left nasal bone and the occipital top (Figs. 1, 5B, 5C).

Referred material　HMV 1442, an old skull and mandible without the mandibular symphysis tip; HMV 1443, a young skull with erupting M3 (Fig. 3B); HMV 1446, a nearly complete adult skull, without the premaxillary tips (Figs. 2, 4C, 5A); HMV 1447, a juvenile skull with DP1-DP4 and erupting M2, but without the right occipital part (Figs. 3A, 4B); HMV 1448, a mandible without the coronoid processes and the left condyle (Fig. 4A).

Etymology　Gansu, indicating the fossils from Gansu Province in northwestern China.

Locality and horizon　Housan, Linxia Basin, Gansu, China; the red clay of the lower part of the Liushu Formation, Late Miocene.

Diagnosis　A moderate-sized dicerotine. Skull brachycephalic, premaxillae reduced and edentulous, nasal notch above the P3/P4 boundary, dorsal cranial profile concave, occipital elevation high, occipital surface vertical, narrow and high, maximum occipital width at the base, occipital crest shallowly concave, paroccipital process short and small, and sagittal keel and tubercle on the basioccipital strong; mandibular symphysis narrow, horizontal ramus thick, and ascending ramus vertical and thin, with a short distance to m3; premolars comparatively small, crista weak, antecrochet absent, metaloph absent on DP1, protoloph isolated on P2, and metaloph narrow on P2 and P3.

Description *Diceros gansuensis* is a moderate-sized (length of nasal-occiput = 591 mm) and brachycephalic (width/length ratio = 0.55) dicerotine. It is close to the living black rhino in size, but much smaller than the living white rhino. Comparatively, width/length ratio of the living black rhino = 0.58, and that of the living white rhino = 0.43 (Guérin, 1980). *Diceros gansuensis* shares numerous cranial, mandibular and dental similarities with other dicerotines (Prothero et al., 1986; Heissig, 1989; Cerdeño, 1995; Antoine, 2002; Geraads, 2005).

The premaxilla is reduced and edentulous. The lower border of the orbit is inclined laterally. The infraorbital foramen is large and near the nasal notch. The lacrimal tubercle is marked, and the supraorbital tuberosity is strongly projected laterally (zygomatic width/frontal width ratio = 1.24). The postorbital process is absent on the frontal. The zygomatic arch is low and narrow, without any postorbital process. The external auditory pseudomeatus is partially closed. The anterior part of the nasals is very broad and rounded, and the nasal horn boss is large, rough, and bulbous. The nasals are totally fused, with a narrow and deep median groove in the anterior part. The nasals are short (length of nasal tip-notch is 165 mm). The frontal horn boss is wide and low. The parietal crests are smooth and widely separate (minimum width = 53 mm). The pit of rectus capitis dorsalis major is deep. The palate is narrow, and the palatine fossa reaches the middle of M2. The vomer is thick and rounded. The postglenoid process is long, strong, narrow transversally, and slightly curved anteriorly, with a strong central crest on the lateral side. The posttympanic process is short, thin, and curved anteriorly, while the paraoccipital process is small, short, and straight. Their bases are fused. The foramen magnum is circular, and the occipital condyle is smooth and rounded.

In a juvenile skull (HMV 1447), the nasal and frontal horn bosses have no any trace, and nasals are narrow. The lacrimal bone is not connected with the nasal bone. The dorsal cranial profile is shallowly concave, with a low occipital elevation. The palate is broad, the pit of rectus capitis dorsalis major is shallow, and the pterygoid valley is wide. The paroccipital process is strong, and the posttymponic process is thick, but not connected with the postglenoid process. The parietal crests are separate more broadly.

The mandibular symphysis is narrow (74 mm) and strongly uplifted, with a concave lingual surface. The posterior border of the symphysis ends at the p3/p4 boundary. The labial surface of the symphysis is flat, with two small nutritive foramina. The small slit-like mental foramen is present below the p2/p3 boundary. The horizontal ramus is low and thick, with a height of 88 mm and a thickness of 73 mm at the p4/m1 boundary, and it has a curved ventral border. The ascending ramus is vertical and thin, with a short distance to m3 (35 mm). The mandibular angle is rounded and rough. The coronoid process is thin (4.5 mm), curved posteriorly, concave laterally, and convex medially. The mandibular condyle is narrow and long, with a wide and deep posterior groove and a strong and rounded posterior crest.

The upper teeth are hypsodont (lightly worn M2 is 70 mm high). The antecrochet and the protocone constriction are absent, and the protoloph is curved posteriorly. The crochet is narrow and short on premolars, while robust and long on molars. The crista is weak on premolars, while absent on molars. The parastyle is sagittal on premolars, while oblique laterally on molars. The premolars are molariform, with separate lingual cusps. The labial cingulum is absent, but a reduced lingual cingulum is present. The posterior valley is deep, narrow, and closed at moderate wear. The protoloph is isolated from the ectoloph on P2. The molars are lacking labial and lingual cingula. The metastyle is long. The metaloph is short, and the posterior part of the ectoloph is concave on M1-2. The posterior cingulum is low and reduced. The labial wall is undulate on M1-2. M3 has a triangular outline. On the lower teeth, the labial groove is deeply V-shaped unto the base; the paraconid and the protoconid are angled, and the trigonid is acute or right-angled; the paralophid is well developed; the lingual and labial cingula are absent. On p2, the paralophid is expanded, and the paraconid is reduced.

On the upper milk premolars, the protocone and the hypocone are not constricted, and they have a similar size with a rounded lingual margin; the labial wall is slightly undulated, with a weak parastyle, but without a paracone rib; the antecrochet and the crista are absent; and the lingual and labial cingula are absent. The protoloph of DP1 becomes a rounded lingual wall, and the metaloph is absent. DP2 has a bridge. The median valley is open on DP3 and DP4. The posterior valley is absent on DP2, and small and closed on DP3 and DP4. DP1 is infrequent in the adult. In the Linxia material, DP1 is present only in the holotype.

Comparison and discussion　Different from *Ceratotherium*, *Diceros gansuensis* has a brachycephalic skull, a strongly concave dorsal cranial profile, a relatively high occipital elevation, an upward tilted braincase relative to the face, a vertical occipital surface, occipital condyles at the same level with the occipital crest, a shallowly concave occipital crest, a high basioccipital crest, a strong basilar tuberosity, vertical and thin ascending rami with a short distance to m3, a weak crista on premolars, a marked paracone fold, and a posteriorly oblique hypolophid.

Geraads (1988) revised *Diceros neumayri* from the Eastern Mediterranean into *Ceratotherium neumayri*. Kaya (1994), Heissig (1996, 1999), Bonis and Koufos (1999), Fortelius et al. (2003), Giaourtsakis (2003), and Antoine and Saraç (2005) adopted *C. neumayri*. In the diagnosis of *Ceratotherium* proposed by Geraads (2005:451), however, almost all characters are shared by *Diceros*; only the paracone rib on the molars of *Diceros* is stronger than on the molars of *Ceratotherium*.

Actually, the different characters of *Ceratotherium* from *Diceros* should be a flat or shallowly concave cranial dorsal profile, a low occipital elevation, a shallow nasal notch above the P2/P3 boundary with a long distance to the orbit, a posteriorly oblique occipital surface, an overhanging occipital crest beyond the occipital condyles, thin postglenoid and paroccipital processes, thick and posteriorly oblique ascending rami with a long distance to m3, posteriorly curved protoloph and metaloph on the cheek teeth, well-developed crista and medifossette, and a nearly sagittal hypolophid on m3. These characters can be seen in the African Pliocene and Pleistocene forms, such as *Ceratotherium mauritanicum* (Geraads, 2005). *Diceros neumayri* lacks these characters, but it is identical with *Diceros*. As a result, *D. neumayri* should be kept in the genus *Diceros*.

The skull and teeth of *Diceros gansuensis* differ from those of *Diceros neumayri*. In *D. neumayri*, the skull is larger, especially from Maragha, Pikermi, and Akkaşdağı (Gaudry, 1862-1867; Weber, 1904; Thenius, 1955; Antoine and Saraç, 2005); the skull is longer; the occipital elevation is lower; the occipital surface is wide and low, and the occipital crest is deeply concave; the paroccipital process is robust; the premolars are comparatively larger; DP1 has a metaloph, and DP2 has a mesostyle; the protoloph is connected with the ectoloph on P2; and the metaloph is wider on P2 and P3.

The teeth of *Diceros gansuensis* are similar to those of *Diceros primaevus* from Bou Hanifia, Algeria (Arambourg, 1959). They share the absence of the metaloph on DP1, and the wide connection of the metaloph with the ectoloph on DP2 and DP3. The teeth of *D. primaevus* differ from those of *D. gansuensis* in having a larger size, a well-developed lingual cingulum and a marked anterior groove of the protocone on the molars.

Diceros gansuensis resembles *Diceros praecox* from Kanapoi, Kenya (Hooijer and Patterson, 1972; Geraads, 2005) with respect to dental morphology, such as the absence of the mesostyle and the posterior valley on DP2. On the other hand, differences exist between the two species. In *D. praecox*, the nasal notch is above the posterior part of P2, the anterior border of the orbit is above M1, the base of the occipital surface is not wider than the top, the crista is absent and the posterior valley is open on the premolars, the protoloph is connected with the ectoloph on P2, the crista and the crochet are strong on the milk premolars, and the metaloph is present on DP1.

The skull, mandible and teeth of *Diceros gansuensis* are distinct from those of the living black rhino *Diceros bicornis*. In the latter, the skull is shorter, the nasal bones are wider, the nasal notch is shallower above the P2/P3 boundary, the anterior border of the orbit is more anteriorly above the middle of M1, the postorbital process is marked on the zygomatic arch, the occipital surface is low, the mandibular symphysis ends at the level of the middle of p3, the mental foramen is large, the horizontal ramus is thinner, and the ascending ramus is narrower.

Lacking fossils, the early evolutionary history of dicerotines is therefore still poorly known. The earliest member of the dicerotines is *Paradiceros mukirii* from the late Middle Miocene of Fort Ternan, Kenya and Beni Mallal, Morocco (Hooijer, 1968; Guérin, 1976). It has a shallow nasal notch above P2, separate postglenoid and posttympanic processes, a vertical occipital surface, an abbreviated and edentulous mandibular symphysis, brachyodont cheek teeth, a constricted protocone, a prominent antecrochet, subtriangular M3, and a mesostyle on DP2 (Hooijer, 1968). But the subsequent evolution of dicerotines has been the subject of much confusion due to rare and fragmentary fossils. During the early Late Miocene, the primitive *Diceros primaevus* from Bou Hanifia, Algeria is very similar to *Paradiceros*, with strong lingual cingula in the premolars and low crowns on the cheek teeth (Arambourg, 1959). *Diceros douariensis* from Tunisia (Guérin, 1966) could be conspecific with *D. neumayri* (Geraads, 2005). The Early Pliocene *Diceros praecox* from East Africa is the ancestor of the living black rhino, and *Diceros bicornis* first appeared in East Africa during the Early Pleistocene (Hooijer and Patterson, 1972; Geraads, 2005).

In Eurasia, some specimens from the Middle Miocene of Anatolia and Chios were considered to be *Diceros*, with anteriorly shortened nasals, a laterally inclined lower border of the orbit, and lack of functional incisors. The skull resembles the living *Diceros*, but the mandible resembles *Ceratotherium* (Heissig, 1989). However, these specimens were indicated to be uncertain, so they should be considered as Rhinocerotidae indet. (Giaourtsakis, 2003). A new species *Diceros gabuniae* was described from a Vallesian locality in Caucasus (Tsiskarishvili, 1987), but it was considered to be a regional variant of *D. neumayri* (Giaourtsakis, 2003). *D. neumayri* expanded its range over the Eastern Mediterranean during the Late Miocene, and it developed rather hypsodont teeth (Geraads, 1988; Heissig, 1989, 1996; Geraads and Koufos, 1990; Antoine and Saraç, 2005).

There are two completely different opinions about the early history of dicerotines. One opinion suggests that the dicerotines were split up into its two living genera already at the beginning of the Late Miocene. *Diceros primaevus* from the Vallesian of North Africa is the ancestor of *D. neumayri* (Heissig, 1999). On the other hand, another opinion believes that the two lineages did not split until the Miocene-Pliocene boundary. "*Ceratotherium neumayri*" from the Late Miocene of the Eastern Mediterranean is the earliest representative of *Ceratotherium* and a likely ancestor for both living dicerotine species, and *Diceros* rises in the Early Pliocene (Geraads, 2005). However, it is questionable for a certain species of *Ceratotherium* as the ancestor of the *Diceros* lineage. *Diceros* has a series of more primitive characters than *Ceratotherium*, such as a vertical occipital surface, a weak crista, a marked paracone fold, a shallowly concave occipital crest, and vertical ascending rami.

Diceros gansuensis is the first fossil species of the *Diceros* lineage ever discovered in East Asia, and it is the best preserved. In *Diceros gansuensis*, the development of a vertical occipital surface brings about the possibility of a browsing mode of life. The material of *D. gansuensis* is collected from the eolian red clay deposits of the Liushu Formation. The locality is localized in the Linxia Basin with the abundant fossils of the *Hipparion* fauna during the Late Miocene. Associated with the new rhino are abundant fossils commonly found in the *Hipparion* fauna, including two weasels *Promephitis parvus* and *Parataxidea sinensis*, two hyenas *Hyaenictitherium wongii* and *Dinocrocuta gigantea*, an elephant *Tetralophodon exoletus*, two three-toed horses *Hipparion chiai* and *Hipparion weihoense*, three other rhinos *Acerorhinus hezhengensis*, *Chilotherium wimani*, and *Iranotherium morgani*, two deers *Cervavitus novorassiae* and *Metacervulus* sp., two giraffes *Samotherium* sp. and *Honanotherium schlosseri*, and three bovids *Hezhengia bohlini*, *Gazella* sp., and *Miotragocerus* sp. (Deng, 2006). All of these animals are steppe or grassland dwellers. This period is an eolian environment, with a dry and hot climate (Liang and Deng, 2005). *D. gansuensis* is no doubt also a steppe dweller.

References

Antoine P O, 2002. Phylogénie et évolution des Elasmtheriina (Mammalia, Rhinocerotidae). Mém Mus Natl Hist Nat, **188**: 1-359

Antoine P O, Saraç G, 2005 Rhinocerotidae (Mammalia, Perissodactyla) from the Late Miocene of Akkaşdağı, Turkey. Geodiversitas, **27**: 601-632

Arambourg C, 1959. Vertébrés continentaux du Miocène supérieur de l'Afrique du Nord. Publ Serv Car Géol Algérie, Paléont, **4**: 1-159

Arambourg C, Piveteau J, 1929. Les vertébrés du Pontien de Salonique. Ann Paléont, **18**: 1-82

Bonis L de, Koufos G D, 1999. The Miocene large mammal succession in Greece. In: Agusti J, Rook L, Andrews P eds. Hominoid Evolution and Climatic Change in Europe. Volume 1: The Evolution of Neogene Terrestrial Ecosystems in Europe. Cambridge: Cambridge University Press. 205-237

Cerdeño E, 1995. Cladistic analysis of the family Rhinocerotidae. Am Mus Novit, (3134): 1-25

Deng T, 2006. Paleoecological comparison between Late Miocene localities of China and Greece based on *Hipparion* faunas. Geodiversitas, **28**: 499-516

Deng T (邓涛), Wang X M (王晓鸣), Ni X J (倪喜军) et al., 2004. Cenozoic stratigraphic sequence of the Linxia Basin in Gansu, China and its evidence from mammal fossils. Vert PalAsiat (古脊椎动物学报), **42**(1): 45-66 (in Chinese with English summary)

Dietrich W O, 1945. Nashornreste aus dem Quartär Deutsch-Ostafrikas. Palaeontographica, **96**: 45-90

Fortelius M, Heissig K, Saraç G et al., 2003. Rhinocerotidae (Perissodactyla). In: Fortelius M, Kappelman J, Sen S et al. eds. Geology and Paleontology of the Miocene Sinap Formation, Turkey. New York: Columbia University Press. 282-307

Gaudry A, 1862-1867. Animaux Fossiles et Géologie de l'Attique. Paris: Savy. 1-472

Geraads D, 1986. Sur les relations phylétiques de *Dicerorhinus primaevus* Arambourg, 1959, rhinocéros du Vallésien d'Algérie. Comp Rend Acad Sci, **302**: 835-837

Geraads D, 1988. Révision des Rhinocerotidae (Mammalia) du Turolien de Pikermi: comparaison avec les formes voisines. Ann Paléont, **74**: 13-41

Geraads D, 2005. Pliocene Rhinocerotidae (Mammalia) from Hadar and Dikika (Lower Awash, Ethiopia), and a revision of the origin of modern African rhinos. J Vert Paleont, **25**: 451-461

Geraads D, Koufos G, 1990. Upper Miocene Rhinocerotidae (Mammalia) from Pentalophos-1, Macedonia, Greece. Palaeontogr Abt A, **210**: 151-168

Giaourtsakis I X, 2003. Late Neogene Rhinocerotidae of Greece: distribution, diversity and stratigraphical range. Deinsea, **10**: 235-253

Gong H J (弓虎军), Zhang Y X (张云翔), Huang L (黄雷), 2005. Paleoenvironment significance of grain-size composition of Neogene red clay in Linxia Basin, Gansu Province. Acta Sediment Sin (沉积学报), **23**(2): 260-267 (in Chinese with English abstract)

Guérin C, 1966. *Diceros douariensis* nov. sp., un rhinocéros du Mio-Pliocène de Tunisie du Nord. Doc Lab Géol Lyon, **16**: 1-50

Guérin C, 1976. Les restes de Rhinocéros du gisement miocène de Beni Mellal, Maroc. Géol Méditerran, **3**: 105-108

Guérin C, 1980. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pleistocène supérieur en Europe occidentale: comparason arec les expèces actuelles. Doc Lab Géol Lyon, **79**: 1-1182

Guérin C, 2000. The Neogene rhinoceroses of Namibia. Palaeont Afr, **36**: 119-138

Heissig K, 1975. Rhinocerotidae aus dem jungtertiär Anatoliens. Geol Jahrb, B, **15**: 145-151

Heissig K, 1989. Rhinocerotidae. In: Prothero D R, Schoch R M eds. The Evolution of Perissodactyls. New York: Oxford University Press. 399-417

Heissig K, 1996. The stratigraphical range of fossil rhinoceroses in the Late Neogene of Europe and the Eastern Mediterranean. In: Bernor R L, Fahlbusch V, Mittmann H W eds. The Evolution of Western Eurasian Neogene Mammal Faunas. New York: Columbia University Press. 339-347

Heissig K, 1999. Family Rhinocerotidae. In: Rössner G E, Heissig K eds. The Miocene Land Mammals of Europe. München: Verlag Dr. Friedrich Pfeil. 175-188

Hooijer D A, 1968. A rhinoceros from the Late Miocene of Fort Ternan. Zool Mededel, **43**: 77-92

Hooijer D A, Patterson B, 1972. Rhinoceroses from the Pliocene of northwestern Kenya. Bull Mus Comp Zool, **144**: 1-26

Jernvall J, Fortelius M, 2002. Common mammals drive the evolutionary increase of hypsodonty in the Neogene. Nature, **417**: 538-540

Kaya T, 1994. *Ceratotherium neumayri* (Rhinocerotidae, Mammalia) in the Upper Miocene of western Anatolia. Turk J Earth Sci, **3**: 13-22

Kretzoi M, 1942. Bemerkungen zum System der nachmiozänen Nashorn-Gattungen. Földt Közl, **72**: 4-12

Liang Z (梁忠), Deng T (邓涛), 2005. Age structure and habitat of the rhinoceros *Chilotherium* during the Late Miocene in the Linxia Basin, Gansu, China. Vert PalAsiat (古脊椎动物学报), **43**(3): 219-230 (in Chinese with English summary)

Mecquenem R de, 1908. Contribution à l'étude du gisement de vertébras de Maragha et de ses environs. Ann Hist Nat Paris, **1**: 27-79

Osborn H F, 1900. Phylogeny of the rhinoceroses of Europe. Bull Am Mus Nat Hist, **13**: 229-267

Pomel A, 1885. Sur la station préhistorique de Ternifine, près de Mascara (Algérie). Assoc Franç Avanc Sci, Comp Rend, **14**: 164

Prothero D R, Guérin C, Manning E, 1989. The history of the Rhinocerotoidea. In: Prothero D R, Schoch R M eds. The Evolution of Perissodactyls. New York: Oxford University Press. 321-340

Prothero D R, Manning E, Hanson C B, 1986. The phylogeny of the Rhinocerotoidea (Mammalia, Perissodactyla). Zool J Linn Soc, **87**: 341-366

Prothero D R, Schoch R M, 1989. Classification of the Perissodactyla. In: Prothero D R, Schoch R M eds. The Evolution of Perissodactyls. New York: Oxford University Press. 530-537

Ringström T, 1924. Nashörner der *Hipparion*-fauna Nord-Chinas. Palaeont Sin, Ser C, **1**(4): 1-159

Schlosser M, 1921. Die *Hipparion* fauna von Veles in Mazedonien. Abh Bayer Akad Wiss, **29**(4): 1-55

Sisson S, 1953. The Anatomy of the Domestic Animals. Philadelphia: Saunders W B Comp. 1-972

Thenius E, 1955. Zur Kenntnis der unterpliozänen *Diceros*-Arten (Mammalia, Rhinocerotidae). Ann Naturhist Mus Wien, **60**: 202-209

Tsiskarishvili G V, 1987. Late Tertiary Rhinoceroses (Rhinocerotidae) of the Caucasus. Tbilisi: Metsnierba. 1-142 (in Russian)

Wagner A, 1848. Urweltliche Säugthiere-Überreste aus Griechenland. Abh Bayer Akad Wiss, **5**(2): 335-378

Weber M, 1904. Ueber tertiäre Rhinocerotiden von der Insel Samos. Bull Soc Imp Nat Moscou, **17**: 477-501

Zeuner F, 1934. Die Beziehungen zwischen Schädelform und Lebensweise bei den rezenten und fossilen Nashörnern. Ber Naturf Ges Freiburg, **34**: 21-79