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甘肃临夏盆地晚中新世貘类化石（奇蹄目、貘科）一新种[1)]

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摘要：描述在甘肃临夏盆地晚中新世地层中发现的貘属新种和政貘（*Tapirus hezhengensis* sp. nov.），它是貘属中已知最小的种之一。在基本特征上，临夏盆地的和政貘与现生貘已相当接近，前臼齿完全臼齿化，门齿、犬齿的数目和形态也与现生貘一致。东亚晚中新世缺少貘科化石的材料，和政貘的发现对中国第四纪貘类的来源提供了重要线索，显示中中新世起源于欧洲的真貘在晚中新世时期已扩散至东亚。貘类通常适应于潮湿的热带森林环境，但和政貘在华北三趾马动物群中的发现说明这类动物也能够生活于干旱的温带草原地区。

关键词：甘肃临夏盆地，晚中新世，柳树组，貘科

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貘科化石的发现与研究虽然已有100多年的历史，但在新近纪地层中发现的貘科化石相当稀少，而且大多是零散的牙齿标本。在欧洲有一些中新世的真貘（*Tapirus*）化石发现，最早的种是Hofmann（1893）创建的*Tapirus telleri*，发现于奥地利Styrian盆地的Göriach和波兰的Opole 2，从未到达过西欧，这个种的时代为Astaracian（MN6）。另一个分布较广的种是Kaup（1833）创建的*Tapirus priscus*，发现于德国的Eppelsheim、Westhofen、Wissberg，西班牙的Can Llobateres，法国的Priay，奥地利的Biedermannsdorf和匈牙利的Rudabanya，这些地点的时代都为Vallesian期（MN9）（Heissig，1999）。Zdansky（1935）在山西武乡晚中新世地层中发现的德氏貘（*Tapirus teilhardi*），其地点和时代都不确切。最近，我们在临夏盆地的广河县官坊乡石磊一带考察时，在该地点柳树组上部的红粘土中发现了貘类的一件幼年个体的头骨和下颌骨前部，后又在和政县买家集乡王家山的相同层位发现一件此类貘的成年头骨前半部。貘类标本在临夏盆地的发现不但证实了中国晚中新世确实产真貘化石，为我们进一步了解真貘属早期种类的性质和时代分布提供了新的关键信息，更重要的是，它填补了貘类在东亚的进化过程中在晚中新世存在的空缺和中断。中国第四纪的貘化石分布广泛，但新近纪的貘化石则非常稀少。发现于山东山旺早中新世晚期的近貘（*Plesiotapirus*）已被认定与

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Tapirus 属没有直接的演化关系(邱占祥等,1991),而产自武乡的德氏貘已经与第四纪的貘类非常接近。所以,此前关于中国第四纪真貘的来源一直是一个悬而未决的问题。

IVPP LX 和 IVPP V 分别为中国科学院古脊椎动物与古人类研究所野外地点编号和化石编号。下颊齿冠面的术语依据邱占祥、王伴月(2007,图7)对奇蹄类的意见。

貘科 Tapiridae Burrett, 1830

貘属 *Tapirus* Brünnich, 1772

属型种　*Tapirus terrestris* (Linnaeus, 1758),现生种,属型分布区为巴西东北部的伯南布哥州(Pernambuco)。

属征　中到大型的貘类;上下吻部不匀称,形成较长的鼻部;前臼齿高度臼齿化;颊齿低冠,但与其他貘类相比较高;上犬齿退化,其功能被强大的I3替代(Heissig, 1999)。

和政貘(新种) *Tapirus hezhengensis* sp. nov.

(图1-4;表1-6)

正型标本　IVPP V 15522,头骨前半部,保存I3、C和P1-M2,DP4刚刚脱落(图1-2)。

副型标本　V 15523,属于同一幼年个体的头骨和下颌骨前半部,从下颌骨保留的齿槽判断,m2刚刚萌出(图3-4)。

产地　V 15522产自甘肃省和政县买家集乡王家山(IVPP LX0501,35°22′34.3″N,103°12′48.9″E,海拔2575 m),V 15523产自广河县官坊乡石磊(LX0031,35°25′19.7″N,103°27′30.3″E,海拔2263 m)。

层位与时代　两件标本均产自上中新统柳树组上部红粘土堆积中。化石层的时代为保德期(晚中新世晚期,NMU10),距今约8.3 Ma,相当于欧洲陆生哺乳动物分期的Turolian早期(MN11)。

名称来源　和政,模式标本产地。

鉴定特征　小型的真貘,是 *Tapirus* 属中已知最小的种之一。前颌骨鼻突短,处于齿隙后部水平,末端截平,插入上颌骨中。下颌联合部长而窄,后部显著收缩,舌面凹陷深。门齿排列紧密,I3加大成犬齿状,上犬齿显著变小,下犬齿发达。齿隙长,C-P1长于P1+P2。P1三角形,长大于宽,无原尖,次尖微弱。其余上颊齿宽大于长。P3和P4矩形,P2、M1和M2梯形,P2前半部收缩,M1和M2后半部收缩。外齿带发达,但不完全,前、后齿带也相当发育。前臼齿完全臼齿化,原脊和后脊几乎平行,中谷开阔而深,前附尖发达。

描述　V 15522头骨仅保留上颌骨和前颌骨(图1-2),带有完整的右I3和残破的左I3,左右I1-2仅保留齿根;带有完整的左右犬齿;带有左右P1-M2颊齿列,左P1和右P2-3残破,DP4刚刚脱落。颊齿磨蚀极轻或未磨蚀,齿冠高度为8.6~11.2 mm。

上颌骨侧面轻微隆突;内面在背腹方向凹入,形成鼻腔侧壁的较大部分。上颌骨前端尖锐,此处与前颌骨结合,共同形成犬齿齿槽。上颌在P1之前突然收缩。上颌骨的腭突从骨体内面下部呈板状突起,形成硬腭基部的主要部分。其鼻侧面光滑,后部非常薄而横向凹陷,在中缝上具有细窄的鼻嵴;前部厚而平,具有一条宽的纵向嵴,左右结合形成犁鼻器的一条浅沟;前、后部之间形成一个高而圆的台阶;腭面轻微凹陷。眶下管几乎水平延伸,位于上颌骨内板

的上缘,其外侧开口眶下孔大,开口向前,有宽短而深的前导沟,位于 P3/P4 界线水平,其水平位置高于眼眶下缘。上颌骨上缘,即鼻切迹下缘呈宽浅的弧形凹陷。眼眶下缘宽大厚实而圆滑,形成强烈突起的面嵴,但在眼眶前很快消失,眼眶前缘位于 P4/M1 界线水平。

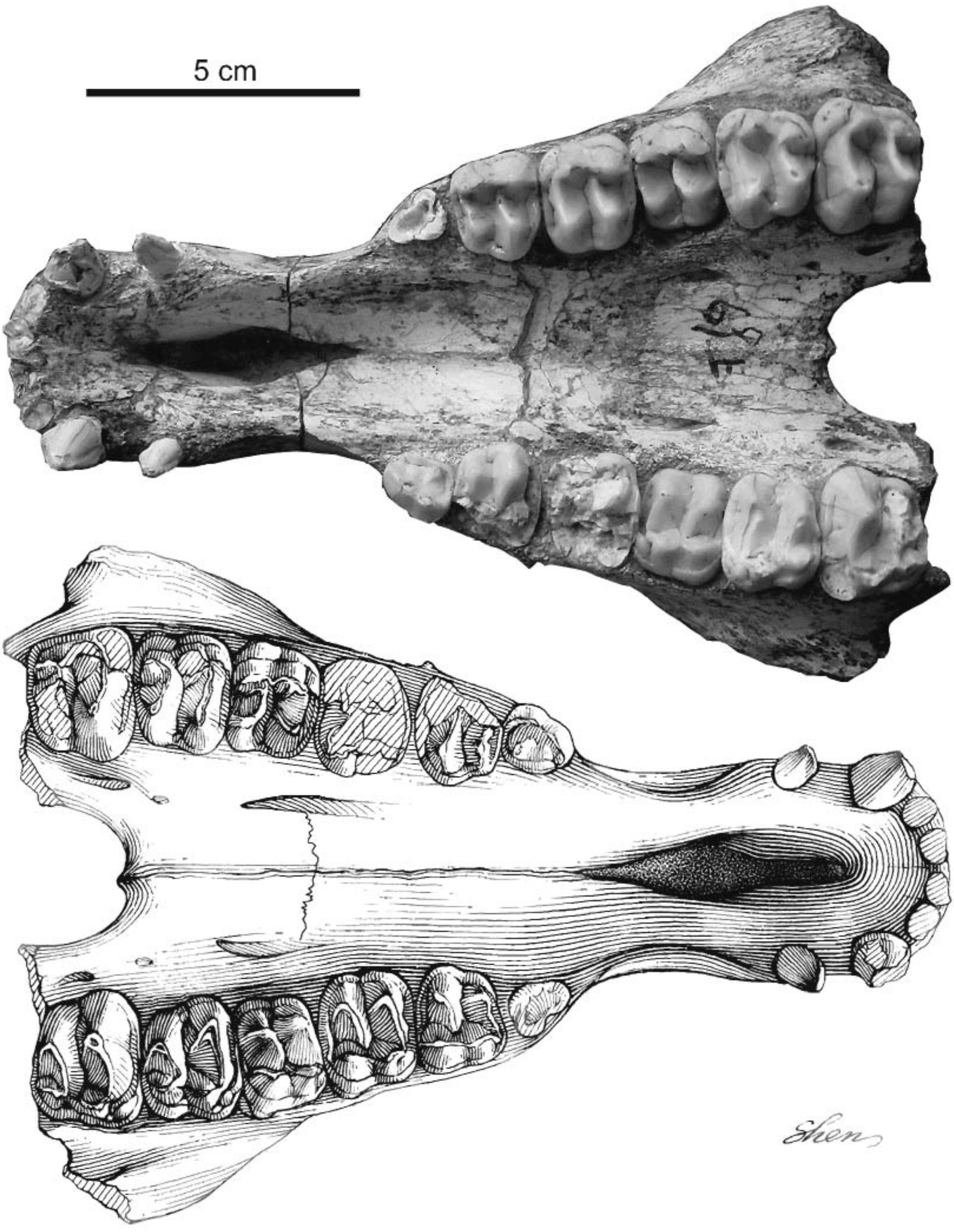

图 1 和政貘(新种)头骨前部,正型(IVPP V 15522)腹视

Fig. 1 Anterior portion of the skull of *Tapirus hezhengensis* sp. nov., holotype (IVPP V 15522), ventral view

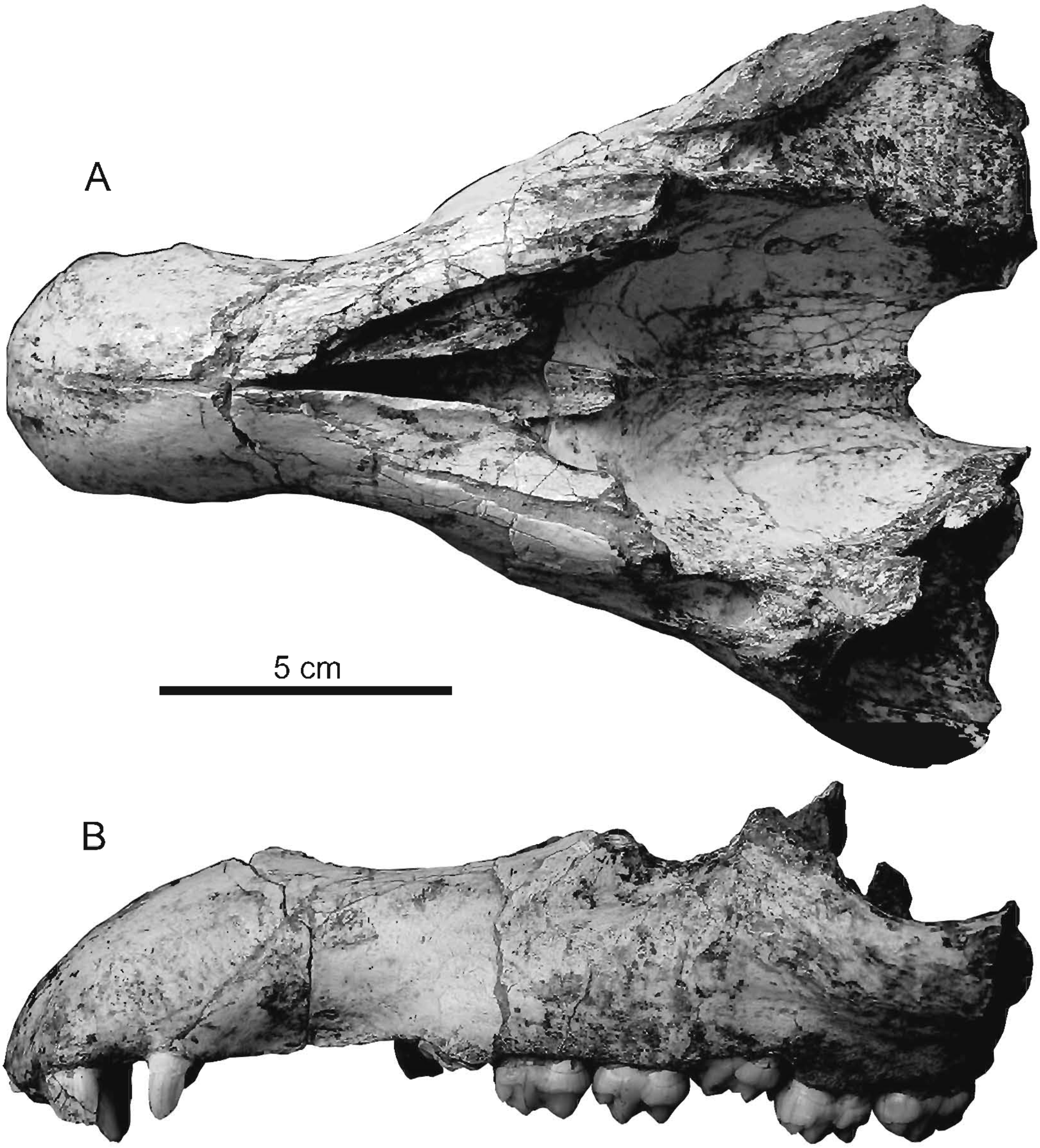

图2　和政貘(新种)头骨前部,正型(IVPP V 15522)

Fig. 2　Anterior portion of the skull of *Tapirus hezhengensis* sp. nov., holotype (IVPP V 15522)

A. 背视 dorsal view; B. 侧视 lateral view

前颌骨的唇面圆隆而光滑,其腭面狭窄而深凹陷。门齿孔窄长而深。齿槽缘薄锐而外倾。前颌骨背缘厚实,后部游离,两侧之间形成一条逐渐向后变宽的沟,鼻突后端截头状,直向后伸,插入上颌骨之中,鼻突后端约在齿隙后 1/3 处水平。相应的上颌骨背部向前伸出的尖锐突起能够在侧面看到,其内缘显著加厚。前颌骨的腹缘与上颌骨的骨缝直,从后上方向前下方倾斜。

腭骨水平部光滑,宽而长;中缝直,中嵴微弱。腭骨横缝锯齿状,位于 P3/P4 界线水

平,腭管前孔位于P4次尖水平,腭管后孔位于M2原尖水平。硬腭后缘位于M1/M2界线水平,呈宽U形。腭骨垂直部的鼻面前部凹陷而光滑。

幼年头骨(V 15523,图3)仅保留上颌骨和前颌骨,带有右I3、右DP2-DP4及M1齿根、左DP1-DP4前半部。乳前臼齿中度磨蚀,齿冠低于恒齿,残余齿冠高度为7.5~8.2 mm,釉质层更薄。从上颌骨破损处可以观察到尚在齿槽底部的左P3,其宽度为21 mm。幼年头骨的形态与成年头骨没有明显差别。下颌骨右侧自水平支中部断失,左侧保留少许上升支,带有右下犬齿、右dp2、dp3及dp4前齿根、左dp2-dp4,下颊齿残余齿冠高度为7.7~8.6 mm(图4)。从下颌骨破损处可以观察到尚在齿槽底部的右p4,其宽度为14.4 mm。由于为幼年个体,各骨之间的骨缝尚未愈合。头骨测量见表1。

表1 和政貘(新种)头骨的测量与对比

Table 1 Measurements and comparison of the skull of *Tapirus hezhengensis* sp. nov. (mm)

Measures	*T. hezhengensis* Adult V 15522	*T. hezhengensis* Juvenile V 15523	*T. telleri* Hofmann, 1893	*T. priscus* Eisenmann and Guérin, 1992	*T. indicus* IVPP 1326
Length of interalveolar space (C-P1)	40	33.4	—	40.2	51.7
Palatal length (P1-choanae)	84.5	74	104	118~124.5	106
Muzzle length	77.5	79	—	73~80	111
Palatal width in front of P2	37.4	38.7	55.4	39	58.7
Palatal width in front of P4	46	46.6	52.4	62.4	67.4
Length of premolar row	64	66.2	68.8	86~69.2	88.5
Length in front of orbit	156	—	—	187	194
Length of premaxilla	78.4	73	—	—	126.3
Minimal width of diastema	39.6	40	—	35~43	54.8
Muzzle width at incisors	42	42.6	~70	44~49	58.5

下颌联合部的舌面光滑而凹陷;唇面隆突,前端具中沟。联合部后部强烈收缩,齿槽缘高而薄锐。齿隙长,颏孔位于dp2前部水平,开口向前。水平支厚实,在dp4后的厚度为21 mm;侧面光滑而轻微隆突;内面光滑,其上部具有微弱的前后向凹陷;腹缘圆厚,轻微弧形弯曲。上升支的侧面前下部凹陷。下颌骨测量见表2。

表2 和政貘(新种)幼年下颌骨的测量与对比

Table 2 Measurements and comparison of the juvenile mandible of *Tapirus hezhengensis* sp. nov. (mm)

Measures	*T. hezhengensis* V 15523	*T. indicus* IVPP 535
Height of horizontal ramus in front of dp3	41.5	45
Height of horizontal ramus in front of dp4	41.8	44
Height of horizontal ramus in front of m1	39	43
Thickness of horizontal ramus in front of m1	21	30.4
Distance between horizontal rami in front of m1	25	46
Length of symphysis	63.6	72
Maximal width of symphysis	39	42
Minimal width of symphysis	30.6	34.3
Length of dp2-dp4	56	75
Length of interalveolar space (c-dp2)	42.5	50

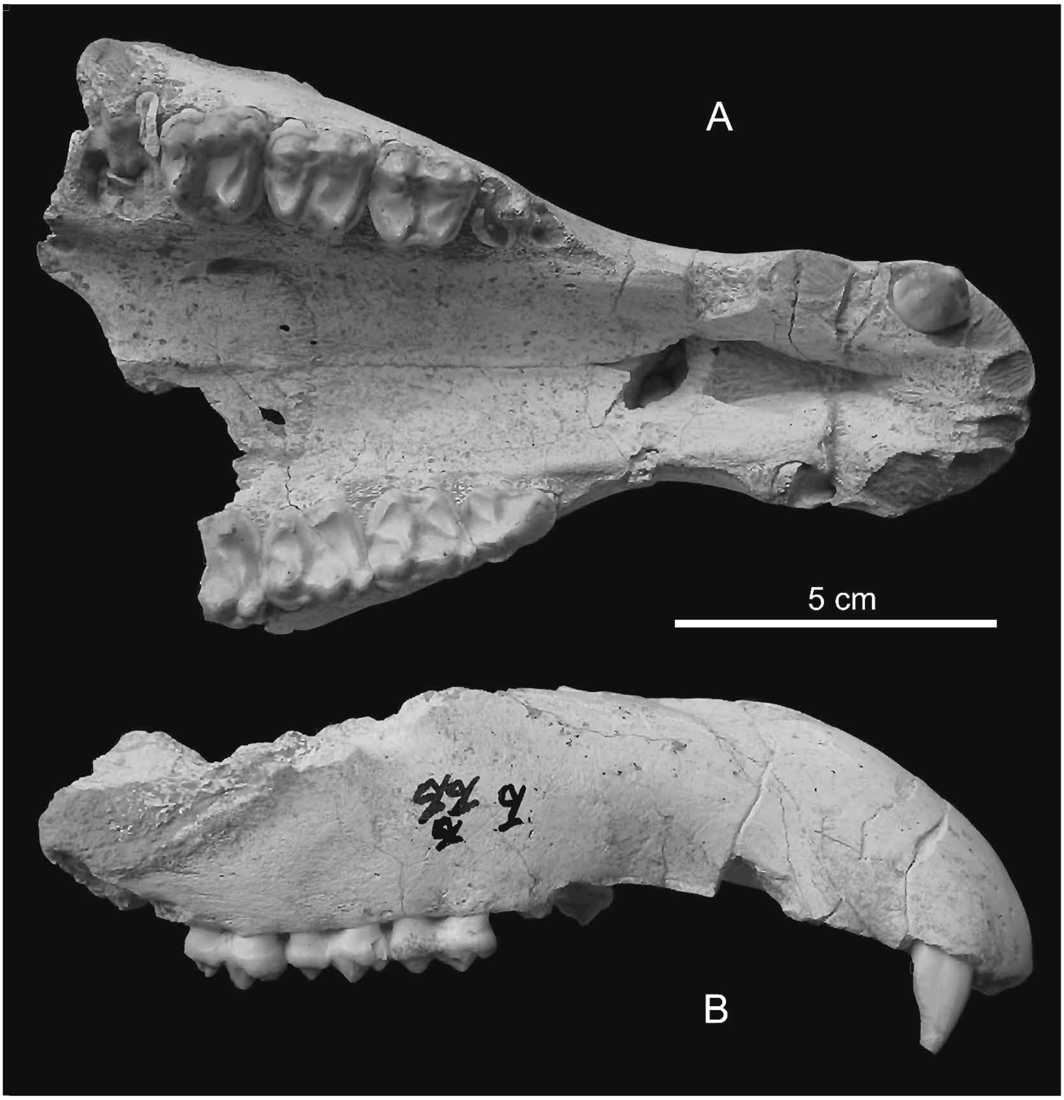

图 3　和政貘(新种)幼年头骨前部,IVPP V 15523

Fig. 3　Anterior portion of the juvenile skull of *Tapirus hezhengensis* sp. nov., IVPP V 15523

A. 腹视 ventral view; B. 侧视 lateral view

从保存完整的右 I3 看,这枚门齿整体上较直立,齿冠高而尖,末梢略向后弯。I1 和 I2 仅在幼年头骨上保留齿槽,在成年头骨上仅保留齿根,均呈长轴在前后方向的椭圆形,尺寸明显小于 I3,基部的大小仅为 I3 的 1/3。从基部判断,I1 略大于 I2。I3 的齿冠基部的横截面呈饱满的椭圆形,齿冠的前后具翼状嵴。翼状嵴在唇、舌侧都以竖沟与隆突的中部相隔,内侧竖沟更显著。犬齿与 I3 的形态完全一致,但尺寸小得多,其基部大小与 I2 相近(表 3)。犬齿与 I3 间的齿槽间隙在幼年头骨为 7.4 mm,在成年头骨为 8 mm。颊齿之前的齿隙长,犬齿与前臼齿间的齿隙在幼年头骨为 33.4 mm,在成年头骨为 40 mm,都大于 DP1 + DP2(30.8 mm)或 P1 + P2(30.3 mm)的长度。

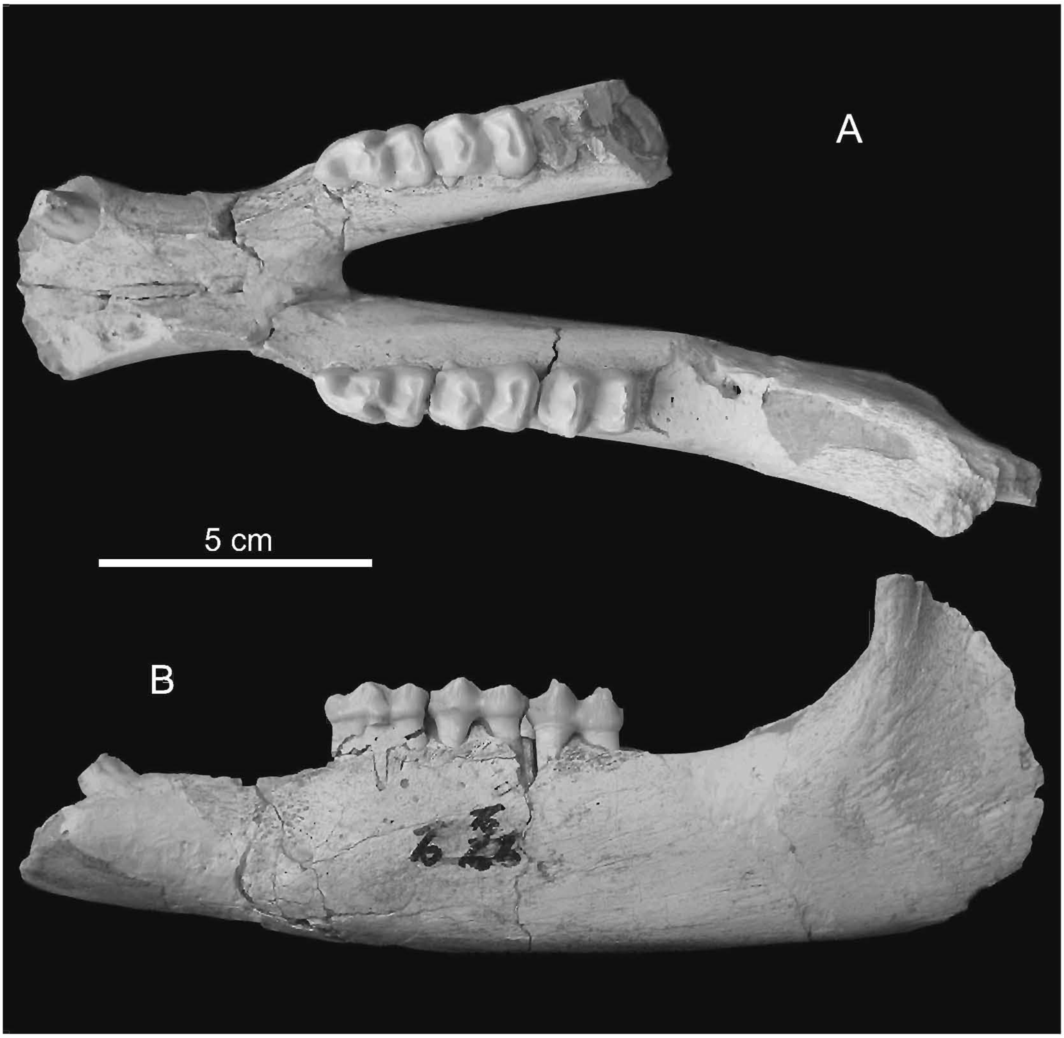

图4 和政貘(新种)幼年下颌骨前部,IVPP V 15523

Fig. 4 Anterior portion of the juvenile mandible of *Tapirus hezhengensis* sp. nov., IVPP V 15523

A. 嚼面视 occlusal view; B. 侧视 lateral view

表3 和政貘(新种)上门齿和犬齿的测量与对比(长×宽×高)

Table 3 Measurements and comparison of upper incisors and canine of *Tapirus hezhengensis* sp. nov. (L×W×H) (mm)

Taxa	I1	I2	I3	C
T. hezhengensis (V 15523)	8.5×7×—	7.8×6×—	11.5×10.3×18	6.4×6.5×11
T. telleri (Hofmann, 1893)	—×10×13.8	12.3×9.4×13.7	14×13.7×18.4	—
T. indicus (IVPP 1326)	10×8.6×10.2	8.6×9×9.5	15.7×13.4×25	10×9×11
E. robustus (Koenigswald, 1930)	—	—	10.3×9×11	—

从成年头骨上的第一前臼齿比幼年头骨的DP1磨蚀程度还要低的情况判断,第一前臼齿确实存在替换。除P1外,其余颊齿的宽度皆大于长度(表4),中谷陡而深,皆开放至牙齿基部。P2-P4的原脊和后脊分别在前尖和后尖前方连接外脊的基部。P2-M1的原尖在4个主要齿尖中最低,次尖最高;M2的后尖最低,次尖仍然最高。

P1的形状为三角形。外脊高耸,向内侧倾斜,中沟显著,将外壁分为前大后小两部分。前尖略高于后尖,中间以一个浅谷相隔,外脊细长。牙齿的舌侧形成一个低矮的平台,原尖和原脊无,次尖细小,后脊微弱。唇侧齿带仅微弱发育于后尖外侧。前附尖非常微弱,在外壁前端形成一条细小的釉质突起。内齿带发达,与同样发达的后齿带连贯。

P2的形状呈梯形,前缘和舌缘略相等,较短,舌缘前部显著收缩;后缘和唇缘略相等,较长;舌缘和唇缘具微弱的中沟。外脊、原脊和后脊高耸。前尖和后尖都为唇侧隆突、舌侧较平的锥形,后尖略大和略高于前尖。前尖和后尖之间以宽谷相隔,外壁中沟宽浅。前附尖与前尖显著分离,前附尖比前尖低得多,以一个浅谷分隔两尖,在外壁上则表现为深沟。前、后齿带发达,内齿带仅发育于中谷口,外齿带在前尖处中断。原尖和次尖皆呈圆锥形,原尖向唇侧偏移,次尖大于原尖。原脊和后脊向后倾斜,后脊显著长于原脊,它们分别在原尖和后尖前部与外脊连接,连接处细弱而低矮。中谷宽阔,谷口略收缩。

P3大于P2,长方形,长度小于宽度。外脊、原脊和后脊高耸,前尖与后尖几乎等大等高,前附尖与前尖完全分离。前、后尖呈舌侧平唇侧隆的半圆锥形,前尖以一条沟与突起较低的前附尖相隔,后尖略向舌侧方向偏移,以宽谷与前尖相隔。前、后齿带发达,外齿带在前尖处缺失,无内齿带。牙齿舌侧高于唇侧,而次尖略高于原尖。原脊近横向,后脊略向后倾斜,两脊几乎等长,它们皆以细窄的颈部分别与前尖和后尖的前部相连。整个中谷宽度均匀,谷口不收缩。

表4 和政貘(新种)上颊齿的测量与对比(长×宽)

Table 4 Measurements and comparison of upper cheek teeth of *Tapirus hezhengensis* sp. nov. (L×W) (mm)

Taxa	P1	P2	P3	P4	M1	M2
T. hezhengensis (V 15522)	14.2×12	17.4×20.3	17.2×21.6	16.6×21.2	17.8×21.4	21×24.5
T. telleri (Hofmann, 1893)	14.5×15	17.9×21.5	20.2×—	18.1×23	20.2×24.7	20.8×26.5
T. arvernensis (average) (Guérin and Eisenmann, 1994)	—	18.1×21	18.1×22.3	18.4×22.8	18.7×22.3	20.7×23.9
T. priscus (Eisenmann and Guérin, 1992)	18.2×16.2	20.1×21.8	20.8×24	20.8×24.5	21×23.8	23.9×27.3
T. yunnanensis (Shi et al., 1981)	13×14	19×20	—	17×20	18×22	19×22
T. sanyuanensis (Huang et al., 1991)	19.1×17	20×24.2	22.3×26.9	22.3×29.2	23.5×29.2	26.7×31.1
T. sinensis (Tong, 2004)	22×20	24×26.5	25×30.5	26×32.5	28.5×33.5	—
T. webbi (Hulbert, 2005)	18.8×16.6	20.7×23.1	21.3×24.7	22.3×26.5	23.4×25.5	26.1×27.7
T. indicus (IVPP 1326)	20.2×15.2	23×—	23×26	24×—	25.3×25.8	27.5×28.3
T. pannonicus (Boeuf, 1991)	—	15×17.8	15.4×19.9	15.5×20.4	17×19.6	18.5×21.7
E. ruber (Cerdeño and Ginsburg, 1988)	12.2×10	13.9×15.5	14.3×17.7	—	—	—
E. robustus (Koenigswald, 1930)	—	18×20.5	17.5×22	17×22	~18×~22	20×—

P4与P3非常相似,仅后脊稍短。上前臼齿已完全臼齿化,P2的原脊和后脊在舌侧也完全分开。

M1 的形状呈梯形,牙齿后壁显著短于前壁,而舌侧在四条边中最短。主要齿尖突起相当高。前附尖发达,向前内方向伸出一嵴与前齿带连贯。前尖与前附尖的分隔沟深。原尖磨蚀后显现发育反前刺。后尖强烈向舌侧方向偏移,以宽谷与前尖相隔。前齿带发达,后齿带仅发育于唇侧,外齿带在前尖处较弱,无内齿带。磨蚀后的原尖大于次尖。原脊近横向,后脊相当短并略向后倾斜。中谷宽阔。

M2 的轮廓和主要特征与 M1 一致,但比 M1 大得多。次尖向后部伸出两嵴,一条到达后谷底部,另一条在后壁中部与后齿带相连。

上乳颊齿齿冠相当低,3 个齿根,DP1 为前面 1 个、后面 2 个,其余乳前臼齿皆为唇侧 2 个,舌侧 1 个,舌侧齿根扁长,强烈中凹,几乎将齿根分为前后两个。外壁表面有釉质竖纹,分别向前尖和后尖顶端汇聚。除 DP1 外,各乳前臼齿比对应的恒齿窄(表 5),磨蚀后的原脊和后脊强烈低于外脊,其主要结构与对应的恒齿相似。

DP1 的原尖非常微小,位于牙齿舌缘中央,而磨蚀后的次尖巨大;舌侧齿带较弱而断续;后脊以一个细短的颈部在后尖前部与其相接。DP2 的前附尖磨蚀后相当大;原尖和次尖磨蚀后呈三角形,原尖小于次尖;原脊向后倾斜,后脊前缘近横向;中谷口狭窄。DP3 显著大于 DP2,牙齿的后缘短于前缘,而舌缘在牙齿的四条边中最短;前尖高于后尖,前附尖与前尖完全分离,同时后尖强烈偏向后侧,其结果是前尖几乎位于外壁中央;内齿带则仅发育于中谷口;磨蚀后的原尖大于次尖。DP4 的原脊宽度显著大于后脊,原尖向后的延伸较弱;前附尖特别发达。

表 5 和政貘(新种)上乳前臼齿的测量与对比(长×宽)

Table 5 Measurements and comparison of upper deciduous premolars of *Tapirus hezhengensis* sp. nov. (L×W) (mm)

Taxa	DP1	DP2	DP3	DP4
T. hezhengensis (V 15523)	15.3×12.6	17×16	18.5×17	17.7×19.2
T. sanyuanensis (Tong, 2004)	21×18.5	—	23.5×27	26×28
T. webbi (Hulbert, 2005)	20×16.5	22.1×20.6	22×21.2	23.2×24.3
T. indicus (IVPP 535)	17.8×16	23×21	22.8×22.2	24.4×23.5
E. bronnimanni (Schaub and Hürzeler, 1948)	15.2×11.4	17×15.7	16.5×15.7	17.3×18.3
E. robustus (Koenigswald, 1930)	—	—	17×17	—

下门齿皆脱落,从保存的齿槽判断,门齿前后向扁长,舌缘宽度明显小于唇缘。下犬齿发达,与 i3 之间没有齿槽间隙,犬齿直,明显向前外方倾斜。齿冠横截面呈长轴在前后向的椭圆形(表 6),舌侧略平,唇侧更隆,前、后端皆具棱嵴。

没有任何 dp1 存在的痕迹。下乳前臼齿双根,除 dp2 的前根以外,前、后根皆横扁。

dp2 呈前端尖锐的窄长三角形,齿带仅微弱地发育于下前尖至下前附尖唇侧。下前附尖高耸而尖锐,下前尖处不突起,而成为下前脊与下原脊交会的最低点。下前脊发达,向后外侧倾斜。下后尖与下原尖之间以窄沟相隔。下原尖为整个牙齿的最高处,下前附尖次之,下后尖更低。下原尖自顶端向前、外后和内后方各伸出一嵴。伸向外后方的嵴延伸至基部形成齿冠最宽处;伸向内后方的嵴与平伸的后脊和向前内侧伸出的次脊形成 3 嵴交会;伸向前方的嵴与下前尖相连形成向前下方倾斜的原脊。下内脊平伸,显著长于下

后脊,其后壁直、前壁凹。

dp3 已高度臼齿化,为纵向的长梯形,前缘短于后缘。齿带仅发育于下前尖唇侧和牙齿后缘。齿尖中以下后尖最高,下原尖次之,下内尖和下次尖的高度依次降低。下前脊细弱而低矮,平伸而微向内侧倾斜。下原脊细长,向前下方陡倾。下后脊粗壮而折曲,在前壁形成中沟,在后壁中央形成向后突出的折角并向后外方伸出一条细嵴与下次脊相接。下内脊宽大而平伸,其后壁平直、前壁中凹。下内脊比下后脊更宽更长,但略低于下后脊。下内尖舌缘平直,前、后角圆润。下次尖在牙齿外后角处形成近似的直角。

表 6 和政貘(新种)下犬齿和乳前臼齿的测量与对比(长×宽)

Table 6 Measurements and comparison of lower canine and deciduous premolars of *Tapirus hezhengensis* sp. nov. (L×W) (mm)

Taxa	c	dp2	dp3	dp4
T. hezhengensis (V 15523)	12×8.8	19.9×10.8	18.2×12.1	18.3×11.8
T. sanyuanensis (Tong, 2004)	—	29×16	23.5×16	25×17
T. webbi (Hulbert, 2005)	—	26.6×13.8	23.3×14.4	24.5×15.6
T. indicus (IVPP 535)	17.5×12.2	28.8×14.2	23.1×14.3	23.5×16.7

dp4 与 dp3 非常相似。差别在于 dp4 呈纵向的长方形;下前脊更发达,其下还有显著的前齿带;下后脊平伸,前壁中沟微弱,后壁无嵴伸出;下后脊和下内脊更加高耸,下后脊略宽于下内脊。下乳前臼齿的测量见表 6。

从 V 15523 的右侧水平支断面上可以观察到尚未萌出齿槽的 p4 的后部情况,其下内脊横向宽、前后向窄,后齿带显著,但很薄,其中央向上伸出一个高度为 1.5 mm 的较厚的齿板。

对比与讨论 亚洲新近纪发现的貘类化石相当少,仅包括在日本本州平牧组和中国山东山旺组发现的近貘(*Plesiotapirus*)(Matsumoto, 1921; 谢万明,1979;邱占祥等,1991)、在山西三趾马动物群中发现的德氏貘(*Tapirus teilhardi*)(Zdansky, 1935)、在云南和陕西晚中新世地层中发现的云南貘(*Tapirus yunnanensis*)和真貘未定种(*Tapirus* sp.)(时墨庄等,1981;祁国琴,1979;宗冠福等,1996;汤英俊、宗冠福,1987)。

从临夏标本显示的情况看,其前臼齿已完全臼齿化,P2-P4 唇侧的两尖,即原尖和次尖完全分离,并形成互相平行的两条横脊,即原脊和后脊。dp2-dp4 也形成完全平行的下后脊和下内脊。前臼齿达到如此臼齿化水平的已知有 4 个属,即晚渐新世至早中新世的 *Eotapirus*、中中新世至现代的 *Tapirus*、晚中新世的 *Tapiriscus* 和第四纪个体很大的 *Megatapirus*。临夏标本的吻部收缩,前颌骨鼻突很短,远未伸达上前臼齿上方;P1 有发育的次尖,原尖则未现;颊齿虽然为低冠,但与其他貘类相比较高;I3 完全犬齿化,上犬齿退化,显著小于 I3;i1 相对增大,i3 相对变小,下犬齿强大;犬齿与前臼齿之间的齿槽间隙相当长。临夏标本的这些特征说明它是 *Tapirus* 属的成员,但其较小的体型却是一个原始的性状(Schlaikjer,1937;Albright,1998)。临夏标本完全臼齿化的前臼齿很容易与貘科中臼齿化程度较弱的属,如 *Protapirus*、*Miotapirus* 和 *Paratapirus* 相区别。产于日本美浓(Mino)可儿(Kani)和中国山东山旺早中新世晚期的 *Plesiotapirus*,其体型约与现生最小的南美貘(*Ta-*

pirus roulili)相近,其I3不特别加大,下犬齿退失,颊齿前的齿隙短(C-P1短于P1+P2),P1原尖大并向唇侧伸出V形脊,P2-P4半臼齿化,中谷仅在上半部开放(邱占祥等,1991)。*Plesiotapirus*的这些特点明显不同于临夏标本。

临夏标本较为接近的属是*Eotapirus*,但它与*Eotapirus*也有显著的差别。*Eotapirus*这个属是Cerdeño and Ginsburg(1988)建立的,他们在建属时指定Schaub and Hürzeler(1948)所建立的*Tapirus broennimanni*为属型种,将其修订为*Eotapirus broennimmani*。属型种的正型标本是Depéret(1902)描述的发现于法国萨瓦(Savoie)省Pyrimont地点Agenian阶(MN2a)的右P2-M1齿列。Schaub and Hürzeler(1948)在建立*Tapirus broennimanni*时的材料也是带有乳齿列的幼年头骨和下颌骨残部,来自瑞士Langenthal的Wischberg。Cerdeño and Ginsburg(1988)在创立*Eotapirus*时研究了产自法国塔尔纳加龙(Tarn-et-Garonne)省Quercy地点的Stampian期的材料,订立一个新种*Eotapirus ruber*,正型标本(Qu 7345)为带有P1-P3的右上颌骨。他们归入*E. broennimanni*的还有以前描述过的很多材料,包括Depéret(1902)描述的*Paratapirus helveticus*和?*Paratapirus intermedius*,Viret and Hürzeler(1937)描述的*Tapirus intermedius* var. *robustus*和*Tapirus* nov. sp.。此后,*Eotapitus robustus*成为一个独立的种(Heissig, 1999)。这样,*Eotapirus*目前只报道发现于欧洲,已知有3个种,即晚渐新世Stampian期的*Eotapirus ruber*,以及早中新世Agenian早期(MN2a)的*E. broennimanni*和*E. robustus*。

应该说,上述这些材料已经相当丰富,足以对*Eotapirus*属的牙齿特征作出比较全面的概括,但Cerdeño and Ginsburg(1988:84)给*Eotapirus*属下的定义却十分简单:"P2原始,轮廓呈斜三角形,发育微弱的原脊;P3和P4强烈臼齿化,轮廓近方形,原脊几乎与后脊等长,原尖与次尖显著分离"。实际上三角形的P2只是该属中最原始的种*E. ruber*的特点,与已知的所有真貘都有明显的区别,在真貘中只有P1是三角形的。因此Heissig(1999:172)将*Eotapirus*的鉴定特征进一步简化,表述为:"小型貘类,上前臼齿强烈臼齿化,具有加长的进步趋势。"

Cerdeño and Ginsburg(1988)描述的新种*Eotapirus ruber*的材料很少,仅有作为正型标本的带P1-P3的右上颌骨,其前臼齿都比临夏标本对应的牙齿小得多(表4)。如上所述,*E. ruber*的P2为三角形(Cerdeño and Ginsburg,1988,fig. 5),与临夏标本完全不同,后者是四边形的(图1);*E. ruber*的P1显著比临夏标本长;*E. ruber*的P2和P3的原脊强烈向后倾斜,而在临夏标本中几乎呈横向;*E. ruber*的P2和P3的后脊完全是横向的,而临夏标本的后脊略为后倾。

*Eotapirus broennimanni*的主要材料是产自瑞士Wischberg的幼年头骨和下颌骨残部(巴塞尔博物馆As. 7),这件标本的头骨带有左、右DP1-DP4和左M1,下颌骨带有左dp1-dp2、右dp1,以及左、右di1,它代表了一种小型的貘类(Schaub and Hürzeler,1948,fig. 3)。*E. broennimanni*的这件标本正好可以与临夏的幼年头骨(V 15523)对比。临夏标本与Wischberg标本相比尺寸更大,如临夏标本的DP1-DP4长67 mm,而Wischberg标本只有60 mm,前者的DP1长15.3 mm、宽12.6 mm,后者的长15.2 mm、宽11.4 mm。它们在形态特征上也有显著的区别:*E. broennimanni*的DP1显著窄长,其长宽比为1.33,而临夏标本为1.21;前者的前附尖相当小,而临夏标本的非常发达,二者之间的差异在DP4

上达到极致;前者 DP2 的唇缘显著长于舌缘,二者之比为 1.95,临夏标本 DP2 唇缘与舌缘长度之间的差距相对较小,其比值为 1.48;*E. broennimanni* 的 DP3 和 DP4 的后脊相当短并强烈后倾,这样的结果也使次尖强烈偏向唇侧,并形成很大而深的后谷;而临夏标本的后脊较长,倾斜程度很低,在 DP4 上接近完全横向,次尖明显偏向舌侧,后谷很小而浅。

Eotapirus robustus 的前臼齿明显比临夏标本更原始(Koenigswald, 1930, pl. III, fig. 1),其 P2 的牙齿前壁强烈向后倾斜,原脊尚未与外脊连接;前臼齿和 M1 的原脊皆显著向后倾斜。在乳齿方面,*E. robustus* 的 DP3 的后脊要比临夏标本的后脊短,其次尖依然偏向唇侧(Koenigswald, 1930, pl. III, fig. 5);*E. robustus* 的 DP3 舌缘强烈中凹,而临夏标本的所有上乳前臼齿的舌缘都相当平直,只有微弱的中凹。*E. robustus* 的 I3 与临夏标本相比要小得多,其冠高远低于临夏标本,形态差异也很大,*E. robustus* 的 I3 呈凿形(Koenigswald, 1930, pl. III, fig. 8)。

Tapirus 最早出现于欧洲的 Astaracian 期的 MN6(Heissig, 1999)。*Tapirus* 大都是中到大型的貘类,其体型显著大于临夏标本。另一方面,与 *Tapirus* 接近的 *Tapiriscus* 的惟一一个种,晚中新世(MN9-13)的 *T. pannonicus* 则小于临夏标本(Made and Stefanovic, 2006, table 2)。Kretzoi(1951)认为 *T. pannonicus* 实际上与 *Tapirus* 在形态上并没有明显区别,只是尺寸较小。但 Made and Stefanovic(2006)将 Boeuf(1991)描述的法国夏朗德(Charente)省 Barro 的 *Tapirus jeanpiveteaui* 也归入 *T. pannonicus*,它有一些原始的性状,如上前臼齿(P2)的横脊不完善等。*T. jeanpiveteaui* 的上颊齿具有发达的小刺,比现生的印度貘的小刺更显著,而临夏标本没有小刺。临夏标本与第四纪的貘类化石相差较大。首先临夏标本的尺寸小得多,如中国貘(*Tapirus sinensis*)、山原貘(*T. sanyuanensis*)以及现生貘都显著大于临夏标本(表1-6)。临夏标本前颌骨的鼻突后端位于齿隙后部,而其他的貘类,如 *Tapirus webbi*(Hulbert, 2005)、山原貘(Tong et al., 2002)和马来貘(*T. indicus*)的鼻突都已伸达前臼齿水平。临夏标本的 P1 具有发达的内、后齿带并连贯形成突起的嵴形,而马来貘 P1 的内、后齿带微弱或缺失。临夏标本上颊齿的外齿带虽然在前尖处有中断的情况,但发育水平相当强大,而第四纪的貘类外齿带都相当微弱甚至缺失。欧洲新近纪晚中新世(MN9)的 *Tapirus priscus*,其体型更大,吻部相对较短,颊齿尺寸更大,P1 的次尖强大(Eisenmann and Guérin, 1992),这些特征显著区别于临夏标本。*Megatapirus* 更是远大于临夏标本。

在真貘化石中与临夏标本在形态和大小上最接近的是 Hofmann(1893)描述的在奥地利 Göriach 地点发现的 *Tapirus telleri*。*T. telleri* 的材料不多,主要有一件带完整左上颊齿列的破碎头骨,一件带门齿的上吻部残段,还有保存颊齿的下颌水平支,以及一些单个的牙齿。*T. telleri* 的前颌骨相当宽阔。*T. priscus* 的吻部宽度在门齿区最大为 46.5 mm,现生的马来貘为 58.5 mm(IVPP 1326),*T. telleri* 的吻部宽度可能超过 70 mm,而后者在整个头骨尺寸上远小于前两个种。这样的前颌骨宽度无论在化石还是现生类型中都未见到,因此这是当初建立这个新种的重要鉴定特征。它的门齿强壮而宽大,I1 和 I2 呈门齿状,而 I3 呈犬齿状。而在颊齿方面,除了尺寸较小,Hofmann(1893)认为 *T. telleri* 与 *Tapirus* 属的其他种没有什么明显的差别。

临夏标本与 *T. telleri* 区别表现在:1)临夏标本的吻部宽度为42 mm,远小于 *T. telleri*;

2)*T. telleri* 的 I3 的横截面圆,而临夏标本 I3 的横截面呈椭圆型;3)*T. telleri* 的前附尖更弱小,而临夏标本的前附尖相当发达;4)*T. telleri* 的 P1 长度小于宽度,而临夏标本 P1 的长度明显大于宽度。

另一方面,临夏标本与 *T. telleri* 相似的性状包括:1)在大小上两者接近,都在 *Tapirus* 属中居于最小之列:*T. telleri* 的 P1-P4 长 69 mm、P1-M2 长 110 mm,临夏标本的 P1-P4 长为 65 mm、P1-M2 长 102 mm;2)都具有紧密排列的门齿,门齿之间无齿隙,而进步的貘类,如现生的马来貘的门齿之间具有显著的齿隙。3)两者的下颌水平支下缘都非常平直,进步貘类的下颌水平支无论是在幼年个体还是成年个体中都具有弧形的下缘。

欧洲中新世最晚期到上新世的 *Tapirus arvernensis* 根据发现于法国 Pérrier-Les Étouaires 的材料创立(Croizet and Jobert, 1828),它的分布时代为 MN13-17(Made and Stefanovic, 2006),其尺寸也大于临夏标本(表4)。

此前在中国发现的新近纪晚期貘化石中,云南禄丰地点仅在化石名单中列有 *Tapirus* sp.(祁国琴,1979),云南永仁的 *Tapirus* sp. 仅有一枚完整下颊齿和另一枚下颊齿的残部(宗冠福等,1996),陕西汉中的 *Tapirus* sp. 仅有一枚 m2(汤英俊、宗冠福,1987),它们都无法与临夏标本对比。时墨庄等(1981)记述的云南昭通的云南貘(*Tapirus yunnanensis*),其材料包括两件带颊齿的下颌水平支和9枚孤立的上颊齿(BPV 276),但原文对部分前臼齿的位置判断有误(其 P2 和 P3 应分别为 P1 和 P2)。云南貘的颊齿尺寸与临夏标本接近,但云南貘的上颊齿相对宽度明显小于临夏标本,即轮廓更接近方形;云南貘上颊齿的外谷比临夏标本更深;云南貘的 P1 长度小于宽度,次尖发达,而临夏标本的 P1 长度大于宽度,次尖微弱。Zdansky(1935, pl. 1, figs. 1-3)记述的山西三趾马动物群中的德氏貘(*Tapirus teilhardi*),化石据称来自武乡县,可能的伴生化石有 *Hipparion* sp., *Acerorhinus palaeosinense*, *Dicrocerus* cf. *D. furcatus*, *Cervocerus novorossiae* 和 *Samotherium palaeosinense*。*T. teilhardi* 的标本只是一件破损的青年个体的右下颌,带有 p3-m2,p2 只残留了齿根,m2 尚在齿槽中未萌出。标本的尺寸相当大,m1 下的下颌最大厚度为 31 mm,显示其比临夏标本大得多,临夏标本的下颌骨在 m1 下的厚度仅为 21 mm。临夏的下颌骨标本虽然是幼年个体,但从它的上颌与成年上颌的比较看,这件幼年标本的尺寸已与成年标本相同。Zdansky(1935)也提到 *T. teilhardi* 比 *T. telleri* 大,而临夏标本略小于 *T. telleri*。

时代与生态 *Tapirus hezhengensis* 化石产地广河县石磊地点与其共生的其他哺乳动物化石包括 *Ictitherium* sp.、*Hyaenictitherium hyaenoides*、*Machairodus palanderi*、*Felis* sp.、*Zygolophodon*? sp.、*Hipparion* sp.、*Acerorhinus hezhengensis*、*Chilotherium wimani*、*Chleuastochoerus stehlini*、*Palaeotragus microdon*、*Gazella* sp. 和 *Hezhengia bohlini*(邓涛等,2004),还有临夏鸵鸟(*Struthio linxiaensis*)等鸟类化石(Hou et al., 2005)。和政县王家山地点与 *T. hezhengensis* 共生的化石目前只记述了粗壮中华马(*Sinohippus robustus*)一个种(侯素宽等,2007)。石磊和王家山地点的化石经过详细的层位追索和对比被划归入杨家山动物群中(邓涛等,2004),相当于中国保德期的 NMU10 上部或欧洲 Turolian 期的 MN11(邓涛,2006)。

和政貘的发现在连接中国真貘化石的演化方面具有相当重要的意义。邱占祥等(1991)指出,新近纪的近貘(*Plesiotapirus*)在系统演化上与第四纪的貘类没有直接联系,

现生马来貘或其祖先,显然是由其他大陆迁移来的。貘科化石的记录始自欧洲和北美的渐新世。欧洲的早期貘类 *Eotapirus* 分布于晚渐新世和早中新世,但在 MN3 晚期或 MN4 至 MN5 早期之间出现貘类的记录空白,随后 *Tapirus* 属的最早代表 *T. telleri* 出现于中中新世的 MN6(Heissig, 1999;Made and Stefanovic, 2006)。在欧洲缺乏貘类的时期,亚洲的中国和日本却有貘类分布(谢万明,1979;邱占祥等,1991),但很快就在中中新世到晚中新世早期出现中断。*T. telleri* 的时代与临夏标本产地相当于 MN11 的层位相比,存在较大的时间差。显然,中国的 *Tapirus* 属应该是在晚中新世时由欧洲逐渐迁徙而来,首先到达华北地区,然后再向南迁徙,产生了南方新近纪晚期及第四纪的类群。北美确切的 *Tapirus* 属化石也是在晚中新世才出现的(Hulbert, 2005),是从欧洲经亚洲扩散的结果。和政貘显然是中国已知最早和最原始的 *Tapirus* 属化石,它的体型居于 *Tapirus* 属中的最小之列,眶下孔具有深而长的前导沟,门齿排列紧密、相互间无齿隙,P1 原尖缺失、次尖微弱,上颊齿外齿带发达,这些都代表了貘类进化中的原始性状(Albright, 1998;Hulbert, 2005),与它在中国真貘化石中最早的地质时代分布吻合。

通常认为貘类喜欢临水的生活,适应于潮湿和植被茂密的热带森林环境,分布范围从海平面至 4500 m 的海拔高度(Eisenmann and Guérin, 1992)。在貘类的生境中,缺乏食树叶的反刍类偶蹄动物,其食物主要包括树叶、嫩芽、小树枝及水生植物等,同时也食果实(Janis, 1984)。北美所有上新世以后的貘类都分布在大陆性冰川以南湿润的中等温度地区(Simpson, 1945)。草原的扩散和草本植物的广泛分布使貘类取食的树木消失,灌木减少。然而,Zdansky(1935)早就指出,如果他描述的德氏貘(*T. teilhardi*)确实是华北晚中新世温带草原(steppe)动物群中的成员,那是相当有意义的发现,因为 Koenigswald(1930:24)曾经强调,早期的貘类似乎生活于沼泽或森林。和政貘在临夏盆地晚中新世三趾马动物群中的发现,肯定了这一重要意义,即证明温带草原环境中也有少量典型的食叶者存在。与和政貘在王家山地点共生的动物还有低冠的中华马,显示有灌丛植物满足这些食叶动物的取食需求(侯素宽等,2007)。

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A NEW SPECIES OF THE LATE MIOCENE TAPIRS (PERISSODACTYLA, TAPIRIDAE) FROM THE LINXIA BASIN IN GANSU, CHINA

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

Summary

The tapirid fossils from the Neogene deposits are relatively scarce, mainly including isolated teeth. In Europe, some Miocene specimens of the genus *Tapirus* were found, among which,

the earliest species was *Tapirus telleri* established by Hofmann (1893) from Göriach in Austria, and Opole 2 in Poland with the age of Astaracian (MN 6). Another widespread species was *Tapirus priscus* established by Kaup (1833) from Eppelsheim, Westhofen, and Wissberg in Germany, Can Llobateres in Spain, Priay in France, Biedermannsdorf in Austria, and Rudabanya in Hungary, with the age of Vallesian (MN 9) (Heissig, 1999). Zdansky (1935) reported the Late Miocene *Tapirus teilhardi* from Wuxiang, Shanxi, but its locality and age were inexact. Recently, the anterior portion of a juvenile skull and mandible (IVPP V 15523) was found from the upper red clays of the Liushu Formation at Shilei (IVPP LX 0031) in Guanghe, Linxia, and then the anterior portion of an adult skull (V 15522) was found from the same horizon at Wangjiashan (LX 0501) in Hezheng, Linxia. The discovery fills the gap and vacuum in evolution of Tapiridae in East Asia, because the origin of the Quaternary tapirs in China has been uncertain.

IVPP LX and IVPP V are the locality and specimen prefixes of Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, respectively. Terminology of lower cheek teeth is according to Qiu and Wang (2007, fig. 7) for perissodactyls.

Tapiridae Burrett, 1830
Tapirus Brünnich, 1772

Type species *Tapirus terrestris* (Linnaeus, 1758), extant, and its type area is Pernambuco, Brazil.

Characteristics Medium- to large-sized tapirids; snout asymmetrical to form a short proboscis; premolars highly molariform; teeth brachydont, but relatively high-crowned compared to other tapirids; upper canine vestigial and functionally replaced by I3 (Heissig, 1999).

Tapirus hezhengensis sp. nov.
(Figs. 1-4; Tables 1-6)

Holotype IVPP V 15522, anterior portion of a skull with I3, C and P1-M2, and its DP4 just fallen (Figs. 1-2).

Paratype V 15523, anterior portion of a skull and mandible of a juvenile individual, and its m2 just erupted judging from the alveoli on the mandible (Figs. 3-4).

Locality Wangjiashan (LX 0501, holotype) in Maijiaji Town, Hezheng County, and Shilei (LX 0031, paratype) in Guanfang Town, Guanghe County in Gansu Province.

Horizon and age Red clay of the upper Liushu Formation of the Upper Miocene; Baodean (late Late Miocene, NMU 10), about 8.3 Ma, corresponding to the early Turolian (MN 11) of the European land mammal ages.

Etymology Hezheng is the county where the locality of the holotype is situated.

Diagnosis A small-sized tapirid, one of the known smallest species in the genus *Tapirus*. Nasal process of the premaxilla short, at the level of the posterior part of diastema, and its posterior end truncate to insert into the maxilla. Mandibular symphysis long and narrow, with a relatively constricted posterior part and a deeply concave lingual surface. Incisors tightly arranged; I3 enlarged and caniniform; upper canine obviously reduced, while lower canine very strong. Diastema of C-P1 longer than length of P1 + P2. P1 triangular, longer than wide, without protocone and with weak hypocone; other upper cheek teeth wider than long. P3 and P4 rectangular; P2, M1 and M2 trapezoid; anterior half of P2 constricted, while posterior half of M1 and M2 constricted. Labial cingulum well developed but discontinuous; anterior and posterior cingula relatively strong. Premolars completely molariform, with nearly parallel protoloph and metaloph; their median valley broad and deep, and parastyle well developed.

Description V 15522 includes the maxilla and premaxilla, with the complete right I3, broken left I3, roots of I1-2, complete canines, and both cheek tooth rows from P1 to M2;

DP4 is just lost and replaced by P4. The height of the cheek teeth is 8.6 ~ 11.2 mm。

The lateral surface of the maxilla is convex. The medial surface of the maxilla is concave dorso-ventrally; it forms the greater part of the lateral wall of the nasal cavity. The anterior extremity of the maxilla is pointed; it joins the premaxilla, and forms with it the alveolus for the canine. The maxilla is abruptly constricted in front of P1. The palatine process of the maxilla projects like a self from the lower part of the medial surface of the maxillary body and forms the greater part of the basis of the hard palate. Its nasal surface is smooth; very thin and concave transversely behind, with the thin nasal crest on its mesial suture; and thick and flat in front, with a wide longitudinal ridge which forms with that of the other side a shallow groove for the vomero-nasal organ. As a result, there is a high and rounded slope between its anterior and posterior parts. The palatine surface is concave from side to side. The suture between the maxilla and palatine bone is situated at the level of the P3/P4 boundary. The infraorbital canal extends almost horizontally. It is placed at the upper edge of the inner plate of the maxilla, and its external opening, the infraorbital foramen, is situated at the level of the P3/P4 boundary. The upper border of the maxilla is shallowly and roundly concave. The lower border of the orbit is situated at the level of the P4/M1 boundary, and it is thick and rounded, with a strongly projected facial crest.

The labial surface of the premaxilla is convex, rounded and smooth. The palatine surface is narrowly and deeply concave. The foramen incisivum is narrow, long and deep. The alveolar border is sharp and laterally oblique in the interalveolar space. The dorsal border is thick and free behind, and forms, with that on the opposite border, a gradually widened groove posteriorly. A broad antero-dorsal projection of the maxilla lies medial to the posterior process of the premaxilla and is visible in lateral view; its medial border is slightly thickened dorso-ventrally. The ventral border is straight and joins the maxilla, oblique from posterio-superiorly to antero-inferiorly.

The horizontal part of the palatine bones is smooth, wide and long. The medial suture is straight, and the medial crest is weak. The transverse palatine suture is dentated, with the anterior palatine foramen at the level of the hypocone of P4. The posterior border (the anterior border of the choanae) is rounded at the level of the M1/M2 boundary. The nasal surface of the perpendicular part is concave and smooth in front.

The juvenile skull (V 15523) has no obvious differences from the adult skull (V 15522). On the juvenile mandible, the lingual surface of the symphysis is smooth and concave, and the mental surface is convex, with a medial furrow in terminal. The symphysis is strongly constricted behind, with high and sharp-edged interalveolar borders. The diastema is long. The mental foramen is situated at the level in front of dp2, opening anteriorly. The horizontal ramus is thick, with a thickness of 21 mm behind dp4; the lateral surface is smooth and slightly convex from edge to edge; the medial surface is smooth, with a very shallow longitudinal depression on its upper part; the ventral border is thick, rounded, and slightly curved. The lower and anterior part of the vertical ramus is somewhat concave.

I3 is straight, with a high and sharp crown, and its tip slightly curved posteriorly. Judging from alveoli, I1 and I2 are much smaller than I3 in size, and I1 is slightly larger than I2. The upper canine is similar to I3 in shape, but much smaller in size. The diastema between C and I3 is 8 mm, and the diastema between C and P1 is 40 mm, longer than the length of P1 + P2 (30.3 mm).

Except P1, upper cheek teeth are wider than long (Table 4); the median valley is steep, deep, and open until the base. The protoloph and the metaloph of P2-4 connect the base of the ectoloph in front of the paracone and the metacone, respectively. Among the four main cusps of P2-M1, the protocone is the lowest, and the hypocone is highest. On M2, the metacone is lowest, and the hypocone still is the highest. Upper premolars have been completely molariform, and the protoloph and metaloph of P2 are also separate lingually.

P1 is triangular in the occlusal outline. Its ectoloph is narrow, long, high, and oblique lingually; paracone is slightly higher than metacone; protocone and protoloph are absent, hypocone is tiny, and metaloph is weak; lingual and posterior cingula are strong and coherent each other.

P2 is constricted lingually at the anterior part. Its ectoloph, metaloph and ectoloph are high; labial wall is shallowly middle-grooved; parastyle is markedly separated from paracone; anterior and posterior cingula are strong, lingual cingulum exists only at the entrance of the median valley, and labial cingulum is discontinuous under the paracone; the protocone is shifted lingually and smaller than the hypocone; protoloph and metaloph are oblique posteriorly, and metaloph is longer than protoloph.

P3 is rectangular, wider than long, and larger than P2. Its ectoloph, protoloph and metaloph are high; paracone and metacone are nearly same in size, and parastyle is completely separated from the paracone; lingual cingulum is absent; lingual side is higher than the labial side, and the hypocone is slightly higher than the protocone; protoloph is nearly transverse, and the metaloph is slightly oblique posteriorly, both of them have a similar length; median valley is wide, without the entrance constriction.

P4 is very similar to P3, with a slightly shorter metaloph.

The upper premolars are completely molariform, and the protoloph and metaloph of P2 are separated lingually.

M1 is trapeziform, with the markedly shorter posterior wall than the anterior wall, and the shortest lingual wall. The four main cusps are relatively high. The parastyle is strong, connected the anterior cingulum via a crest, and separated from the paracone by a deep groove; the protocone has an antecrochet after wear; the metacone is obviously shifted lingually. The anterior cingulum is well developed, the posterior one occurs only labially, the labial one is weak under the paracone, and the lingual one is absent. The protoloph is nearly transverse, and the metaloph is very short and slightly oblique posteriorly. The median valley is broad.

M2 is similar to, but much larger than M1. The hypocone of M2 extends two crests posteriorly, one reaching the bottom of the posterior valley, and another connecting the posterior cingulum at the middle of the posterior wall.

The crown of the upper deciduous cheek teeth is relatively low, with three roots. DP1 has one root anteriorly and two posteriorly, while other deciduous premolars have two roots labially and one lingually. Except DP1, each deciduous premolar is narrower than the corresponding permanent one (Table 5), and its worn protoloph and metaloph are much lower than its ectoloph. The protocone of DP1 is very tiny and located in the middle of the lingual margin, while the worn hypocone is relatively large; the lingual cingulum is weak and discontinuous; the metaloph is connected with the metacone anteriorly by a narrow and short neck.

The lower canine is strong and oblique anterio-labially, without diastema between it and i3. There is no any trace of dp1. The lower deciduous premolars are double-rooted. The dp2 is a narrow and long triangle with a sharp anterior end, and its labial cingulum is weakly developed by the paraconid and parastylid; the parastylid is high and sharp; the paralophid is oblique postero-labially; the protoconid extends three crests oriented anteriorly, postero-labially and postero-lingually, respectively; the entolophid is transverse and obviously longer than the metalophid. The dp3 is molariform, and its anterior margin is shorter than the posterior margin; the cingula occur only on the labial side of the paraconid and the posterior margin of the tooth; the metalophid is highest among the cusps; the paralophid is narrow and low, the protolophid is narrow and long, the metalophid is wide and flexural, and the entolophid is wider and longer than the metalophid. The dp4 is similar to dp3, but dp4 has a marked anterior cingulum.

Comparison and discussion The Neogene tapirids were scarcely found in Asia, including *Plesiotapirus* from the Hiramaki Fm. in Honshu, Japan, and the Shanwang Fm. in Shandong, China (Matsumoto, 1921; Xie, 1979; Qiu et al., 1991), *Tapirus teilhardi* from the *Hipparion* fauna in Shanxi, China (Zdansky, 1935), *Tapirus yunnanensis* and *Tapirus* sp. from the Upper Miocene in Yunnan and Shaanxi (Shi et al., 1981; Qi, 1979; Zong et al., 1996; Tang and Zong, 1987).

The premolars of the Linxia tapir have been completely molariform with the parallel transverse protoloph and metaloph. The dp2–dp4 also have the two parallel transverse lophids. Such molarisation appears only in *Eotapirus* from the Late Oligocene to the Early Miocene, *Tapirus* from the Middle Miocene to the Recent, *Tapiriscus* from the Late Miocene, and *Megatapirus* from the Quaternary.

The Linxia tapir is different from *Eotapirus ruber* from Quercy, France in having larger cheek teeth, shorter P1, quadrangular P2, and transverse protoloph of P2 and P3; it is different from *Eotapirus broennimanni* from Wischberg, Switzerland in having larger size, shorter and wider DP1, stronger parastyle, and longer metaloph; it is different from *Eotapirus robustus* in having straight anterior margin of P2, protoloph connecting with the ectoloph, and transverse protoloph on the premolars and M1. The Linxia tapir is obviously larger than the European *Tapiriscus*, but much smaller than the Asian *Megatapirus*. *Tapiriscus pannonicus* (= *Tapirus jeanpiveteaui* Boeuf, 1991) from Barro, France has a well-developed crista on each upper cheek teeth, while *T. hezhengensis* has no crista.

The Linxia specimen is also distinctly smaller than *Tapirus* of the Quaternary, such as *Tapirus sinensis*, *T. sanyuanensis* and *T. indicus* (Tables 1–6). The posterior end of the nasal process of the premaxilla is located within the posterior part of the diastema in *Tapirus hezhengensis*, while reaches to the level of the premolars in other species of *Tapirus*, such as *Tapirus webbi* (Hulbert, 2005), *T. sanyuanensis* (Tong et al., 2002) and *T. indicus*. P1 of *T. hezhengensis* has well-developed lingual and posterior cingula that connect each other to form a prominent crest, while P1 of *T. indicus* has weak lingual and posterior cingula or lacks them. The labial cingulum of the cheek teeth is discontinuous but strong in *T. hezhengensis*, while it is weak or absent in the Quaternary tapirs. The Late Miocene (MN 9) *Tapirus priscus* of Europe has a larger size, a shorter muzzle, and a strong hypocone of P1 (Eisenmann and Guérin, 1992), which are different from those of *T. hezhengensis*.

Among the species of *Tapirus*, *T. telleri* from Göriach, Austria (Hofmann, 1893) is the closest to *T. hezhengensis* in shape and size. The premaxillae of *T. telleri* are relative wide, with a width over 70 mm, larger than 46.5 mm of *T. priscus* and 58.5 mm of *T. indicus*, but the skull of the former is much smaller than the latter two species. *T. hezhengensis* is similar to *T. telleri* in having the similar size, tightly arranged incisors, and straight lower border of the mandibular horizontal ramus. On the other hand, *T. hezhengensis* has some different characters from *T. telleri*, such as a narrower muzzle (42 mm), an oval cross section of I3, strong parastyle of cheek teeth, and longer than wide for P1. The European *Tapirus arvernensis* of MN13–17 (Made and Stefanovic, 2006) also is larger than *T. hezhengensis* (Table 4).

The size of *Tapirus yunnanensis* (Shi et al., 1981) is close to that of *T. hezhengensis*, but the cheek teeth of the former are proportionately narrower than those of the latter, the labial valley is deeper, P1 is wider than long, the hypocone of P1 is strong. *Tapirus teilhardi* from the *Hipparion* fauna of Shanxi (Zdansky, 1935, pl. 1, figs. 1–3) is obviously larger than *T. hezhengensis*.

Age and ecology *Tapirus hezhengensis* is accompanied with *Ictitherium* sp., *Hyaenictitherium hyaenoides*, *Machairodus palanderi*, *Felis* sp., *Zygolophodon*? sp., *Hipparion* sp., *Acerorhinus hezhengensis*, *Chilotherium wimani*, *Chleuastochoerus stehlini*, *Palaeotragus microdon*, *Gazella* sp., *Hezhengia bohlini* (Deng et al., 2004), and *Struthio linxiaensis* (Hou et al., 2005) at Shilei, and with *Sinohippus robustus* at Wangjiashan (Hou et al., 2007). The fossils of Shilei and Wangjiashan belong to the Yangjiashan fauna, corresponding to upper NMU 10 of

China or MN 11 of Europe (Deng, 2006).

The discovery of *T. hezhengensis* is significant for the recognition to the evolution of the Chinese Tapiridae. Qiu et al. (1991) indicated that the Neogene *Plesiotapirus* had no direct connection with the Quaternary tapirs in phylogeny. The record of the Tapiridae began from the Oligocene of Europe and North America. Europe has a successive sequence of Tapiridae: *Eotapirus*, the early member of the Tapiridae was distributed from the Late Oligocene and Early Miocene, but there was a "tapir-vacuum" from late MN 3 or MN 4 to early MN 5 (Made and Stefanovic, 2006); *T. telleri*, the known earliest species of *Tapirus* appeared first in MN 6 of the Middle Miocene (Heissig, 1999), much earlier than the horizon of *T. hezhengensis* (corresponding to MN 11). During the European "tapir vacuum", tapirs survived in China, but subsequently there was no any record from the Middle Miocene to the early Late Miocene. As a result, the Chinese *Tapirus* should migrate from Europe during the Late Miocene. *T. hezhengensis* is the earliest and most primitive species of *Tapirus* in China, and its primitive characters include small size, long and deep front groove of infraorbital foramen, tightly arranged incisors, absent protocone and weak hypocone of P1, and strong labial cingulum of upper cheek teeth (Albright, 1998; Hulbert, 2005).

Generally, tapirs favor to live near water and they are adapted to wet and dense tropic forests from the sea level to the elevation of 4500 m (Eisenmann and Guérin, 1992). In the habitat of tapirs, there is a paucity of folivorous ruminant artiodactyls, and the diet of tapirs includes leaves, fresh sprouts, small branches, and aquatic plants, as well as fruit (Janis, 1984). In North America, all post-Pliocene tapirs are distributed in the humid mesothermal region south of the continental glaciers (Simpson, 1945). The expanse of grasslands and the widespread distribution of herbaceous plants caused trees disappeared and shrubs decreased, which were the food of tapirs. On the other hand, Zdansky (1935) has indicated that it should be a significant discovery, if *T. teilhardi* was a member of the Late Miocene steppe fauna in northern China, which was different from the emphasis of Koenigswald (1930:24) that early tapirs seemed to live in swamps or forests. The discovery of *Tapirus hezhengensis* in the Late Miocene *Hipparion* fauna of the Linxia Basin affirms the significance, i. e., there were a few typical browsers in steppe habitats. The brachyodont horse *Sinohippus* coexisted with *Tapirus* at Wangjiashan, which showed that some shrubs could provide food for these browsers (Hou et al., 2007).

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