

## *Machairodus horribilis* Schlosser, 1903 头骨材料记述<sup>1)</sup>

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**摘要:** Schlosser 于 1903 年根据不明地点的零散牙齿所创建的 *Machairodus horribilis* 种一直没有得到古生物学家们的认同。最近发现了产自山西保德的两个剑齿虎头骨及一件下颌。其中的 m1 和 *M. horribilis* 者在大小和形态上都非常接近, 据此把上述新材料归入了 *M. horribilis*。在与中国及欧洲已知各种对比后, 确信 *M. horribilis* 应为一有效种。

**关键词:** 中国山西保德, 晚中新世, 剑齿虎

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*Machairodus horribilis* (恐剑齿虎) 系 Schlosser 于 1903 年所建。依据的材料是从药铺购得的一些零散牙齿。Zdansky 在记述山西保德的剑齿虎材料时把其中的 P4 (还有 C?) 归入他所创建的 *Machairodus palanderi* (巴氏剑齿虎), 而把其中的门齿、p4 和 m1 看作是另外的未知属、种 (Zdansky, 1924: 115)。后来, 张席禔 (1957) 和童永生等 (1975) 在记述巴氏剑齿虎时都没有提到这个种。国外的学者则几乎完全忽略了这个种的存在, 极少有人提到它。

1991 年本文前一作者在整理中科院古脊椎所三趾马动物群的库存标本时, 发现了两件尚未修出的剑齿虎头骨。标本系该所技工武英于 1965 年自山西保德采得, 详细地点已不可考。修理后发现这两件头骨都很大, 形态很接近。有意义的是, 其中和一件头骨连在一起的下颌上的 m1 竟然和 Schlosser 记述的 *M. horribilis* 的 m1 非常接近。这表明上述材料都应归入 *M. horribilis* 这个种。这样一来, 终于有了比较完整的 *M. horribilis* 的头骨和下颌的材料, 足以使我们对于该种的特性及其有效性作进一步的讨论。

促使作者现在发表本文的另一个原因则是, 直到最近我们才有可能将我国与欧洲的剑齿虎头骨化石进行比较可靠的对比。目前绝大多数古生物学家都认为在欧洲最常见的只有两个种, 即属型种 *M. aphanistus* 和 *M. giganteus*。它们的化石很多, 分布也很广, 但多为零散的牙齿, 完整的头骨及连在一起的下颌极为稀少。最早的一个 *M. giganteus* 的头骨发现于希腊的 Halmyropotamos 地点, 但描述过于简短 (Melentis, 1968)。这种情况直到最近才有所改变。两个种的头骨和下颌的较详细描述或图版已于近期发表 (Antón et al., 2004; Geraads et al., 2004)。

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在古北区晚中新世地层中还记录过 *Machairodus* 属的其他许多种,总数接近 20 个。其中大多数种的材料很少,其分类地位还有待进一步研究确定。我们在查阅了有关文献后,认为它们和上述保德头骨在大小及特征上都有明显的区别。本文的主要目的是确立 *M. horribilis* 种的有效性,故不再对这些材料少而分类地位存疑的种进行比较和讨论。

文中某些头骨测量项的定义取自 Osborn (1912); L, W, H 分别代表长、宽和高。

## 1 系统描述

### **Felidae Fisher de Waldheim, 1817**

#### **Machairodontinae Gill, 1872**

#### ***Machairodus* Kaup, 1833**

#### ***Machairodus horribilis* Schlosser, 1903**

*Machairodus horribilis* Schlosser, 1903 (partim), p. 37-39, pl. I 15-16 (only ml)

*Machairodus palanderi* Zdansky, 1924 (partim), p. 112-116, pls. XXVI 3-4

*Machairodus palanderi* Tung et al., 1975, p. 34, 36, pl. I 1

*Machairodus tingii* Zdansky, 1924, p. 116-120, pls. XXVII 3-4 (?), XXVIII, 1-2

*Machairodus tingii* Chang, 1957, p. 196-197, pl. III-IV

*Epimachairodus palanderi* Teilhard de Chardin and Leroy, 1945 (partim), p. 11-14, fig. 5

*Epimachairodus tingii* Teilhard de Chardin and Leroy, 1945 (partim), p. 14

**选型** 左 m1 (Schlosser, 1903, pl. I 15-16; 本文图 2F), 产地不明。

**本文记述标本** V 15642 (图 1), 近于完整的头骨, 仅第一、第二对门齿, 右第三门齿及两侧犬齿齿冠缺失, 右 P3 稍破损, 中年个体。V 15643 (图 2A-E, 3, 4), 残破头骨及下颌, 中年个体, 比 V 15642 稍年轻, 头骨左上颌及以后的部分和右侧颧弓以后的部分缺失, 门齿除左 I3 外, 齿冠顶端均破失; 下颌右支完整; 左支 p4 以前和 m1 后半部以后的部分保留, m1 前半部之下的部分缺失。下牙中左 i3 以右的门齿及犬齿的齿冠部分破损, 右 p3 前附尖断失, 左 m1 破损。

**特征** 本属中尺寸最大, 头骨全长  $\geq 350$  mm, P3-P4 长  $\geq 65$  mm, p3-m1 长  $\geq 90$  mm。头骨较宽, 颧弓处宽与顶长比约为 65%。鼻骨近长方形, 前窄后宽; 向中缝方向急剧加厚。鼻咽窝后窄前宽, 硬腭后缘 U 形。乳突特别粗壮, 其远端腹面附着臂头肌的粗糙面大并延伸至外侧面; 副枕突较大, 远离枕髁, 其下端超过枕髁下缘。下颌冠状突退化, 其后缘较垂直, 顶端位于关节髁之前。I1-I2 舌侧有 V 形齿带, 但小尖位于近中和远中侧基部。P2 保留, P3-P4 和 p3-m1 相对较长。颊齿齿壁上偶有不规则粒状突起。P3 和 p4 具 5 个齿尖; P3 舌侧后半部几乎不向内凸出, P4 原尖退缩为向内的弱隆起(不为尖锥形), 但具独立齿根。p4 内后角有较大粒状突起; m1 前缘以较大角度斜向后上方, 具分离下后尖残迹。

**描述** 头骨背面: V 15642 保存完好(图 1A)。两鼻骨组成长大于宽的长方形; 最大长(带前侧突)96 mm, 后端最大宽 61 mm, 前端宽 50.5 mm; 鼻-额骨缝在近中 2/3 处大致

垂直于头骨长轴,额骨中尖突几乎不发育,但插入鼻骨及上颌骨的侧尖突却很明显,长约 16 mm,使鼻骨外后角呈圆形。两鼻骨前缘形状复杂:有中矢凹,凹两侧为一对尖突,尖突之外为一对较深的凹,最外侧为一对细长的侧突。自前面看,鼻骨向中矢方向急剧变厚,最厚达 14 mm,使两鼻骨前端形成三角形粗糙面(图 1F)。鼻骨背面中部微隆,仅在最后端的中矢部微微凹陷。前颌骨插入鼻骨和上颌骨的部分在背面可以看到(图 1A)。额骨宽,眶后突粗壮而厚,末端不尖锐,其上的粗糙面大并转向侧方。眶后突处头宽 130 mm,眶间最小宽 104 mm。额骨前部的中矢凹陷很大,中矢长 17 mm,其后缘界限清楚。脑颅在眶后突之后不急剧收缩,脑颅侧缘几乎平直地斜向近中后方。脑颅在颞骨处微弱膨大,最大宽达 90 mm,亦即窄于眶间宽。额嵴以较强的弧形向后趋中,至关节窝前端上方处形成单一矢状嵴。额-顶骨缝已愈合。矢状嵴最前端有很短的中矢深槽。颧弓较直地斜向外后方,最突出处位于后端,此处头骨宽(修复)约 230 mm。

侧面: V 15642 保存较完整,仅矢状嵴后端顶部破损(图 1B)。V 15643 仅右侧关节突以前的部分保存,而且前颌骨和眼眶以上的部分破损较多(图 2A)。头骨若以门齿齿槽至枕髁下缘连线为水平线定位(以下皆如此),V 15642 头骨顶缘自鼻骨前端至眶后突后端以约 30°角斜向后上方,自此向后头骨顶缘较平直,仅矢状嵴后部微微下斜。鼻骨前端位于上犬齿中部之前。门齿齿槽区不特别向前突出,使前颌骨前上缘弯曲和斜度都较弱。前颌骨鼻支宽大而长,在鼻骨前端处宽 15 mm,自此向后延伸长约 50 mm,和额骨鼻突之间的距离为 21 mm。眶下孔后缘位于 P4 前附尖上方;眶前缘大致位于 P4 前尖上方。眼眶卵圆形,眶前缘稍稍斜向后上方,与眼眶长轴平行,后者长轴约 45 mm。在眼眶前下角稍上,泪骨的上端有棱脊状的泪结节。眼眶面微微斜向内上方。颧弓在 V 15642 标本上保存不完整,后半部由石膏修补(图 1B 阴影区);V 15643 标本上右颧弓保存基本完整(图 2A)。颧弓上的眶后突与额骨上的接近,低宽,末端不尖,其后缘不形成宽深的凹陷。颧弓在眶后突以前的部分短而高,而眶后突以后的部分较细长,斜向后下方伸延。矢状嵴向后急剧变高,呈垂直板状,最高处约 45 mm。

眶部各孔在 V 15642 中均保留。泪孔位于泪结节后下方,离边缘较远,深入眶内。眶下孔在眶内的后开口很大,圆三角形,高、宽接近。后腭孔在眶内的后开口小,位于蝶腭孔的前下方,后者差不多是前者的一倍大,两者分开较远。筛孔很小,裂隙状。视神经孔处保存不好,其后为很大的眶裂(蝶裂),再后则为圆孔。卵圆孔和圆孔一样大,两者相距较远,后者面向前方。没有翼蝶管。关节后突和乳突之间的距离小,在远端两者更为接近,但不将外耳道封闭。乳突粗大而下伸较远,自外侧将听泡大部分遮住,乳突远端的粗糙面近三角形,大部分位于腹面,部分转至侧面。因此粗糙面自侧面可以很清楚地看到。副枕突扁三角形,末端伸向下方,微微前弯。乳突和副枕突相距较远,两者以一宽大的弧形嵴相连。关节后突、乳突和副枕突末端大约组成一略微斜向后上方的直线。枕面自侧面看斜向后上方。

腹面: V 15642 保存完整(图 1C-D), V 15643 仅保留腭部及右颧弓部分(图 2B)。V 15642 的门齿中度前凸,其齿槽前缘为弱凸弧形, I3-C 齿隙长约等于 I3 近中远中宽,其唇缘微凹,因此门齿与犬齿齿槽唇缘几乎形成连续平滑弧形。前颌骨-上颌骨骨缝自犬齿内面中央向内伸至前腭孔后缘。前腭孔椭圆形,位于犬齿前半部之内,左、右两孔互相

靠近;其前方的腭窝(fossa palatina)长于前腭孔,但较浅,直抵 I1 后缘。腭骨深陷于颊齿之下,颊齿齿根暴露在外。后腭孔位于 P4 稍前。此外,腭面上还具有多个滋养小孔,在后腭孔之后每侧至少还有 5 个较大者。腭面上有一对突出的棱嵴,自前腭孔内后角延伸至后腭孔的内侧。腭面中央凹陷明显,凹陷之后的腭骨中缝突起为很窄的弱嵴,向后一直延伸至硬腭后缘。上述 3 条纵嵴都不及 *Smilodon* 者高锐。上颌骨-腭骨骨缝中央部分为 M 形,其中凹部分大约与后腭孔位于同一水平,而两侧向前突出的部分离后腭孔不超过 10 mm。硬腭后缘 U 形,没有中尖突和明显的中矢凹缺;最前缘位于 M1 水平。鼻咽窝(内鼻孔)前宽后窄。在 V 15643 标本上,前腭孔部分破损;上颌骨-腭骨骨缝几近平直,小滋养孔较少,腭面上的嵴发育弱。这可能与较年轻有关。

V 15642 的基枕部保存非常好(图 1D)。基枕骨后半部变为隆凸的三角形,与枕髁相接;中嵴在三角形之前为锐嵴形,两侧为深凹陷,而其前端消失于附着头腹直肌的一对粗糙隆起之间。后者大而互相接近,其前方的平面在前端以明显的弧形弱嵴为界。基枕-基蝶骨缝不清。卵圆孔位于关节窝和翼突后缘之间,由于主要面向前方,自腹面只能部分看到。肌咽鼓管(canal musculotubarius, 见 Davis, 1964:51)很大,位于翼突基部的后外方和关节后突的内方。鼓室腹壁最隆凸处位于前 1/3 的后端,其后的部分斜向背上方,因此自侧面看,鼓室腹壁的后 2/3 斜向后上方。鼓室腹壁的前和前外方为一相当宽大的粗糙平面,面向前下方。这一部分可能相当于猫科外鼓骨的腹壁。内颈动脉孔位于后破裂孔的前端,与其相通。关节突不特别向腹侧伸出,因此关节窝的内面面向内下方,而不是接近垂直。关节突和乳突之间的距离较窄,远端留有 6~7 mm 的距离。乳突特别粗大,位于听泡的前 2/3 之外,腹面为附着臂头肌的大粗糙面。茎乳孔和鼓舌窝斜向排列,位于乳突中部内面的一个大的凹陷内。副枕突位于鼓室的外后端,末端弱钩状高出于鼓室,距离乳突相当远。它和枕髁及乳突间的距离大致相等。

枕面:V 15642 的枕面保存完整(图 1E)。若以乳突外缘为下端,枕面的形状约为一相当高的等边三角形,但接近顶端有一对向外的突起。枕面周边附着肌肉的粗糙部分和中央枕髁附近的光滑面(容纳寰-枕滑囊)之间没有非常明显的界限。中央光滑面分为两对凹陷区,一对位于枕髁的外侧,另一对则位于枕髁的上方。枕外中嵴仅在中部微弱可见。该处有一对较深的凹陷,应为头背直肌等的附着处。其他附着伸展头部肌肉的粗糙面很难区分,在顶缘之下也没有附着肌肉的深坑。枕大孔上缘有一对嵴形突起,但不特别发育。

头骨测量见表 1。

下颌:V 15643(图 2C-E)非常低长,冠状突小,而联合部高而宽大。左、右下颌支在联合部虽留有清晰的骨缝,但愈合紧密。下颌联合的后缘可以分为以约 45°角斜向后下方的上半部及垂直向下或稍向前凹入的下半部。这样,联合部的上半部较平,其后缘大约位于下犬齿之后 12 mm,联合部的下半部则为附着颏舌骨肌(m. genioglossus)和颏舌肌(m. geniohyoideus)的凹陷。联合部前端为近四方形的平面,下半部面向前方,上半部稍面向前下方;面上有许多小的滋养孔。有两对比较大而规则:一对位于上半部每侧的中部;另一对位于下半部靠近侧缘处(图 2E)。下颌联合中缝大部分为浅沟,但在下端稍稍隆凸。自侧面看,联合部前缘与水平支下缘形成稍大于 90°的角,边缘处为棱脊状,伸出于联

表 1 某些剑齿虎头骨的测量与比较  
Table 1 Measurements and comparison of some *Machairodus* skulls

	<i>M. palandri</i>		<i>M. horribilis</i>		<i>M. qufanensis</i>		<i>M. giganteus</i>		
	Baotie		Baotie		Huoixian		Pikermi		
	Ex. 1	V 905	V 15643	V 15642	V 4567	Batallores-1		Halmyp.	
	Zhdansky, 1924	Chang, 1957	1)	this paper	Tung et al., 1975	Antón et al., 2004	Roth et al., 1854	Melentis, 1968	
1. 顶长 vertex L.	261*(280?)	335.6*		353					355
2. 基枕长 condylobasal L.		314*		318	~305°	236~313(271)			
3. 基长 basilar L.		286.6*		299	~290°				285
4. 腭长 palatal L.	123*	158		163	~160°				160
5. I3 处宽 W at I3	36*	54.1*		60					
6. C 处宽 W at C-C	60.9*	76.3*		90	70**				64
7. P4 后端处宽 W at post. end of P4	102.5*	120.8*		138	108**				104
8. 颧弓处宽 W at zygom.	141.8*	187.4*		230	175**				210
8/1(%)	50.6?	55.8		65.2					59.2
9. 眶后突处宽 W at postorb. pr.		108.5*		132	80**				118
10. 乳突处宽 W at mast. pr.	91.5*	111.9*		127	109.3**				128
11. 枕面高 occip. H		100.7*		120					
12. 乳突处高 H at mast. pr.		124.4*		142	131.5				122
I3 L.	12.8	14		17.2	12.6				
I3 W	10.6	13		14.2	11				
C-P3 齿隙 diastema	8°	20°		19.3	17.2	~11			18.7
C L	30.5	45		38	49.8	39.5	25.4~35.7(30.9)	35	35.2
C W	10.5*	16.5		13.5	15.9	16	10.7~14.5(12.4)	15	14.3
CW/CL(%)	34.4	36.7		35.5	31.9	40.5	35.8~49(40.8)	42.9	40.6
P3 L	22.5	23		26	24.3(alv)	24.3	21.1~25.9(23.7)	23	23.7
P3 W	9.5	9.4		11	9.6	10.2	9.9~13.8(12)		10.6
P4 L	40	41		45	47	44.8	31.7~40.9(36.4)	42	43.1
P4 W	16.5	17		15?	19.7	15	13.3~19.3(17.4)		14.8
M1 L	6.5	7		6.5	5.4				7.2
M1 W	10.8	12		11.3	9.4			11	?
P3L/P4L(%)	56.3	56.1?		57.8	51.7	57.6	63.7	54.8	55

1) Zhdansky's Ex. 3 of *M. palandri*; \* measured and/or calculated by the present authors; \*\* compressed; ^ estimated; alv. measured at alveoli; numbers in the brackets represent the means.

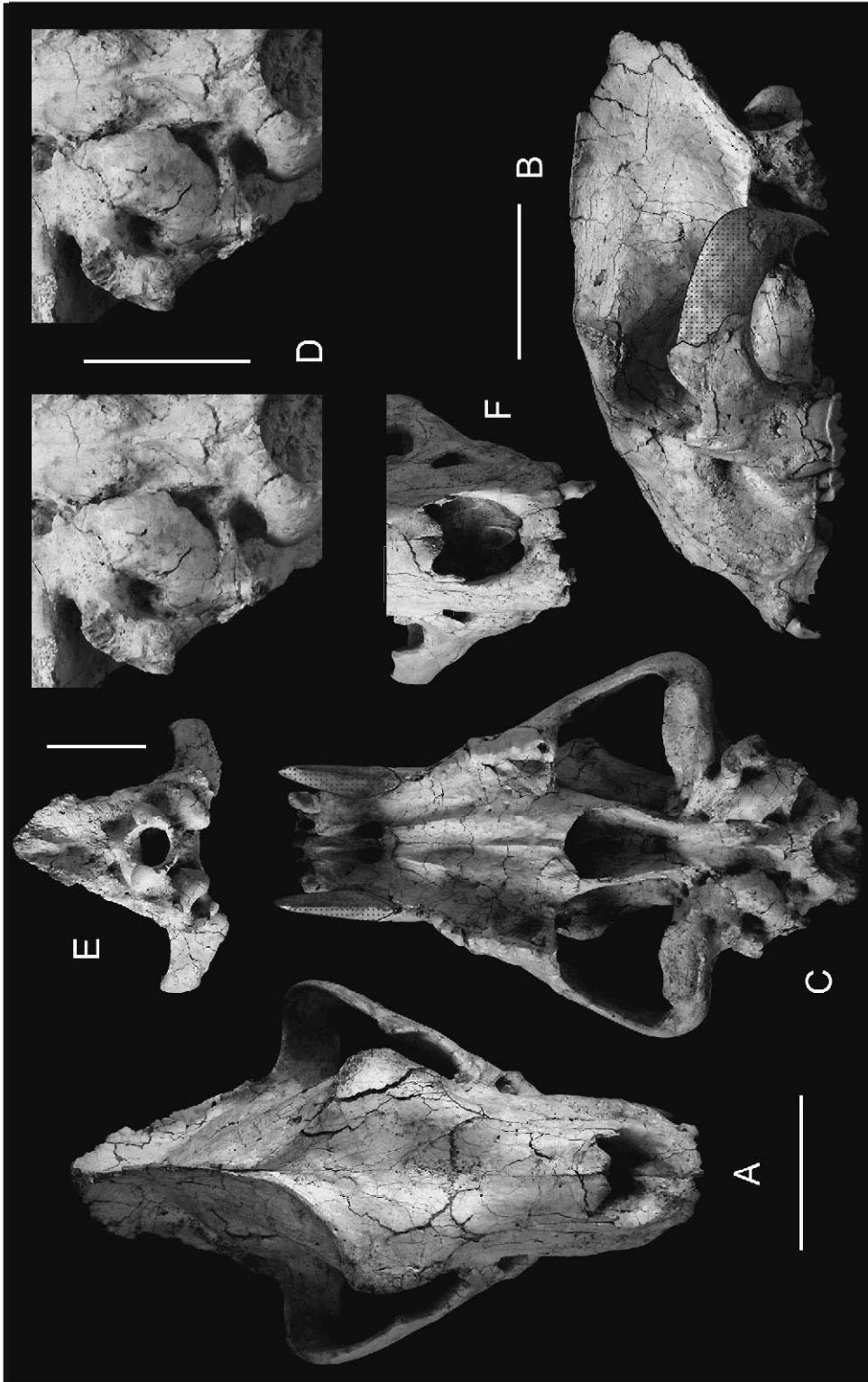


图1 恐剑齿虎头骨, V 15642

Fig. 1 Skull of *Machairodus horribilis*, V 15642

A. 顶面 dorsal view; B. 左侧面 left lateral view; C. 腹面 ventral view; D. 枕面 occipital view; E. 枕面 occipital view; F. 吻部前上侧视 anterosuperior view of muzzle; 阴影区示修复部分 dotted area indicating restored part; 标尺 scale bars = 5 cm

合部和水平支下缘之下。水平支薄,在 c-p3 齿隙处最薄。齿隙很长,56 mm;齿槽缘形成锐嵴。颞孔两个,都很大,前者稍大于后者。后者位于 p3 后半部之下,前者位于齿隙后 1/3 的前端处之下。咬肌窝宽大,其下缘有棱嵴形边界,此棱嵴向后一直延伸至关节髁的外端。下颌角伸向后下方,但末端缺失,不知向后延伸及向内弯曲的程度。冠状突高约 50 mm(自关节髁顶面测量),仅相当于 m1 加 1/3 p4 的长之和。冠状突后缘接近垂直,仅顶端略微斜向后上方。关节髁位于冠状突之后很远,其髁的前缘位于冠状突之后(图 2C)。

测量见表 2。

上牙齿: V 15642 标本的上门齿中只保留了左 I3(图 1C);在 V 15643 标本中仅左 I3 保存完整,其他上门齿都不同程度地缺失(图 2B)。V 15643 的门齿从近中向远中方向增大,但 I3 显著大于近中侧的两个。I1 和 I2 的舌侧基部都没有小尖,但在两侧有棱形突起,并在基部会合,从保留的部分看,至少 I2 内、外两侧近基部处有突出的附属小尖。上述两件标本上都有 I3,但 V 15643 的 I3 高远大于 V 15642 者。前者具弱的前近中嵴和较锐利的后远中嵴;两嵴下半部均经磨耗,未见锯齿。在近中侧基部有附属小尖,小尖的后部形成斜向后下方延伸的棱嵴,其上有锯齿。V 15642 的 I3 构造和 V 15643 者同,但齿冠低小,前近中附属小尖似不发育,齿冠两侧的嵴也较弱。上犬齿在 V 15642 中齿冠部分完全缺失;在 V 15643 中保存完好。上犬齿非常大而长:牙齿直线全长约 205 mm,从齿槽中部至顶端直线长 130 mm。牙齿弯曲明显。齿冠外面前端较隆凸,内面较平,使齿冠断面前端较宽,向后变薄。齿槽处断面长 50 mm,宽 16 mm。珐琅质在基部变得很薄,和齿质的界限不规则:在外侧,前缘界限下降最甚,此处齿质出露高约 35 mm;在中部齿质出露高约 25 mm;而在后端珐琅质伸入齿槽内。舌侧亦大致如此。前嵴自齿槽之上约 50 mm 处开始向内偏转。前、后嵴珐琅质均有锯齿。自齿槽判断,V 15642 标本的犬齿明显小于 V 15643 者(见表 1)。从 I3 和 C 的大小判断,V 15643 应为雄性,而 V 15642 应为雌性。

P2 在两件标本上都有齿槽保留。在 V 15642 中齿槽表明该齿为双根。两根接近等大,总长 6 mm。在 V 15643 中仅右 P2 两齿槽保存,长约 8 mm。它们和 P3 间只有很小的距离。左、右 P3 在 V 15642 中均保存。其中右侧者齿冠稍破损,而左侧者完整。P3 为双根 5 尖齿:除主尖和前、后两主要附尖外,在前附尖的前方还有一个很低的突起,在后附尖的后方则有一个较高的后附属小尖。此外,在前附尖的内、外壁基部各有一很小的粒状突起。牙齿外缘较平直,内缘中部微凹,后半部比前半部稍更向内突出。P4 具前前附尖和由单独一根支持的已很退化的原尖。V 14562 的 P4(图 1B-C)在前附尖的外面基部有两个小粒状突起。牙齿内面磨耗深,原尖的珐琅质已完全磨光。从根部看,在前外根和原尖根之间形成 V 形凹槽。在 V 15643 中 P4(图 2A-B,3)磨耗轻,前前附尖、前附尖和原尖前半部的内面尚未磨耗。前前附尖很小,高约为前附尖的一半。前附尖高约为前尖高的一半(图 3A-B)。原尖的前半部已磨耗为一凹坑,后半部尚未磨耗。此处可见原尖的齿冠部分不为孤立锥状,而只在内壁上形成微弱的隆起(图 3B-C)。后附尖外壁有中凹。外壁前端有不规则的粒状突起。V 15642 的右 M1 已破碎,很小,位于 P4 后端内侧;左侧只有齿槽,椭圆形,长 5 mm,宽 8 mm。其位置比右者稍更靠后。在 V 15643 中右 M1 保存完整,冠面磨耗,在内后侧已磨至基部,磨面面向前内下方。最大长(中部)7.7 mm,最大宽 14.5 mm。

表 2 某些剑齿虎下颌的测量与比较  
Table 2 Measurements and comparison of some *Machairodus* mandibles

	<i>M. horribilis</i>		<i>M. irtyshensis</i>		<i>M. palanderi</i>		<i>M. apfhanistus</i>		<i>M. giganteus</i>	
	V 15643 this pupet	lectotype Schl., 1903	No. 2413/115 Oidov, 1936	No. 2413/115 Oidov, 1936	Zhdansky, 1924 Ex. 2	Autón et al., 2004	Autón et al., 2004	Gerauds et al., 2004	UEK-124	
1. 全长 total L.	275				190*	192.2-238.8(209.4)				
2. 冠状突处高 H at coron. pr. 2/1(%)	97				65.7*	79.3-104.7(89.1)				82
3. 犬齿后缘处高 H at post. end of c	35.3				34.6	42.6				
4. p3 前缘处高 H at ant. end of p3	65.5				42.3*					
5. i3 近中远中宽 mesiodist W	43.5				30*					
6. i3 L	12		10.4		9.2					9.2
7. c L	11.8		10		9.9					7.8
8. c W	21.2		19.5		14.3		16-21.1(17.6)			15
9. e-p3 齿隙长 diastema	14.4		13		10.3		9.7-13.1(11.3)			11
10. p3 L	53.7		59		35.5					~32
11. p3 前宽 ant. W	20		21.5		15.1		18.4-20.8(19.4)			18.5
12. p3 后宽 post. W	8.7									
13. p3 主尖高 H of main cone 12/10(%)	9.9		10.5		7.4		7.7-9.3(8.7)			7.5
13/10(%)	14.4		48.8		9.3*		11-13.9(12.8)			
14. p4 L	49.5				49		44.8			40.5
15. p4 前宽 ant. W	72				61.6		66			
16. p4 后宽 post. W	31.7		32		25.7		22.7-26.6(24.7)			27.2
17. p4 主尖高 H of main cone 16/14(%)	12.4									
17/14(%)	13.5		14		10.4		10.3-12.5(11.5)			>11.2
18. m1 L	>17		43.8		14.4*		14-18.1(16.3)			
19. m1 最大宽 max. W	42.6				40.5		46.6			>41.2
20. m1 下原尖后端高 H of post. end of protoconid 19/18(%)	>53.6				56		66			
20/18(%)	36.7	35.5	35.5		28.8		28.7-33.4(30.5)			
10/14(%)	14.7	15	15.5		12.9		12.2-15.3(13.6)			
10/18(%)	20	42.3	43.7		16.4*		15-22.5(18.3)			
14/18(%)	40				44.8		44.6			
	54.5				56.9		60			
	63.1				58.8		78.5			68
	54.5				52.4		63.6			
	86.4				89.2		81			

\* Measured and/or calculated by the present authors; numbers in the brackets represent the means.



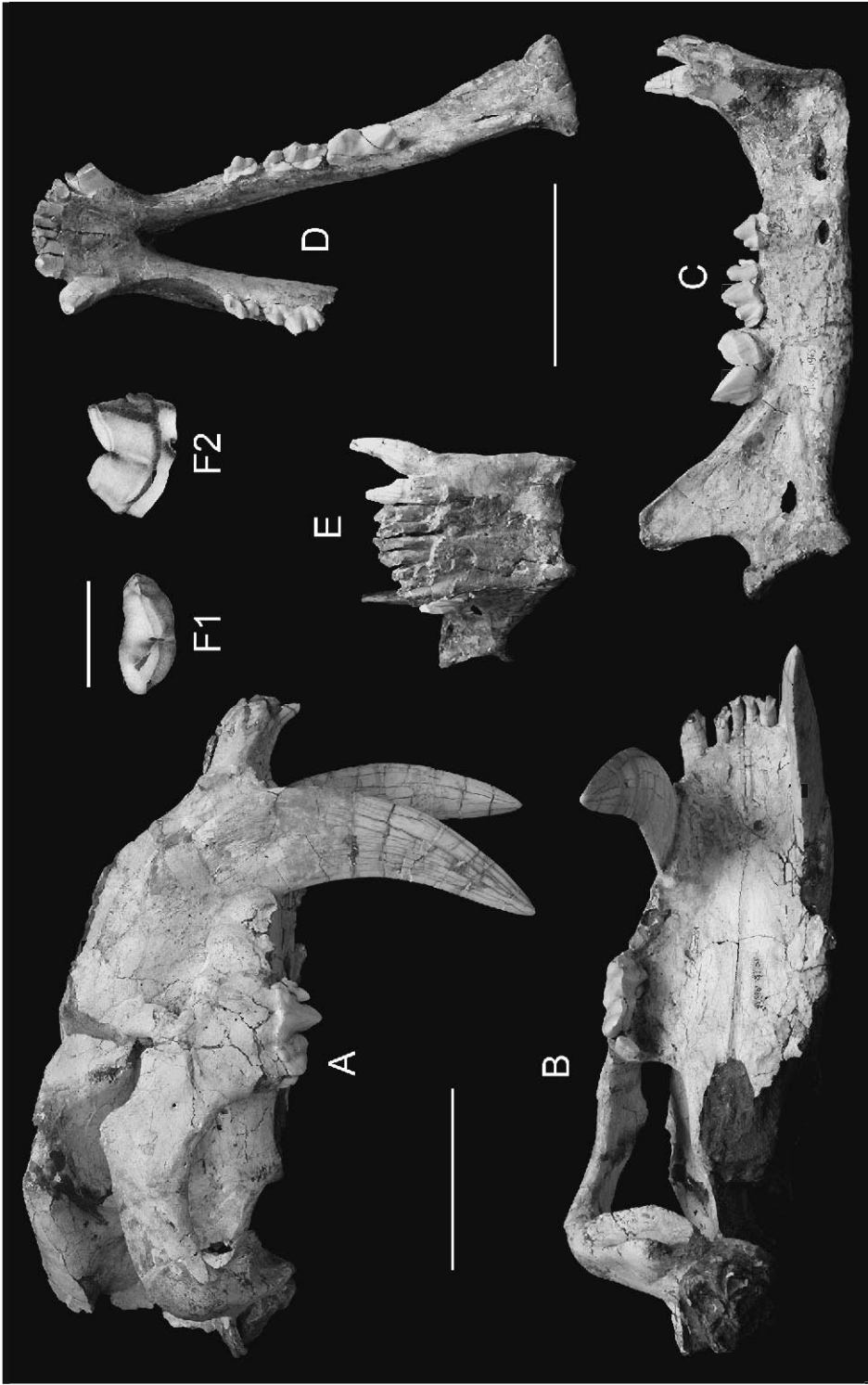


图2 恐剑齿虎选型(1900XII 501) (F) 及头骨和下颌(V 15643) (A-E)

Fig. 2 Lectotype (F) and skull with mandible of *Machairodus horribilis* (V 15643, A-E)

A. 头骨右侧面 right lateral view of skull; B. 头骨腹面 ventral view of skull; C. 右水平支外侧侧面 lateral view of right ramus horizontalis; D. 下颌顶面 top view of mandible; E. 联合部前面 anterior view of symphysis; F. 左左 ml, after Schlosser 1903, F1. 冠面 crown view, F2. 唇侧 labial view; 标尺 scale bars: A-E = 10 cm, F = 3 cm

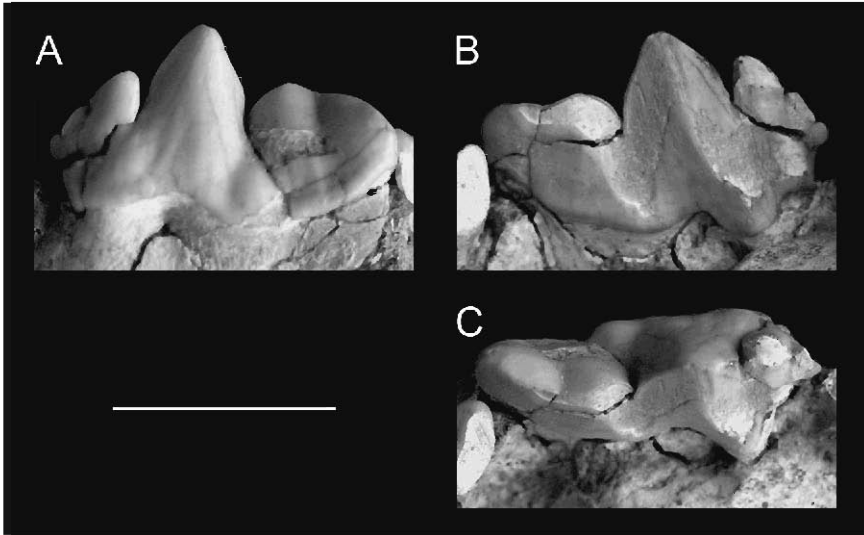


图3 恐剑齿虎左 P4, V 15643

Fig. 3 Left P4 of *Machairodus horribilis*, V 15643

A. 唇面 labial view; B. 舌面 lingual view; C. 冠面 crown view; 标尺 scale bar = 3 cm

下牙齿: 仅在 V 15643 中保存(图 2C-D, 4)。下门齿自近中向远中逐渐增大, 但 i3 不像 I3 那样急剧增大。i1 冠面已大部破碎。i2 舌侧有很微弱的侧嵴, 但比 I2 者弱。i3 仅左侧者保存。其近中嵴和远中嵴均已磨耗, 但明显发育; 近中嵴基部无小尖, 远中嵴基部则有, 但比 I3 者小。左侧 c 与 i3 间有 8 mm 的齿隙, 而右侧者没有齿隙。c 显著大于 i3。

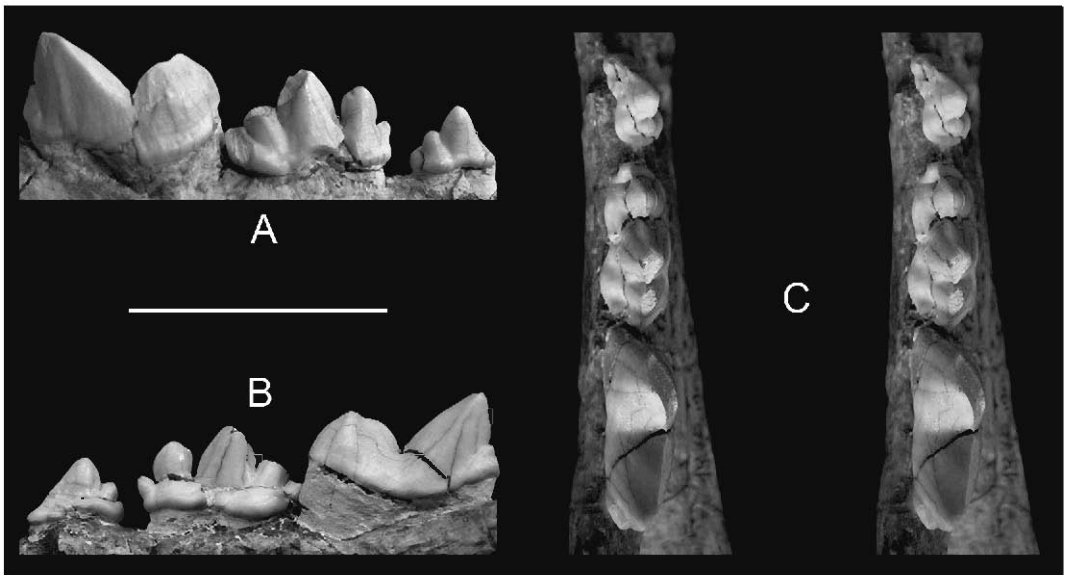


图4 恐剑齿虎右 p3-m1, V 15643

Fig. 4 Right p3-m1 of *Machairodus horribilis*, V 15643

A. 唇面 labial view; B. 舌面 lingual view; C. 冠面, 立体视图 crown view, stereopair; 标尺 scale bar = 5 cm

近中缘前端有嵴,仅基部较明显,且有锯齿;后嵴长而显著,具锯齿。无 p2 存在的迹象。右 p3 前端破损,左侧者虽破裂,但保存完好。p3 和 p4 间留有 3~4 mm 的齿隙。p3 前齿根稍斜向前下方,齿冠长轴斜向外后方,和下颌支长轴轻微斜交。p3 冠面轮廓椭圆形,舌面中部微凹。主尖很高大,前附尖小,弯向内方,后附尖比前附尖稍大而高,其后还有一个由齿带形成的小尖。上述 4 个尖均由纵嵴相连。主尖的前、后嵴上均可见锯齿。牙齿舌侧齿带较发育,但在中凹处不显;颊侧齿带仅在后半部明显。p4 非常长大,由 5 个尖组成。前附尖非常大而高,超过主尖的一半大小;后附尖小于前附尖;前前附尖小而突出;后齿带尖与前前附尖大小接近。在后附尖和后齿带尖之间的内部,自齿冠基部伸出一粒状尖突。主尖后半部和后附尖顶端的外面磨耗。后齿带小尖的外面一直磨耗至齿冠基部。右 m1 保存完整。牙齿前宽后窄,最宽处位于牙齿中部。磨耗后下前尖明显低于和短于下原尖部分。下前尖的前缘较钝圆,以约 45°角斜向后上方,而下原尖的后缘尖锐,有很微弱的锯齿,方向则接近垂直。基部有一小尖,应为下后尖的残迹。其下方稍稍隆起(图 4)。

## 2 比较与讨论

### 2.1 与中国材料的比较

中国真正的剑齿虎属化石(包括部分错误地归入 *Epimachairodus* 的材料,但不包括后来归入 *Paramachairodus* 的材料),除了未定种之外只有 3 个种,即 Schlosser 于 1903 年创建的 *Machairodus horribilis* 和 Zdansky 于 1924 年创建的 *M. palanderi* 及 *M. tingii*。后来记述的一些材料(Teilhard de Chardin and Leroy, 1945;张席提,1957;童永生等,1975)都被归入到 Zdansky 的两个种中。但中国这些剑齿虎的种和欧洲剑齿虎的关系一直没有很好地解决。前两个种虽然在国内已被广泛采用,但在国外,从 20 世纪 70 年代起就被大多数学者归入到欧洲的 *M. giganteus* 种中(详见 de Beaumont, 1975; Morlo and Semenov, 2004)。

Schlosser 据以建立 *Machairodus horribilis* 的材料保存在德国慕尼黑古生物博物馆内。本文前一作者 1983 年 12 月访问该馆时,曾对这些材料作过观察。观察的情况如下:

1) 编号 1900XII 506-507 的标本(Schlosser 文中没有图版)应为同一个体的两块,带有左 I2+I3 和 P3-M1 的齿槽。骨为黑色,牙齿亮黑色。门齿相当大;I2 的两侧有锯齿,基部有小尖,但舌侧没有 V 形齿带。根据上述门齿的特征判断,这件标本应该属于 *Homotherium*。

2) 1900XII 505 为一段上犬齿(Schlosser, 1903, pl. I 9),灰黑色,具前、后锯齿。根据其前后长度向下收缩较快判断,可能也属于 *Homotherium*。

3) 1900XII 502-503(Schlosser, 1903, pl. I 10, 13)为由前、后两半组成的 P4。前半牙冠为黑色,而后半牙冠为黄色。前半可能为 *Machairodus* 者,而后半,根据裂凹以后的部分较短(长 14 mm)、齿冠基部斜向后下方较剧等判断,可能是某类鬣狗者(如 *Adcrocuta*)。

4) 1900XII 501(Schlosser, 1903, pl. I 15, 16)为左 p4 和 m1。p4 齿冠灰白色,m1 则为黑色。两者不见得为同一类。p4 可能是某类 *Machairodus* 者,但很难鉴定到种。m1,正如 Schlosser 所指出的,无疑是 *Machairodus* 者,但比当时已知各种者都大(图 2F)。它应该是 Schlosser 建立 *Machairodus horribilis* 新种的主要依据。我们将这颗 m1 定为选型。

有意义的是,在大小上能够和这颗 m1 (1900XII 501) 相比的只有 V 15643 及 *M. irtyschensis* (Orlov, 1936) 者(见表 2)。在形态上这颗 m1 比较原始,其下后尖小,但与下原尖后脊清楚分离;既不像在 *M. aphanistus* 中那样发育,也不像在后期种中那样退化。在这一点上,这颗 m1 和 V 15643 更为接近,而不同于 *M. irtyschensis* 者。此外,根据图片(见 Orlov, 1936, fig. 1)判断,*M. irtyschensis* 的 m1 的冠面轮廓相当特殊:其唇缘前半部强烈向外隆凸,而舌缘则接近平直,致使牙齿的最宽处位于牙齿前半部。这和 1900XII 501 及 V 15643 下颌的 m1 都不同:它们的唇缘比较平均地向外隆凸,而舌缘中部微凹,牙齿最宽处位于中部。在形态上,1900XII 501 和 V 15643 的 m1 之间惟一可以看得出来的区别是,前者的前、后缘向上趋中得更明显些,特别是后缘,亦即下原尖后缘倾斜稍更明显些。上述对比使我们倾向于把 V 15643 下颌归入 *M. horribilis* 种。V 15642 头骨比 V 15643 者稍小,但形态上非常接近,也应该归入该种。新材料的归入进一步表明 *M. horribilis* 和 *M. irtyschensis* 确应为不同的种。在后者中 p3 和 p4 的附尖明显更为退化变少。Orlov 曾考虑到它们归属同一种的可能(Orlov, 1936:116)。即便如此,*M. horribilis* 这个种名也具有无可争议的优先权。将来我们也许应该把 V 15643 头骨和下颌作为新型(neotype),而把 V 15642 头骨作为配型(allotype),以填补选型仅为一个 m1 的缺憾。

Zdansky (1924) 所创建的 *Machairodus palanderi* 由若干标本组成。其中保存最好的是 Ex. 2, 一个带下颌的幼年头骨(Zdansky, 1924, pls. XXV, XXVI 1-2)。这件标本和上述归入 *M. horribilis* 的头骨和下颌差别十分显著。首先应该指出,Zdansky 所记述的这件头骨的修复可能有误(头骨后部和前部之间有石膏粘接的痕迹,见 Zdansky, 1924, pl. XXV 1)。其关节突距离颧弓的眶后突特别近,而且与齿列相比位置太高,这使得其颧弓变得异常短(见 Zdansky, 1924, pl. XXV 1)。从腹面看,其 M1 和关节突的距离也异常地近,仅稍长于 P4 之长(见 Zdansky, 1924, pl. XXV 2)。在 V 15642 中这一距离大约与 P3 + P4 等长。如果把这件头骨的后部下移并稍稍后移至正常位置,那么该头骨就应该更长(比根据图版测量得出的 260 mm 更长,可能应该接近 280 mm?)。其顶缘也应该呈更弯曲的弧形。这样,这件头骨的长大约只有 V 15642 的 4/5 左右(见表 1)。这件头骨的眶下孔和眶前缘的位置都更向前。前者在 P4 前端,而后者在 P4 中部。在 V 15642 中它们分别位于 P4 前尖前半部和裂凹之后的上方。此外,在 Zdansky 这件头骨上,鼻咽孔的侧缘互相平行,而在 V 15642 中,该孔明显向前变宽。Zdansky 这件头骨的基枕部和枕部保存不好,无法和新记述的标本对比。两者在牙齿上也有区别。在 V 15642 的 P3 前附尖之前还有一个附加小尖,在 Zdansky 的头骨上没有这个小尖。但是最明显的区别还是在下颌及下牙上。和 V 15643 下颌相比,Zdansky 所记述的下颌除了明显较小(见表 2)外,其后颞孔很小;p3 没有前附属小尖;p4 的前、后附尖相对于主尖都较小,而且没有前附属小尖;m1 的下后尖-下跟座隆起与下原尖后缘呈逐渐过渡,而没有分隔沟。这些都和 V 15643 者明显不同。总之,Zdansky 所记述的这个头骨和下颌在尺寸小、p3 前附尖退失等方面和欧洲的两个种也可以区别开来。Zdansky 作为 *M. palanderi* 描述的其他标本的性质则不很清楚。其中的 Ex. 1 和上述头骨差不多大小,也许应该归入巴氏剑齿虎这个种;但 Ex. 3 的尺寸则大得多,可能应该归入恐剑齿虎内(见表 1);其他标本由于保存较少,其种的地位目前很难确定。综上所述,*M. palanderi* 应该是一个有效的独立种。我们建议

将 Ex. 2 的头骨和下颌作为该种的选型(lectotype)。

Zdansky 所创建的 *Machairodus tingii* 的材料中没有很完整的。其中 Ex. 1(头骨和下颌的前部)保存最好(Zdansky, 1924, pls. XXVII 3-4, XXVIII 1-2)。Zdansky 建种的主要理由是:1) 其上犬齿前缘没有锯齿,而仅在后缘有;2) 下颌上两个颞孔都很大,差不多大小;3) p3 具前附尖,整个牙齿斜向前下方,而且和 p4 之间有齿隙;p4 的前附尖大而高。现在已有足够的证据表明,剑齿虎上犬齿前缘的锯齿是可以磨光的(在榆社 V 906 标本上可以看得非常清楚)。而在其他两点上,这件标本和 V 15643 相当接近。惟一的差别是其 p4 没有前附尖。我们倾向于把它们归入同一个种。这样,*Machairodus tingii* 就应该是 *Machairodus horribilis* 的后出同物异名了。

1957 年张席提记述了一件采自山西保德的头骨,被鉴定为 *M. palanderi*。这个头骨保存完好,没有受到挤压。其头骨在总体形态上和 V 15642 接近。但有如下区别:头骨在比例上明显窄长,特别是眶后突部,耳部等;鼻咽窝前后差不多等宽,而不向前变宽;M1 较大,位于 P4 之后等。这些特点使其更接近于 *M. palanderi* 的选型,而与 *M. horribilis* 不同。童永生等(1975)所记述的一件采自山西霍县的头骨也被鉴定为 *M. palanderi*。这件标本因受侧向挤压变得很窄,其鼻咽窝也被挤扁,但其牙齿在大小和构造上更接近于 V 15642 者。这件标本大概应该归入 *M. horribilis* 中。同样,Teilhard de Chardin 和 Leroy (1945, fig. 5)也记述了一件采自山西榆社的头骨,被鉴定为 *Epimachairodus palanderi*。这件头骨在大小、长宽比例及牙齿特征上都和 V 15642 很接近,应该归入 *M. horribilis* 中。

## 2.2 与欧洲材料的比较

*Machairodus* 属由 Kaup 在 1833 年创建于欧洲。分布最广而又获得绝大多数古生物学家承认的只有 2 个种,即:*M. aphanistus* 和 *M. giganteus*。前者主要发现于晚中新世 Vallésian 期,后者则主要在 Turolian 期的地层中。前者原始,后者进步。由于研究历史悠久,这两个种的化石已经积累了很多。但大多是零散的牙齿和下颌,完整的头骨,特别是和下颌在一起者,十分稀少。长期以来人们对它们的了解大多局限于牙齿的特征。这种情况直到最近才有所改变。最近在西班牙马德里之南的 Cerro de los Batallones-1 地点发现了 10 余个 *M. aphanistus* 的头骨及下颌,其初步研究结果已经发表(Antón et al., 2004)。*Machairodus giganteus* 的第一个头骨发现于希腊的 Halmyropotamos 地点,其记述见于 1968 年,但记述过于简单(Melentis, 1968)。最近在土耳其的 Kemiklitepe 地点上部地层中发现了与下颌在一起的头骨化石(Geraads et al., 2004)。现在终于有可能将中国的材料和欧洲的经典种在头骨和下颌的特征上进行对比了。

根据 Antón 等(2004)的描述,*Machairodus aphanistus* 在头骨和牙齿上比中国上述两个种都更原始。除了总体尺寸较小外(见表 1-2),其鼻骨较细长,后端窄于前端,后缘呈弧形;额骨深入鼻骨和上颌骨的前突宽大而长;乳突较小,其前端位于内鼓骨前端之后;副枕突仍然较大,其末端伸至乳突之下;下颌冠状突仍然很大,其长约与 p4 + m1 之长相等等;冠状突斜向后上方,其后端伸达关节髁之上或之后。P3 舌侧后半部向内明显凸出;P4 的原尖很大,冠部仍呈锥形,使 P4 的宽大于其长的 1/2。所有这些在剑齿虎的进化过程中都是近祖性状。

*Machairodus giganteus* 的头骨, 根据 Melentis (1968, 最初鉴定为 *M. aphanistus*, 但个体显然比 Bataallones-1 地点的所有头骨都大, 因此可能应该归入 *M. giganteus* 种) 和 Geraads 等 (2004) 的记述, 与中国的两个种在大小和形态上都比较接近。和 *M. palanderi* 最明显区别在于它的 P2 已退失, 而在后者中 P2 总是存在。它和 *M. horribilis* 的区别也较明显。一方面, 它的尺寸没有达到 *M. horribilis* 那样大 (见表 1)。另一方面, 其头骨中部 (包括鼻咽窝) 不特别加宽; 乳突末端亦不变宽, 其远端附着肌肉的粗糙面基本限于腹面, 然而副枕突却更为退化, 其末端与枕髁下缘大体在同一水平上 (见 Melentis, 1968, pl. XXXI 1-2; Geraads et al., 2004, fig. 2A-B)。在牙齿上, *M. giganteus* 没有 P2, 其 P4 和 p3-p4 没有 *M. horribilis* 那样长大且无多余附属小尖。

## DESCRIPTION OF SKULL MATERIAL OF *MACHAIRODUS HORRIBILIS* SCHLOSSER, 1903

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### Summary

*Machairodus horribilis* was erected by Schlosser in 1903, based on isolated teeth purchased from some drugstores in China. Zdansky attributed some of these teeth (P4 and C?) to his new species *M. palanderi*, but left the others (incisors, p4 and m1) as specifically indeterminate (Zdansky, 1924:115). Otherwise, few paleontologists paid attention to Schlosser's species at all.

While curating the Chinese *Hipparion* fauna fossils in IVPP during the early 1990's, the senior author of the present paper accidentally found two machairodont skulls collected from Baode in 1965, still unprepared. One of them turned out to be a perfectly preserved skull, while the other, a larger one, though only about half preserved, was associated with its mandible. Both were exceptionally large and possessed features shared exclusively by them. It was of particular interest that the m1 of the 2<sup>nd</sup> skull seemed considerably close to that of Schlosser's *M. horribilis* in size and morphology. This renders it plausible to refer these two skulls to *M. horribilis*, and this would, in turn, rehabilitate Schlosser's *M. horribilis*.

The other reason for presenting the present paper now is the recently emerged possibility of making more detailed comparison between the Chinese and the classical European *Machairodus* species. For this we owe much to the two recently published articles on the skulls and mandibles of *M. aphanistus* and *M. giganteus* (Antón et al., 2004; Geraads et al., 2004).

### 1 Systematic description

**Felidae Fisher de Waldheim, 1817**

**Machairodontinae Gill, 1872**

***Machairodus* Kaup, 1833**

***Machairodus horribilis* Schlosser, 1903**

**Lectotype** Left m1 (Schlosser, 1903, pl. I 15-16; Fig. 2F of this paper), from China,

but exact locality unknown.

**Described specimens** V 15642 (Fig. 1), an almost complete skull of middle-aged individual without I1's, I2's, right I3 and crowns of both C. V 15643 (Figs. 2A-E, 3 and 4), partial skull with mandible of younger age. The left half of the skull is mostly broken off, while the part posterior to the zygomatic arch of the right half is also missing. Of the mandible only the middle part of the left ramus under the anterior half of the m1 is missing. Of the incisors only the left I3 and i3 are more or less complete; the canines are well preserved; and the cheek teeth are well preserved, though with cracking.

**Diagnosis** The largest so far known of the genus, with vertex L (length) of skull  $\geq 350$  mm, P3-P4 L  $\geq 65$  mm, and p3-m1 L  $\geq 90$  mm. Skull proportionally broader, with greatest W / vertex L around 65%. Nasals roughly rectangular in form, slightly wider at posterior end; bone-plates sharply thickening sagittally. Nasopharyngeal fossa (term of Davis, 1964) considerably widened anteriorly, ended with a U-shaped anterior border. Distal end of mastoid process enlarged, with elongated rough area for muscle attachment, extending to lateral side; paroccipital process prominent, extending downward beyond the occipital condyle. Height of mandibular coronoid process only slightly longer than L of m1, with its posterior border being almost vertical, and condyle lying far behind the coronoid process. Lingual cingula in I1-I2 V-shaped, giving rise to basal cusplets on mesial and lateral sides respectively. P2 present. P3-P4 and p3-m1 relatively long. Cheek teeth occasionally with irregular granular tubercles on enamel surfaces. P3 and p4 5-cusped. P3 without evident posterolingual bulging, and P4 has a weakly bulged protocone supported by a separate root, without forming a real conical tubercle. Large granular tubercle present on posterolingual side of p4, and m1 with strongly oblique anterior border, almost vertical posterior border, and well separated rudimentary metaconid.

**Description** Skull Frontal view (Fig. 1A): Maximum L of nasals is 96 mm, W at posterior end is 61 mm, and at anterior end is 50.5 mm. The mesial 2/3 of fronto-nasal suture is roughly transverse. No sagittal processes of frontals are evident, but the lateral process inserting between the nasal and maxilla is prominent, L of which is  $\sim 16$  mm. The anterior border of the nasals forms a strong zigzag, with a sagittal notch bordered bilaterally by pairs of wide concavities and lateral processes. Seen from the front, the nasals are rapidly thickened sagittally, forming a isosceles triangle, H (height) of which reaches 14 mm (Fig. 1F). The sagittal depression in the border area between the nasals and frontals is well developed. The frontals are broad, with robust and blunt postorbital processes. Sagittal crest very long, beginning at the level above the anterior end of the glenoid cavity. The largest W of the skull at the posterior ends of the zygomatic arches (partly restored in plaster) is  $\sim 230$  mm.

Lateral view (Figs. 1B, 2A): Nasal process of premaxilla is 50 mm long, W at the anterior end of the nasal being 15 mm. The interspace between the nasal processes of the premaxilla and frontal is 21 mm. The infraorbital foramen is above the P4 parastyle, while the anterior border of the orbit above the P4 paracone. The postorbital process of the zygomatic bone is like that of the frontal. The sagittal crest becomes higher and higher posteriorly and plate-like, maximum H of which reaching  $\sim 45$  mm. The foramina and fissures on the mesial wall of the orbit are well preserved, description of which is omitted here because of space limitation.

Ventral view (Figs. 1C-D, 2B): The labial border of the premaxilla is arched, without an evident concavity in the area of the I3-C diastema. The premaxillo-maxilla suture runs from the middle part of the canine to the posterior border of the anterior palatal foramen. The paired anterior palatal foramina are large and oval in form, roughly parallel with each other. The palatal fossae situated anterior to the above foramina are very long, reaching the posterior borders of the I1's. The posterior palatal foramina are situated slightly anterior to the P4's. In addition, numerous small nutrient foramina can be seen posterior to the posterior palatal foramina, at least 5 on each side. The palato-maxilla suture is roughly M-shaped, with its middle portion lying at

the same level as the posterior palatal foramina and the lateral portions ~10 mm anteriorly protruded. The 3 crests, a sagittal one and a pair of lateral ones, are clearly shown, but far less sharp than in *Smilodon*.

The basicranium in V 15642 is well preserved (Fig. 1D). The posterior part of the basioccipital forms a strongly bulged triangle, which is confluent with the occipital condyles. The sagittal ridge is crested anterior to the bulged triangle and bordered bilaterally by deep depressions. Then it fades out between the pair of the muscular tubercles. The foramen ovale is situated between the glenoid cavity and the posterior part of the pterygoid plate, opening mainly anteriorly. The tympanic bulla is oval in form, strongly bulbous, with its apex lying in the anterior 1/3 of the bulla. The anterolateral portion of the bulla is rather large and flat, finely sculptured. This may be the external wall of the ectotympanic. The carotid foramen is confluent with the posterior lacerated foramen, which shares a common large depression with the condyloid foramen as well. Both the postglenoid and mastoid processes are strongly downward extended, 6 ~ 7 mm separated from each other at their distal ends. The distal end of the mastoid process is widened, with large muscle attachment area on distal and lateral sides. The anterior 2/3 of the bulla is covered up by the enlarged mastoid process from outside. The paroccipital process is still quite large, with its extremity extended beyond the lower border of the condyle. The mastoid and paroccipital processes are connected by an upward convex ridge at their lower ends. Therefore, the line connecting the distal ends of the three processes (postglenoid, mastoid and paroccipital) goes only slightly upward and posteriorly.

Occipital surface (Fig. 1E): It roughly forms a high isosceles triangle, but with a pair of small outgrowths at the lower borders of the upper 1/3 of the lateral sides. The area around the condyles is smooth, subdivided into two pairs: one pair is above the condyles, while the other pair lying lateral to the condyles. Otherwise, the occipital surface is highly rugose, especially at the peripheral areas and above the depressions above the condyles.

Mandible (Fig. 2C-E): The only mandible (V 15643) is generally very long and low, with highly reduced coronoid process. The two rami are tightly coalesced, although suture remains clearly traceable in symphyseal part. The posterior surface of the symphysis can clearly be subdivided into an upper, rather flat surface facing upward and posteriorly, and a lower, deeply excavated part, where the geniohyoid and genioglossus muscles are to be attached. The anterior surface of the symphysis is roughly rectangular in form, with the middle of its lower border slightly projected. The surface is covered by numerous nutrient foramina, of which two pairs are more prominent: the upper pair are located equidistant between the mid-line and the lateral borders, while the lower pair are closer to the lateral borders. Seen from the lateral side, the angle formed by the anterior border of the symphysis and the lower border of the ramus is slightly more than 90°. The mental flange projects over the symphysis, especially in its lower part. The ramus is thin, particularly so in the area under the c-p3 diastema, which is 56 mm long. There are two mental foramina: the anterior one is larger, situated below the anterior end of the posterior 1/3 of the diastema; while the posterior one is smaller, under the posterior half of the p3. There is a small diastema between the p3 and p4, which is only 3 ~ 4 mm. The lower ridge of the masseteric fossa is very prominent, extending to the lateral end of the condyle. H of the coronoid process, measured from the condyle to the top of the process, is only 50 mm, about the same length as the m1 + one third of the p4. The posterior border of the coronoid process is almost vertical, with its top lying well anterior to the condyle.

Dentition (Figs. 3, 4): None of the incisors are well preserved, except for the left I3 and i3. So far as can be judged from what is preserved, the incisors can be briefly described as follows. They gradually increase mesiodistally in size, with greater gaps between the 3<sup>rd</sup> and the 2<sup>nd</sup> ones. On the lingual sides in I1-I2 there are V-shaped basal cingula, branches of which terminated as serrated cusplets on mesial and distal sides. In I3 the mesial basal cusplet is lar-



ger and higher situated, and the distal one is less prominent. There are no V-shaped lingual cingula in the lower incisors, nor are the bilateral ridges very sharp. In i3 the mesial accessory cusp is hardly noticeable, while the distal one is small.

The C in V 15643 is exceptionally large (see Table 2), with its total rectilinear L ~205 mm, and the L from alveolus to the crown top 130 mm. The enamel becomes very thin toward the crown base and fades out before it reaches the alveolus, except near the posterior edge. Both anterior and posterior edges are cutting and serrated. The anterior ridge turns mesially at the level ~50 mm above the alveolus. The c is much larger and higher than the i3 and separated from the latter by a diastema of 8 mm long. There are anteromesial and posterior ridges, cutting and serrated in their lower halves.

The cheek teeth are relatively large, occasionally covered by granular tubercles, especially on their labial surfaces. The P2 is always present. The P3 is 2-rooted and 5-cusped, the anteriormost supplementary cusplet is the smallest, while the posterior cingular cusplet is the next smallest. The bulge on the posterolingual part of the tooth is hardly noticeable. The P4 is 3-rooted, with one anterolingual root supporting the highly reduced protocone, which takes the form of a weak lingual bulge, without forming a conical tubercle. The pre-parastyle is prominent, while the metastyle is longer than the paracone. The M1 is highly reduced, retreated to the inner side of the posterior end of the carnassial. All the lower cheek teeth are two-rooted. The p3 is 4-cusped, with the anterior accessory cusp being the smallest and hardly seen from the labial side. The p4 is very long and 5-cusped. The anterior accessory cusp is the largest cusp next to the main cusp and the anteriormost supplementary cusplet is well set and clearly separated. The anterior border of the m1 slopes strongly posteriorly, but the posterior edge of the protoconid is almost vertical, with a well differentiated rudimentary metaconid near its base. The talonid is highly reduced and no clear separation between it and the metaconid is detectable.

## 2 Comparison and discussion

### 2.1 Comparison with other Chinese materials

There are 3 species of *Machairodus* so far officially described from China: *M. horribilis*, *M. palanderi* and *M. tingii*. Among them the 1<sup>st</sup> one has been the least known and the most often neglected.

During his study visit to the Paleontological Museum of Munich University in 1983, the senior author of the present paper had the chance to survey the specimens based on which Schlosser created his *M. horribilis* in 1903. There were altogether 4 specimens labelled as belonging to *M. horribilis*, all bearing the prefix 1900XII: 501, left p4 and m1, but of different colors (Schlosser, 1903, pl. I 15-16); 502-503, a left P4 composed of 2 pieces of different colors (Schlosser, 1903, pl. I 10, 13); 505, a piece of upper canine (Schlosser, 1903, pl. I 9); 506-507, two pieces of left maxillae with I1-I2 and alveoli of the P3-M1 (unfigured). Of them only the m1 (501) appeared to be diagnostic enough for establishing a new *Machairodus* species, while the others should either belong to other forms (*Homotherium*, *Adcrocuta*, etc.), or inadequately distinctive for erection of a new species. Fortunately enough, the m1 (501), stood out from the other specimens compared with the other known *Machairodus* species. The m1 (501) was so large that only those of V 15643 and *M. irtyschensis* from Pawlodar (Orlov, 1936) were comparable with it in size. On the other hand, morphologically it remained rather primitive in having a metaconid-talonid complex, clearly set off from the posterior ridge of the protoconid, a feature closer to that of V 15643 than to that of *M. irtyschensis*. According to fig. 1 given by Orlov, the m1 of *M. irtyschensis* seems to be rather peculiar in crown configuration, with the anterior half of its labial side being strongly bulged, while its lingual side almost

totally straight. In both m1's (V 15643 and 1900XII 501) the labial side bulges more or less evenly and the lingual side shows a shallow concavity at the middle (Fig. 2D, F, Fig. 4). Furthermore, in the mandible of *M. irtyschensis* both p3 and p4 lack the anteriormost supplementary cusplets (Orlov, 1936, pl. I 1, 3). This is quite opposite to the case in V 15643, where the supplementary cusplets and granular tubercles are excessively developed. Therefore, we are in the opinion that *M. irtyschensis* may really be a valid species, morphologically different from that represented by V 15642–15643, which are to be included in Schlosser's *M. horribilis*. Were *M. irtyschensis* conspecific with *M. horribilis*, as once suggested by Orlov (1936:116), *M. horribilis* is certainly to be chosen because of its year priority over the former (1903 vs 1936).

The materials referred by Zdansky to *Machairodus palanderi* are apparently heterogeneous. The best and most diagnostic specimen is Ex. 2, consisting of a skull in association of its mandible of young age. It is small in general size (see Tables 1–2), and its diagnostic features are best shown in its mandible; the small posterior mental foramen, the lack of anterior supplementary cusplets in p3 and p4, and the confluence of the metaconid with the talonid without clear separation from the posterior edge of the protoconid in the m1. As typified by this Ex. 2, *M. palanderi* is to be considered a valid species.

The validity of *Machairodus tingii* as a separate species is still an unresolved problem. The material consists of 3 specimens, only one of which (Ex. 1, muzzle parts of skull and mandible) is described in more detail and figured. It is rather large in size, but slightly smaller than V 15643. In morphology the two specimens are quite close, with probably the only distinction that in the former the p4 lacks the anteriormost supplementary cusplet (broken?). It cannot be totally excluded that they might belong to the same species.

## 2.2 Comparison with the European species

Thanks to the new discoveries in Spain (Antón et al., 2004), the skull and mandible features of *Machairodus aphanistus* are well known. It differs from *M. horribilis* in having a number of plesiomorphic characters, such as the comparatively long nasals, narrowing posteriorly; the larger and long anterolateral processes of frontals inserting between the nasals and maxillae; the smaller mastoid but larger paroccipital processes; the long and posteriorly slanting mandibular coronoid process; P3 being considerably widened posteriorly; P4 with large protocone etc.

*Machairodus giganteus* is now better known through the additional find of skull with mandible in Turkey (Geraads et al., 2004). As a rule rather than exception, there is no P2 in *M. giganteus*, while in most specimens from China, *M. horribilis* included, the P2 does exist. Furthermore, *M. giganteus* differs from *M. horribilis* in being narrower in the middle part of the skull, especially clearly shown in the narrowness of the anterior part of the nasopharyngeal fossa; the less robust mastoid process; the stronger reduction of the paroccipital process, lower end of which lying at the same level as the lower border of the condyle; and the less development of the supplementary cusplets in the cheek teeth.

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