

记山东山旺貘类一新属

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关键词 山东山旺 中新世 貘化石

内 容 提 要

作者把最近在山东山旺发现的貘类标本和谢万明在1979年记述的两颗上颊齿以及松本彦七郎1927年记述的一个貘类的下颌归并成一个种，并主要依据头骨上的一些独特性状为它们建立了一个新属——*Plesiotapirus*。根据命名法则，其种名应为*Plesiotapirus yagii* (Matsumoto, 1921)。*Plesiotapirus* 代表了貘科进化中的一个绝灭的旁支。本文指出了这一发现在中、日动物群对比上的意义。

作者1985年在清理山旺古生物博物馆库存标本时，发现了一件貘类化石，它包括呈自然关联状态的头骨、下颌、颈及胸的前部。和山旺的大部分其它标本一样，也是被包覆在薄层状硅藻土之中，侧向受压变扁。头部仅鼻骨因受挤压而末端向上翘起，其它部位仅有轻微错动。头骨左侧面在发现过程中受到了较多的损坏。上、下颌紧紧咬合在一起。为了研究的方便，主要将左侧齿列修出，在修理过程中，下前臼齿损坏较多。虽然如此，它仍不失为貘科化石中少有的保存完好的标本。貘科化石的发现与研究虽然已有百余年的历史，但第三纪地层中，特别是在晚第三纪早期的地层中，发现的貘化石几乎全是零散的牙齿，因此我们对貘类早期进化历史的了解还很少。山旺发现的材料，是目前亚洲第三纪地层中保存最好的貘类的头骨。这一发现为我们提供了貘科早期进化的新信息，它表明在其进化中存在着现已灭绝的进化旁支。

本文由杨明婉女士绘图，张杰先生照相，在此一并致谢。

一、标本记述

貘科 *Tapiridae* Burrett, 1830

近貘属(新属) *Plesiotapirus* gen. nov.

矢木氏近貘 *Plesiotapirus yagii* (Matsumoto, 1921)

1921 *Palaeotapirus yagii* Matsumoto

1979 *Palaeotapirus ziejaheensis* Xie

属型种 *Plesiotapirus yagii*

正模 左下颌(具 P_2-M_2) 和属于同一个体的 M_3 。保存地点不详, 可能收藏于日本仙台 Tohoku Imperial University。

归入标本 左 P^4-M^1 。标本保存在上海自然博物馆。标本编号: 1020。

本文记述标本 1. 呈自然关联状态的头骨、下颌、颈和胸前部。标本保存在山东省山旺古生物博物馆。标本编号: 85005。2. 一 $MtIII$ (?) 远端, 标本保存在中国科学院古脊椎动物与古人类研究所。标本编号: V 9475。

特征 大小约与现生最小的南美貘 (*Tapirus roulini*) 相近。眶前面部很高, 眶下孔大约位于面高的中部, 自 Prosthion 至鼻切迹后端为向上隆凸的曲线。鼻骨窄短、舌状, 后端两侧具小凹陷以容纳鼻憩室之后端。鼻骨后移, 其后端在 M_3 之后的上方, 而前端约位于眶前缘附近; 无眶后突。前颌骨鼻突插入上颌骨之中, 其后端达 P^3 处。下颌颏孔位于 P_2 之前。门齿排列紧密, 前两对门齿唇面冠高而平直, I^3 不特别加大, I_3 不变小; 上犬齿很小, 距 I^3 不远, 下犬齿退失。颊齿前之齿隙短: $C-P^1$ 短于 P^1+P^2 。上前臼齿宽大于长; 后尖位置内移, 但基部向外扩展, 使后尖外壁明显倾斜; 内齿带发育, 但不完全。 P^1 原尖大, 向外伸出 V 形嵴, 其后有很小的“次尖”。 P^2-P^4 半臼齿化, 内中谷仅在上半部开放, 两横脊接近平行。下前臼齿后脊脊形明显, 但低于前脊。下臼齿中仅 M_3 前脊宽于后脊。

地点与层位 正模产于日本 Mino 省 Kani 县 Tonohira 地点的平牧组 (Hiramaki) 中, 时代为早中新世末期; 其余材料均产自山东临朐山旺含优质硅藻土的夹层中, 时代大约相当于欧洲陆相哺乳动物分带的 MN 5。

描述 头骨鼻—额缝以前的部分很长, 额顶部大约只占头全长的 $1/4$, 面部很高。鼻骨是头骨受压变形最厉害的部位, 致使两鼻骨都竖立了起来。它们的腹面相向迭压在一起, 只是左鼻骨比右侧者更向上错动了一些。鼻骨短小, 中缝处最长约 4 cm。前端圆钝, 侧缘中部稍稍凹入。鼻—额骨缝较平直, 自中矢缝向外并稍稍向后倾斜。鼻骨背面微隆, 其侧后端没有大多数貘类所具有的容纳鼻憩室后端部的弧形凹槽, 但在额骨上, 在鼻骨后外角之外方, 有一小凹缺, 代表了容纳鼻憩室后端的部位 (图 Ia)。鼻骨的位置很向后移。以鼻—额骨缝外端为准, 它位于 M^3 之后; 而鼻骨前端复原后的位置大约在眼眶前缘附近。额—上颌骨缝自上述的小凹缺向前缓缓下降, 在眶后突之前转入眼眶。额—上颌骨缝在眶后突之上及其以后隆起呈嵴状, 构成容纳鼻憩室凹区之外界。此嵴和眼眶上缘之间也为一凹面, 宽约 13 mm。眶前缘位于 M^1 后端上方。泪骨在面部的出露为一小三角形, 位于眼眶之前上方。泪骨在眶缘上大约有两个泪孔, 上面的一个大, 通向前下方。上颌骨顶缘隆凸, 其后端伸入鼻切迹中, 其前端上方伸至前颌骨之内。自顶面看, 从前颌骨鼻突后端稍前方开始, 上颌骨的顶缘转向中矢方向, 因此将鼻孔分成上、下两部分。向后此转向中矢方向的部分逐渐变窄, 大约于眶后突的上方即行消失。眶下孔在眼眶之前约 30 mm 处, 与眼眶下缘大约处于同一水平上, 距上颌骨顶缘约 40 mm。前颌骨有一细长的鼻突, 斜向后上方并插入上颌骨之中, 其后端达 P^3 的上方。颧弓细弱, 其前端起始于 M^1 和 M^2 之间, 先向后平伸, 自眼眶后斜向后上方, 使关节窝远高于齿槽缘。关节后突下端向前弯曲, 下颌关节突和头骨关节后突上半部之间留有宽的空隙。关节后突和乳突在下方不封闭, 留有宽的开口。乳突与副枕突愈合, 看不出它们的界限, 表面粗糙。乳突前

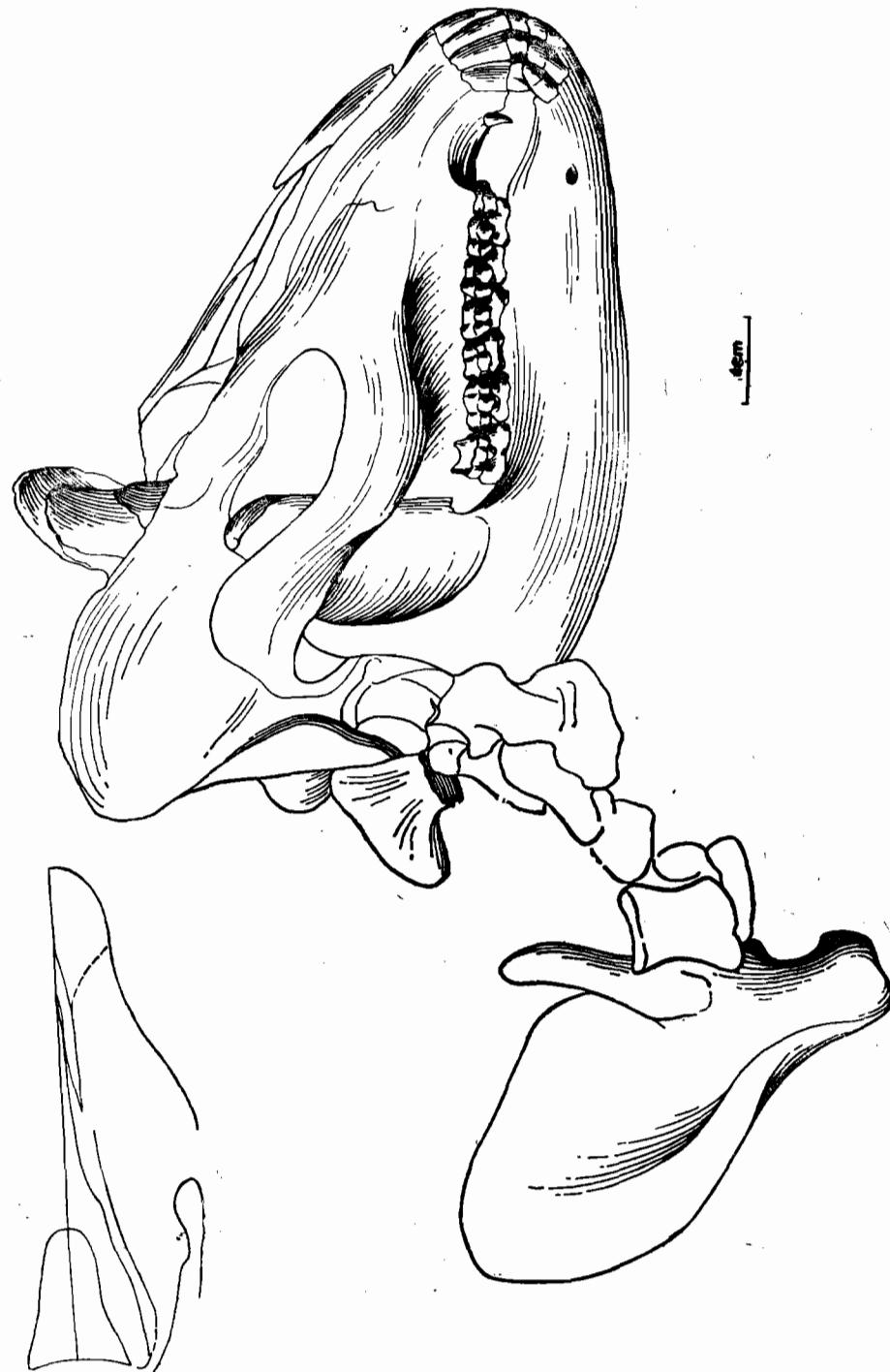


图 1 *Plesiotapirus yagii*, 85005
a. 右侧面 (right side); b. 复原后头骨正面视(鼻部) (top view of nasal part after restoration)

端有一斜向前下方的嵴；副枕突后缘平直，末端锥形。头骨顶缘自鼻骨以后向后平伸，仅在枕顶部向下弯曲。颞嵴大约在枕面前约 85mm 处形成单一的矢状嵴。

下颌粗壮。外侧面圆隆，最隆处位于 M_3 的后下方。下缘较平直，最隆处位于 M_2 和 M_3 之下方。颏孔位于 P_2 之前约 10 mm 处。垂直支前缘近于垂直；后缘在关节突之下凹入，然后斜向后下方。

上门齿近于垂直。 I^1 和 I^2 形态接近(图版 II)。齿根断面都是以唇侧为底的等腰三角形，但唇面稍凸，而两侧面则有浅的中凹。齿根和齿冠之间的界限明显。齿冠宽于齿根。齿冠断面也为等腰三角形，但底(唇面)长于两腰。自侧面看，齿冠的唇缘为脊形，而脊内的部分为凹形，亦即唇侧冠高远大于舌侧。舌侧有齿带。 I^1 稍大于 I^2 。 I^3 齿冠破损，其根的断面区别于 I^1 和 I^2 者，近椭圆形，向末端收缩缓。因此 I^3 的根显得比 I^1 和 I^2 者稍粗壮些。 I_1 和 I_2 与上门齿在形态上大体相同，但尺寸稍小，且齿冠与齿根不在同一轴线上，它们的唇侧壁也更圆凸。 I_3 由于保存得太差，其形状不能十分肯定，其齿冠与 I_1 、 I_2 不同，可能更近一锥形，而不为三角形，它的齿根至少在唇面也是圆凸的，而不是平的。它在齿槽中着生的位置也有别于它前面的门齿：更近水平些，与 I_2 齿根间有较大的空隙。虽然如此，我们根据咬合关系仍把它视作 I_3 。由于颊齿处于正位咬合状态，门齿的咬合也应是正常的。上述牙齿与 I^2 和 I^3 咬合，而不是与 I^1 和上犬齿咬合。这表明它应为 I_3 ，而不是下犬齿。

上犬齿很小，圆柱形；齿根细长，齿冠则很小。根长至少是冠高的两倍。牙齿稍向前下方倾，并稍向后弯曲。它与 I^3 间齿隙约 7 mm。

如果关于 I_3 的判断无误，下犬齿则已全然退失。

颊齿前的齿隙短：上者为 28 mm，下者为 47 mm。

P^1 形状接近三角形，只是前内缘向内凹入。外壁高耸，向内上方倾斜。前尖和后尖在外壁上以沟相分开。此沟至齿冠基部斜向后方。前尖和后尖在外脊内壁上也以一浅沟相隔。前附尖分离不太明显，外壁上也见到它和前尖之间有一浅沟。原尖近锥状，位于前尖之内方。两者之间以一纵沟相隔。自原尖顶端向前外和后外方各伸出一条短嵴，前者和前齿带之外半部相连，后者伸向后尖的基部。原尖远低于外脊。次尖很小，瘤状，附于原尖之内后方。内齿带和后齿带连成一弧形将牙齿包围。后尖处外齿带也发育。

P^2 为一前窄后宽的梯形。外脊与 P^1 者相似，只是外壁上的沟表现得更明显，前附尖已从外脊中较明显地分离了出来，只是还很小。原脊斜向内后方，它的外端并不与前尖直接融合，而是以一窄的纵沟分开。后脊弱而短，已磨蚀到齿质暴露。次尖本身较高。自内侧面看，次尖高于原尖，两尖仅在上半部分开，下半部互相愈合，但留有一很深的分隔沟。后齿带与后尖处的外齿带的情况与 P^1 者大体一样，前齿带较 P^1 者更为发育，并与前附尖连为一体。内齿带在原尖和次尖最隆处消失。齿根三个，外侧两个，大小相近；内侧一个横向扁，在内侧面上有一弱的中沟，在其外侧面上中沟深，几乎将此根分成前、后两个。

P^3 和 P^4 很难辨别。为了不影响陈列的效果，我们只将左侧牙齿修理摘取，由于修理时没有关于牙齿位置顺序的记录，而右齿列 P^3 和 P^4 从外壁又很难区分，因此，我们只能依据牙齿接触面的吻合情况、磨蚀的程度和臼齿化的程度来判定 P^3 或 P^4 。这种判定不一定十分可靠。 P^4 与 P^3 的区别在于：1) 从内侧面看， P^4 的齿冠稍高于 P^3 者(但在外

侧面却不易区别)。2) 它的两条横脊更互相平行。在 P^3 中其内端稍趋近。3) 它的前附尖在比例上稍大些。4) P^4 更近长方形, 而 P^3 前半部窄于后半部。根据上述的判断, P^3 稍宽于 P^4 。这曾使我们怀疑对 P^3 和 P^4 的判定是否准确。但 P^3 的次尖磨蚀比 P^4 者深, 而且 M^1 在宽度上也小于 P^4 , 这又使我们相信我们的判断是可信的。 P^3 和 P^4 明显地区别于其它上臼齿: 1) 整个牙齿的轮廓更趋向横宽; 2) 后尖外壁明显地向内侧倾斜; 3) 横脊在内端不完全分开, 自内面看, 内壁的下 $2/3$ 或 $3/4$ 都是相连的, 将中谷部分地封闭起来。总之, P^3 和 P^4 还处于半臼齿化的水平。

M^1 的宽小于 P^3 和 P^4 。齿冠自外侧看, 低于 P^3 和 P^4 者, 但自内侧看, 则高于 P^3 和 P^4 者, 亦即原尖, 特别是次尖较高, 外脊和横脊在高度上差别不象在前臼齿中那样明显。自冠面看, 前附尖、前尖和后尖组成一条斜向后内方的脊, 其倾斜程度大于前臼齿者。但由于 M^1 的外缘也是斜向后内方的, 所以后尖的外壁不像前臼齿那样明显地向内上方倾斜。两横脊间距离宽, 后脊内端向后方歪斜显著。中谷向内完全开放。外、后齿带比前面齿发育弱; 前齿带与前臼齿者同; 内齿带前半部较发育, 将原尖包围。齿根可能是四个。

M^2 明显地大于 M^1 , 齿冠也更高。横脊更长, 更近于互相平行。内齿带仅在中谷处有一残迹, 后齿带几乎完全消失。 M^3 的后尖明显变小变扁。牙齿的后缘较隆凸, 齿带较发育。齿根四个, 内侧有两个。

下颊齿在修理过程中损失较大。左 P_2 仅剩下了下次脊的部分, 但右侧者保存较完整, 仅下前尖缺损。从内侧面看, 下前尖与下原尖明显地分开。下原尖高大, 自顶端向外后, 后和内后方各伸出一短嵴。伸向外后方的嵴延伸至基部形成齿冠最宽处; 伸向后方的

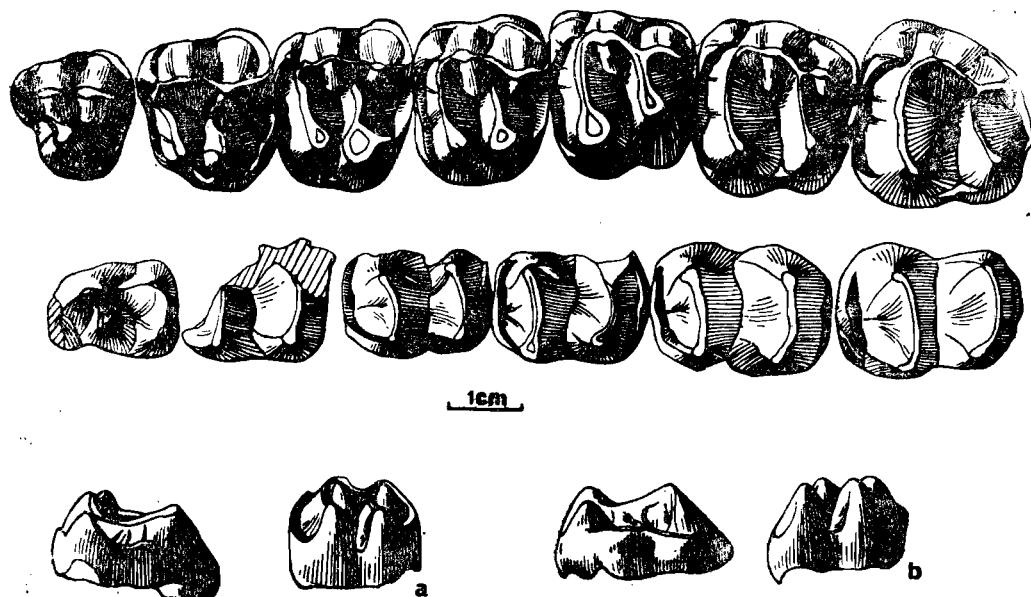


图 2 *Plesiorapirus yagii*

1. 85005 左上、下颊齿, 冠面视 (left upper and lower cheek teeth, crown view)

2. 85005 (a) 和 1020 (b) P^4 之比较 左: 前面视; 右: 舌侧视

(comparison of P^4 , a: 85005; b: 1020 upper: anterior view; lower: lingual view)

嵴与下次尖相连；而伸向内后方的嵴则伸向下后尖。下次脊已形成，但明显低于下原尖。下次尖和下内尖间以一脊相连，使次脊作L形。

左 P_3 保存得更不完整：下前尖、下后尖和下内尖皆已破失。从保留的部分看，两个横脊已经形成，但下后脊的纵脊部分，亦即下前尖还相当长。下次脊和 P_2 者接近，明显低于下后脊，并以嵴与下原尖相连。

左 P_4 保存完整，已高度白齿化。前脊前面有中沟，其后缘内侧有一小的下后附尖的残迹。后脊明显低于前脊，但较前脊更宽。下前嵴齿带状，真正的前齿带位于下前嵴之下，但表现很不明显。后齿带较明显，其中部升高，几乎达到后脊中凹的高度。外齿带仅在外中谷处发育，呈小瘤状。

左 M_1 内壁破损。前脊前壁更陡直，相对也更宽。后脊与前脊几乎等高。前、后齿带都较发育，后齿带中部仅稍稍向上凸起，离横脊顶端还很远。左 M_2 明显大于左 M_1 ，齿冠也更高。左 M_3 是颊齿中最大者，后端收缩变圆，后脊也短于前脊。

表1 猛类头骨及下颌的测量及比较 (单位：毫米)
(Measurements of some tapirid skulls and lower jaws, in mm)

	<i>Plesiotapirus yagii</i> (85005)	<i>Paratapirus helveticus</i> (Schaub, 1928)	<i>Miotapirus harrisonensis</i> (Schlaikjer, 1937)	<i>Tapirus indicus</i> (IVPP 1326)
头长 (Prosthion-condyle)	360			422
眶前长 (Prosthion-orbit)	172	125.3*	148	185
眶后长 (Condyle-ant. rim of orbit)	193			245
鼻骨最大长 (Max. L. of nasal)	~48	87	91.3	117
鼻切迹长 (L. of nasal notch)	260	171		268
前颌骨长 (L. of premax.)	154	121		127
齿隙长 (C-P ¹)	25	19	27.4	53
眶前缘—眶下孔 (Orbit-infraob. for.)	32	26		31
P ¹ —P ³	127	112	113.2	~160
P ¹ —P ⁴	68	58.6	60.2	89
M ¹ —M ³	~60	54	54.7	~72
下颌全长 (Max. L. of lower jaw)	290			348
齿隙长 (I ₁ —P ₂)	49		37.8 (C—P ²)	60 (C—P ²)
P ₂ 处下颌高 (H. at P ₂)	48		32.4*	59
P ₄ 处下颌高 (H. at P ₄)	53	~46	41	66.5
P ₂ —M ₃	118		103.2	~150
P ₂ —P ₄	54.5		47	73.5
M ₁ —M ₃	64		56.1	

* 依图测数据。

和头骨在一起的还有颈椎、胸椎、肋骨和右肩胛骨。寰椎被压挤在头骨之下，难以辨认。枢椎仅背棘及右后关节突可以看出来。背棘长不少于 65 mm。第三至第七颈椎都保存得不好，但大体仍处于正常互相关联的位置。 C_6 具很发育的板状横突，背棘高约 50 mm。 C_7 背棘高大，长不少于 100 mm，其基部前后宽不少于 25 mm。颈椎全长约 240 mm。胸椎和肋骨只保存了前部的几个。肩胛骨后缘较平直，没有大的向后伸出的角状突起。后缘

的上 1/3 和下 2/3 之间组成约 150° 之角。顶缘圆，前缘中部向前伸出很远，颈部明显凹入，肩胛结节不发育。肩胛冈自颈凹区上方开始，至肩胛上 1/3 处形成大的结节，再向上又变低并延伸至顶缘。肩胛骨最大长 285 mm，最大宽约 140 mm，颈部最窄处宽 48 mm，关节窝前后径长 41 mm。

表 2 貘类牙齿的测量(长×宽) (单位: 毫米)
(Measurements of some tapirus teeth, length × width, in mm)

	<i>Plesiotapirus yagii</i>			<i>Paratapirus helveticus</i> (Schaub, 1928)	<i>Miotapirus harrisonensis</i> (Schlaikjer, 1937)	<i>Tapirus indicus</i> IVPP 1326
	85005	1020	type (Matsumoto, 1921)			
I ¹	15.2×—				11.8×—	10.9×9.8
I ²	14.2×—				12.5×—	10.8×8.8
I ³						15.3×12.7
C	5.8×—			6.5×—		8.8×7.2
P ¹	15.6×17.3			16.3×13.9	14.1×13.3	20.9×15.0
P ²	17.6×21.9			17.4×17.1		23.8×24.1
P ³	17.6×24.1			16.0×19.1		23.6×26.5
P ⁴	17.7×23.7	18.5×23.0		16.4×19.6	16.5×20.5	
M ¹	18.6×23.4	19.5×22.5		18.2×20.0	16.3×20.3	24.4×27.5
M ²	20.8×24.3			18.9×21.6		27.8×29.8
M ³	22.3×24.7			20.3×22.5	19.0×23.5	
I ₁	12.1×—				10.5×—	11.8×—
I ₂	10.9×—				9.6×—	9.3×9.2
I ₃	7.6×—				6.8×—	6.3×5.6
C	—				9.0×—	17.9×12.4
P ₂	~19.0×13.0		19.5×13.5		16.0×11.6	26.3×15.0
P ₃	~19.0×—		18.0×15.5			26.0×17.2
P ₄	19.5×14.5		18.0×17.0		16.1×14.7	
M ₁	20.4×15.0		21.0×16.0		16.3×13.4	24.3×18.5
M ₂	23.4×17.1		22.5×16.5	18.5×—		27.6×20.6
M ₃	25.0×17.2		25.0×17.0	19.5×—		

V 9475 根据其对称的形态和扁宽的程度判断，它可能是中蹠骨的远端。它与杨钟健 1936 年研究发表的山旺标本保存在一起，标本上写有 Loc. 37，显然是杨钟健未曾鉴定遗漏的材料。阎德发等 1983 年发表的山旺脊椎动物化石名单中的 *Anchitherium* sp. 即指这件标本。经进一步对比，它应属貘类，而不为安琪马类。它和安琪马者区别如下：1. 比例上更扁宽；2. 远端关节面前上缘较平直，而后上缘位置低，大约与前上缘等高或稍低。在安琪马中，远端关节面的前上缘为弧形，而后上缘显然高于前者。3. 侧韧带凹及凹上方的结节都更接近前缘，而在安琪马中它们位于中部。

V 9475 远端最大宽 25.9 mm，关节面宽 22.3 mm，厚 16.3 mm。

比较 亚洲晚第三纪早期的貘类化石发现极少，现将描述发表的分别讨论如下：

1921 年松本彦七郎 (H. Matsumoto) 记述了采自日本本州平牧组中的一些貘类化石。材料是带有颊齿的下颌。松本彦七郎将其归入了一个欧洲的属，但定了一个新种：*Palaeotapirus yagii*。它与新发现的标本中的下颌，无论在大小还是在形态上都几乎无法

分辨。它们表现在牙齿上的共同特征是： P_2 下后尖离下原尖较远，位于下原尖的内后方，下内尖和下次尖已组成脊，而不再为锥形； P_3 可能仍保留较大的下前尖部分，后横脊脊

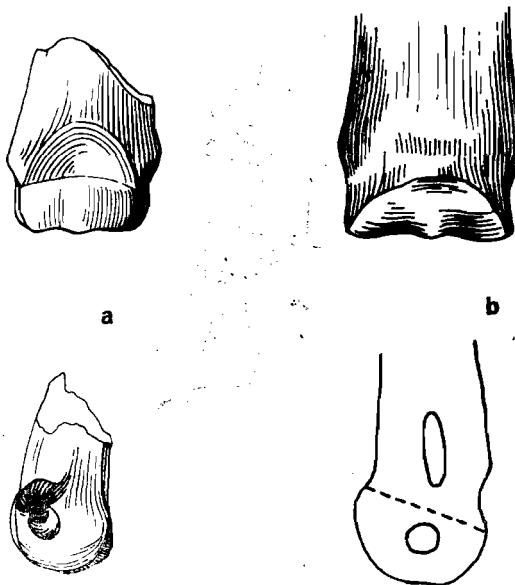


图 3 *Plesiotapirus yagii* 和 *Anchitherium* 中
蹠骨远端之比较 a: V9475; b: *Anchitherium*
(依 Sondaar, 1968)

(Comparison of the distal ends of *Plesiotapirus yagii* (a) and *Anchitherium* (b) upper:
dorsal view; lower: lateral view)

上：背面视；下：侧面视

形清楚，相当宽； P_4 — M_2 都是前窄后宽，只有 M_3 ，前脊宽于后脊。下前臼齿的后脊虽为脊形，但低于前脊。下颊齿上未发现明显的下后附尖。两者颊齿的大小和冠高也很接近。两者下颌的高度稍有差别，但差别很小。两者在 P_4 处高分别为 48 mm (日本) 和 53 mm (中国)。应该承认，下颊齿在貘的分类中，所能提供的鉴别性状有限，因而主要根据下颊齿的相似而把它们归入同种并不一定可靠。但另一方面，我们也不能把区别不大的标本强行分成不同的种，更不要说属了。松本彦七郎把它归入 *Palaeotapirus* 的理由并不充分。他只是觉得日本的这件标本比 *Protapirus* 进步，而比 *Tapirus* 又原始，就归入了这个代表了进化的中间阶段的欧洲的属。山旺的新材料表明，在亚洲颊齿处于相似进化阶段的貘类，在头骨的构造上可以是很不相同的。考虑到相似程度和地理因素，在没有其它可供对比材料的情况下，我们姑且把日本和山旺的标本归为同属同种。

1979 年谢万明记述了采自山旺的貘类的两枚上颊齿。和松本彦七郎一样，谢万明把这两枚貘类的上颊齿也归入了欧洲的 *Palaeotapirus* 属中。由于无法和日本的下颊齿直接比较，谢万明又建了一个新种：*P. xiezhaheensis*。多少有些使我们感到意外的是，这两枚牙齿虽然在总的形态上和新发现的头骨上的牙齿很相似，却又存在着一些差别，而且差别的程度比后者与日本标本之间还大些，这主要表现在谢万明材料中的 P^4 的臼齿化程度更高些，它的牙齿轮廓更近于方形，原尖和次尖相当高，从前或后面看，它们和前尖及后尖差不多一样高；自内面看，它们分开得较深，使中谷更开放（见图 22）。而 M^1 的差别很小，谢万明材料中的 M^1 之内齿带在原尖内壁处已消失，而新发现的头骨上的 M^1 的内齿带将原尖包围起来。如何解释这些差别？我们曾试图将谢万明材料中那个 P^4 看作是乳齿或臼齿，但都没有成功。看来，谢万明的鉴定是准确的。这颗牙齿的前附尖小，后尖外壁特别倾斜，中谷内开口半封闭，这都说明它不是一颗上臼齿；另一方面它没有乳齿所特有的外长内短以及前、后缘较圆隆的形状，因此也不是上乳齿。我们不能排除在山旺存在

着两种摸的可能性。但是在目前,由于谢万明的材料实在太少,我们宁愿相信表现在 P^4 的差异,是为种内个体间的变异。

二、*Plesiotapirus* 的性质

人们早就认识到,摸科动物在从渐新世至今的进化过程中,牙齿上的变化不大,而且变化主要表现在上前臼齿。这一演化过程可以分为三个阶段:开始其内侧只有一个尖,带有呈V字形伸向外侧的两条嵴;其次内侧尖在上半部分分离,两横脊形成,但其内端靠得较近;最后则是内侧完全分为两尖,两横脊互相平行,亦即完全臼齿化。对于第一阶段, H. Filhol 1877 年创立了 *Protapiro*s 的属名。后来在北美也发现了一些具有类似进化水平的上前臼齿的摸类动物,虽然在细微构造上还有差异,也被归入了这个属。属于最后一个阶段的是现生摸属和第四纪个体更大些的 *Megatapiro*s。属于第二阶段的则有欧洲的 *Paratapiro*s 和北美的 *Miotapiro*s。新属的上前臼齿显然是属于第二演化阶段的,因此下面的对比主要集中在它与 *Paratapiro*s¹⁾ 和 *Miotapiro*s 上。

这三个属虽然在颊齿的进化程度上大体处于同一水平,但仍有一些差异。新属的 P^1 和后两个属的 P^1 都不同: *Plesiotapiro*s 的 P^1 宽大于长,原尖大,有向外伸出的V形嵴,“次尖”很小。而 *Paratapiro*s 和 *Miotapiro*s 的 P^1 和现生属者形态接近:长等于或大于宽,原尖小而次尖大。在其它的颊齿上 *Plesiotapiro*s 和欧洲的 *Paratapiro*s 更接近,有时很难区分。根据我们的统计,欧洲这个属至少包含有进化水平不等的六个种。其中大部分都比新属的颊齿稍原始而小,但较进步的种则与新属很接近,例如 *P. intermedius*、*P. robustus*。可以指出的区别大概只有在欧洲这些种中内齿带普遍发育的较好,而在下颊齿上常有下后附尖。美洲的 *Miotapiro*s 在颊齿上和新属的区别较明显。根据 E. M. Schlaikjer 1937 年的记述和插图可以看出,它的上前臼齿后尖的位置不那么强烈地内移,上、下前臼齿的原尖、次尖和下次尖及下内尖的锥形形态还保留得较清楚。

最明显的区别还是在头骨的构造上, *Plesiotapiro*s 和 *Paratapiro*s 及 *Miotapiro*s 的区别是: 1. 眼眶前的面部很高,从 Prosthion 至鼻切迹后端为一向上升起的弧线,而不是向下的凹线。2. 门齿靠得紧, I^3 不特别大,下犬齿完全退失。3. 鼻骨短,位置特别靠后,其前端仅达眶前缘,而在后两个属中鼻骨的后端离眶前缘不远。

如果和现生属作一比较,那么可以看出,首先,上面的前两个特征不仅是新属和上述两个属,而且也是和现生属的区别。在这两方面,新属区别于所有已知的摸科的化石。但是在第三个特征上,新属与现生属更接近。另一方面我们还可以看到上面三个化石属也有一些与现生属不同的共同性状: 1. 它们的吻部都相对较短,这主要表现在门齿、犬齿之间以及犬齿之后的齿隙较短上。2. 它们都没有深的容纳鼻憩室的凹槽,特别是在鼻骨上不形成弯向中矢线的弧形凹。3. 它们的前颌骨鼻突都很长,不同程度地伸达上前臼齿

1) 这里采用了 *Paratapiro*s, 而没有采用 *Palaeotapiro*s。后者建属时的模式种是 Filhol 1888 年定的 *P. buxovillanus*。事实上,这个种的正模乃是一件始新世,属于 Lophiodontidae 的上颌,因之 *Palaeotapiro*s 不是摸科的有效属名。1902 年 Ch. Depéret 为 von Meyer 的 “*Tapiro*” *helveticus* 所建的新属名 *Paratapiro*s, 才是代表上前臼齿处于第二演化阶段的摸类有效属名。

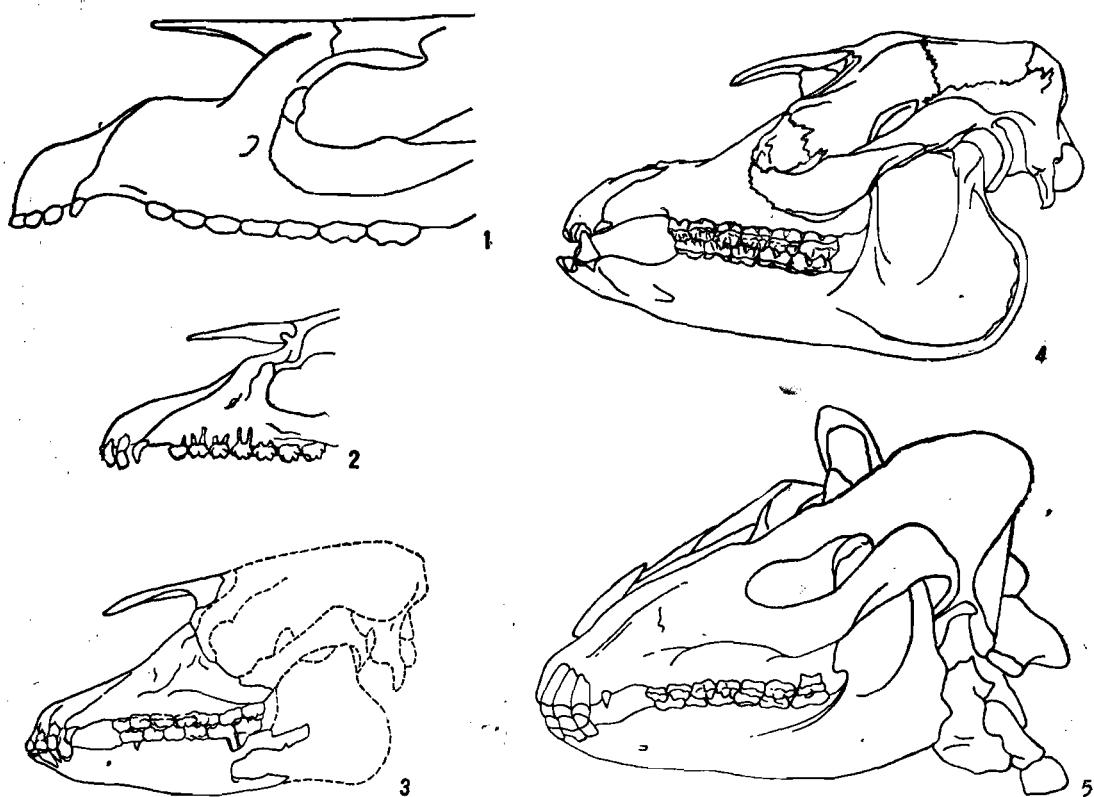


图 4 犀科各属头骨侧面之比较 (comparison of skulls of major tapirid genera)
 1. "Prototapirus" validus (依 Radinsky, 1965) $\times 1/2$, 2. Paratapirus helvetius (依 Schaub, 1928) $\times 1/4$, 3. Miotapirus harrisonensis (依 Schlaikjer, 1937) $\times 1/4$ 4. Tapirus indicus (依 Hatcher, 1896) $\times 1/4$, 5. Plesiotapirus yagii (85005) $\times 1/4$

的上方。4. 下颌的颏孔都位于颊齿列之前。

上述的比较充分说明了 *Plesiotapirus* 乃是犀科进化中的一个旁支。它以一系列特征区别于已知的犀科中的各属。在进化水平上, 它大体与 *Miotapirus* 和 *Paratapirus* 相当。它没有留下后代, 也不可能进化成现代的犀。它的分布范围可能仅限于亚洲中间地带的东部。现生马来犀或其祖先, 显然是由其它大陆迁移来的。

三、*Plesiotapirus yagii* 在山西发现之意义

犀科化石的记录始自欧洲和北美的渐新世。在欧洲, 从晚渐新世开始出现前臼齿半臼齿化的 *Paratapirus*, 到早中新世的 Aquitanian 期 (MN 1,2), 这个属分化成若干种。此后, 发现的化石很零星, 其分类位置也不十分可靠 (R. von Koenigswald, 1930, p.22—23), 但是到中中新世 (MN 6) 就已出现真正的犀 (*Tapirus*), 这就是 A. Hoffmann 1893 年记述的采自奥地利 Göttingen 的 *Tapirus telleri*。在北美, 前臼齿半臼齿化的 *Miotapirus* 出现于早中新世的 Harrison 组 (距今约 22 百万年)。*Plesiotapirus* 虽

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1) 这里采用了 *Paratapirus*, 而没有采用 *Palaeotapirus*。后者建属时的模式种是 Filhol 1888 年定的 *P. buxovillanus*。事实上,这个种的正模乃是一件始新世,属于 Lophiodontidae 的上颌,因之 *Palaeotapirus* 不是摸科的有效属名。1902 年 Ch. Depéret 为 von Meyer 的 “*Tapirus*” *helveticus* 所建的新属名 *Paratapirus*, 才是代表上前臼齿处于第二演化阶段的摸类有效属名。

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A NEW GENUS OF TAPIRIDAE FROM SHANWANG, SHANDONG

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Summary

While helping to curate the jumbled specimens accumulated at the Shanwang Paleontological Museum in 1985, the senior authors of the present paper were happy enough to find a tapirid specimen. Through careful preparation it turned out to be a part of articulated skeleton consisting of skull, lower jaw, cervical and some anterior dorsal vertebrae and a scapula. As most of the other fossils from Shanwang, it is laterally compressed, therefore, no width could actually be measured. The nasal bones of the skull have become vertically oriented through compression. Otherwise the skull is little deformed. In order to study the tooth morphology closely, we had to extract most of the teeth from the left side of the tightly occluded tooth battery. All this notwithstanding, the skull represents one of the few well preserved specimens among the tapirid fossils ever found.

Description

Tapiridae Burnett, 1830

Plesiotapirus gen. nov.

Plesiotapirus. yagii (Matsumoto, 1921)

1921 *Palaeotapirus yagii* Matsumoto

1979 *Palaeotapirus xiejiacheensis* Xie

Holotype A left lower jaw with P_2-M_2 , with a M_3 of probably the same individual. The specimen is possibly kept at Tohoku Imperial University, Sendai, Japan.

Referred specimen Left P^4-M^1 , kept in Shanghai Natural Museum, Cat. no. 1020.

Described specimens 1) Skull, lower jaw, cervical and anterior dorsal vertebrae and right scapula in natural articulation, kept in Shanwang Paleontological Museum, Cat. no. 85005; 2) A distal end of $MtIII(?)$, undescribed specimen from Prof. Young's 1937 collection, kept in IVPP, v 9475.

Diagnosis Size comparable with that of the smallest extant species, *Tapirus roulini*. Its facial part anterior to the orbit remains unreduced and high, with the lower border of the nasal notch strongly convex upward. The nasals are short, tonguelike, strongly retracted backward, with their posterior border situated approximately above the posterior margin of the M^3 , far behind the anterior border of the orbit. The paired depressions for lodging the diver-

ticulum nasi are present, but weakly developed, without encroachment upon the posterior portion of the nasals. The postorbital process is hardly discernible on the zygomatic arch. The nasal process of the premaxilla is thin and long, and inserted into the maxilla, reaching as far back as above the P^3 . The mental foramen is located anterior to the P_2 . The incisors are closely implanted. I^1 and I^2 are rather highcrowned labially. I^3 is not especially enlarged, and neither is the I_3 strongly reduced. The upper canine is small, situated not far from I^3 , while the lower canine is probably totally lost. The diastem is short. $C-P^1$ is shorter than P^1+P^2 . All the upper premolars are wider than long. The protocone of the P^1 is large, with two transverse ridges diverging labially. A tiny "hypocone" is present behind the protocone. The metacones of the premolars are markedly skewed lingually at their tops. Their labial walls slant strongly, forming bulged post-external corners in these teeth. P^2-P^4 semimolariform, with two transverse lophs almost parallel, but the medisinus lingually half-blocked. The posterior transverse lophids of the lower premolars are ridge-like, but lower than the anterior ones. Only in M_3 , the anterior lophid is longer than its posterior one.

Localities and ages The holotype was found from the Hiramaki Formation, Kani District of Mino Province, Japan. Its age is now believed to be the latest Early Miocene. All the other material came from the famous Shanwang quarry of diatomaceous earth. Its age is roughly equivalent to the European MN5.

Description The part of the skull anterior to the frontal-nasal suture is particularly long, about 3/4 of the total skull length. The nasals are very short, only about 40 mm long along their sagittal suture. Their tips are blunt, while their posterior border, the frontal-nasal suture, is rather straight, weakly slanting post-laterally. The lodgement of the posterior end of the diverticulum nasi is represented only by a pair of small notches situated lateral to the post-lateral border of the nasals. The maxilla-frontal suture stretches from that notch anteriorly, forming the lateral border of the diverticulum nasi. The lacrimal bone is exposed on the face in form of a triangle, a little larger than in the extant tapirs. It is perforated by two foramina, a large upper one and a smaller lower one, like in the extant tapirs. The maxilla is particularly large. Its upper marginal part is not only strongly curved upward, but also turns sagittally, forming a horizontal plate partly subdividing the nostril into an upper and a lower partitions. The zygomatic arch is weak. Posterior to the orbit, it ascends rapidly, so that the glenoid cavity is far higher than the alveolar border. The postglenoid process is not straight, but curved posteriorly, leaving a large unoccupied space between it and the condyle of the lower jaw. The postglenoid and the mastoid processes remain open the whole length, while the mastoid and the paroccipital processes are completely ossified. The mastoid part is provided with an anterior ridge immediately posterior to the external meatus. The paroccipital process stretches longer downwards. An unified sagittal crest is probably present, about 85 mm long.

The lower jaw, especially its horizontal ramus, is particularly robust. Its lower border is rather straight, the most convex portion being below the M_{2-3} . The mental foramen is situated 10 mm anterior to P_2 . The anterior border of the ascending ramus is vertical, while its posterior border slants posteriorly and downward, forming a wide angular lobe.

It is rather unexpected to find only three pairs of anterior teeth in the lower jaw. Our study has revealed that the last pair of these teeth are I_3 , but not canines. The argument is that the upper and lower teeth of the described specimen are in normal state of occlusion and the last pair of the anterior teeth occlude with I^3 and I^2 , but not I^3 and canines. It is a pity that the lower premolars are all somewhat damaged during preparation. However, it is still

clear that their posterior transverse lophids are well developed and all ridge-form, although lower in height.

The total length of the cervical vertebrae is about 240 mm. The scapula is large, about 285 mm long and 140 mm wide, with high spina scapulae. v. 9475 is probably a distal end of a MtIII, judging from its flatness and symmetrical form of the articulation surface. Originally it was thought to belong to *Anchitherium* sp., and as such was listed by Yan Defa et al. in 1983. Detailed comparison revealed that it was quite different from that of *Anchitherium*. The differences are the following: 1. v 9475 is proportionally wider and flatter. 2. The anterior margin of the articulation surface is straight and situated at about the same level as its posterior margin in v 9475, while in *Anchitherium* the anterior margin of the surface is markedly curved and situated lower than its posterior margin. 3. The prominence and the depression for attachment of ligamentum laterale are both located in the anterior half of the lateral side in v9475, while in *Anchitherium* they are almost in the centre.

Comparison So far as we can judge from the description and pictures, the lower jaw described by Matsumoto under the name of *Palaeotapirus yaqii* is almost identical to our new specimen in morphology and equal in size. They share the following common features: The metaconid is widely separated from the protoconid and the hypo- and endo-conid form a low, but clear ridge in P_2 . All the posterior transverse lophids are still lower than the anterior ones in premolars. No clear metastyloid is discernible in lower cheek teeth. Only in M_3 the anterior transverse lophid is wider than the anterior one. It is to admit that the lower cheek teeth can provide only a few diagnostic features important for classification, therefore, the identification based on lower cheek teeth can not be considered entirely reliable. However, under the present circumstance, it is difficult for us to intentionally separate two almost identical specimens into two different taxa. Since the new material from Shanwang proves widely different from all so far known tapirid genera, we naturally assign the Japanese specimen to our new genus rather than to the European *Palaeotapirus*.

As Matsumoto, Xie Wanming also assigned two upper teeth from Shanwang to *Palaeotapirus*. Since no direct comparison was then possible, he erected a new species, *P. xiejiaheensis*. While basically similar to those of the new specimen in morphology, the differences between them were even bigger than those between our new specimen and the Japanese one. This is clearly shown in the higher degree of molarization of the P^4 in Xie's specimen. It is more quadrate in shape, with considerably high protocone and hypocone, and deeper separated transverse lophs (text fig. 2). The possibility to find two tapirid forms in Shanwang can not be ruled out, but the paucity of Xie's material renders it dangerous to view them as belonging to two taxa.

Affinity of *Plesiotapirus*

Paleontologists have long been aware of the fact that the tapirids evolved slowly and their evolution as evidenced by tooth morphology is demonstrated mainly in premolars. During the first step of their evolution the upper premolars had a single inner tubercle, the protocone, with a V-shaped ridge descending from it labially. *Protapirus*, proposed by H. Filhol in 1877, is used to represent the animals of this stage. During the next stage the premolars were semimolariformed, i.e. the V-shaped ridge turned into two transverse lophs, however, half connected lingually. The European *Paratapirus* and the American *Miotapirus* belong to this stage.

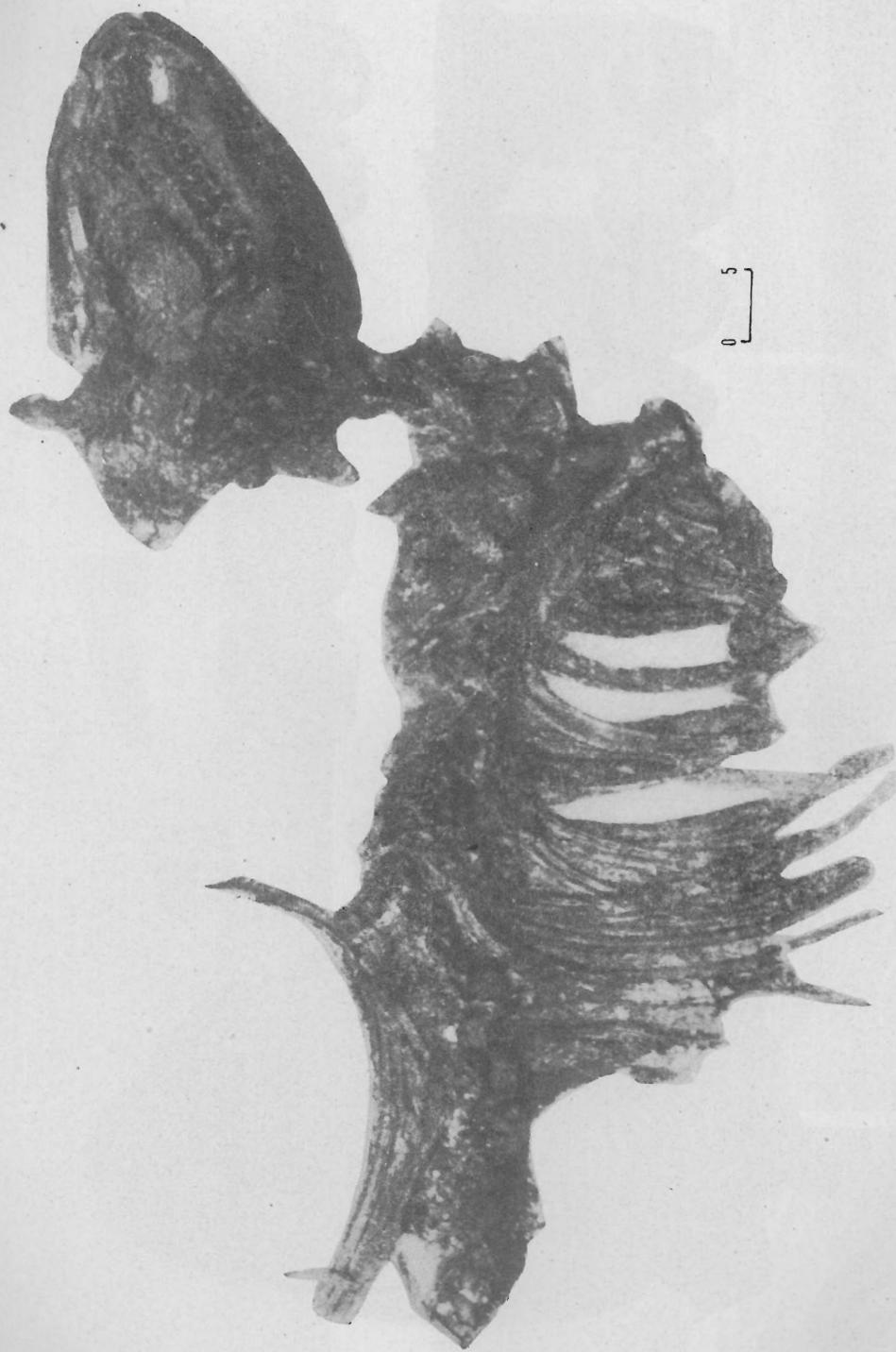
Note that we use *Paratapirus* instead of *Palaeotapirus*. The reason for doing so is that the type specimen of the type species of the genus, *Palaeotapirus buxovillianus* (Filhol, 1888), actually belong to Lophiodontidae. *Paratapirus* was erected by Ch. Depéret in 1902, based on von Meyer's *Tapirus helveticus*. Though later, it is the legitimated genus name for the European animals of the second stage. The last stage is characterized by fully molarized premolars. *Tapirus* and *Megatapirus* are the representatives of that stage.

Judging from the evolutionary level of its premolars, the tapir of Shanwang belong evidently to the second stage, but it differs widely from the other two known genera. Starting from the teeth, which show less differences than the skull, we may point the following. Unlike all the other tapirs, the Shanwang form has a rather peculiar P^1 , which is wider than long and possesses a large protocone followed by a tiny "hypocone". The morphology of the other teeth of the Shanwang form is quite similar to that of the second stage forms in general, especially to that of some advanced forms in Europe, as *P. intermedius* and *P. robustus*. Some minor differences are, for example, the better development of the inner cingulum on the upper premolars and the frequent presence of the metastylids on the lower cheek teeth in these European forms. If the text figures given by E. M. Schlaikjer are correct, the premolars in *Miotapirus* are apparently less advanced. The protocones and hypocones on the upper, and the hypoconids and entoconids on the lower premolars remain still half cone-shaped. The most striking differences between the Shanwang form and the other genera are shown on the skull morphology. The Shanwang form differs from the others by the following features. 1) The facial part anterior to the orbit is particularly high, the lower border of the nasal notch forms an upward convex line. 2) The incisors are closely situated together, I^3 is not particularly enlarged and the lower canine is lost. 3) The nasals are small and short, strongly retracted backward, with their anterior tips situated just above the anterior margin of the orbit. If we compare the Shanwang form with the extant representatives, we may note that the first two characters of the Shanwang form differ not only from those of the above mentioned fossils, but also the extant forms. However, in the third character, it is similar to the extant tapirs. On the other hand, the three forms, *Paratapirus*, *Miotapirus* and *Plesiotapirus*, share the following characters, by which they differ from the extant tapirs. 1) They all have a comparatively short snout, which is clearly demonstrated by the brevity of the diastems. 2) There are no large depressions on the nasal bones to accommodate the diverticulum nasi. 3) The nasal process of the premaxilla is very long, reaching the back part of the premolars in position and 4) The mental foramen is situated anterior to P_2 (text fig. 3). All this shows that *Plesiotapirus* is evidently a side-branch in the tapirid evolution, leaving no descendant in recent time. It is at about the same evolutionary level as *Paratapirus* and *Miotapirus*. It may be an endemic form of the Asian continent.

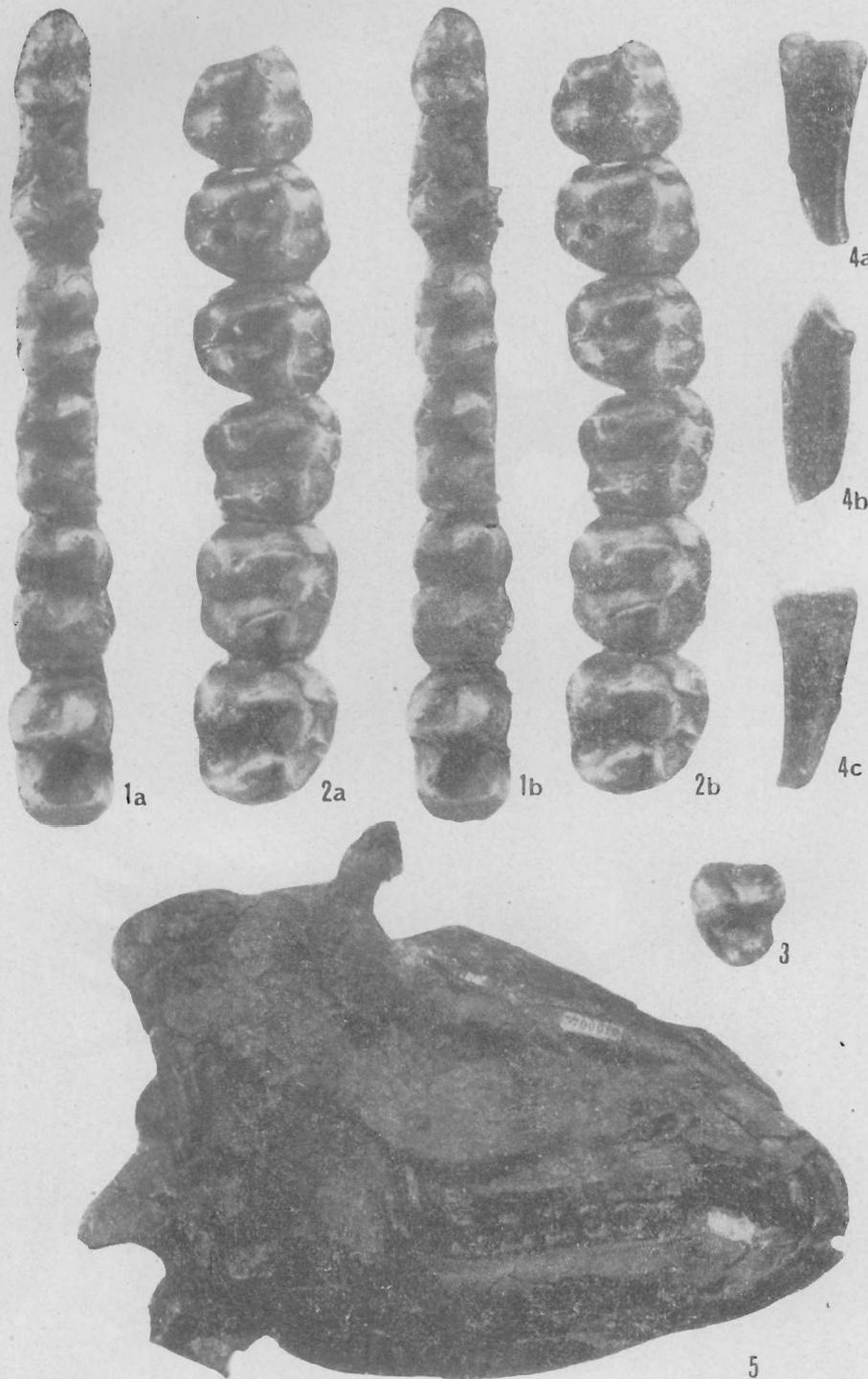
Significance of the Discovery

The faunal exchange and correlation between the Japanese islands and the Asian continent has been a difficult problem, mainly because of the poor fossil records allowing direct comparison. The best documented Neogene mammalian fauna in Japan is probably the Hiramaki fauna. Altogether 5 forms were described: *Anchitherium hypohippoides*, "*Palaeotapirus*" (= *Plesiotapirus*) *yacii*, "*Teleoceras*" (= *Brachypotherium*) *pugnator*, *Amphitraqus minoensis* and "*Hemimastodon*" (= *Gomphotherium*) *annectens*. So far these forms have been considered as

comparable with those of the Eurasian continent at generic level. However, few direct comparison has been made. In 1964, Chow M. C. and Wang B. Y. referred some isolated teeth from Sihong, Jiangsu, to *Brachypotherium pugnator*, but one year later, Wang B. Y. reassigned these teeth to *Plesiaceratherium shanwangense*, but at the same time she expressed the opinion that the Japanese rhino species possibly also belong to *Plesiaceratherium*. If our identification is correct, *Plesiotapirus yagii* is the first form common to the Hiramaki and Shanwang fauna at the species level. Taken as a whole, the east coastal area of North China might well be a source area for the Japanese Hiramaki fauna. In recent years the Hiramaki Formation is dated as 15—16 Ma B. P., The Shanwang Formation may be a little older than that in age (roughly equivalent to the European MN 5). This again accords with the age assignment obtained from other sources.



Plesiotypus yagii (Matsumoto, 1921)
头骨，下颌，颈和胸前部 (Skull, lower jaw, cervical and anterior dorsal vertebra and right scapula in natural articulation)



Plesiotapirus yagii (Matsumoto, 1921)

1a, 1b. 下齿列立体照片 (Lower cheek teeth, stereo photographs); 2a, 2b. 上齿列立体照片 (Upper cheek teeth, stereo photographs); 3. 右 P^1 冠面观 (Right P^1 , crown view); 4a. I^1 唇侧观 (Labial view); 4b. I^1 侧面观 (Lateral view); 4c. I^1 舌侧观 (Lingual view); 5. 完整头骨 (Lateral view of skull), $\times 1/3$