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山东山旺 *Palaeomeryx* 化石的初步研究

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关键词 山东 中新世 山旺动物群 古鹿

内容提要

Palaeomeryx 在含义、性质和分类位置上，一直是一个争论较多的属。最近在山旺发现的 *Palaeomeryx* 完整骨架，为解决上述问题提供了有价值的资料和证据。*Palaeomeryx* 雄性具有一对眶上"皮骨角"和单一的"枕顶角"。根据共近裔性状的分析，本文作者认为 *Palaeomeryx* 应该归入长颈鹿，作为这一支中最早分出的一个旁支。长颈鹿和鹿科有较近的亲缘关系，而和牛科的关系较远。*Palaeomeryx* 大概位于 *Blastomeryx* 和 *Leptomeryx* 之间，从反刍类主干中分出。山旺的材料，代表本属中一个较原始的新种：*Palaeomeryx tricornis*。它的时代，可能相当于欧洲的 MN4 或 MN5。

一、前 言

Palaeomeryx 是 Hermann von Meyer 1834 年根据德国巴州 Georgensgmünd 发现的一些下牙而建立的一个属。他认为这类鹿的下臼齿及第四乳齿在下原尖后壁上，有一斜向后内方的褶状构造(后来被称为古鹿褶即: *Palaeomeryx*-Wulst 或-fold)，这一特征在现生鹿类中是没有的。由于当时没有同时发现角化石，他确认这个属是无角的。但后来发现中新世和上新世鹿类中，具有古鹿褶这一特征的很多。此后的一个多世纪，从这个属曾划分出很多角形各异的属。*Palaeomeryx* 作为剩下的一些种的属名，在概念上就变得相当模糊了。其中最主要的原因是，虽经百余年的努力，却一直没有发现这类动物比较完整的头骨，当然，就不用说完整的骨架了。近年来，特别是 1966 年 L. Ginsburg 和 E. Heintz 把两个在性质上和长颈鹿的角相同的"皮骨角"(ossicone) 归入了 *Palaeomeryx*，并把 *Palaeomeryx* 归入了长颈鹿超科，此后，围绕着 *Palaeomeryx* 分类位置的争论日趋激烈，成为当前古哺乳动物学中颇为引人注目的争论点之一。

Palaeomeryx 在我国，除山旺外，曾有过三次零星材料的报道: 1885 年 E. Koken 的 *Palaeomeryx oweni* (采自云南?)、1976 年陈冠芳和吴文裕(河北磁县九龙口)和 1978 年李玉清和吴文裕记述的 *Palaeomeryx* sp. (陕西蓝田冷水沟)。

山旺的 *Palaeomeryx* 化石，是德日进 (Teilhard de Chardin, P.) 1939 年提出的，不过德氏对这一鉴定并无十分把握。因为当时只发现了 *Lagomeryx* 的角，但却有大、小两

类牙齿。这两类牙齿在形态、构造上几乎无法区分,其中大者,照德日进的话说:"如在欧洲发现,无疑应订为 *Palaeomeryx*"。德氏因此怀疑 *Lagomeryx* 和 *Palaeomeryx* 是否分别代表了同一种鹿的角和牙齿。所以德氏把它们定为 *Palaeomeryx* (? *Lagomeryx*) A 和 B 种。此后就再无人真正涉及这个问题了。因此,山旺的 *Palaeomeryx* 化石,一直是个悬而未决的问题。

最近几年,在山旺不仅发现了 *Palaeomeryx* 带有角的头骨,而且也找到了好几具保存相当完整的骨架。这些发现将有助于我们了解 *Palaeomeryx* 的真正性质,得以比较确切地讨论它们的分类位置,并使我们对山旺动物群的地质时代也有了较前不同的认识。鉴于这些骨架的修理还不是很快能完成的,本文仅就能观察到的,对 *Palaeomeryx* 的主要特征予以介绍。

Palaeomeryx 骨架的发现,曾引起法国巴黎自然历史博物馆的 L. Ginsburg 博士和荷兰乌德列支地学研究所的 J. J. M. Leinders 博士的极大兴趣。他们除与作者就 *Palaeomeryx* 的分类位置交换了意见外,还为作者提供了未曾发表的手稿和数据,这使本文作者十分感动。沈文龙同志为山旺这一形态特殊的鹿形动物绘制了精美的头部复原图,杜治同志为化石标本照相,在此一并致谢。

二、化 石 记 述

Giraffoidea Simpson, 1931

Palaeomerycidae Lydekker, 1883

***Palaeomeryx tricornis* sp. nov.**

***Palaeomeryx* (? *Lagomeryx*) sp. A. Teilhard de Chardin, 1939**

(图: 1、2、3、4、表: 1、2、3 图版: I. II. III. IV.)

正型标本 头骨及下颌(下颌在修理过程中大部破损),带有三个颈椎,雄性。古脊椎动物与古人类研究所标本编号 V7728。

其它材料

(1) 完整骨架,雌性(图版 IV)。临朐古生物博物馆临时编号(下同)820831。

(2) 完整骨架,雄性(图版 III),830009。

(3) 完整骨架,雄性,840002。

(4) 骨架,雌性,脊柱中段及四肢远端缺失,840015。

(5) 不完整骨架,雄性。临朐古生物博物馆标本编号 LV80003。

(6) 很不完整骨架,820837。

(7) 残破头骨(仅右侧出露),V7729。

(8) 一不完整左上齿列(具 P^2—M^3),V7730。

(9) 一不完整左下齿列(具 P_4—M_3),V7730.1。

地点与层位 山东临朐县山旺,中中新统山旺组中段。

特征 个体在本属中,中等偏小,有时有 P_1,它与 P_2 间的齿隙可很小,也可长至 10mm 左右。下前臼齿的下后尖发育弱,不形成封闭的内谷。上前臼齿内嵴的内中沟发育弱;上

臼齿较短宽，原尖后脊内有珐琅质小褶。颊齿齿带及附柱发育较弱。雄性有一对短粗侧扁的“皮骨角”，位于眼眶之上方，角的前缘向后倾斜，其基部伸达眼眶之前，后缘呈向前凹入的弧形，基部位于眼眶后缘，“皮骨角”的顶端稍有膨大，角表面粗糙。枕部顶端向后上方延伸，形成末端膨大的“锤形”角状突起。

描述 整个骨架侧向压扁，各部分多保持原先连接状态，脱落开的部分很少。化石本身，除牙齿外，都较疏松，化石表面常常覆盖有一层铁质硬壳，致使化石不易从中修出。这种保存状况使许多细部构造无法观察，在多数情况下，长骨的宽和厚无法确切地测量。

头骨 保存最好的是正型标本。这件标本的右半部已完全修出，整个头骨因受压而侧扁，眶上缘被推压向上，基枕部、耳区和颧弓均不同程度地破损。头骨腹面因侧向压扁已无法观察。鼻骨在 830009 标本上也保存较好，鼻骨前达上犬齿前缘水平，末端延伸于前颌骨上端之前，形成小的鼻颌切迹；鼻骨前端宽 18mm，向后仅稍稍加宽；鼻上颌缝近一直线，鼻骨后端约 24mm。鼻上颌缝的后方，在 P^2 和 P^3 的上方，岩石从骨下呈长条形裸露，大概代表了“筛窗”（Fenetre ethmoidal 或 ethmoidal vacuity），前颌骨为一长条状骨，与鼻骨约成 45° 角，其宽度变化不大，吻端向前伸出，大概不特别向两侧扩展。

上颌骨前半部较高，齿隙处仅稍稍向内收缩凹陷。眶下腺窝大，边缘清晰，此窝在所有标本上皆可不同程度地观察到。它位于眼眶的前方稍偏下，其下缘低于眶下缘，后上角紧接眼眶前缘中部，稍高于泪孔，其前缘达 P^3 后部。窝呈卵圆形，长轴为后上前下方向，长约 50mm，短轴宽约 20mm。眶下孔位于 P^2 前缘上方。

眼眶大约位于头骨基长的正中，如从顶面测量，即包括枕顶角（雄性）在内，则位于头骨顶长的 2/5 处。这表明它的脑颅部分是相当长的。眼眶可能较小，圆形，面向侧方，眶缘不特别向侧方伸展。眶前缘中部破损，仅见于眼眶内面，接近前缘中部处有一袋状凹陷，凹陷正中则是一相当大的孔，此孔当为泪孔（lacrimal orifice）。此孔明显地位于眼眶内壁，离眶前缘已有一定距离。如果 Leinders 和 Heintz（1980）对泪孔形式的概括是正确的话，*Palaeomeryx* 的泪孔应是“眶内单孔”型，而不是“眶缘双孔”型，亦即此处在眶缘不

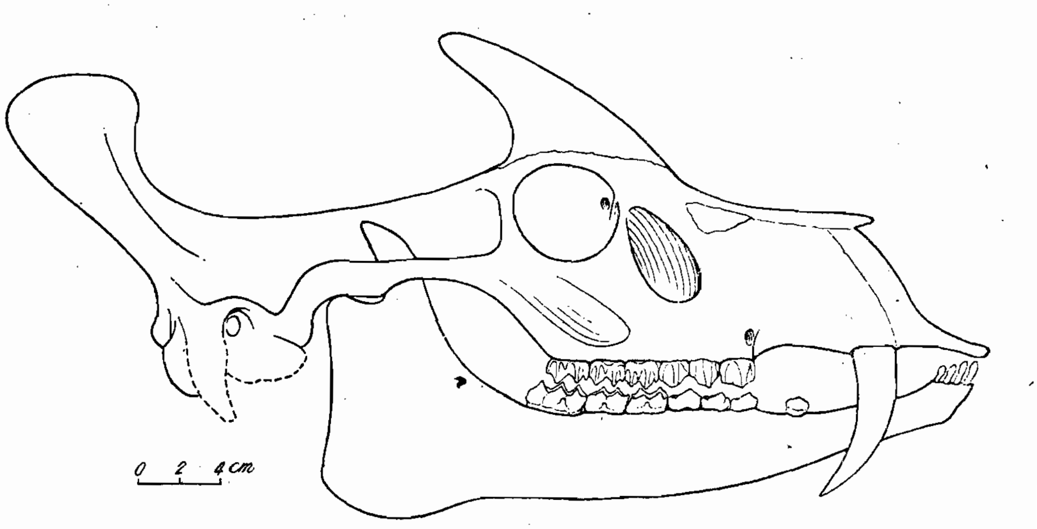

图 1 *Palaeomeryx tricornis* sp. nov. 头骨♂

会再有泪孔了。眶后桥及颧弓,从保留部分看,比较细弱。

颅顶部形成矢状嵴。分叉处约位于关节窝水平。基枕骨在枕髁之前有一对相当发育的结节,结节的后壁陡,前壁平缓。

雄性个体的枕部,都向后上方伸出,末端膨大,可称之为"枕顶角"。在其基部侧面,还可清楚地辨认出枕部后延的形态:枕嵴自乳突处斜向后上方,延伸至"枕顶角"的中部,然后消失。"角"之表面只有微弱的粗糙面,和正常的骨表面差不多,所以这种"角"应该和雷兽的骨质隆起相似,而不同于已知偶蹄类中所见之角。"枕顶角"的后缘,超出枕髁后缘约130mm。但横向宽度,以及是否也象 *Triceromeryx* 那样,顶端分叉,不得而知。不过可能还是不分叉的。

雄性个体眼眶上方,有一对"皮骨角"。这种角表面粗糙,没有规则的沟纹或瘤状物,而是布满了不规则排列的孔,事实上,整个角都是近蜂窝状的。在角和额骨之间,至少在正型标本上(已为老年个体),有一向上隆起的不规则面,极似骨缝合线,表明这种角并不是额骨膨大形成的,角和额骨在成年个体中也不是完全愈合的。这种角的形状、结构以及与头骨的关系都和长颈鹿者相同。这种角是由真皮下另一个骨化中心形成,它和头骨在一生中大部分时间里是分离的。为了把这种角和其它的角区别开来,Lankester 1907 年把这种角称之为 ossicone。我们把它译为皮骨角。在正型标本上,这对角比较细长,末端稍稍膨大。其左侧者更向后倾,右侧者几近垂直。鉴于头骨右侧明显因挤压变形,考虑到在其它标本上的角也多倾斜较剧,所以应该认为左侧的角,更接近其自然状态。虽然在不同个体上"角"的形态和大小是变化的,但其基部前缘都达于眼眶之前,而其基部后缘大体都在眼眶后缘。

下颌骨在 830009 中保存最好。下颌底缘向下隆起,齿槽缘也下凹,所以水平支在颊齿区的高度变化不大。P_2 前高为 32mm,M_3 之后则为 40mm。下颌角圆大、突出。下颌角后缘至门齿区中央处长为 280mm,关节突至下颌下缘的高为 82mm。垂直支在关节面下最窄处,前后长为 42mm。

齿列 无上门齿,雄性上犬齿发育,相当扁长,其最粗壮处位于齿根之中部(20×10 mm),齿根长约 50mm。齿冠和齿根的分界不太明显,仅以珐琅质的有无为度。齿冠更扁,前缘较圆钝,后缘锐利,自前后方向看,犬齿中部向内凹,下端明显外翘。整个看来,犬齿外面较平,内面更圆隆些。在雌性个体中,犬齿退化成极小的柱形。

P^1 无,C 至 P^2 的齿隙长约 40mm。

P^2 外壁中肋粗壮,肋前有一深沟。在正型标本中,内脊较粗壮,但其内侧没有中沟,在 LV80003 标本上有一微弱的中沟。

P^3 与 P^2 接近,只是内脊更向内突出,使齿冠面更接近一等边三角形。

P^4 短宽,自外面看,前附尖为一尖端向下的三角形隆起,其后缘形成陡坎,前尖肋向前覆盖在它前方的沟上。内脊前支为单脊,后支则由双脊组成,前外者高于内后者,但它们之间的沟很浅,稍经磨蚀即可变为一宽的磨蚀面。有微弱的前、内、后齿带。

三枚上臼齿的构造基本一致。前附尖比中附尖稍小,但都相当粗壮,自外侧面看,为近一尖端向下的三角形,基部相当宽,前附尖的后缘和中附尖的前、后缘界限都很分明。前尖肋与 P^4 者同,覆盖在它前方的沟上。后尖脊斜度较大,其唇侧也有一微弱的细肋。

原尖为不对称的V形脊，其后支伸向后方，指向后小尖脊(也见之称次尖脊者)前支的中央，(E. Heintz 把它看作是原尖脊的附脊 Pli protoconal)，在它的唇侧，还有一个不规则的脊形物 (E. Heintz 相反，却把它视作原尖脊的后支)。这一脊形物由 M^1 向 M^3 逐渐增大，形状也有所变化。在 M^1 中，它很小，在 M^2 它为倒L形，而在 M^3 中则為倒Y形。当磨蚀不深时，它们和原尖脊不怎么连接，磨蚀后，它们把后小尖脊和原尖脊连在一起。原尖比后小尖更向舌侧伸展。后小尖脊的前支并不伸达外脊，甚至在磨蚀相当深时，两者仍不相连。后小尖本身在唇侧可以看出有一弱肋，肋的后方有一沟，脊的后支也是二分的，一支成为齿冠的后缘，另一支则斜向前外方，抵达后尖基部。齿带在前缘和后缘发育，内谷中附柱发育较弱。

下门齿仅保留齿根。在 820831 标本上可见三个细齿根紧靠在一起。犬齿紧接其后，齿根与门齿者同样粗细。估计犬齿齿冠不会有双叶式构造。

P_1 至少在三件标本上是有的。牙齿很小，为单尖纵脊状。它与 P_2 间的齿隙大小不等，在正型标本中，齿隙长约 10mm。在 840015 标本上 P_1 与 P_2 几乎紧接，在另一标本中，齿隙长度界于前二者之间。

P_2 在正型标本中只保存了后半部，在 840015 标本中则仅可见外侧面。牙齿冠面构造简单：自下原尖向内方伸出的脊斜向后方，下内小尖脊细而短，为一发育不完全的脊。

P_3 横脊已相当发育。连接下原尖和下后尖的脊也斜向后方，下后尖已隐约分出。下内尖脊和下内小尖脊之间的沟，向齿冠内侧变浅，形成半封闭的盆状。外壁在下原尖和下次尖之间的沟，不易分辨。

图 2　*Palaeomeryx tricornis* sp. nov. (830009) 右下颌

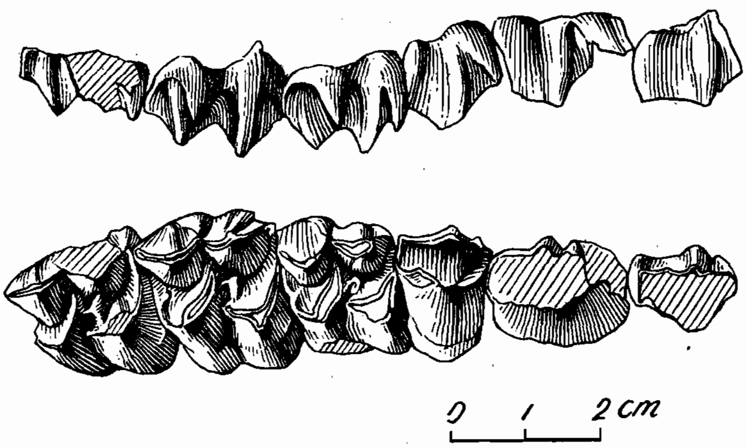

图 3　*Palaeomeryx tricornis* sp. nov. (830009) 右上颌

P_4 和 P_3 基本相同，但个体更大些。在下前附尖之后，已形成一个下前尖脊。下后尖更大，近一纵向片状，但不封闭内谷。外壁在下原尖和下次尖之间的纵沟已较明显。三角座内壁基部，下前尖和下后尖之间，有一段齿带。

M_1 和 M_2 构造相同。下原尖后支首先和下后尖前端相连，然后通过一珐琅质小柱再与下前尖后端相接。古鹿褶很发育。下原尖脊的前端和下次尖后支的后端不与前尖脊和后尖脊直接相连，留有明显的空隙，后者可以清楚地从内侧看见，前者由于前一牙齿后端的覆盖难于观察。下前尖和下后尖呈覆瓦状排列，两者在舌侧均有肋状突起。下前附尖不发育，下中附尖却很大，其后缘形成陡坎。齿冠前、后缘有齿带，也有外中附柱。

M_3 第三叶为椭圆形封闭环状，其内支与下后尖相连，外支与下次尖脊后支中部相连。

头后骨骼

脊柱 颈椎七个，没有加长的迹象。其自然连接状态的总长度，仅稍长于头骨之基长。枢椎的棘突向前悬垂，在雄性个体中，已与“枕顶角”相接触。C_{III-IV} 的棘突都较发育，但较粗短。C_{VI} 横突的下支呈板状，C_{VII} 的棘突很高。

胸椎 13 个。肋骨仅最后 5—7 个断面呈圆形，前边的肋骨多少都有些扁板状。腰椎六个，棘突很宽大，棘突间所留的空隙很小。荐椎数目不清，尾椎短小而数目亦少，尾椎末端超出盆骨后缘不多。

前肢 肱骨比肩胛骨短，远端关节面的中嵴，自前面看，斜向前外方，而不象现生鹿中那样，为垂直方向。与此相对应，桡骨近端关节面的中凹也不那么深而直。这表明这类动物的肘关节单向运动的适应性不很强。尺骨细，但骨干及远端依然完整。腕骨中仅保存

表 1 ***Palaeomeryx* 颊齿的测量与对比**（单位：毫米）

	P^2	P^3	P^4	M^1	M^2	M^3
V7728	16.2/16.0	16.0/—	13.9/16.9	17.5/19.3	20.2/—	21.5/21.3
	16.8/14.2	15.5/—	13.4/18.8	17.8/20.5	—	20.8/24.0
	16.0/—	—	13.3/18.4	17.9/21.2	21.8/25.0	21.8/—
Teilhard de Chardin, 1939	—	17.0/—	13.0/18.0	17.0/22.0	22.0/—	—
Artenay (MN 4a)*	16.5/13.7	16.9/14.4	14.2/16.9	18.4/19.3	20.5/22.6	—
Sansan (MN6)*						
Sa 4153*	22.3/16.9	20.8/19.2	~17.5/22.7	22.8/25.6	25.6/27.1	—
Sa 4156*	—	19.3/19.1	15.0/20.6	23.9/24.5	26.5/26.2	—

	P_2	P_3	P_4	M_1	M_2	M_3
LM 80015	—	17.0/9.2	17.1/10.0	18.0/12.8	19.7/15.2	29.6/14.4
V7729	—	—	16.9/11.0	17.4/13.8	19.7/16.6	29.5/16.1
V7730	—	14.2/—	16.0/—	17.0/—	—	—
Teilhard de Chardin, 1939	15.0/7.0	16.0/9.0	16.0/9.5	17.0/12.5	20.0/14.0	31.0/16.0
Artenay (MN4a)						
Ar 1608*	13.7/7.2	16.1/10.0	17.0/10.8	17.4/12.5	19.4/12.8	27.1/12.7
Baigneaux (MN4b)						
Ba 867*	—	18.3/10.8	18.0/11.2	18.2/13.4	20.5/15.7	27.6/15.0
Sansan (MN 6)						
Sa 4399*	17.3/9.5	21.2/13.0	21.9/15.0	21.4/16.9	24.4/18.9	34.1/18.5

* After the unpublished data provided by L. Ginsburg

有舟状骨、头状骨＋小多角骨、楔骨和豌豆骨。这些腕骨的形态皆为典型的鹿型，而无长颈鹿的特化特征。第三、四掌骨已完全愈合，背面中沟在远端封闭为孔状，远端关节面中嵴通过中凹(粗糙面)。第二和第五掌骨完整，位于炮骨后面的两侧，均退化成细条状，远端关节面的两个中嵴发育不完全，但每指都有三个指节骨。肘关节至足尖的长度约为600mm。

表 2　头骨及头后骨骼的长度

The Lengths of Skull and Postcranial bones（单位：毫米）

	820831 ♀	830009 ♂	840002 ♂	*P. eminens* (Sansan)
头全长 L. of Skull				
Basion—Prosthion	342	377	355	
Acranion—Prosthion	395	438	437	
颈　长 L. C.I—VII	350	323	375	
胸腰长 L. D. I—XIII+L. I—VI	825	825	750	
荐尾长 L. S.+Caud.	—	290	310	
肩胛长 L. Scapula	—	273	252	
肱骨长 L. Humerus	239	237	270	274*
桡骨长 L. Radius	237	242	—	331.5*
掌骨长 L. Mc_{III+IV}	219	221	221	300.5*
股骨长 L. Femur	—	315	300	
胫骨长 L. Tibia	—	335	325	396*
蹠骨长 L. Mt_{III+IV}	264	260	249	323.5*

* After the unpublished data provided by L. Ginsburg

表 3　*Palaeomeryx* M_3 长度递增对比表(单位：毫米)

		(mean)		
MN 8	La Grive	37.0		
MN 7	Simorre	36.9		
MN 6	Sansan	35.2		
MN 5	Pontlevoy	31.4	Teilhard de Chardin, 1939	31.0
MN 4b	La Romieu	26.0	v7729	29.6
	Baigneaux	26.9	v7730	29.5
MN 4a	Artenay	26.8		
MN 3	Neuville	24.0		
	Chilleurs	25.5		

后肢　各部分都比前肢的相应部分要长些。胫骨比股骨稍长。附骨中保存有跟骨、距骨、舟状骨＋骰骨和外楔骨。外楔骨不与舟状骨＋骰骨相愈合，基本与鹿类者一致(*Muntiacus* 除外)。第三、四蹠骨也愈合为炮骨，但较第三、四掌骨者长，背面中沟亦在远端封闭成孔。第二、五蹠骨与相应的掌骨同。膝关节至足尖的长度约为 750mm 左右，比前肢相应部分长约 150mm。

三、讨　论

(一) 关于 *Palaeomeryx* 的含意及其特征的订正

Palaeomeryx 确实是一个曾经引起过许多争论的属。如前所述，人们很快就发现，事情并不象它的定名人，von Meyer 定名时想象得那么简单。首先是 Lartet 于 1851 年报道了法国著名的中新世哺乳动物化石地点，桑桑盆地 (Sansan) 的一种双叉，但无真正角环的鹿角，他将其命名为 *Dicrocerus*。1859 年 Hensel 又根据德国 Schlesien 的材料定了 *Prox* 属，这种鹿的角也是双叉的，但却具有真正的角环，而且角柄也很长。从 1862 年开始，Fraas 发现德国 Steinheim 也有一种有角的鹿 (后来证明是 *Lagomeryx*)。Gaudry 1878年又将一类角柄很高，无角环，末端分叉的鹿定名为 *Procervulus*。这些鹿的下臼齿毫无例外地都是有古鹿褶的。这样，就产生了两种相反的意见，以 Fraas 为首的一些德、奥古生物学家 (A. Hofmann, O. Roger 等) 倾向于应该扩大 von Meyer 关于 *Palaeomeryx* 的含意，他们把古鹿褶看成是"第三纪反刍类极好的鉴别特征"，角的发现只是证明了 von Meyer 原先关于 *Palaeomeryx* 无角的判断是错误的，他们相信 *Palaeomeryx* 本来就应该是有角的，因此，他们把具有各式各样不同分叉的角的鹿，只要具有古鹿褶的，都归入了 *Palaeomeryx* 属。另一方面，法国的古生物学家(包括中欧的 F. Toula 和 R. Hoernes 等) 则认为古鹿褶是"意义不大的性状"。他们根据角的差异，把上述那些鹿又全都从 *Palaeomeryx* 中分了出来，他们还把法国一些小个体的，无角，但具古鹿褶的鹿类，也从 *Palaeomeryx* 中分了出来，如 *Drematherium* (G. St. Hilaire, 1832), *Amphitragulus* (Pomel, 1846) 和 *Micromeryx* (Lartet, 1832) 等，在他们看来，只有剩下的，那些头上无角，大个体的，具有古鹿褶的鹿类才是 *Palaeomeryx*。

到本世纪的上半叶，问题才逐渐明朗。人们逐渐接受了法国人的观点，更多地根据角的特征来划分属。此后，从 *Palaeomeryx* 中又划分出了 *Lagomeryx* (O. Roger, 1904), *Heteroprox* (G. H. Stehlin, 1928), *Euprox* (=Hensel 的 *Prox* Stehlin, 1928) 等。

1966 年 Ginsburg 和 Heintz 对欧洲的 *Palaeomeryx* 材料进行了整理，他们认为过去已经划分出的属 (见前)，都是可以成立的。*Palaeomeryx* 在欧洲实际上只有三个种：*P. kaupi* von Meyer (=*P. bojani* von Meyer、*P. garsonini* Mayet); *P. magnus* lartet (=*P. sansaniensis* Filhol) 和 *P. eminens* von Meyer (=*P. nicoleti* von Meyer)。

另一方面，Ginsburg 和 Heintz 却认为德日进记述的山旺的 *Palaeomeryx* (? *Lagomeryx*) sp. A 以及 Whitworth 记述的非洲的 *Palaeomeryx africanus* 都不是真正的 *Palaeomeryx*，而应该从这个属中划分出去，因为上述的材料都有 P_1，而欧洲的材料则都没有 P_1。山旺最近发现的材料进一步证实了，德日进关于山旺大个体的"鹿类"的牙齿，和欧洲狭义的 *Palaeomeryx* 的牙齿极为相似的观点，事实上，除了一些细微的特征外，山旺的标本很难与欧洲的 *Palaeomeryx* 相区分。山旺新发现的材料还证实了，这种大个体的"鹿类"的角和 *Lagomeryx* 的角根本不同，不能归人同一个属。另外，山旺的 *Palaeomeryx* 也不是都具有 P_1 的，因此，不能依 P_1 的有无而将山旺的标本从 *Palaeomeryx* 划分出去。*P.*

africanus 和山旺的情况大体相同，看来也应继续留在 *Palaeomeryx* 属。

山旺的材料数量较多，保存完整，它们所显示的特征应该更为可靠。

我们根据对山旺标本的观察，对 *Palaeomeryx* 属的特征，作如下的补充订正：

个体与现生马鹿大小相近。脑颅长，眼眶居中，颅基面与腭面几乎位于同一平面上，有眶下腺窝及"筛孔"；原始种中保留有 P_1，P_1 与 P_2 之间常有齿隙；颊齿低冠，珐琅质表面皱纹发育，齿带及附柱也较发育；前臼齿臼齿化程度弱，P_4 前谷仅在进步种中趋于封闭；上臼齿原尖后支后伸，其外方有一小的珐琅质褶，外侧前附尖、中附尖和前尖肋发育强；下臼齿及下第四乳齿具明显的古鹿褶。颈、四肢，特别是肱骨、股骨以下部分，都不特别伸长，后肢比前肢长，炮骨背面中沟在远端封闭成孔状，其远端关节面嵴发育完全，前、后侧趾(指)，II 和 V 退化成细条状，位于炮骨后面两侧，但各有三节指(趾)节骨。

雌、雄异型：雄性眼眶上方有一对粗短的"皮骨角"，枕部有由枕骨向后延伸形成的末端膨大的"枕顶角"。具马刀状的上犬齿。雌性无上述特征。

（二）*Palaeomeryx* 的性质及其分类位置

虽然 *Palaeomeryx* 和长颈鹿之间的某些相似性早就引起了人们的注意（O. Hofmann, 1870、M. Schlosser, 1903、Teilhard de Chardin, 1939、G. Pilgrim, 1941），它还是一直被人们习惯地放在鹿科或鹿超科里。1966年 Ginsburg 和 Heintz 才第一次明确地提出，把 *Palaeomeryx* 放在长颈鹿超科，他们认为，*Palaeomeryx* 在下列各点上是具有长颈鹿性质的：

（1）可能具有"皮骨角"(ossicone)。他们在清理有关欧洲的 *Palaeomeryx* 材料时，在奥而良砂层（Sables de Orleanais）的采集物中，发现了两个"皮骨角"。他们认为这两个"皮骨角"可能是属于 *Palaeomeryx* 的。因为这种类型的角是长颈鹿所特有的，这一特征成了他们这种分类设想的主要依据。

（2）他们认为 *Palaeomeryx* 头骨上没有"筛孔"，长颈鹿科和牛科亦然，而鹿科都是有"筛孔"的。

（3）*Palaeomeryx* 的牙齿构造，如低冠，珐琅质表面多皱，附尖特别发育，上臼齿原尖后支不分叉等，接近长颈鹿者，特别是 P_4 臼齿化程度在后期进步种中尤甚。

（4）肱骨远端中沟比鹿类者深，上髁退化。

（5）桡骨远端背面，通过掌前侧伸肌腱的沟变浅。

（6）中掌骨近端关节面中嵴位于中央粗糙面之外方。

（7）掌骨后面逐渐变平。

（8）中蹠骨近端关节面后方，被 Heintz 称作 diathrodinal facet 的那个小面缺如。

（9）掌、蹠骨接近等长。这些肢骨上的特征，根据 Ginsburg 和 Heintz 的意见，都和长颈鹿(有些甚至和牛科)接近，而与鹿科者不同。

Hamilton 1973 年在研究北非 Gebel Zelten 的偶蹄类时，就采用了 Ginsburg 和 Heintz 的意见。而且 Hamilton 认为，最原始的长颈鹿，*Zarafa* (Leinders 认为是 *Canthumeryx* 的同物异名)在上牙的构造上，恰恰介于 *Palaeotragus* 和 *Palaeomeryx* 之间，这更说

明了长颈鹿和 *Palaeomeryx* 在系统关系上十分接近。

1955 年 Frechkop 首先提出,长颈鹿和牛科的关系接近,他认为它们的角,在发生上更为接近,而和鹿角的发生相距较远。这一观点,后来曾得到了生物学方面的支持: Gaastra 1975 年发现,长颈鹿和牛科动物的细胞中,核氧核糖氨基酸序列更为接近,而与鹿者相去较远。很多人都附合这种观点, Hamilton 本人,1978 年也转而支持这种观点,其中 Leinders 和 Heintz 是最积极的支持者,他们特别强调了砲骨和泪孔在分类上的作用。这样,对于 *Palaeomeryx* 归属的矛盾就更趋激化,要么 *Palaeomeryx* 归入鹿类而和长颈鹿的关系甚远(因为长颈鹿更接近牛科),要么它就和长颈鹿一起归入牛超科。然而无论是哪一种方法,都和我们对 *Palaeomeryx* 的习惯看法,即把它看作在形态上介于鹿与长颈鹿之间的一种动物,是大相径庭的。

Leinders 是前一种观点的代表,最近(1984 年)他在研究意大利的一种十分特殊的反刍类化石时,对 Ginsburg 和 Heintz 1966 年关于 *Palaeomeryx* 应归入长颈鹿类的观点逐条地进行了分析:

(1) Leinders 承认"皮骨角"是重要的衍生性状,但他更相信,这或许是通过平行进化产生的,也可能仅仅是有角鹿类在开始阶段与长颈鹿的"皮骨角"外形相似的一类角而已。

(2) Leinders 认为"筛孔"的有无不甚重要,因为现生鹿中也有缺之者。

(3) 对于牙齿, Leinders 只分析讨论了上臼齿原尖脊后支是否分叉问题,他指出, Kretzoi 1974 年记述的 *Palaeomeryx* 的上臼齿原尖脊后支就是分叉的,此外, *Triceromeryx* 的上臼齿原尖脊后支也是分叉的,所以他认为 Ginsburg 和 Heintz 对这一点的记述是不确切的。

(4) Leinders 认为 Ginsburg 和 Heintz 所列举的头后骨骼的特征,在区分鹿和长颈鹿时都不大可靠,例外的情况很多。

Leinders 还注意到 Ginsburg 和 Heintz 所提到的 *Palaeomeryx* 的许多与长颈鹿接近的特征,都只在后期较进步的种中才出现,亦即从 MN6 才开始有的。现有的化石资料表明,早在 MN5 长颈鹿科就已经形成了(Gebel Zelten)。这表明长颈鹿不可能从进步的 *Palaeomeryx* 中产生。

Leinders 特别强调了炮骨背中沟在远端封闭成孔状的这一特征。他说 *Palaeomeryx* 已有这一特征,这使 *Palaeomeryx* 不能和具有开放型炮骨背中沟的长颈鹿类放在一起。

总之, Leinders 认为 Ginsburg 和 Heintz 1966 年提出的理由说服力不大, *Palaeomeryx* 还应置于鹿科中(Leinders, 1984, fig. 4)。Ginsburg 最近在致本文作者之一,阎德发的信中依然坚持他 1966 年提出的看法。而 Heintz 大概已转而倾向 *Palaeomeryx* 应归入鹿科了。

山旺发现的新材料为 *Palaeomeryx* 的分类提出了新的证据:

(1) 它证实了 *Palaeomeryx* 头上确实有角,而且也确实是一对长在眼眶上方的"皮骨角"。这对角在着生位置、表面形态、内部构造以及与头骨的关系(以骨缝相接)等方面与现生长颈鹿完全一致。此外,还有一"枕顶角",此角与"皮骨角"在性质上完全不同,到目前为止,仅出现在西班牙中中新世的 *Triceromeryx* 和北美中新世的 *Cranioceras* (*Procra-*

nioceras）的标本中。前者肯定应归入长颈鹿科，C. S. Churcher 说，它的“牙齿及头后骨骼在特征上完全是 Palaeotragine 型的”（Churcher, 1970, p. 84）这可能有些过分，但至少在 P_4 的构造上，已是长颈鹿式的了：它的下后尖已经与下原尖分离，而下内尖脊反而与下原尖相连，而且很倾斜，下内小尖几乎完全分离等特征（Crusafont, Pairo, 1952, Pl. XIII）清楚地说明了这一点。关于 *Cranioceras* 的性质，目前还不十分清楚，但它在形态上，似乎比 *Triceromeryx* 更接近于山旺的标本，这无论从不分叉的“枕顶角”，下前臼齿的进化程度，还是从炮骨背中沟远端封闭等特点上都可以看出。不过，我们的标本眶上方的“皮骨角”和上述两者都不相同。总之，从“角”看，山旺标本无疑最接近长颈鹿。过去，长期以来没有发现 *Palaeomeryx* 的角，一方面可能因采集不够，另一方面仅雄性有角，可能也是一个重要原因。

(2) 头骨长头型，眶后部分特别长，眼眶位于头骨全长之中点附近，颅部和面部的基底几乎位于同一直线上。这种长而近水平的颅部，可能是长颈鹿(特别是早期类型)的特征之一，类似的头骨还见于 *Zarafa* (Hamilton, 1973, Pl. 2)和 *Giraffokeryx* (E. H. Colbert, 1933, fig. 1) 在这一点上 *Cranioceras* 也与上述标本接近 (Ch. Frick, 1936, fig. 11) 本来眼眶位于头长的中部，颅部与面部的夹角很小，这可能是反刍类的原始性质，但头骨如此伸长，却仅发现于上述这些类别中，而在别的类群中没发现过，这很可能是长颈鹿类的近裔性状之一。

(3) *Palaeomeryx* 头骨上有筛孔。 这点 Ginsburg 和 Heintz 1966 年对 *Palaeomeryx* 的推断是不确切的。过去，一般都认为长颈鹿和牛科动物是没有筛孔的。事实上，在长颈鹿中，有的属种确实具有筛孔。*Okapi* 就具有筛孔，我们在现生长颈鹿 *Giraffa* 头骨上也观察到了筛孔。另外，在 *Zarafa* (Hamilton, 1973, p. 87), *Giraffokeryx* (Colbert, 1933, p. 7), *Palaeotragus* (Bohlin, 1926, p. 11)的头骨上也都有筛孔。筛孔在鹿类的头骨上普遍都存在，但 Leinders (1984, p. 40) 指出，在鹿中也见之无筛孔者。在牛科中则通常是没有筛孔的。筛孔可能是一种原始特征，这一特征在绝大部分鹿中都还保留，在长颈鹿中亦然，而在牛科中则已消失。虽然在这一点上 *Palaeomeryx* 和长颈鹿及鹿最接近，但由于是近祖性状，它并不能说明，这两者比它们与牛科的关系更近。

(4) *Palaeomeryx* 的泪孔为眶内单孔型。 这和现生多数牛科动物是一致的。 但已知最原始的长颈鹿 *Zarafa*，也是眶内单孔型泪孔。 Hamilton (1973) 描述为双泪孔，但 Leinders 说，经他观察 *Zarafa* 实为单泪孔 (Leinders, 1984, p. 38) 甚至 *Prolibytherium* 也是单泪孔。鹿类中的原始类型，*Hyaemoschus*, *Moschus* 等都是具有单泪孔的，但在后期类型中则都为眶缘双泪孔型了。显然，单泪孔是近祖性状，而双泪孔则是近裔性状。因此，在这一点上，*Palaeomeryx* 和牛科动物的相似，并不能说明它们的共近祖关系。

(5) *Palaeomeryx* 具有明显的眶前窝，雄性具有马刀状的上犬齿。前者在大部分鹿中都存在，后者则常见于原始的鹿类中。但在长颈鹿和牛科中从未发现过。不过这两个特征显然都是近祖性状，它既不能证明牛科与长颈鹿是否关系更接近，也不能说明 *Palaeomeryx* 就和鹿类更接近。这两个原始特征，无论在哪一个支系的原始种类中，都可能被保留下来。

(6) *Palaeomeryx* 的上、下颊齿，正如 Hamilton 1973 年指出的，和 *Zarafa* 在大小，形

态上都最为相似。其中有些共同点,如上臼齿原尖后支的形态,特别是 Hamilton 称之为 h 形的珐琅质褶形物,在其它类别中,从来没有如此明显,它可能是长颈鹿早期类型的特征。有一些共同特征,如颊齿附尖及前尖外肋的特别发育等,是在牛科中所不见的(后期牛亚科的附尖及肋,是后来平行产生的)。它们很可能是中新世阶段的鹿和长颈鹿类的共同近裔性状,说明它们和牛科的关系更远。最后还有一些共同性状,是整个反刍类的相对近祖性状,如低冠,齿带较发育,前臼齿臼齿化程度较低等…。这些特征只能说明 *Palaeomeryx* 处在比 *Hyaemoschus*, *Gelocus* 以及 *Leptomeryx* 等原始反刍类稍高的阶段。

(7) *Palaeomeryx* 炮骨背中沟在远端封闭。Heintz 和 Leinders 认为这是把长颈鹿科和牛科放在一起,而与鹿类分开的主要依据。因为长颈鹿和"牛"炮骨背面中沟在远端是开放型的,而鹿类则是封闭型的。这也是 Heintz 和 Leinders 把 *Palaeomeryx* 和鹿类放在一起的主要理由。

这种观点值得商榷。首先,Heintz 和 Leinders 对炮骨背中沟的敞开型和封闭型,没有进行极性分析。我们认为:敞开型显然是近祖性状,而封闭型则是近裔性状。从鹿类的进化来看,在炮骨形成的最初阶段是敞开型的,如渐新世的 *Gelocus* (Kowalevsky, 1876—1877, Tab. 11, 19), *Leptomeryx* (Matthew, 1908, fig. 9) 等,在此之后才出现封闭性的炮骨。如果具敞开型中沟的炮骨是近祖性状,那么就不能用它作为把长颈鹿和牛类归在一起的根据。另外,现有的资料还表明,封闭型的中沟这一近裔性状,也可以在不同的支系中平行产生,最明显的例子是叉角羚。现在叉角羚的炮骨中沟是封闭型的,这也是 Leinders 把它放入鹿科的主要依据。但叉角羚的祖先中,却有开放型的炮骨:Furlong 1927 年记述了 *Merycodus* cf. *furcatus* [＝*Cosoryx* (*Paracosoryx*) *furlongi* Frick, 1937] 一不完整的骨架,它的炮骨就是开放型的 (Furlong, 1927, fig. 16)。这种动物都被公认是叉角羚的祖先类型:双叉型的角,位于眼眶之上方,角表面被以皮毛,终生不脱落。这表明,叉角羚这一支系从反刍类主干中分出时,炮骨中沟还是开放型的,只是后来才变为封闭型的,而不是从开始就是封闭型的。

Palaeomeryx 封闭型的炮骨背中沟,究竟是由哪一种方式产生的? 是从已经变为封闭型的鹿类获得的近裔性状,还是从具有开放型中沟的炮骨,通过平行进化,像叉角羚那样产生的呢! 这要看对其它性状的综合分析,根据简约性原则才能决定。

(8) 头后骨骼的其它特征,根据我们对山旺标本的观察,全都和鹿类的没有什么区别。Ginsburg 和 Heintz 1966 年所推测的一些 *Palaeomeryx* 和后期长颈鹿相似的特点,或是差别很细微,不足以作为分类上的依据,或是推测不够准确,如前肢变长等…。事实上,*Zarafa* 的脊柱和四肢骨也和 *Palaeomeryx* 的很相近。Hamilton (1973, p. 98) 指出,*Zarafa* 的跟骨和距骨与 *Palaeomeryx* 相似。其实在颈椎和四肢的比例上,它和 *Palaeomeryx* 也很接近。这都证明了鹿和长颈鹿的系统关系更为接近。

综上所述,*Palaeomeryx* 和长颈鹿至少有三个近裔性状,即上述 (1)、(2) 和颊齿中的个别特征(如 h 形构造),它和鹿及长颈鹿共有的近裔性状是颊齿上特别发育的附尖及肋。*Palaeomeryx* 和牛科没有共近裔性状,但是 *Palaeomeryx* 有一个性状是只和鹿科的近裔性状相同的,这就是封闭型的炮骨背中沟。考虑到 *Palaeomeryx* 和原始的长颈鹿有更多的共近裔性状,根据简约原则,炮骨背面封闭型的中沟,只能看作是平行进化的产物。

Palaeomeryx 作为长颈鹿科中，构造最原始的一员(封闭型的炮骨背中沟除外)，它同时也决定了长颈鹿从反刍类主干中分出的位置：它应在蹠骨已愈合为炮骨，但尚为开放型背中沟之后，而在炮骨进化成封闭型背中沟之前产生的。在反刍类中，开放型炮骨背中沟，出现在渐新世的 *Gelocus* 和 *Leptomeryx* 中，此时它们的掌骨还没有愈合，为四指型，显然它们比 *Palaeomeryx* 更原始，而第一次出现封闭型炮骨的则是 *Blastomeryx*，它的前肢也和 *Palaeomeryx* 达到同样的水平，即第三、四掌骨已愈合，而退化的侧指 (Mtc II, V) 还全长保留。长颈鹿类从反刍类主干中分出时应该是前、后肢侧指(趾)已相当退化，并已形成炮骨 (背中沟尚为开放型)，但已产生了"皮骨角"。*Palaeomeryx* 是这一支系中，最原始的代表，但是它的炮骨却向着鹿的方向特化，变为封闭型的背中沟。另一支则是真正的长颈鹿类，它的上犬齿完全退化，眶前窝消失，下犬齿为双叶状，第四下前臼齿逐渐进化为特殊的长颈鹿型构造…。*Palaeomeryx* 是否应为独立的一个科，它应包括哪些属，这个问题需要在对一系列有关的属进行研究后，才能肯定。

上述这种分类意见的一个直接后果，就是把牛科与长颈鹿类分开了。牛科无疑既保留一些近祖特征(开放型炮骨背中沟和眶内单孔型泪孔)，同时也有一系列特化特征，如高冠齿及角的发育等。从已有的化石资料判断，如果牛科的产生是单系发生的话，它应该有相当早的历史。因为在中渐新世，已有齿冠很高的牛科动物了 (黄学诗，1982)，另一个可能的推测是：叉角羚还是和牛科更为接近，它和鹿类有共同的特征(指炮骨封闭型的背中沟)，是独立地平行进化获得的，而它的"角"，高冠的牙齿等，都和牛科为共近裔性状。

(三) *P. tricornis* 与有关种的比较和关于地质时代的估计

欧洲的 *Palaeomeryx* 只有 *P. kaupi*、*P. magnus* 和 *P. eminens* 三个种。后两个种的牙齿大小和山旺的标本差别很大，形态上也显得更进步些。这主要表现在上、下前臼齿臼齿化的程度上。遗憾的是，这两个种角的情况不明。*P. kaupi* 的材料很少，近来在法国北部，早中新世地层中又有不少的发现，但一直没见研究发表。Ginsburg 和 Heintz 1966 年记述的"角"化石，显然应属 *P. kaupi* 的，因为他们是从 Artenay (MN 4) 发现的，这一层位里只有这一种 *Palaeomeryx*。这种"角"在形态上和山旺的标本有所区别。它显然比较细长，而山旺者基部宽大，为低短的三角锥形。根据 Ginsburg 提供给我们，从 Artenay 发现的牙齿标本的模型来看 (P^3—M^3, Sa. 4156, Sansan P_2—M_3, Artenay)，几乎和山旺的标本完全一样，但它没有 P_1。Ginsburg 和 Heintz 也把缺失 P_1 作为欧洲 *Palaeomeryx* 的特征之一。

Whitworth 1958 年记述的东非 Sohghor, Burdigalian 期的一类 *Palaeomeryx*: *P. africanus*。Hamilton 1973 年把它归入了牛科的 *Walangania*，其中有两个牙齿，Hamilton 定了一个新种，*Gelocus whitworthi*。从形态上看，这些牙齿不大像牛科的。它们在个体上要比山旺的标本小得多，前臼齿臼齿化的程度也低，M_3 的第三叶还没有完全和第二叶相连接。这个种也是有 P_1 的。总之，它和山旺的标本还是易于区别的。Hamilton 1973 年还建立了一个新属：*Canthumeryx*。Leinders 1984 把它和 *Zarafa* 等同了起来。后者则是真正的长颈鹿，不管 *Canthumeryx* 是不是 *Zarafa*，它的下颊齿的中附尖特别突出，这一点和

山旺的标本区别明显。Stromer, Whitworth 和 Hamilton 都描述过一些属于 *Propalaeoryx* 的牙齿，这个属也被归入到 Palaeomerycidae 中。它的个体也小，大体上和 *Palaeomeryx africanus* 差不多，但齿冠相对较高一些。

由于山旺的标本区别于 *Palaeomeryx* 属的各个已知种，因此，我们把他视为这个属的一个新种：*Palaeomeryx tricornis* sp. nov。

Ginsburg 和Heintz 1966 年曾提出，欧洲的 *Palaeomeryx* 在个体上有规律地逐步增大，并以 M_3 的长作为例证予以说明。Burdigalian 的 *P. kaupi* 的 M_3 长度在 23.9—29.0 mm 之间，下 Helvetian 的 *P. magnus* 长度为 26—35 mm，而晚些，从中 Helvetian 至 Tortonian 的 *P. magnus* 和 *P. eminens* 则为 32.7—40.0mm。从整个齿列的大小看（表 1、3），山旺的标本似乎与下 Helvetian 亦即 Pontlevoy（=MN 5）最接近，有些数字还落在 Burdigalian 亦即 Baigneaux（= MN 4b）的材料的变异范围之内。而显然要比桑桑或更晚地层（MN6—MN8）中的小。

长期以来，我们习惯于把山旺和桑桑（MN 6）相对比。如果我们以欧洲 *Palaeomeryx* 个体增大的规律对山旺的 *P. tricornis* 进行推测，那么它的时代，就应该比原先想象的要早些，也许把山旺放在 MN 5 或 MN 4 更合适些。考虑到亚洲的 *Palaeomeryx* 的一些特殊性质（"角"的形态和 P_1 的存在等），它也可能代表一个不同于欧洲的单独支系。如果是这样的话，那么它的时代也有可能更早些或者更晚些。

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参 考 文 献

Bohlin, B., 1926: Die Familie Giraffidae. *Pal. Sin.*, Ser. C vol. IV (1): 1—178.

Chen, G. F. and W. Y. Wu, 1976: Miocene mammalian fossils of Jiulongkou, Ci Xian district, Hebei. *Vert. PalAs.*, **14** (1): 6—15.

Churcher, C. S., 1970: Two new Upper Miocene Giraffids from Fort Ternan, Kenya, East Africa: *Palaeotragus primaevus* n. sp. and *Samotherium africanum* n. sp. In Leakey and Savage, 1970, Fossil Vertebrates of Africa. 2: 1—105.

Colbert, E. H., 1933: A skull and mandible of *Giraffokeryx punjabiensis* Pilgrim. *Amer. Mus. Nov.*, No. 632: 1—14.

——————, 1938: The relationships of the okapi. *J. Mammalogy*, **19** (1): 47—64.

Crusafont-Pairo, M., 1952: Los Jirfidos fosiles de *Espana. Mem. y Com. del Inst. geol.*, VIII: 1—239.

Filhol, M. H., 1890: Études sur les mammifères fossiles de Sansan. *Bibl. de l'école des Hautes Études*, Sec. sci. nat. **37** (1): 1—319.

Fraas, O., 1870: Die Fauna von Steinheim. *Württ. naturwiss. Jh.*, **26** (2/3): 145—306.

Frechkop, S., 1955: Ruminantia. In: Grasse, P. (ed.): *Traite de Zoologie*. t. XVII (1): 636—638.

Frick, C., 1937: Horned ruminants of North America. *Bull. Amer. Mus. Nat. Hist.*, 69: 1—669.

Furlong, E. L., 1927: The occurrence and phylogenetic status of *Merycodus* from the Mohave desert Tertiary. Univ. Calif. Publ., *Bull. Dept. Geol. Sci.*, **17** (4): 145—186.

Ginsburg, L., 1974: Les faunes de mammifères burdigaliens et vindobоniens des bassins de la Loire et de la Garonne. *Mem. B. R. G. M.*, vol. **78** (2): 153—167.

Ginsburg, L. and E. Heintz, 1966: Sur les affinités du genre *Palaeomeryx* (Ruminant du Miocène européen). *C. R. Acad. Sc.* Paris, vol. 262: 979—982.

Hamilton, W. R., 1973: The lower Miocene ruminants of Gebel Zelten, Lybia. *Bull. Brit. Mus. Nat. Hist (Geol.)*, **21**: 73—190.

Heintz, E., 1963: Les caractères distinctifs entre métatarses de Cervidae et Bovidae actuels et fossiles *Mammalia*, **27**(2): 200—209.

Huang, X. S., 1982: Preliminary observations on the Oligocene deposits and mammalian fauna from

Alashan Zuoqi, Nei Monggol. *Vert. PalAs.*, **20**(4): 337—349.
Koken, E., 1885: Über fossile Säugetiere aus China. *Pal. Abh.*, **3**(2):
Kowalevsky, V., 1876: Osteologie des *Gelocus aymardi*. *Palaeotogr.*, n. ser. 4: 145—162.
Lankester, R., 1910: Monograph of the okapi. London.
Lee, Y. Q. et W. Y. Wu, 1978: Miocene Artiodactyla of Lintong and Lantian, Shensi. Professional papers of stratigr. paleont., 7: 127—135.
Leinders, J. J. M., 1984: Hoplitomerycidae fam. nov. (Ruminantia, Mammalia) from Neogene fissure fillings in Gargano (Italy). *Scripta Geol.*, 70: 1—51.
————, and E. Heintz, 1980: The configuration of the lacrimal orifices in pecorans and tragulids (Artiodactyla, Mammalia) and its significance for the distinction between Bovidae and Cervidae. *Beaufortia*, **30**(7): 155—162.
Loomis, F. B., 1925: Dentition of artiodactyls. *Bull. Geol. Soc. Amer.*, **36**: 583—604.
Macewen, W., 1920: The growth and shedding of the antler of the deer. Glasgow. p. 1—109.
Matthew, W. D., 1908: Osteology of *Blastomeryx* and phylogeny of the American Cervidae. *Bull. Amer. Mus. Nat. Hist.*, **24**: 535—562.
von Meyer, H., 1952: *Palaeomeryx eminens*. *Palaeontogr.* **2**: 78—81.
Pilgrim, G. E., 1941: The relationship of certain variant fossil types of 'horn' to those of the living Pecora. *Ann.* and *Mag. Nat. Hist.*, **11**, 7: 172—184.
Ridewood, W. G., 1904: Some observations on the skull of the giraffe. *Proc. Zool. Soc.* London: 150—157.
Roger, O., 1898: Wirbeltierreste aus dem Dinotheriensande der bayerisch-schwabischen Hochebene. *Bericht Naturwiss. Vereins Schwab. u. Neuburg in Augsburg*, 33: 1—46.
Sigogneau, D., 1968: Le genre *Dremotherium* (Cervoidea), anatomie du crane, denture et moulage endocranien. *Ann. Pal. (Vert.)*, **54** (1): 39—100.
Teilhard de Chardin, P., 1939: The Miocene cervids from Shantung. *Bull Geol. Soc. China*, **19** (3): 269—278.
Webb, S. D. and B. E. Taylor, 1980: The phylogeny of hornless ruminants and a description of the cranium of *Archaeomeryx*. *Bull. Amer. Mus. Nat. Hist.*, **167**(3): 121—157.
Whitworth, T., 1958: Miocene ruminants of East Africa. In: Fossil Mammals of Africa, No. 15: 1—50.
Yan Defa et al., 1983: Miocene stratigraphy and mammals of Shanwang, Shandong. *Vert. PalAs.*, **21** (3): 210—222.
Young, C. C., 1937: On a Miocene mammalian fauna from Shantung. *Bull Geol. Soc. China*, **17** (2): 209—238.

PRELIMINARY OBSERVATIONS ON THE NEWLY FOUND SKELETONS OF *PALAEOMERYX* FROM SHANWANG, SHANDONG

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Key words Shandong, Miocene; Shanwang Fauna; *Palaeomeryx*, Skeleton

Summary

Palaeomeryx was erected by Hermann von Meyer in 1834, who based his new genus

chiefly on the presence of a "Würst" on the posterior wall of the protoconid of DP_4 and the lower molars (later called the "*Palaeomeryx*-fold"). The fact that no associated antlers were found led von Meyer to believe that *Palaeomeryx* might possibly be hornless. Subsequent discoveries of various kinds of "antlers" in association with teeth bearing the *Palaeomeryx*-fold made the genus *Palaeomeryx* conceptually ever-changing, and sometimes very confusing. L. Ginsburg and E. Heintz's referral of two ossicones, allegedly pertaining to *Palaeomeryx* from Artenay, France, resurrected the dispute as to the content, affinity and taxonomic position of the genus *Palaeomeryx*. One of the main reasons for the controversy lies in the lack of complete skulls, to say nothing of skeletons.

Till now there have been few records of the genus in China. E. Koken reported in 1885 several isolated teeth from Yunnan (?) and erected a new species for them, *Palaeomeryx oweni*. Chen G. F. and Wu W. Y. (1976) and Li Y. Q. and Wu W. Y. (1978) mentioned some material of *Palaeomeryx* spp. from Cixian, Hebei, and Lantian, Shaanxi, respectively. All the above mentioned materials are too scanty to be helpful with regard to the problems concerned.

The presence of *Palaeomeryx* fossils in Shanwang was first noticed by P. Teilhard de Chardin in 1939. There were two kinds of jaws, both with the *Palaeomeryx*-fold. The larger one, according to Teilhard de Chardin, "Would, without any hesitation, be determined as *Palaeomeryx*", "if they had been found in an European site". However, there was only one type of "antler", pertaining, judging by its size, only to the smaller form. As a result, he identified them as *Palaeomeryx* (?*Lagomeryx*) spp. A and B.

The excavations carried out in the last years have luckily resulted in finding not only complete skulls, but also skeletons of *Palaeomeryx*. The significance of the discoveries is self-evident. Owing to the extremely fragile nature of the fossil bones and the technical problems in their preparation, we are tempted to publish the first observations on the most important aspects of the skulls and the skeletons before they can be available for detailed study.

Description

Palaeomeryx tricornis sp. nov.

Holotype V 7728, skull and associated lower jaw (much damaged during preparation) with three cervical vertebrae. (Pl. III)

Other Material

1. 820831* complete skeleton, female (Pl. VI).
2. 830009* complete skeleton, male (Pl. III)
3. 840002* complete skeleton, male
4. 840015* skeleton, female, the middle part of the vertebral column and the distal parts of the limbs are lacking
5. LV 8003* incomplete skeleton, male
6. 820837* part of skeleton
7. V 7729 skull, only the right side is exposed

* stored in Linqu Paleontological Museum.

8. V 7730 left P^2—M^3
9. V 7730.1 left P_4—M_3

Diagnosis of the species Size smaller than the medium-sized species of the genus. P_1 present (but not always), with or without a short diastema to P_2. Teeth brachyodont, corrugated. Metaconids on P_2—P_4 weakly individualized, forming no closed valleys on the inner side of the teeth. *Palaeomeryx*-fold well developed. Inner crests of P^2—P^4 barely divided by grooves on their inner walls. Upper molars propotionally wider. Accessary conules of irregular form, but very well developed, labial to the posterior ridge of the protocone on upper molars. Cingulum and style (id) comparatively weak. Male with a pair of ossicones above the orbits and an occipital bony "horn" (may be characteristic for the genus in general). The ossicone is very wide at its base, tapers rapidly and inclines backward. The occipital "horn" long, much dilated at its end.

Description

The only discernible sutures on the skull are those between premaxilla and maxilla, and between them and nasals. The nasals are flattened dorsally, and extend anteriorly to the level of the front of the upper canine, forming a small nasal notch over the premaxilla. The width at its anterior end is 18 mm, that at its posterior part is 24 mm. The premaxilla forms an oblique parallelogram, forming an angle of 45° with the alveolar border, but its anterior tip is rather pointed. The maxilla is rather high. At the posterior end of the nasal-maxilla suture a strip of matrix is exposed beneath the bones, evidently representing the ethmoidal vacuity (fenester ethmoidale). A large, oval (50 ×20 mm) and sharp-edged preorbital fossa is situated in front of the orbit. The fossa extends beneath the lower border of the orbit. The infraorbital foramen lies in front of P^2. The orbit is situated approximately in the middle of the skull (measured from basion to prosthion). The orbit is not outward protruded. The anterior edge of the orbit is damaged, but judging from the preserved parts it can be concluded that there is only one rather large lacrimal orifice on the inner wall of the orbit. Though the back part of the skull is more compressed, a forked sagittal crest is still traceable. The point of bifurcation lies at the level of the glenoid cavity. The delicate parts of the skull, the ear region and the basicranium are too crushed to provide useful informations.

Sexual dimorphism is clearly shown by the presence or the absence of the "horn" structures. In the male, there are a pair of ossicones and an occipital "horn". The ossicones are situated just above the orbits. The surface of the ossicones is rough and cancellous. On the type skull a rough suture can be observed, which separates the ossicone from the skull. Since the skull belongs to a rather old individual, judging by the strongly worn teeth, it must mean that the ossicone was unankylosed to the skull roof until late in life. Unfortunately we could not find a similar suture in the other male skulls at our disposal. Probably the ankylosis may occur irregularly, earlier or later in life. Seen from the lateral side, the ossicone is triangular in form, slanting strongly backward. Its anterior margin is far beyond the anterior border of the orbit, while its posterior margin which is concave anteriorly, lies approximately at the level of the posterior border of the orbit. The ossicone is strongly compressed laterally. In the type skull the tip of the ossicone is a little swollen, in other skulls the tips may be pointed. So the ossicone varies in form. The occipital "horn" is morphologically and histologically different from the ossicones. The surface of the "horn" is smooth, like the surface of any ordinary bone. The lambdoid crest extends upward to the middle of the "horn". The uppermost part of the "horn" is ornamented with fine knots and striations, but this is the usual roughening of the bone surface, as in the case of the "horn" of brontotheres. Seen from the side, the "horn" resembles a large bulb sitting on a stout pedicle. Laterally it is compressed, and seemingly unforked, unlike that in *Triceromeryx*.

The upper canine in male is large and sabre-like, with a stout root. The most robust part of the tooth is in the middle of the root (20×10 mm). The demarcation between the root and the crown of the tooth is vague. The anterior margin is rounded, while the posterior is trenchant. The crown is rather flat externally, but convex internally (opposite to Teilhard de Chardin's description). Seen from the antero-posterior direction, the tooth is bent, with its tip turned externally. The upper canine of a female individual is very small and peg-like.

There is no P^1, the diastema between canine and P^2 on the type skull is about 40 mm. The P^2 is provided with a very strong paracone rib on the labial wall and deep groove in front of it. There is no clear central groove on the lingual wall of the tooth on the type specimen, while on other specimens the groove is very weakly developed. P^3 resembles P^2, with the inner crest more robust, making the tooth more triangular in form. P^4 is markedly shorter than its preceding teeth, but wider. There are two prominent swellings on the labial wall: the parastyle and the paracone rib. Seen from the labial side, the former takes a form of low triangle, while the latter is long and ridge-like. They converge at the base of the crown. The paracone rib overlaps the groove which lies in front of it. The posterior wing of the protocone is composed of two ridges. The labial one is higher than the lingual one, but the valley between them is very shallow, so that slight wear will change the two ridges into one broad wear surface. A weak cingulum runs along the anterior, lingual and posterior sides of the tooth.

The three molars are alike in structure. Parastyle and paracone ribs resemble those in P^4. The mesostyle resembles the parastyle in form, but more robust, forming the most labial point of the tooth. The metacone has a more oblique orientation than the paracone, and has a fine rib on its outer wall. The posterior wing of the protocone is directed more posteriorly than postero-labially, furthermore, it points to the middle of the anterior wing of the metaconule, rather than to its labial end. Labial to the posterior wing of the protocone there is a conule of irregular form. The form of the conule changes from M^1 to M^3. For the M^1 it takes the form of a knob with two short arms, one of which points lingually, the other posteriorly to the anterior wing of the metaconule. In M^2 this conule has the form of an upside-down "L", while in the M^3 it changes into an upside-down "Y". In later deer the posterior wing of the protocone is constructed differently, consisting of two well formed ridges; the labial one stronger than the lingual one. E. Heintz called the labial ridge the protocone ridge proper, and the lingual one protocone-fold. It is opposite to what we observed in *Palaeomeryx*. The anterior wing of the metaconule does not reach the inner side of the mesostyle. The metaconule has a fine rib on its labial wall. Its posterior wing divides into two thin ridges at its posterior end. One stretches toward the metastyle, while the other, and smaller one, points to the base of the inner wall of the metacone. The cingulum is developed on the anterior and posterior sides. An entostyle is variably developed, but in general it is rather weak.

No complete lower incisors and canines are preserved. What left are only their roots. They are rod-like, and stand in a row tightly one after the other. There is no diastema between I_3 and the lower canine. Judging from the small part of the preserved crown, the lower canine seems to be single-cusped, not double-lobed, as in giraffids.

P_1 is present at least on three of these specimens. It is small, laterally compressed and single-cusped. A small diastema occus between it and P_2, not longer than 10 mm. In one specimen, LV 8003, P_1 stands close to P_2. On the type specimen only the posterior half of P_2 is still preserved, while in another specimen, LV 8003, only the outer wall can be seen. The protoconid, which is centrally situated, sends a low crest posterolingually. There is no metaconid, and the entoconulid-crest is not fully developed. The P_3 has three fully developed transverse crests. The crest, which connects the protoconid and metaconid, is diagonally oriented. The metaconid is poorly individualized from the crest, and is situated behind the protoconid. The posterior two crests are not strictly parallel: the entoconulid forms a curve, and approximates the entoconid at both its extremities. The valley between the two crests is shallow. P_4 resembles P_3 in structure, but it is larger. Its posterior two crests are parallel. The protoconid forms an independent crest, and there is a clear groove on the labial wall, just opposite the entoconid. An internal cingulum is present only before the metaconid, which is much better individualized.

The molars, except the third lobe of M_3, are structurally alike. The protoconid first connects with the metaconid, then through a tiny enamel tubercle with the posterior end of the paraconid. *Palaeomeryx*-fold is alway very well developed. The connections between the anterior ends of proto-and paraconid, and between the posterior ends of hypo- and metaconid are both very low, leaving gaps on the outer wall of the tooth. The former can not be seen owing to the overlapping by the preceding tooth, but the latter can be clearly seen from the side. The mesostylid is strong, and forms the most lingual point of the tooth. A weak cingulum is present on the anterior and posterior sides. The ectostylid is always present between the two lobes. The third lobe of M_3 takes the form of a horse-shoe, the inner arm of which is low and connects with the posterior end of the metaconid, while the labial arm goes to the middle of the posterior wall of the hypoconid.

No indication of the special prolongation of the neck is observed. The length of the seven associated cervical vertebrae is only about as long as the basial length of the skull. All the neural spines of cervical vertebrae II—VII are well developed and platelike, among which that of the axis is especially broad (antero-posteriorly), with the top strongly overhanging anteriorly. The thoracic vertebrae are 13 in number, lumbar vertebrae probably 6, the neural spines of which are broader than those of the cervical ones. The number of the caudal vertebrae is unknown, but it must be very short, probably extends not much beyond the posterior end of the pelvis. The humerus is shorter than scapula. The intermediate ridge on the distal articular surface of the humerus, seen from the front, stretches not vertically, but with its upper extremity turned laterally. The shaft of the ulna is thin, but fully preserved. Among the carpal bones there are only scaphoideum, magnum, triquetrum and pisiform, which are detached. Morphologically they are quite deer-like. McIII and IV are completely fused, with the central groove on the front face of the bone distally closed. McII and V are slender, but preserve their full length, and each with a complete set of phalanges. The proximal part of the two lateral metacarpals has shifted to the posterior side of McIII—IV, The hind limb is longer than the fore limb in general. The tibia longer than the femur. The metatarsals are similarly constructed to the metacarpals. The central groove on the frontal face of the canon bone is distally closed as well.

Discussion

For more than half a century after the erection of the genus most of the German language speaking paleontologists adhered von Meyer's original concept of the genus, that is, they lumped all species having the teeth with a *Palaeomeryx*-fold into the genus *Palaeomeryx*, regardless of the marked, sometimes even radical, differences in the "antlers" of these species. However, gradually a series of genera have been extracted from the overly lumped aggregation. These genera are, for example, *Amphitragulus* Pomel, 1846, *Dicrocerus* and *Micromeryx* Lartet, 1851, *Procervulus* Gaudary, 1878, *Prox* Hensel, 1859 (=*Euprox* Stehlin, 1928), *Lagomeryx* Roger, 1904 and *Heteroprox* Stehlin, 1928, among others, A historical review of the vicissitudes of these genera is given in the text in Chinese.

We adopted the conception of the genus proposed by L. Ginsburg and E. Heintz in 1966, with the only emendation that both Asia and Africa may well have their local representatives of the genus. According to the two French paleontologists, there are only three species: *P. kaupi* (=*P. bojani*, =*P. garsonini*), *P. magnus* (=*P. sansaniensis*) and *P. eminens* (=*P. nicoleti*). Since the Shanwang material provided for the first time so much reliable informations for the genus, it is desirable to give a revised diagnosis for the genus:

A primitive group of giraffoids. Size comparable with medium to large deer. Skull dolichocephalic, orbit central in position. Angle between the basicranial and the palatal surfaces almost 180°. Both preorbital fossa and ethmoidal vacuity present, one lacrimal oriface within the orbit. P_1 present in primitive species. Teeth brachyodont, strongly corrugated, with well developed cingulum and style (stylid) and paracone rib. Molarization of premolars low, transverse valleys seldom closed lingually. Posterior arm of protocone directed posteriorly, a prominent conule situated labially to it. Prominent *Palaeomeryx*-fold. Neck and limbs not specially elongated. Hind limb longer than foreleg. Canon bone with distally closed groove on dorsal face, its distal condyle with strong keel. Lateral metapodia (II & V) slender, but preserved full length, with full set of phalanges. Sexual dimorphism. A pair of orbital ossicones and an occipital bony " horn" as well as sabre-like upper canine in males.

The affinity, hence the systematic position of *Palaeomeryx*, as stated above, has been the subject of controversy. There are two main contradictory points of view, represented by L. Ginsburg and J. Leinders respectively. The former insists that *Palaeomeryx* should be included in Giraffoidea, while the latter argues that *Palaeomeryx* is a member of Cervoidea, and Giraffidae must be placed with the Bovidae. The reader, who is interested to know these points of view in detail, is referred to the papers written by L. Ginsburg and E. Heintz (1966) and by J. Leinders (1984).

The discovery of the *Palaeomeryx* skeletons in Shanwang contributes the following information to this problem:

1. The discovery has proved the correctness of Ginsburg and Heintz's attribution of a pair of ossicones to *Palaeomeryx*. The Shanwang material shows clearly that *Palaeomeryx* has ossicones of definitely giraffid type. The form, structure, position and the relationship of ossicones to the skull bones are all uniquely conformable with the ossicones of giraffids. What is more, an occipital bony "horn" has been found so far only in two ruminants forms: *Triceromeryx* and *Cranioceras* (*Procranioceras*). As to the affinity of *Triceromeryx,* the opinion is still controversial. However, its giraffid type of P_4 (Crusafont-Pairo, 1952, Pl. XIII) supports its inclusion in the lineage of giraffids. Unfortunately, the true nature of the American genus *Cranioceras* and its like is still not clear. The presence of giraffid ossicones in *Palaeomeryx* is Ginsburg's main argumentation for his inclusion of *Palaeomeryx* in Giraffoidea. In this respect our new discovery substantiates strongly his point of view. The extreme rarity of the occurrence of ossicones in the fossil record lies, at least partly, in the phenomen of sexual dimorphism.

2. The dolichocephaly, the central position of the orbit and the gentle bend of the cranium relative to the facial portion, which we observed in *Palaeomeryx tricornis,* may constitute a complex of correlated features, characteristic of the giraffids. In general the last two features are considered plesiomorphic for the Ruminantia. However, they are never combined with so long a skull as in *Palaeomeryx.* Therefore, the combination of the three features is probably to be considered as apomorphic for giraffids. Similar combination of features can be found, for example, in *Zarafa* (Hamilton, 1973, Pl. 2) and *Giraffokeryx* (Colbert, 1933, fig. 1), both genuine giraffids.

3. Contrary to Ginsburg and Heintz's assertion, *Palaeomeryx* does have an ethmoidal vacuity. Ginsburg and Heintz were not correct either, when they stated that giraffids are lacking this vacuity. In fact, not only in recent forms, *Okapi,* and sometimes *Giraffa* (for example, in one of the skulls in our institute), but also in fossil forms, *Zarafa* (Hamilton, 1973, p. 87), *Giraffokeryx* (Colbert, 1933, p. 7) and *Palaeotragus* (Bohlin, 1926, p. 11) may possess this vacuity as well. However, it is evidently a plesiomorphic character within the Pecora. It plays thus no role in deciding whether *Palaeomeryx* belongs to Giraffidae, or Cervidae or even Bovidae.

4. *Palaeomeryx* has one lacrimal orifice within the orbit. In this respect it is similar to Bovidae. However, from what we learned from the evolutionary trends in Cervoidea it can be safely deduced that the direction of transformation of this feature is from one orifice within the orbit to two orifices on the orbit margin. It is well known that the primitive Cervoidea always possess one orifice in the orbit, as in members of the Tragulidae, and even *Moschus,* but the true deer have only the second type of lacrimal orifices. So, again, the character is plesiomorphic.

5.. *Palaeomeryx* possesses a preorbital fossa and a sabre-like upper canine in males. The former is one of the characteristic features of the Cervoidea, while the latter is very common among the members of the group. Neither have been found in the Giraffidae, or Bovidae. The polarities of these two characters are unknown to us. Since

Cervidae, taken as a whole, is considered as an archaic group in Pecora, the above mentioned characters may well be retentions of plesiomorphic features.

6. The cheek teeth of *Palaeomeryx*, as indicated by Hamilton (1973, p. 94), are very similar to those of *Zarafa*. In fact, in morphology of the cheek teeth, *Zarafa* links *Palaeomeryx* with the later forms of Giraffidae so well, that Hamilton, after having described his *Zarafa* material, was convinced of the giraffid affinity of the genus *Palacomeryx*. However, later, based on the belief that these similarities in the cheek teeth were only of plesiomorphic features, he favoured the opinion that *Palaeomeryx* could be classified with Bovoidea (Hamilton, 1978). It seems to us that the similarities in the cheek teeth between *Palaeomeryx* and *Zarafa* are much more than those between *Palaeomeryx* and *Triceromeryx*, although many paleontologists were strongly impressed by the similarities between the latter two forms, when *Triceromeryx* was first described. We are inclined to believe that the common features of *Palaeomeryx* and *Zarafa* are not totally plesiomorphic. Some of them could be synapomorphies, for example, the extremely developed style (stylid) and ribs, and the prominent accessary conules labial to the posterior wing of protocone on the molars. They have never been so strongly developed in Cervidae, to say nothing of Bovidae.

7. The central groove on the dorsal face of canon bone is here distally closed, as in all advanced forms of deer. This is the main, and in fact the sole criterion, on which J. Leinders moved *Palaeomeryx* into the Cervidae. Leinders has never unequivocally deciphered the polarity of the character concerned. From the context one can see that he seems to consider the closed-groove as a derived character relative to the open one. The question rises: why he based his Bovoidea (=Giraffidae+Bovidae) on a plesiomorphic character (open-groove)? This led us to inquire in more detail into the problem relating to the polarity of the canon bones. The results are: (a) The polarity is from open-groove type to closed-groove one. This polarity is clearly demonstrated by the presence of open-groove type in the most primitive forms of deer, like *Gelocus* Kowalewsky, (1876—77, Tab. II, 19) and *Leptomeryx* (Matthew, 1908, fig. 9). Thus Leinders' Bovoidea (=Bovidae+Giraffidae) is based on plesiomorphic character (open-groove) and hence questionable. b) Although the closed-groove type is a derived character, it could be independently derived, through parallel evolution in different phyla within the Ruminantia. The Antilocapridae provide a good example in this respect. While the recent pronghorn has a closed-groove type canon bone, some primitive fossil forms may have an open-groove type, for example, the canon bones of *Merycodus* cf. *furcatus* (=*Cosoryx* (*Paracosoryx*) *furlongi*, Frick, 1937) are of open-groove type (Furlong, 1927, fig. 16). The identigfication of Furlong's material as belonging to a primitive form of Antilocapridae is irrefutable, because the skull, which was associated with the above mentioned foot bones, is evidently of antilocaprid affinity. The inevitable conclusion to be drawn from the foregoing statments is that, when Antilocapridae branched off from the general stem of Pecora, it must still have an open-groove canon bone, and then at some later time changed into the closed-groove type characteristic of the living pronghorn.

8. Our observations on postcranial skeletons reveal no principal differences between *Palaeomeryx* and the typical Cervidae. Some of the differences listed by Ginsburg and Heintz as characters shared with giraffids are untanable. Contrary to the

statment of Ginsburg and Heintz, the hind limb of *Palaeomeryx tricornis* is evidently longer than its forelimb. However, this should not present an obstacle to the linkage of *Palaeomeryx* with Giraffoidea, as the true giraffid, *Zarafa*, has no less deer-like postcranial bones than *Palaeomeryx*.

As a result, the available evidence is in favour of Ginsburg's point of view that *Palaeomeryx* may share more derived characters with giraffids than with cervids, to say nothing of bovids. At the same time it should be noted that *Palaeomeryx* must be very primitive, with many plesiomorphic characters shared with cervids. In this case the closed-groove type of the canon bones must be considered as the result of parallel evolution.

One of the consequences of the present hypothesis is the separation of giraffids from Leinder's Bovoidea. Judging from the evolutionary level of *Palaeomeryx*, it is to be inferred that the giraffids, *Palaeomeryx* included, originated after *Gelocus* and *Leptomeryx*, and before *Blastomeryx* and Eupecora in the sense of Webb and Taylor (1980).

In comparison with the European species, *Palaeomeryx tricornis* is comparable only with the small species, *P. kaupi*. The other two species. *P. magnus* and *P. eminens*, are much larger and more advanced than ours. The molarization of the premolars, especially P_4, in the two larger species is evidently higher than in ours. Unfortunately, *P. kaupi* has not been properly studied. At any rate the distinction between the Shanwang species and the European ones is clear. In none of the European species there exists a P_1, a primitive character of *Palaeomeryx tricornis*. Furthermore, the cingulum is generally weak in our form, while it is markedly developed in European species. It seems that the upper molars of the Shanwang specimens are proportionally wider. Probably there are also some differences in the form and size of the ossicones or "horns" between them. The only record of the ossicones, from Artenay (Ginsburg and Heintz, 1966), belongs most probably, to *P. kaupi*, because at that locality the only recorded species is *P. kaupi*. The above mentioned ossicones are proportionally slender at their bases. No occipital "horn" has been so far reported from Europe. These differences, it seems to us, warrant the separation of the new material as a new species: *Palaeomeryx tricornis*. sp. nov.

According to Ginsburg and Heintz, the European *Palaeomeryx* increased regularly in size, and this may serve as good indicator of geological age. In size our specimens are comparable to those from Pontlevoy (MN 5) and Baigneaux (MN 4b). Strictly speaking, our specimens are among the smaller of Pontlevoy material, but a little larger than those from Baigneaux. In case the Chinese form represents a separate lineage, different from its European relatives phylogenetically, its age may be older or younger.

Acknowledgments

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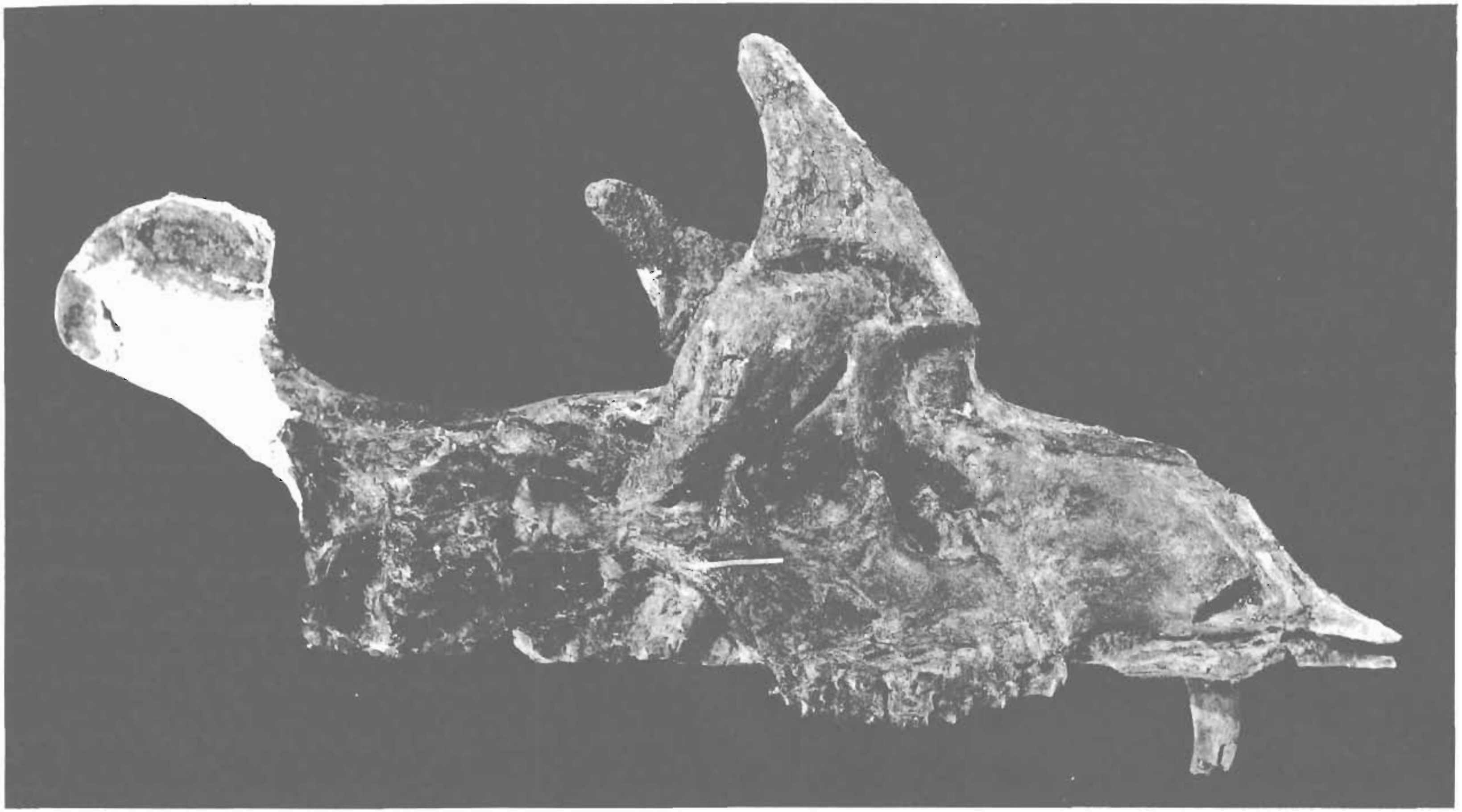
Palaeomeryx tricornis sp. nov. 头骨复原图



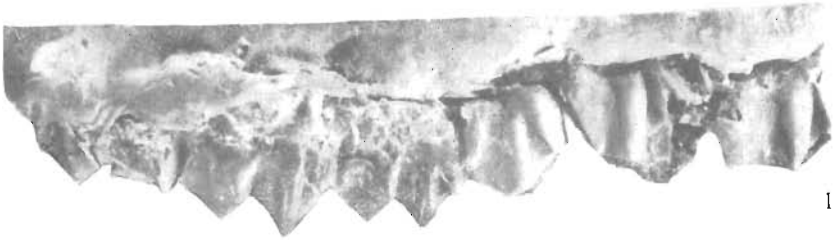
Palaeomeryx tricornis sp. nov. 头骨 v 7728，×1/2，雄性

***Palaeomeryx tricornis* sp. nov.**

完整骨架，雄性，840002 约 1/9

***Palaeomeryx tricornis* sp. nov.**

完整骨架，雌性，820831 约 1/9



1a

1

1b

2a

2

2b

***Palaeomeryx tricornis* sp. nov.** ×1

1. 右上齿列顶面观、 1a. 唇侧观， 1b. 舌侧观；
2. 右下齿列顶面观、 2a. 唇侧观， 2b. 舌侧观