figs. 1-6, p1. I-III

江苏泗洪下草湾中中新世脊椎动物群 ——8. Dorcatherium (Tragulidae, Artiodactyla)

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关键词 江苏泗洪 中中新世 鼷鹿

内 容 提 要

本文记述了江苏泗洪下草湾动物群中最常见的一种化石,羚鼷鹿 (Dorcatherium)。材料包括六段破碎颌骨、若干肢骨和四百余颗单个牙齿。根据齿冠低、上颊齿齿带弱、下臼齿 Σ 形结构清楚等特点,将它订为一新种:东方羚鼷鹿 (Dorcatherium orientale sp. nov.)。其地质时代大约相当于欧洲的 MN4。文中还讨论了鼷鹿科的分类问题,指出在牙齿构造上有三个类群: Dorcatherium, Dorcabune 和现生鼷鹿。

1983 年李传夔等在下草湾发掘报告的动物群名单中列举了羚鼷 鹿 (Dorcatherium) 的两个未定名种,所据材料是四段破碎颌骨和少量单个牙齿。此后,本文后一作者多次赴该地区工作,所采化石中最多的就是羚鼷鹿的牙齿。到目前为止,已修复的共有颌骨六段,完整的单个牙齿约 370 个,不完整的百余个以及十几块肢骨。这些化石中的绝大部分都发现于松林庄地点(见李传夔等,1983),只有极少数发现于郑集。郑集是 1983 年以后发现的一个新地点,它位于松林庄东北约两公里。其岩性和松林庄者相近,所产的鼷鹿化石也和松林庄者没有什么区别。所以这两个地点大约是同时代的。

研究中发现,1983 年根据少量材料划分的两个种,在材料大大增加后已不适宜了。我们注意到同位牙齿在大小和形态上的差异是相当显著的,但这些差异大多是连续的,而且其变化幅度均在现今生物种的变异范围之内(见后)。虽然个别牙齿形态特殊,但由于材料本身的局限(主要为单个牙齿),无法组成足以建立不同种的齿列。在这种情况下,只能把所有这些材料当作一个种来处理。材料的特殊性使记述的方法也不得不作相应的改变,即:按照牙齿定位的难易程度确定记述顺序并讨论其变异情况。

现生鼷鹿仅残存在东南亚和西非两地。但在欧洲中新世时曾繁盛一时,并且是生物 地层分带的标准化石之一。在亚洲,这类动物的化石发现很少,研究的程度也低。泗洪地 区羚鼷鹿丰富材料的发现表明,这类动物在亚洲也有自己的繁盛时期,并成为动物群中数 量上占优势的分子。这一发现对于研究亚洲和欧洲鼷鹿类的关系以及确定下草湾动物群 的时代都提供了新的资料。

本所韩德芬女士热情地向本文作者提供了她所收藏的中国和西瓦利克鼷鹿类的化石和模型。沈文龙同志绘图,张杰同志照相,本所计算机室帮助处理测量数据,在此一并致谢。

一、标本记述

1. 上臼齿(图版 I, 1-6; 图版 II, 1-2)

标本中有采自松林庄的两段上颌: 一段带 M²-M³ (图版 II, 2); 另一段带 DP⁴-M¹ (图版 II,1)。 从这两段上颌可以看到: 1) M¹ 较明显地小于 M² 和 M³, 它的前附尖更向前伸,使牙齿前缘不为直线状,而是外部向前突出。2) M³ 的后附尖较明显,有时甚至反卷向前,外后根经常斜向后方;相反,后小尖(有人称它为次尖)变小,使牙齿内缘后半部向外方退缩得更显著。3) 有些性状,或性状出现的频率是递变的。 例如原尖后脊自 M¹ 向 M³ 逐渐变长,末端常形成弯向外方的小钩。小钩的出现在 M³ 中较多。齿带,特别是内齿带前半部,自 M¹ 向 M³ 逐渐变强,在 M³ 中将原尖完全包围的情况较多。

根据上述区别,我们从松林庄的材料中区分出 63 个 M^1 (左 24, 右 39), 37 个 M^2 (左 15, 右 22) 和 13 个 M^3 (左 7, 右 6); 从郑集的材料中区分出右 M^1 和左 M^2 各一枚。

上臼齿的共同特征是: 1)低冠、丘一脊形齿。以齿冠最高的 M³ 为例,其未磨蚀的外壁的高仅为牙长的 2/3。这和丘形齿的 Dorcabune 的齿冠的高/长比例较接近,而与脊形齿的 Dorcatherium 相比则是较低的。例如我们根据 D. minus 的模型 (AMNH39865)算出的比是 4/5。四个主尖中只有前尖由于有膨大的外肋而呈锥形;后尖因外肋弱而呈半锥形;两个内侧尖都为脊形,其舌侧顶端较尖削,唇侧面上常出现小瘤状物(图版 I, 6)。原尖近一直角的 L 形,其后脊短,伸向后小尖前脊的中部,末端常向外弯曲成钩状。2)前、中附尖都很发育,在前尖肋之前有一深而窄的沟。中附尖低,锥形,随着磨蚀的加深,愈来愈比前附尖大,并成为外壁的最突出部。后附尖仅在 M³ 上较清楚(图版 I, 1,2)。3)珐琅质表面褶纹发育。4)齿带发育。但在本种中齿带是较弱的。原尖在内侧被齿带包围起来的情况,在 M¹ 中有 5 个,M² 中有 9 个,M³ 中 5 个。从出现的频率看,越往后越高: M¹ 为 8%,M² 为 25%,而 M³ 为38%。5)牙齿具三根:内根扁平并向内方斜伸,其舌面还有一纵沟将根分为前大后小的两部分。

2. 上前臼齿(图版 I, 7—12)

标本中没有保存在颌骨上的上前臼齿,因此只能根据形态确定其位置。

采自松林庄的 P⁴共 20 个(左、右各 10 个),采自郑集的左、右各一个。P⁴(图版 I,7—9,11)构造很特殊,容易鉴定。轮廓为一横宽的不对称三角形:内角较尖,后外角伸出较远。原尖的后脊不是伸向牙齿的后外角,而是伸向外侧主尖(前尖)的内后端。在磨蚀很轻的牙上可见有一短嵴自前尖内后壁向内伸出并与原尖后脊相连,磨蚀后则完全连成一脊。前尖肋形成外壁最隆凸处,其前方有一深沟。前附尖发育,后附尖弱。后齿带很发育,但变化大:有的完整,有的分为内、外两段,有的只有外半段(图 1)。

在归入 P⁴ 的牙齿中有一个构造相当特殊 (V9462.22,图 1,D;图版 I,8)。它的轮廓 近一正三角形,有一相当高的后附尖,后附尖之前有一深沟将其和主尖分隔。这使该牙在 外侧形成三个彼此分离的尖。原尖的后脊很靠前,其外端很靠近前尖。这使由前尖和原 尖所组成的中凹几乎全限在牙齿的前半部。后齿带粗大,但只有外半段。这颗牙齿的基本构造仍是鼷鹿的,而不是其它鹿类的。但它究竟是泗洪这个种的种内个体变异,抑或代表了另一个种的存在还很难断定。此外还有两个 P⁴,轮廓也是近于正三角形,但却没有 明显的后附尖。

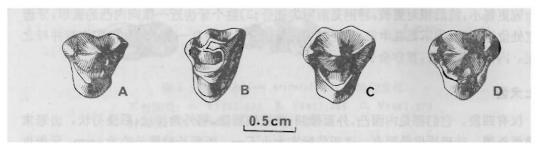


图 1 Dorcatherium orientale 的左 P⁴
A. V9462.23; B. V9462.24; C. V9462.25; D. V9462.22

P³ 共 13 个(左 7, 右 6; 图版 I, 10),均采自松林庄。轮廓近一扁长的等腰三角形。前尖位于外侧中央,明显地高大于前附尖,两者以一深沟相隔;后附尖不显著。原尖很低小,向内伸延的程度不一,但多数都很小,它的基本形态仍与 P⁴ 者同,但前脊已退化得与齿带无法区别,后脊更短小。后齿带低小,延伸至原尖后壁。齿根有三,内根通常最细小,位于内侧中央,有时与外后根差不多粗细,在一个牙齿上它与外后根完全愈合在一起。牙齿磨蚀最重的部分是后半部,常常形成宽大的磨平面,面向内后方。前半部磨蚀则主要在前附尖上。

有一个牙齿特别扁小,其原尖已完全消失,内齿带也不发育。但其基本形态仍是双根三尖形。鼷鹿类是没有 P^1 的,因此,这颗牙齿是羚鼷鹿的 P^1 的可能性很小。 从构造上看也不像是乳齿。它很可能是泗洪这个种变异较大的一个 P^2 。

3. 上乳齿(图版 II, 3,5,7,9)

按照 L. Rütimeyer (1883, P.16) 的意见,鼷鹿类乳齿的特征比恒齿还明显,它们的形态各异,区别起来并不困难。

 DP^4 共 25 个(左 16, 右 9; 图版 II, 3),均产自松林庄。形态和 M^1 几乎完全一样,但 更小些。它的前附尖比 M^1 的更向前突出,齿带发育弱,没有发现内齿带将原尖完全包围起来的情况。

DP³ 共 12 个(左 5, 右 7; 图版 II,5,7), 采自松林庄。形态很特殊。外侧由三个差不

多大小的尖组成,最前边的一个可以看作是膨大的前附尖,后面的两个分别是前尖和后尖,因为在它们之间有一中附尖,而在前尖肋之前也还可以看到不大深的窄沟。后小尖较小,V形脊的夹角较小而尖角的顶尖指向内后方。在后小尖和原尖之间有一凹缺,此凹缺在深浅上变化颇大。齿带的变化也大,在前附尖的内方有一细弱的齿带。内齿带向后可延伸至后小尖的前壁上,亦可呈瘤状断续发育。牙齿只有三根:前根、后外根和内中根。外侧中央通常无第四根,但在个别牙齿上此处有一小突起。

DP² 只有四枚(左、右各 2; 图版 II,9),均采自松林庄。它和 P² 相似,但有以下区别: 1)齿冠更低小,前后相对更长,特别是前附尖部分;2)整个牙齿近一微向内凸的弧形,牙齿最宽处位于后端,而不是在中部;3)在前尖内壁的前、后各有一条小嵴伸向内齿带并与之相连。内齿带较显著,贯穿全长。

4. 上犬齿

仅有四段。它们都是内面凸,外面微凹,前缘较圆隆,前外角棱状,后缘刃状,齿冠末端微微外翘。珐琅质仅外面有。这四件标本大小不一,断面长轴最长的为6mm,牙齿也显得粗短;断面长轴短者只有4mm,牙齿较细长。它们可能都是雄性犬齿。

5. 下臼齿(图版 II, 10; 图版 III, 1-6)

松林庄材料中有带 M_1 和 M_2 的下颌段(图版 II,10)。这使我们有可能将 M_1 和 M_2 区别开来。1) M_1 的尺寸较小。2) M_1 的前端更窄,整个牙齿更近一三角形;三角座凹窄小,前齿带在磨蚀轻时很向前突出。3) M_1 前齿根细小,断面近圆形,在外侧面中央有时有一退化的小根。根据这些差别我们区分出 25 个 M_1 (左 8,右 17),68 个 M_2 (左 32,右 36,其中 5 个采自郑集)。 M_3 共有 29 个(包括郑集的 2 个,左 18,右 11)。

下臼齿是鼷鹿类特征最明显的牙齿。 这主要表现在所谓的 Σ 形构造上(M. Mottl 称之为 M 形构造)。它是指在下臼齿第一和第二叶之间一种特殊的连接形式,即从下后 尖和下原尖的顶端向后各伸出两条脊,其中下原尖唇侧的一条脊与下次尖前脊相连;下后 尖舌侧的一条脊常游离;而中央相邻的两条脊在后端相汇并与下内尖的前脊相连(图 3)。 在泗洪的标本上这一 Σ 形构造表现得都很清楚,即使在磨蚀很重的情况下。除此之外,下 臼齿还有以下共同特征: 1)齿冠相对较低。从侧面看,中谷较深,低于冠面的一半;而前、后外的前、后缘都较缓。在内侧面由下后尖内、外两脊所夹之小三角形面(图 2),由于中谷 深而变得很低小。在高冠齿中此面则较高大。2) M_2 和 M_3 下次尖后脊相对较短,常常不

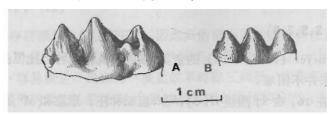


图 2 右 M₃ 内侧面之比较

- A. Dorcatherium minus (HGSP 16000, 哈佛大学模型);
- B. Dorcatherium orientale (V9462.273)

达下内尖即终止,使第二叶的后方在内面不封闭,留有一小的开口。3)下原尖的内壁和下内尖的外壁较平滑,没有 Dorcabune 属中常有的深沟。4)前、后齿带通常很突出,外中谷口有瘤状突起。

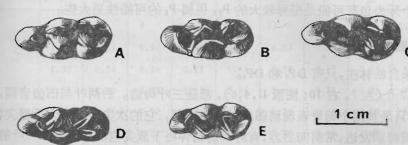


图 3 Dorcatherium orientale M, 跟座的变化 不封闭型: A. V9462.273 B. V9462.265 C. V9462.274 封闭型: D. V9462.266 E. V9462.275

M₃的跟座部分变化相当大。 基本上有两种型式: 跟座和第二叶间在舌侧封闭和不封闭。每种型式中次尖后脊的形态又有许多变化(图版 III, 3-6; 图 3)。

6. 下前臼齿(图版 III, 7-10)

P4 共 20 个(左、右各 10; 图版 III, 7,8),采自松林庄。鼷鹿类 P4 最显著的特征是在主尖之后有一长而深的中沟。此中沟后端弯向内侧并在牙齿的内侧面后端形成 一个 开口。沟外侧的脊形态变化较大:有的分为两段,在外壁上形成一条沟;有的在内壁上形成一个突起使纵沟在中部收缩(图 4)。下前附尖相当大,脊状,斜向前内方,与主尖之间在内侧以一深谷相隔。自外侧看,前附尖只比主尖前缘的最低点稍高一点。主尖高耸,其外壁后方有一纵沟,沟的基部前方常有瘤状齿带。

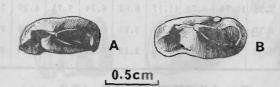


图 4 Dorcatherium orientale 的右 P₄
A. V9462.179; B. V9462.180

P₃ 共 7 个(左 3, 右 4; 图版 III, 9), 采自松林庄。P₃ 在比例上比P₄ 更细长, 为两根三 尖形齿。前附尖与P₄ 者接近, 但稍小。主尖明显地低于P₄ 者。内、外壁上将主尖和主尖 以后部分分开的纵沟短浅。后附尖则比P₄ 者更明显。从侧面看, 三尖分得较清楚。自后 附尖顶端伸出两脊: 一条伸向内后方; 另一条先伸向后再转向内。两脊间夹一凹面, 此凹 面向内方开口。这一凹面大体上与P₄ 主尖后的中沟相当, 只是更短小。齿带不发育。

P₂6个(左 4, 右 2; 图版 III,10),采自松林庄。P₂只有两个尖: 主尖前脊相当长,其前端稍稍向内弯曲,但不形成独立的前附尖;后附尖部分与P₃者相近,只是更小,其脊和

凹表现得更弱。

 $?P_1$ 3 个(左 1, 右 2), 采自松林庄。形态与 P_2 同, 仍是双根双尖齿, 但更小。后附尖部分的两脊和小凹几乎完全消失。 *Dorcatherium* 属中确实有 P_1 双根的(见 C. Aramburg, 1933), 这三个牙齿也有可能是变异较大的 P_2 , 但属 P_1 的可能性更大些。

7. 下乳齿(图版 II,4,6,8)

乳齿全采自松林庄,只有 DP3 和 DP40

DP4 共 17 个(左 7, 右 10; 图版 II,4,6),都是三叶构造。后两叶与臼齿者同,具清楚的 Σ 形构造,只是其两个侧脊表现稍弱。与臼齿不同,它的次尖显著地大于原尖;它们之间的外齿带瘤特别发达,常斜向后方,有时向前延伸将下原尖包围起来。第一叶的两个尖中内侧者大,大小接近其后的下后尖和下内尖,形态也接近,都是扁长形;外侧的一个和下原尖相近,而小于下次尖。外侧第一和第二谷之间也常见不规则的瘤状或脊状的齿带。无内齿带,但在牙齿的前外角和后缘有齿带。齿根三个,中间的一个很小,位于外侧中央。

 DP_3 共 9 个(左 5, 右 4; 图版 II,8)。它是所有牙齿中最细弱的。 具双根和大体等长的三个齿尖。前附尖是最小的一个,前端偏向内侧。主尖内后方有一弱沟,主尖的后脊高,与后附尖的前脊相连。后附尖向内及后方各伸出一脊。它的后半部很像 P_3 者,但更细弱。在后附尖外壁的后方有时还可见到一附属小脊。齿带仅在牙齿前外角 和 后 缘 发

	UP2		UP3		UP4		UM1		UM2		UM3	
	长	宽	长	宽	长	宽	长	宽	长	宽	长	宽
n	8	8	12	12	19	20	61	60	33	33	11	11
X	7.58	3.36	7.18	5.01	6.48	6.94	7.18	8.74	8.06	10.05	8.09	10.32
SD	0.71	0.36	0.34	0.59	0.39	0.44	0.41	0.55	0.48	0.65	0.34	0.56
V	9.36	10.71	4.74	11.77	6.02	6.34	5.71	6.29	5.96	6.47	4.20	5.43
Range 最小值	6.10	2.68	6.48	3.77	5.85	6.14	6.30	7.70	7.20	8.90	7.35	9.56
最大值	8.20	3.80	7.80	5.80	7.10	7.72	8.06	10.24	9.60	11.67	8.58	11.12

表 1 东方羚鼷鹿上颊齿测量 (单位: mm)

表 2 东方羚鼷鹿下颊齿测量	(単位:	mm))
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	L	P1	LI	2	LI	23	LI	24	L	Mi	LN	M 2	LM3	
	长	宽	长	宽	长	宽	长	宽	长	宽	长	宽	长	宽
n	4	4	6	6	5	7	16	17	24	24	54	54	17	17
x	5.76	2.23	6.43	2.76	7.44	3.01	7.64	3.54	7.33	4.59	8.39	5.39.	11.94	5.50
SD	0.67	0.24	0.67	0.24	0.52	0.17	0.60	0.30	0.40	0.43	0.54	0.44	1.14	0.33
	11.63	10.76	10.42	8.70	6.99	5.65	7.85	8.47	5.46	9.37	6.44	8.16	9.55	6.00
Range 最小值	5.10	2.02	5.42	2.50	6.46	2.77	6.80	3.16	6.64	4.00	7.18	4.52	8.33	4.98
最大值	6.34	2.65	7.44	3.14	8.00	3.30	9.10	4.20	8.20	5.52	9.66	6.72	13.08	6.20

	· UDP2		UDP3		UI	DP4	LD	P3	LDP4	
	长	宽	长	宽	长	宽	K	宽	长	宽
n	4	4	9	12	22	21	6	6	16	15
X	7.65	3.01	8.30	4.98	6.88	6.97	7.37	2.39	9.25	3.96
SD	0.37	0.34	0.24	0.27	0.41	0.39	0.47	0.15	0.71	0.34
V	4.84	11.30	2.89	5.42	5.96	5.60	6.38	6.28	7.68	8.59
Range 最小值	7.12	2.54	7.82	4.70	6.10	6.24	6.75	2.22	8.10	3.00
最大值	7.92	3.36	8.72	5.44	7.74	7.56	8.12	2.60	10.82	4.42

表3 东方羚鼷鹿乳颊齿测量 (单位: mm)

育,很细弱。

在一件带有 DP_3 的下颌残段上还保留着 DP_2 的一个齿槽。 鼷鹿类 的 DP_2 和 DP_3 很难区分。上述牙齿中也许就有 DP_2 。

8. 肢骨

鼷鹿类的肢骨有些是特征相当明显的。从松林庄的不多的肢骨材料中发现以下几块 是可以归入鼷鹿类的:

距骨:两个左侧者,都保存不完整。它的近、远端两滑车的轴线不互相平行:近端滑车的轴线斜向外下方。近端滑车的内脊细,而脊间凹开阔。载距面横向凹。近端滑车外脊的外光滑面小,附着短外侧韧带的凹坑位置低。这些特征都和我们用于比较的*Tragulus*的距骨一致。

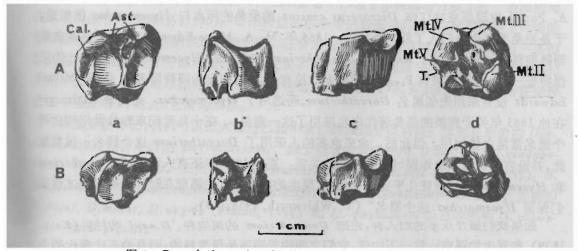


图 5 Dorcatherium orientale V9462.375(A) 与 Tragulus sp.IVPP 1433(B) 的舟一骰一外楔骨比较

a. 顶面; b. 外侧面; c. 背面; d. 底面 T. 腓长肌腱沟 (Groove for the M. peroneus longus tendon)

舟一骰一外楔骨(图 5): 两个右侧者。这三块跗骨愈合在一起是鼷鹿类最显著的特征。和 Tragulus 的一样,它的近端与跟骨关节的面几乎完全转到了前面,其前端形成一个深窝,而且向下延伸得很低。远端与 MtV 关节的小面有两个: 一个紧挨在与 MtIV 关节面之后;另一个则位于腓长肌腱沟之后。这样,腓长肌腱是从 MtV 近端上方通过的,而不像在其它鹿类中那样,是穿过 MtIV 和 MtV 之间的。远端与 MtIII 和 MtIV 的关节面相对较小,面的波曲度大。但是与现生 Tragulus 者相比,松林庄的标本也有些不同之处。首先,它尺寸较大,相对较高而厚;它的与 MtII 相关节的小面较大,但腓长肌腱沟却较浅,外侧面上仅隐约可见。

此外还有几个第二指节骨和蹄骨。它们的关节面都比较短宽。蹄骨的远端面横向凹,其近中和远中侧不象后期鹿类中那样不对称,表明了第三、第四趾的蹄骨不那样镜面对称。

二、比较与讨论

1. 关于化石鼷鹿的分类问题

鼷鹿科现今仅包含五个属。 两个现生属: 西非的 Hyaemoschus 和东南亚的 Tragulus 及三个化石属: Dorcatherium, Dorcabune 和 Yunnanotherium。 在属一级分类上的问题主要是: Dorcatherium 和 Hyaemoschus 究竟是什么关系? 它们是否是同物异名? 以及 Dorcabune 是否是一个独立的属?

Dorcatherium 这个属现在都认为是 J.J.Kaup 于 1833 年创建的。实际上 Kaup 对这个属的描述和图版直到 1839 年才问世。但是早在 1834 年 H. von Meyer 就引用了这个属名,而且记述了它的主要特征。当创建这个属时,人们对现生鼷鹿的特殊性还不了解。Tragulus 和 Hyaemoschus 是 J.E.Gray 分别于 1836 年和 1843 年建立的。1851年 A. Pomel 发现原来被订作 Dicrocerus crassus 的桑桑的标本与 Hyaemoschus 很相近,于是把桑桑这个种归入了后一个属中。1864 年 M. A. Milne-Edwards 在创立并系统整理鼷鹿科的材料时指出,Kaup 的 Dorcatherium 和桑桑的 Hyaemoschus crassus 的牙齿特征一致,只是前者有 P₁,而后者大多数没有 P₁。它们应为同物异名。 但 是 Milne-Edwards 没有采用先创属名 Dorcatherium,而选用了 Hyaemoschus。此后 R. Rütimeyer 在他 1883 年关于鹿类的经典著作中也采用了这一意见。 在十九世纪末和廿世纪初这两个属名常常交替使用。但此后,愈来愈多的人采用了 Dorcatherium 这个属名。虽然如此,并没有人认真系统地探讨它们之间的关系。直到 1958 年还有人说:"Dorcatherium 和 Hyaemoschus 的特征几乎完全一致","现生的和中新世的鼷鹿在时间上的隔离才使我们保留 Hyaemoschus 这个属名" (T. Whitworth, 1958, p.3)。

如果我们撇开众多的归人种,先把 Dorcatherium 的属型种, D.naui 的材料(Kaup, 1839)和现生的鼷鹿比较一下的话,它们之间的差别还是很清楚的,而且绝不比现生两个属之间的差别小。这些差别是: 1)化石属的眶后部分明显拉长而且向后下方倾斜显著。2)化石属的鼻骨更长,其后端距眼眶前缘很近,而且后端向上翘起,使鼻一额缝处形成坎状下降。3)化石属的下颌水平枝向后明显变高,其下缘最隆处位于 M₃ 之后,而不是在 M₂

下方。4)化石属虽然较大,但齿冠相对较低。这从外侧面看得更清楚。在化石属中外肋及附尖都为锥形,亦即近根部加宽;而在现生属中它们都是柱形,上、下接近等宽。5)化石属下臼齿的 Σ 形构造特别清楚,至磨蚀相当深时仍清楚;在现生属中 Σ 形构造稍经磨蚀就变得模糊不清了。这也是为什么这一 Σ 形构造首先是从化石材料中发现,而在现生属中反而发现得晚的原因。6)化石属上牙的前尖肋和中附尖都特别粗壮,原尖V形脊的后支更多地向后伸,这使原尖和后小尖两个V形脊在形态上差别较大;在现生属中前尖肋和中附尖细窄,原尖和后小尖两个V形脊形态差别不大。7)化石属牙齿上的齿带通常很发育,在上牙中常将原尖包围起来,在下牙的外谷基部则有瘤状突起。8)化石属中常有 P_1 ,现生属中无。

Dorcabune 是 G.E. Pilgrim 1910 年根据西瓦利克的化石建立的一个属。它的主要特征是齿尖强烈丘形。从形式上看,没有什么人反对这个属的独立性。实际上在欧洲人们只承认 Dorcatherium,把一些明显是丘形齿的种都归入了这个属。最近 Mottl(1961)已经提出了欧洲存在着两个鼷鹿的支系的可能。她指出,欧洲最早出现的 Dorcatherium guntianum (MN4)已具进步型的 Σ 型结构,而稍晚些的 D.crassum (MN5)的 Σ 形构造还是原始型的:即脊的连结不完全。V. Falbusch (1985)则进一步把 D.crassum 与典型的丘形齿的种,例如 D.peneckei 等从系统上联系起来。与此同时还有以属型种 D.naui为代表的脊形齿的一支,但是他们都没有采用 Dorcabune 这个属名。我们在研究了上述有关种之后,认为这两个支系的后期类型区别很显著,但早期类型则很接近,不大容易区分。尽管如此,它们是并行存在的,代表了不同的进化方向,因此也应该划分为不同的属。

根据我们的观察,这两个属的区别如下: 1) 丘形齿者同时齿冠也低而且比例上较短宽。以 M_3 为例,其宽总是长的一半以上,而在脊形齿者,宽则小于长的一半。2)丘形齿的上臼齿有几乎与前尖肋一样粗壮的后尖肋,上内和下外齿带都很粗壮;在脊形齿者中后尖肋几乎不发育,齿带也相对较细弱。3) 丘形齿者下臼齿下原尖的前脊由于有一条深沟而变成了两条脊(见韩德芬,1986)。 Σ 形构造的两条中央脊先自行交会,然后再与下内尖的前脊相连,而两条侧脊则相对较短而弱。在脊形齿者中在下原尖舌侧的前端只有一条很浅的沟,所以前脊并不分成两条;两条中央脊不先行交汇,而直接与下内尖前脊相连接。4) 在丘形齿者中,除在最原始的种类 (MN5) 中还有单根的 P_1 外,其余的均无 P_1 ,而在脊形齿者中总是有 P_1 的,而且常为双根。

根据上述特征,我们可以把大部分已知中新世的鼷鹿分成两类: 低冠丘形齿的 Dorcabune 和高冠脊形齿的 Dorcatherium。 属于前者的有欧洲的 D.crassus, D.vindobonensis 和 D. peneckei, 亚洲的 D. anthracotheroides, D. nagrii (Pilgrim, 1951), D. progressus 和 D. liuchengensis; 属于后者的有欧洲的 D.guntianum, D. naui, 亚洲的 D.majus, D.minus, D.nagrii (Prasad, 1968) 和 D. puyhauberi 以及非洲的 D. chauppuisi 和 D.pigotti。

还有几个种似乎很难归入上述任何一个属。D. parvum 是非洲早中新世的一个种。根据 Whitworth 的记述,它的个体特别小,下颌水平支特别低小,下臼齿 Σ 形构造的侧脊都很弱,无外谷齿柱,齿尖脊形,齿冠较高。这些特征和现生鼷鹿很一致。D. songhorensis

也是非洲早中新世的一个种。 如果 Whitworth(1958) 的插图 7 是正确的,它也是没有真正的 Σ 形构造的。 D.minimus 是最近从西瓦利克地层中发现的,材料只有一个 M^3 。这是目前所知最小的一个种。它的前附尖和前尖肋都很细窄,齿尖为脊形,也没有将原尖包围起来的内齿带。最近韩德芬记述的产自禄丰古猿地点的 Yunnanotherium 的下臼齿也是高冠, Σ 形构造发育不完全(图 6)。上述这些种使我们相信,除了 D or cabune 和 D or catherium 之外,还有另一个与现生鼷鹿形态更接近,系统上可能也更直接有关的支系:其个体都很小,齿冠相当高,而 Σ 形构造发育不甚完全。 Yunnanotherium 是这一支系的一个属。非洲的那两个种是否也应该归入这个属,还需要更多材料的证实。

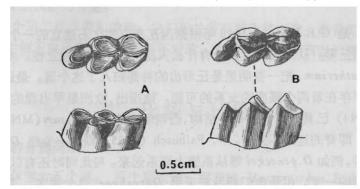


图 6 Tragulus sp. IVPP1433(A) 和 Yunnanosherium simplex V8134.1(B)的右 M, 上,冠面视; 下,外侧视

2. 泗洪鼷鹿的分类地位

我们在本文的开头已经指出过,泗洪鼷鹿的牙齿在大小上差异是相当显著的。测量表也清楚地显示了这一点:它们的变异系数的范围是 2.88-11.77,均值是 7.32。我们没有鼷鹿方面现成的资料可供对比。 H. S. Pearson 1928 年曾引用了古埃及部落一个墓葬居群牙齿测量的资料,其变异系数范围为 5-12.5。这表明,从统计学的观点看,泗洪鼷鹿牙齿大小的变异仍在种的范围之内。此外,从表中可以得知,变异较大的主要是前边的牙齿,即 P^{2-3} 和 DP^2 以及 P_1-P_2 ,其余牙齿的变异系数大体都在 5-6 之间。 在鹿类中前边的前臼齿处于退化的过程之中,变化较大也是可以理解的。

从形态上看,泗洪这些材料无疑应该归入 Dorcatherium 这个属。它们的粗壮 的下颌,下臼齿上清楚的 Σ 形构造,外中谷的瘤状突以及上牙中特别粗壮的前附尖和前尖肋(后尖肋很弱) 等都说明了这一点。在这个属中在大小和形态上与泗洪标本最接近的是发现于印巴次大陆的 Dorcatherium nagrii 和欧洲的 Dorcatherium guntianum。 泗洪这个种比欧洲的这个种个体更小,上臼齿内齿带发育得细弱,而且 P_1 是双根的。Colbert 1935年记述的 Dorcatherium sp.,在大小和形态上都和泗洪的标本很接近,遗憾的是材料太少。1980年 R.M. West 把它归入了 Prasad 1968年订的 Dorcatherium nagrii 中。但是 Prasad 的材料比泗洪的还小,而且 Prasad 的材料比泗洪的还小,而且 Prasad 的大于宽 Prasad 的材料比泗洪的还小,而且 Prasad 的材料是否应该属于 Prasad 还不得而知。在这种情况下,我们建议将泗洪的材料定一新种:Prasad Prasad Prasad

Tragulidae Milne-Edwards, 1864 Dorcatherium Kaup, 1833 Dorcatherium orientale sp. nov.

正型 左下颌带 M₂-M₃, V9462.281。

众型 共约 370 个牙齿及少量肢骨。

特征 个体比 D.guntianum 还稍小些。颊齿低冠,上臼齿内齿带发育弱。将原尖包围的频率低。 P_1 具双根,下臼齿 Σ 形构造清楚。

地理及地史分布 目前仅发现于江苏泗洪。这很可能是鼷鹿类在东亚发现的最北的一个地点。 考虑到欧洲的 D. guntianum 是从 MN4 开始出现的,而泗洪这个种在进化水平上大体与它相当,因此,松林庄和郑集这个种的地质时大概也应该与此相当,即相当于欧洲生物地层划分的 MN4。

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THE ARAGONIAN VERTEBRATE FAUNA OF XIACAOWAN, JIANGSU ——8. DORCATHERIUM (TRAGULIDAE, ARTIODACTYLA)

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Summary

Key words Sihong, Jiangsu; Middle Miocene; Dorcatherium

In their preliminary report on the Xiacaowan vertebrate fauna in 1983, Li Chuankui et al. listed two unnamed *Dorcatherium* species, based on 4 jaw fragments and a few isolated teeth. Since then, the junior author of the present paper has intermittently visited this site with the aim to collect as many fossils as possible. As a result, she not only succeeded in finding rich material from the most fossiliferous site, Songlinzhuang, but also collected some specimens from Zhengji, a new locality, about 2 km northeast to the first site. Now the specimens identified as belonging to *Dorcatherium* amount to 6 jaw fragments, 370 isolated teeth, about one hundred fragmentary teeth and some foot bones. They are the most frequently uncountered fossils in the Xiacaowan fauna, and *Dorcatherium*, therefore, seems to be the most representative animal of that fauna.

Detailed study of the sample does not seem to favour the viewpoint of Li et al. that there existed two *Dorcatherium* species. We failed to find a way to further divide the sample into groups. In the following we deal with the whole sample as of one species and describe the teeth in an order from the teeth whose loci determination is more reliable to the teeth whose loci are less certain, since the majority of the teeth are isolated ones.

Description

1. Upper molars

There are altogether 64 M¹, 38 M² and 13 M³. Their identification is based on two jaw fragments with DP⁴-M¹ and M²⁻³ respectively. The three upper molars differ from each other slightly in morphology. The M¹ is smaller than the other two teeth, but with a more forward projecting parastyle, while the M³ is characterized by a pronounced metastyle, often a little forward curved, and by a reduced metaconule (or hypocone) crescent. In addition, from M¹ to M³ the posterior arm of the protocone crescent becomes gradually longer and often turns outward at its end. The cingulum becomes stronger and also occurs more frequently. However, as a whole the three upper molars are quite characteristic in morphology and share the following common features. 1) They are low-crowned and buno-selenodont teeth. The height of M³, which is the most high-crowned among the three, is only about 2/3 of its length. Owing to the presence of a strong rib, the paracone takes a form of a cone but all the other three are crescentic in shape. 2) The protocone crescent is approximately L-shaped, i.e. its posterior

arm is short and perpendicular to its anterior half. 3) The parastyle and mesostyle are well developed, the latter of which is pyramid in shape, with a wide base. In front of the well developed paracone rib there is a deep and narrow groove. 4) As a rule, the crown surface is strongly wrinkled, particularly the labial surface of the protocone crescent. 5) In comparison with other species, the cingulum of the present species is to be considered as weakly developed. The complete encircling of the protocone by the inner cingulum occurs here apparently less frequently than in other species. In M¹ it is only 8%, for M²: 25% and for M³: 38%. 6) Each tooth is supported by three roots: one inner and two external. The inner root inclines mesially and is subdivided by a marked groove on lingual side into a wide anterior and a narrow posterior part.

2. Upper premolars

The upper premolars in tragulids are easily distinguished by their differences in morphology. There are altogether 22 P⁴, 13 P³ and 8 P².

The P⁴ is triangular in form. The paracone rib forms the most projecting part of the external wall. As in molars, in front of it there is a deep and narrow groove. The parastyle is better developed than the metastyle. The protocone is crescentic in form. Its posterior arm stretches not to the very post-external corner of the tooth, but a little anterior to it. The posterior cingulum is generally well developed, but varies considerably in strength (see text fig. 1). One P⁴ (V 9462.22) is quite unusual in structure. It has a remarkable metastyle, bordered by a deep groove anteriorly. The posterior arm of the protocone is rather anteriorly situated, making the inner half of the tooth rather unsymmetric. The posterior cingulum is strong, but limited in external half of the tooth. It is difficult for us to erect a new species for it, unless we know it better through its combination with teeth demonstrating similar or equally distinctive features.

The P³ differs from P⁴ by its strongly reduced protocone. However, the reduction varies from specimen to specimen. Sometimes, the protocone is no more than an enlarged cingulum, but sometime, it remains still rather large. The tooth is supported by three roots. In only one tooth the inner root is coalesced with the post-external one. The P² is further smaller than P³. It is supported by only two roots. Occasionally, a rudiment of the third root, the inner one, can be seen. The protocone is further reduced.

3. Upper milk teeth

The sample contains 25 DP⁴, 12 DP³ and 4 DP². The DP⁴ is fully molariform, but smaller than M¹ in size and with a more protruding parastyle. The DP³ is rather unusually constructed. Labially it has three cusps: a smaller parastyle and two equally big paracone and metacone. Between the latter two cones there is still a small mesostyle. There is a pronounced V-shaped metaconule (or hypocone) crescent situated lingual to the metacone. In front of the metaconule the tooth narrows down abruptly. The parastyle and paracone seem to be encircled only by a lingual cingulum. The tooth has usually only three roots: the anterior, the post-external and the inner one. Occasionally a small rudiment of the fourth root can be seen between the two external ones. The DP² is similar to P² in form, with the following distinctions. It is more low-crowned and longer proportionally. The tooth is a little concave externally and the inner wall of the paracone is provided with two fine ridges and a rather continuous cingulum.

4. Upper canines

There are four pieces of canines referred to that species. Their commonly shared characters are the convex inner, but concave outer surfaces, the blunt anterior, but sharp posterior

edges. The longest piece is only 22mm long. The maximum length of their cross-section is only about 6mm.

5. Lower molars

The M₃ is readily distinguished from the other molars by its presence of a third lobe. The M₁ is similar to M₂ in morphology, but smaller in size. In addition, its anterior part is narrower, supported by smaller anterior root. The sample contains 25 M1, 68 M2 and 29 M3. They all have the so-called Σ structure (Mottl calls it M structure), remarkably demonstrated even in considerably worn teeth. The other common features shared by these teeth are: 1) They are comparatively low-crowned, just as the uppers. This can easily be seen from the inner side (see text fig. 2). 2) The posterior arm of the hypolophid is comparatively short, often without reaching or connecting the endoconid, leaving a cleft between the second and the third lobes lingually. 3) The grooves on the anterior half of the lingual wall of the protoconid and on the posterior half of the labial wall of the endoconid, which are generally well developed in Dorcabune, are hardly discernible. 4) The cingulum is generally well developed. The anterior and posterior cingula are always quite pronounced. The external cingulum, often in form of tubercles, exists in the valleys between the lobes. The talonid of the M₃ varies considerably in form and structure. Basically there are two types: talonid directly connecting with the endoconid lingually and talonid leaving a cleft between the second lobe and the talonid lingually (see text fig. 3).

6. Lower premolars

We have found 20 P₄, 7 P₃, 6 P₂ and 3?P₁. The identification of P₂ and P₁ can not be considered as fully reliable for the reason that they are not quite distinctive in morphology.

The P₄ is very characteristic by its long posterior valley bordered by a labial and a lingual ridge. The valley opens postlingually, leaving a small cleft at the posterior end of the tooth. The labial ridge of the groove is longer than its lingual counterpart and sometimes subdivided into two parts (see text fig. 4). The paraconid is prominent, clearly separated from the main cusp by a lingual groove. Tubercles may be present at the base of the above mentioned groove and somewhere behind the main cusp on the labial side. The P₃ is more slender than P₄. It is a three-cusped tooth, but the central main cusp is much lower than that of P₄. However, its metastylid is larger than that of P₄. From the top of the metastylid two small ridges descend posteriorly and lingually gespectively. It reminds us of the valley-ridges structure in P₄. The P₂ has only two cusps. The paraconid is reduced to a rudiment. Otherwise it is similar to the P₃, but smaller in size. The P₁ is similar to P₂ in morphology, but smaller in size. It is a two-cusped tooth supported by two roots.

7. Lower milk teeth

Among the lower milk teeth there are 17 DP₄ and 9 DP₃. As in all the other cervids, Dor-catherium has a tri-partite DP₄. The two posterior pairs of the lophids are apparently homolongous with those of the lower molars and with clearly shown Σ structure. The anteriormost pair of the lophids is an addition to the normal structure. On the bottom of the valley between the two lophids there exist always irregular tubercles. The DP₃ is the most slender among the cheek teeth. It is a three-cusped tooth, similar to P₃ in morphology.

8. Postcranial skeleton

A few skeleton bones have been found together with the above mentioned teeth. Among .

them are 2 astragala, 2 cubo-naviculo-ectocuneiform bones and several phalanges. The astragala are not perfectly preserved, but show the characteristic features of the Tragulidae. These are the horizontally concave sustentacular facet, the slanting proximal pulley in relation to its distal block and the low position of the attachment scar for the ligamentum laterale etc. Another tarsal bone characteristic of the Tragulidae is the fused bone of the cuboid, navicular and ectocuneiform. In common with those in extant tragulids, our specimens show the following:

1) The articulation facet for calcaneum faces rather anteriorly than upwards, stretches considerably downward and forms a rather deep fossa at its anterior and lower end. 2) The articulation facet for MtV is separated by the transverse groove for the tendon of the M. peroneus longus. 3) the articulation facets for MtIII and MtIV are comparatively small and not very flattened. However, our new specimens are bigger in size, especially higher and thicker in proportion. The articulation facet for MtII seems here to be larger and the groove for the tendon of the long peroneous muscle is much shallower, without clear indication on lateral side (see text fig. 5)

Comparison and Discussion

As far as the classification of the Tragulidae at the generic level is concerned, two problems seem to be especially critical for any further discussion. 1) Whether *Dorcatherium* is a valid genus, in other word, whether it is the synonym of the extant *Hyaemoschus*. 2) Whether *Dorcabune* is a valid genus, or is it only a junior synonym of *Dorcatherium*.

Dorcatherium was generally considered to have been erected by J. J. Kaup in 1833. As far as we know, detailed description and figures had not been made available until 1839. However, since H. von Meyer cited it as early as 1834, Kaup's priority has never been seriously challenged. The originality of the extant tragulids had not been recognized untill J. E. Gray erected Tragulus and Hyaemoschus in 1836 and 1843 respectively. In 1851 A. Pomel found that the specimens originally referred to Dicrocerus crassus from Sansan were quite similar to Hyaemoschus and hence referred this species to Hyaemoschus. While systematically revising the tragulids in 1864, M. A. Milne-Edwards pointed out the overall similarity between Kaup's Dorcatherium and Pomel's Hyaemoschus crassus. It is a pity that Milne-Edwards preferred Hyaemoschus to Dorcatherium. Later in 1883, L. Rütimeyer adopted this point of view in his classical treatise on the cervids in general. For a long time since then the two genus names have been indifferently used. As late as in 1958, T. Whitworth still maintained that "The diagnosis of Dorcatherium, when thus emended, agrees almost exactly with that of Hyaemoschus" and "the recent and Miocene tragulids are sufficently isolated in time to warrant the retention of the generic name, Hyaemoschus."

If we compare the type specimens of the type species of the fossil genus, Dorcatherium naui, with the extant Hyaemoschus, striking differences can easily be observed. To list just a few of them. 1) The cranial part of the skull posterior to the orbit is much lengthened and bends more downwards in Dorcatherium than in the extant genus. 2) The nasal bones in the fossil genus are much longer, approaching the level of the orbit and raising stepwise at their posterior end, while in the extant genus they are short and flat. 3) The horizontal ramus of the lower jaw in the fossil genus is robust, the most convex part of its lower border is behind the Ms, while in the extant genus it is slender and the most convex point lies under the Ms. 4) In the former the teeth are low-crowned, with the ribs and styles rapidly widening in the direction to roots. In the latter the teeth are more high-crowned and their ribs and styles are more

or less pilar-shaped. 5) In the former the Σ structure in the lower cheek teeth is much more clearly shown than in the latter. 6) In the extant genus the teeth are generally more selenodont and with weaker cingulum than in the fossil genus. 7) In the extant genus no P_1 has ever been found, while in the fossil genus it is present as a rule. The foregoing comparison renders it convincing enough to separate them into two genera rather than lump them into one.

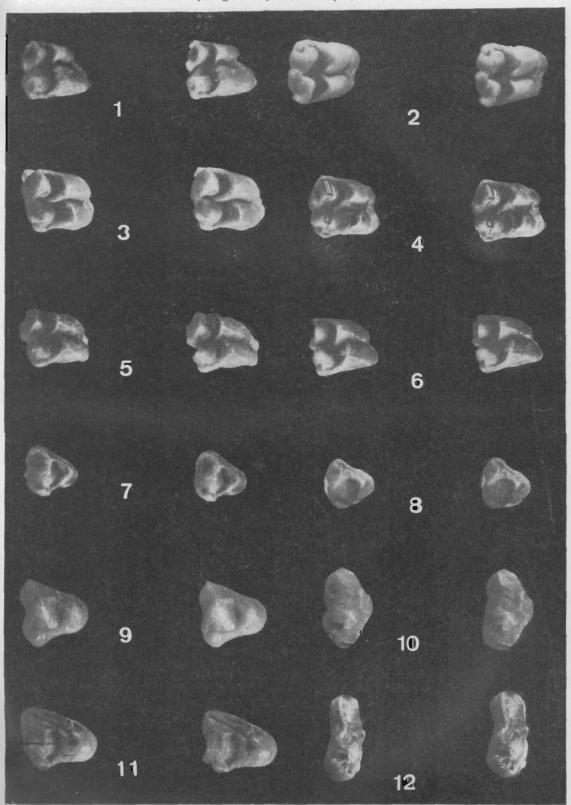
Dorcabune was erected by G. E. Pilgrim in 1910. Its diagnostic feature has been believed to be the bluntness of its tooth cones. Officially, nobody opposes its validity. However, no European paleontologist has ever applied the genus name Dorcabune to European forms, although it is no doubt that there are such forms there. Recently some paleontologists have admitted the possible presence of at least two lineages within the European Dorcatherium (M. Mottl, 1961 and V. Fahlbusch, 1985). It seems to us that two types could well be distinguished morphologically, though forms with some intermediate characters do exist in Europe, such as D. crassus. One is characterized by its low-crowned and bunodont teeth, while the other has high-crowned selenodont teeth. They differ further by the following characters. 1) The bundont type has its cheek teeth also proportionally wider and shorter than the selenodont type has. 2) former type has more developed cigulum as a rule than the latter one. In addition, there is a rib on the external wall of the metacone in the former type. 3) The Σ structure in the two groups is also a little different: in the former, the central two arms unit with each other first, then unit with the entoconid, while the lateral two arms are comparatively weaker developed. In the selenodont group the Σ structure is typically constructed and fully developed. 4) In the bunodont group P1 is usually absent, or in case it is still present, it is strongly reduced and one-rooted. In the selenodont group P1 seems to be always present and two-rooted. It is appropriate to call the first Dorcabune and the second Dorcatherium. In our opinion, the first genus should include the European D. crassus, D. vindobonensis and D. penekei and the Asian D. anthracotheroides. D. nagrii (Pilgrim, 1915), D. progressus and D. liuchengensis. Dorcatherium is to include the European D. guntianum and D. naui, the Asian D. majus, D. minus D. nagrii (Prasad, 1968) and D. puyhauberi and the African D. chappuisi and D. pigotti. Some poorly known forms are for the moment difficult to assign to any of the two above mentioned genera, for example, the African "D." parvum and songhorensis. The nature of the Siwalik "D." minimus is also unclear. It is interesting to note that all they are very small in size, their lower teeth lo not have typical and fully developed Σ structure and their upper teeth have only weak cingulum. These characters are nothing else but distinctive features of the extant tragulids. The most interesting material in this regard is the recently genus Yunnanotherium from the famous locality Lufeng. It possesses the same characters as we just mentioned. This has led us to think, whether theses forms, or some of them represent the third group of the fossil tragulis which is closer to the extant forms phylogenetically.

It is to be noted that the Sihong sample of the *Dorcatherium* teeth varies considerably in size, as demonstrated by its variation coefficients: 2.89—11.77 (see Tables). Without statistic data of tragulids at hand, we may use the data cited by H. S. Pearson (1928) from an ancient Egyptian Naqada population as an example of the variation range of a homogeneous population. In given case, the variation coefficients for the tooth measurements range from 5 to 12.5, higher than those of the Sihong sample. Furthermore, the highest coefficients in the Sihong sample are those for the first to third premolars. Since these teeth are in process of degeneration, it is understandable to have higher variation for them.

Our new species seems to be close to the European D. guntianum both in size and mo-

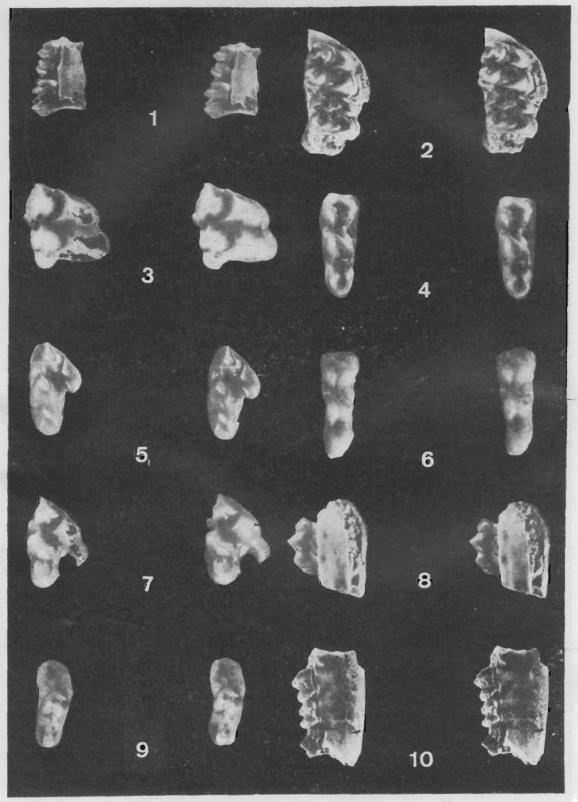
phology. However, there are still some differences between them. Our species is still smaller, with weaker cingulum and well developed P₁ supported by two roots. The few specimens described by E. H. Colbert in 1935 under the name of *Dorcatherium* sp. resemble the Sihong specimens both in size and morphology very much. R. M. West referred them to *Dorcatherium nagrii*, a species erected by Prasad in 1968. However, the M³ of Prasad's material, as is cited by West himself, measures only 7.1mm (L)×7.0mm (W), smaller than the smallest M² in the Sihong sample. Under the present circumstances we incline to erect a new species for the Sihong sample: *Dorcatherium orientale*. Judging from its evolutionary level, we believe it is appropriate to assign its age to a time-span approximately equivalent to the European MN 4.

8. Dorcatherium (Tragulidae, Artiodactyla)



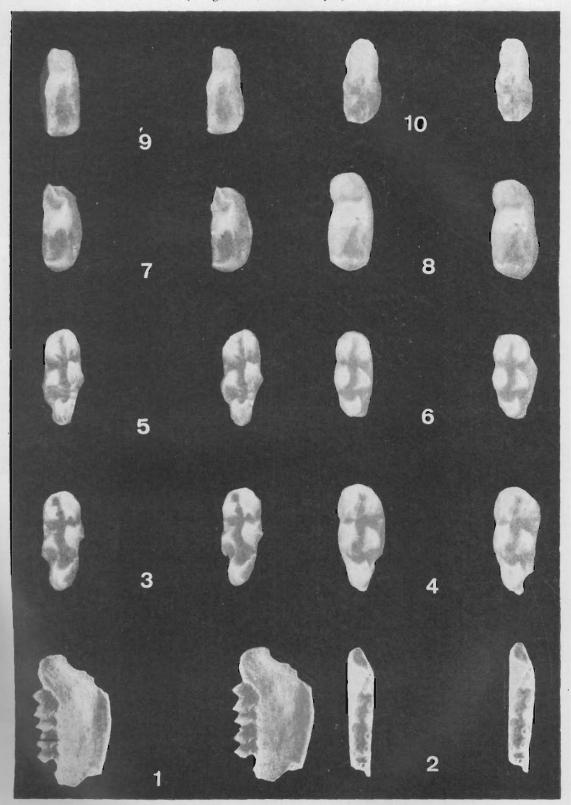
Dorcatherium orientale sp.nov. V9462 1-8×2; 9-12×3
1.1.M³; 2.r.M³; 3-4.1.M²; 5-6.1.M¹; 7-9,11.1.P⁴; 10.1.P³; 12.1.P²(立体照片)

8. Dorcatherium (Tragulidae, Artiodactyla)



Dorcatherium orientale sp.nov. V 9462 1-2,10×1; 3-9×3
1.1.DP4-M1 (labial side); 2.1.M2-M3; 3.1.DP4; 4.r.DP4; 5.1.DP3; 6.r.DP4; 7.1.DP3 (with inner root); 8.1.DP3 (lingual side); 9.1.DP2; 10.1.P4-M2(labial side) (立体照片)

-8. Dorcatherium (Tragulidae, Artiodactyla)



Dorcatherium orientale sp.nov. V9462 $1-2\times1;3-6\times2;7-10\times3$ 1-2.r. lower jaw fragment with M_2-M_3 (lingual and crown sides); 3.5.1. M_3 ; $4,6.r.M_3$; $7-8,r.P_4$; $9.r.P_3$; $10.r.P_2$ (立体照片)