

广西百色盆地及永乐盆地始新世反刍类的 再研究, 兼论 *Indomeryx*, *Notomeryx*, *Gobiomeryx* 和 *Prodremotherium* 的系统位置¹⁾

郭建崑¹ 齐 陶¹ 盛泓洁²

1 中国科学院古脊椎动物与古人类研究所 北京 100044

2 北京教育学院生物系 北京 100044

摘要 为鉴定广西百色、永乐两盆地新采集的始新世反刍类,重新研究了中科院古脊椎动物与古人类研究所以往发现于该地的全部有关标本,将原订的右江印度麋鹿 (*Indomeryx youjiangensis*) 并入百色南方麋鹿 (*Notomeryx besensis* Qiu, 1978), 记述了大南方麋鹿 (新种) (*Notomeryx major* sp. nov.) 和戈壁原驰鹿 (未订种) (*Gobiomeryx* sp.), 将印度麋鹿属 (*Indomeryx*)、南方麋鹿属 (*Notomeryx*)、戈壁原驰鹿属 (*Gobiomeryx*) 和原驰鹿属 (*Prodremotherium*) 从 *Gelocidae* 科中分出并归为一个新科: 原驰鹿科 (新科) (*Prodremotheridae* Fam. nov.).

关键词 广西, 百色盆地、永乐盆地, 始新世, 反刍类

中图法分类号 Q915.876

1 简介

1995年2~3月, 广西壮族自治区地质研究所的邝国敦高级工程师、美国卡内基自然历史博物馆的 Christopher Beard 博士、芝加哥大学的 Daniel Gebo 博士和本文第一、二作者在广西考察时在百色盆地和永乐盆地采到一批中始新世最晚期~晚始新世 (童永生等, 1995) 反刍类化石。在鉴定化石的过程中, 笔者认为有必要对包括邱铸鼎 (1978) 研究过的 *Indomeryx cotteri*、*Indomeryx youjiangensis*、*Indomeryx* sp. 和 *Notomeryx besensis* 以及童永生、翟人杰和 Savage D. E. 等在 80 年代初采集的标本在内的所有百色盆地和永乐盆地的中始新世最晚期~晚始新世反刍类加以重新研究和讨论, 以明确 *Indomeryx*、*Notomeryx* 以及与之相关的 *Gobiomeryx* 和 *Prodremotherium* 的系统关系。

1) 本项研究得到的资助有: 中国国家自然科学基金 (49372070号)、中国科学院古生物学和古人类学科基础研究特别支持基金 (课题号为970302) 和美国国家自然科学基金 (SBR9221231)。

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2 系统记述

偶蹄目 Artiodactyla Owen, 1848

反刍亚目 Ruminantia Scopoli, 1777

有角次目 Pecora Linnaeus, 1758

原驰鹿科(新科) *Prodremotheridae* Fam. nov.

科的特征 同科型属。

科型属 原驰鹿属 (*Prodremotherium* Filhol, 1877)。

归入属 印度麋鹿属 (*Indomeryx* Pilgrim, 1928), 南方麋鹿属 (*Notomeryx* Qiu, 1978), 戈壁原驰鹿属 (*Gobiomeryx* Trofimov, 1957)。

科型属的特征(据 Viret, 1961; Janis, 1987; Janis, *et al.*, 1987 修订) 上臼齿丘~新月形, 低冠, 横向不特宽; 前尖外侧中肋粗壮, 后尖外侧中肋明显; 齿带不连续; 具中附尖和小而锥形的内附尖。P3 前叶不收缩, 内侧较发育。下臼齿内侧主尖(下后尖和下内尖)侧扁; 无“*Dorcatherium* 褶”; 具下后附尖; 外侧主尖(下原尖和下次尖)呈简单的新月形, 无古鹿褶; 下内尖后部在其后棱唇侧向前方缩入呈很浅的凹沟; 下内尖后棱后端未伸达齿后缘, 而下次尖后棱延伸到牙齿后舌侧, 因此后齿谷在牙齿的后~内侧角有一很小的开口; 具前齿带。跖骨愈合, 跖骨沟封闭。

印度麋鹿属 *Indomeryx* Pilgrim, 1928

柯氏印度麋鹿 *Indomeryx cotteri* Pilgrim, 1928

(图 1)

1978 *Indomeryx* sp. Qiu, p. 7~12

材料 一残破的右 M2 (V4954.1); 一存有 p3~m3 的残破的左下颌骨 (V4954.2); 存有 m2~3 的残破的左下颌骨两件 (V4954.3, V4954.4); 同一个体的一左 p4 和一左 m3 (V4954.5); 一存有 m1~3 的残破的右下颌骨 (V4956.1); 一存有 m1 和 m3 的残破的右下颌骨 (V4956.2); 一左 m2 (V4956.3); 一右 m1 (V11482.1); 一左 m1 (11482.2) 和一右 M2 (V11482.3)。

地点和层位 广西田东塘烧 (73081)、浮塘北 (73080)、却林 (73086)、却林北 (74067), 广西联雄弄禄 (广西区燃化局第一地质队编号 74-1-古-13); 中始新世最晚期那读组 (童永生等, 1995)。

修订特征 M2 无后附尖; 内齿带与前、后齿带均不相连。下臼齿具锥形的下后附尖和小的下外附尖。m3 第三叶仅有下次小尖, 该尖两侧前伸的环状嵴围成一个向前的浅凹, 该浅凹由下内尖后棱与第二叶的齿谷隔开, 此处下内尖后棱终端形成多样的珐琅质褶; 无后齿带。p4 下原尖高耸, 向后伸出内外两条急骤倾斜的嵴, 两嵴在齿后缘封闭, 将跟座围成盆状; 小的下后尖位于内嵴前端舌侧。

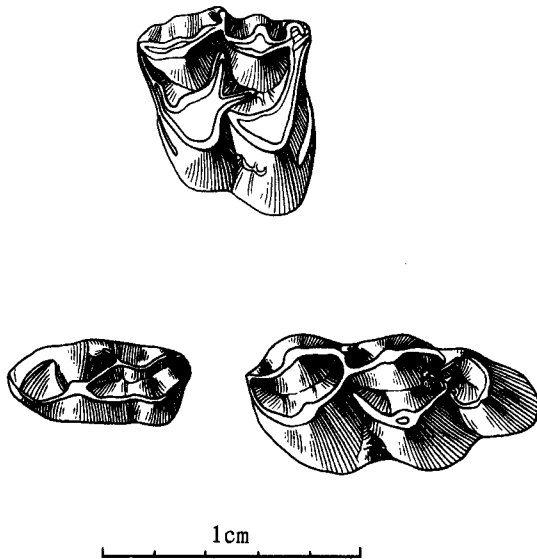


图1 柯氏印度麋鹿

Fig.1 *Indomeryx cotteri* Pilgrim, 1928 (Upper, V11482.3; Lower, V4954.1)

描述 M2 低冠, 略呈梯形, 前缘宽于后缘、唇侧缘略宽于舌侧缘。唇侧主尖(前尖和后尖)丘形; 舌侧主尖(原尖和后小尖¹⁾)新月形。原尖最大, 向舌面突出; 其前棱长, 几乎横向地延伸至牙齿的唇侧, 汇于前尖前棱与前附尖的连接处; 其后棱较短, 向后~唇侧方伸出不久即止于后小尖前棱上。后小尖前棱伸入前尖后棱与后尖前棱之间, 但与二者均未相交; 在原尖后棱终点唇侧, 后小尖前棱向前方又出一珐琅质褶, 伸向前齿谷。后小尖后棱伸向牙齿唇侧与后尖后棱相连。前尖唇侧中肋很发达。后尖唇侧中肋较弱但仍明显。前附尖和中附尖相当发育, 无后附尖; 内附尖极弱。前、后齿带长; 内齿带仅存于舌侧两主尖之间, 与前、后齿带均不相连。

p3 狭长, 主尖位于中部。

p4 主尖(下原尖)高耸, 位于牙齿中部稍前; 下原尖前棱形成牙齿前部向内弯曲的弧形嵴, 前端与下前尖相连; 下原尖向后伸出内外两条急剧倾斜的嵴, 两嵴在齿后缘封闭, 将跟座围成盆状; 小的下后尖位于内嵴前端舌侧。

下臼齿舌侧主尖(下后尖和下内尖)侧扁, 唇侧主尖(下原尖和下次尖)呈简单的新月形; 下原尖的前、后棱分别与下后尖的前、后棱相连, 无古鹿褶和“*Dorcatherium* 褶”; 斜棱汇于下原尖而不是下内尖。锥形的下后附尖开始出现于下后尖后棱末端舌侧。小的下外附尖在不同的标本上以不同的程度出现于下原尖与下次尖之间的牙齿基部。下内尖后部在其后棱唇侧向前方缩入呈很浅的凹沟; 某些个体上该凹沟比其他个体略深, 因此显得这些个体下内尖后部在其后棱的唇侧存在一锥形的珐琅质褶。下内尖后棱后端未伸达齿后缘, 而下次尖后棱延伸到牙齿后舌侧, 因此后齿谷在牙齿的后~内侧角有一很小的开口。前齿带不明显到发育, m1 和 m2 具后齿带。m3 第三叶仅有下次小尖, 该尖两侧前伸的环状嵴围成一个向前的浅凹, 该浅凹与第二叶的齿谷之间由变化多样的珐琅质褶隔开; 无后齿带。

比较与讨论 上述反刍类化石与 Pilgrim (1928) 所订的以及 Colbert (1938) 所描述与讨论的 *I. cotteri* 个体大小相当(表 1), 而且显示出的性状完全一致, 因此, 将它们归入 *I. cotteri* 是合理的。当然, 由于广西的材料无论数量还是完好程度均超过邦唐的材料, 因此我们得以对 *I. cotteri* 有了如描述中所指出的更为全面的认识。

邱铸鼎 (1978) 认为 V4956.1~3 号标本可能是不同于 *I. cotteri* 的种: *Indomeryx* sp.,

1) 邱铸鼎 (1978) 原认为是次尖, 似有误。

表1 百色的柯氏印度麋鹿牙齿测量及其与邦唐材料的比较(长/宽)
Table 1 Measurements of the teeth of *I. cotteri* from Baise Basin and comparison
with the fossils of Bondaung beds (Length/Width) (mm)

	M2	p3	p4	m1	m2	m3
V4954.1	6.1/-	-	-	-	-	-
V4954.2	-	6.3/2.6	6.2/3.0	5.7/4.2	6.8/4.6	10.6/4.7
V4954.3	-	-	-	-	7.3/4.9	10.9/5.1
V4954.4	-	-	-	-	7.3/4.4	10.0/4.4
V4954.5	-	-	6.9/3.2	-	-	11.0/4.9
V4956.1	-	-	-	6.8/4.3	7.1/4.8	-
V4956.2	-	-	-	6.5/4.4	-	9.4/4.6
V4956.3	-	-	-	-	7.1/4.7	-
V11482.1	-	-	-	6.8/4.0	-	-
V11482.2	-	-	-	6.3/3.8	-	-
V11482.3	6.5/8.3	-	-	-	-	-
G. S. I. B765	-	-	-	6.6/3.4	6.9/4.2	9.7/4.3
A. M. 20023	-	-	-	-	-	11.5/5.4
A. M. 32521	-	-	-	6.5/4.4	-/4.5	-

他认为这些标本具有如下不同于 *I. cotteri* 的特征: 下臼齿具有比较发育的外齿带和珐琅质褶皱, m3 有一个短小而低矮的后跟(即第三叶)。据笔者观察, 1) 珐琅质褶皱也同样存在于一些被归入 *I. cotteri* 的标本(如 V4954.3 和 V4954.5); 2) 邦唐的 *I. cotteri* 标本下臼齿上也有较为发育的外齿带; 3) 所谓的 *Indomeryx* sp. 中唯一保存有 m3 第三叶的标本是 V4956.2, 但其第三叶后部却恰恰有所破损, 因此“m3 有一个短小而低矮的后跟”不足以成为所谓的 *Indomeryx* sp. 区别于 *I. cotteri* 的判断特征。

南方麋鹿属 *Notomeryx* Qiu, 1978

百色南方麋鹿 *Notomeryx besensis* Qiu, 1978

(图 2)

1978 *Indomeryx youjiangensis* Qiu, p. 7~12

1985 *Notomeryx youjiangensis* Tong (根据 Russell and Zhai, 1987)

材料 一存有 p4~m3 的残破的右下颌骨(V4955.1); 残破的右 M3 两件(V4955.3 和 V11485.4); 残破的左 m3 两件(V4955.4 和 V11483.11); 一存有 m1~3 的残破的右下颌骨(V4955.5); 一存有 p3~m3 的残破的左下颌骨(V11480); 一存有 M1~3 的残破的左上颌骨(V4957.1); 一存有 m2~3 的残破的右下颌骨(V4957.2); 一左 M2(V4957.3); 一存有 p3 和 m1~2 的残破的右下颌骨(V4957.4); 存有 dp4~m1 的残破的左下颌骨两件(V4957.5 和 V11483.14); 左 m2 三件(V4957.6a, V11483.17 和 V11483.19); 一右 m1 (V4957.6b); 右 m2 五件(V4957.6c, V11483.18, V11483.21, V11485.1 和 V11485.2); 一残破的右 p3(V11479); 一存有 p3~m3 的残破的右下颌骨(V11483.1); 一存有 dp4~m2

的残破的右下颌骨(V11483.2);同一个体的右 M1、M2 和左 m2(V11483.3);存有 m1~3 的残破的左下颌骨两件(V11483.4 和 V11483.16);一右 M2(V11483.5);同一个体的右 M2 和 M3(V11483.6);一残破的左 m2(V11483.7);右 m3 两件(V11483.8 和 V11483.9);一残破的右 m3(V11483.10);存有 m1~2 的残破的左下颌骨两件(V11483.12 和 V11483.15);一存有 m1~2 的残破的右下颌骨(V11483.13);一左 M3(V11483.20);一右 M1(V11485.3);一残破的左 M2(V11485.5);左 M1 两件(V11485.6 和 V11485.7);一左 m1(V11485.8)以及一残破的右 m2(V11485.9)。

地点和层位 广西田东却林(73086)、却林北(74067)、那桑(73078)、浮塘,广西百色东笋(广西区燃化局第一地质队编号 74-1-古-18)、六塘(73072),广西永乐晚江、洞郁;中始新世最晚期那读组(童永生等,1995)。

修订特征 M1 无外齿带,内齿带与前、后齿带均不相连;无后附尖。M2 内齿带与前、后齿带均不相连,在后尖唇侧、中附尖与后尖后棱末端之间存有弱的外齿带;无后附尖。M3 内齿带与前齿带相连,外齿带在后尖唇侧非常发育;后附尖开始出现于一些个体。下臼齿下后附尖较发育;下内尖后部在其后棱唇侧向前方缩入的凹沟或深或浅,以致一些个体下内尖后面形成明显的双嵴。m3 第三叶单尖,具后齿带。p4 仅后唇侧嵴延至齿后缘,舌侧仅在斜棱与下后尖连接处向后伸出一短褶,因此跟座不呈盆状。p3 各齿尖的唇侧棱相连构成牙齿的纵嵴;下原尖和下次尖均另具舌侧嵴;牙齿后部由下次尖舌侧嵴、纵嵴及与后者相连的横向齿后嵴围成三角形齿谷。

描述 个体明显地较 *I. cotteri* 大(表 2)。

上臼齿低冠,略呈梯形,前缘宽于后缘,唇侧缘略宽于舌侧缘。唇侧主尖(前尖和后尖)丘形;舌侧主尖(原尖和后小尖)新月形。原尖最大,向舌面突出;其前棱长,几乎横向地延伸至牙齿的唇侧,汇于前尖前棱与前附尖的连接处;其后棱较短,向后~唇侧方伸出不久即止于后小尖前棱上。后小尖前棱伸入前尖后棱与后尖前棱之间,但与二者均未相交。在牙齿中央由前尖的后舌侧面、原尖齿谷和后小尖前棱围成的区域内或多或少有珐琅质褶发育。后小尖后棱伸向牙齿唇侧与后尖后棱相连。前尖唇侧中肋很发达。后尖唇侧中肋较弱但很显著。前附尖和中附尖相当发育,内附尖较弱;后附尖在 M1 和 M2 上不存,在 M3 上出现于一些标本。前、后齿带长;内齿带在 M1 和 M2 上仅存于舌侧两主尖之间,与前、后齿带均不相连,但在 M3 上则与前齿带连接,围绕原尖的前、内侧;外齿带在 M1 上不存,在 M2 上存于后尖外侧、中附尖和后尖后棱末端之间,而在 M3 上则显著发育于后尖外侧。

p3 三尖:下前尖、下原尖和下次尖;前者的齿棱与后二者的唇侧齿棱连接成一条纵向齿嵴;下原尖(主尖)和下次尖均另具舌侧嵴,其中下次尖舌侧嵴后向倾斜延伸至齿后缘,并与牙齿的纵嵴以及与之相连的横向齿后嵴围成三角形齿谷。

p4 仅后唇侧嵴延至齿后缘;舌侧仅在斜棱与下后尖连接处向后伸出一短褶,因此跟座不呈盆状。

下臼齿舌侧主尖(下后尖和下内尖)侧扁,唇侧主尖(下原尖和下次尖)呈简单的新月形;下原尖的前、后棱分别与下后尖的前、后棱相连,无古鹿褶和“*Dorcatherium* 褶”;下次尖后棱以单嵴与下内尖连接,但斜棱以单嵴汇于下原尖而不是下内尖。下后附尖明显,在

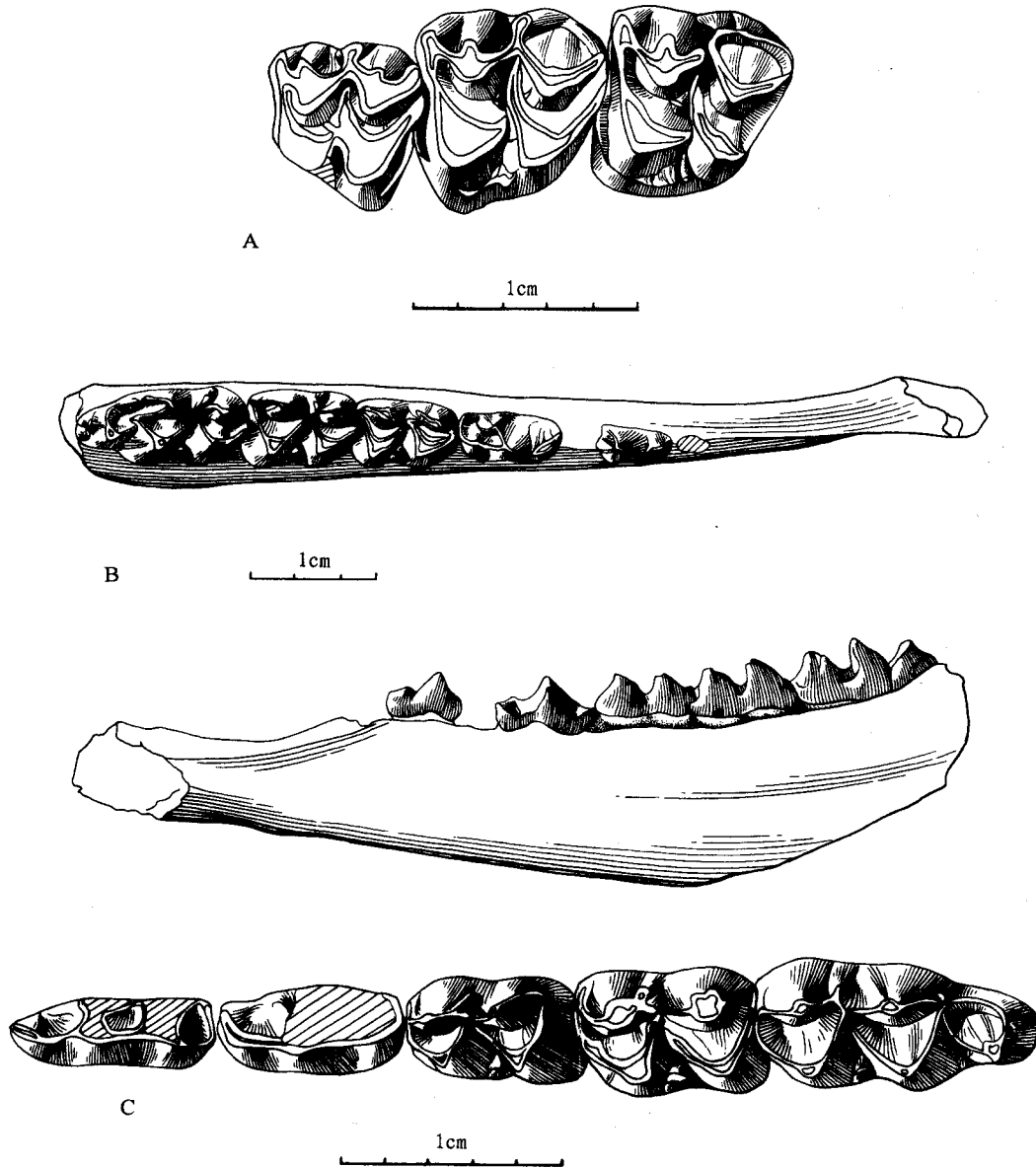


图2 百色南方麋鹿

Fig.2 *Notomeryx besensis* Qiu, 1978 (A. V4957.1; B. V11483.1; C. V11480)

一些标本上相当发育。下外附尖在不同的标本上以不同的发育程度出现于下原尖与下次尖之间的牙齿基部。下内尖后部在其后棱唇侧向前方缩入呈或深或浅的凹沟, 使得下内尖后部在其后棱的唇侧形成一珐琅质褶; 此褶在一些标本上非常发育, 使得下内尖后部呈双峰状态。下内尖后棱后端未伸达齿后缘, 而下次尖后棱延伸到牙齿后舌侧, 因此后齿谷在牙齿的后~内侧角有一很小的开口(个别牙齿该处无此开口, 如 V11480)。前、后齿带发育。m3 第三叶仅有下次小尖, 该尖两侧前伸的环状嵴围成一个向前的齿谷, 该齿谷与第二叶的齿谷以下内尖后棱隔开。

表2 百色南方麝鹿牙齿测量(长/宽)

Table 2		Measurements of the teeth of <i>N. besensis</i> (Length/Width)							(mm)
	M1	M2	M3	p3	p4	m1	m2	m3	
V4955.1	-	-	-	-	8.2/4.1	7.7/5.4	8.3/6.0	12.9/6.3	
V4955.5	-	-	-	-	-	7.1/5.2	8.1/5.8	/6.0	
V11480	-	-	-	9.0/3.2	8.3/4.2	7.2/5.0	8.1/6.1	12.9/6.1	
V4957.1	7.8/	8.5/9.6	8.3/9.3	-	-	-	-	-	
V4957.2	-	-	-	-	-	-	8.5/5.7	12.3/6.1	
V4957.3	-	8.5/10.0	-	-	-	-	-	-	
V4957.4	-	-	-	/3.4	-	7.6/5.3	8.1/5.5	-	
V4957.5	-	-	-	-	-	8.4/4.9	-	-	
V4957.6a	-	-	-	-	-	-	9.1/5.6	-	
V4957.6b	-	-	-	-	-	8.4/4.9	-	-	
V4957.6c	-	-	-	-	-	-	8.5/5.8	-	
V11483.1	-	-	-	-	8.0/3.9	7.7/5.1	8.1/5.9	13.0/6.0	
V11483.2	-	-	-	-	-	7.9/4.9	8.8/6.0	-	
V11483.3	7.3/8.8	8.2/10.2	-	-	-	-	8.0/5.6	-	
V11483.4	-	-	-	-	-	7.0/4.9	7.9/5.5	12.7/5.6	
V11483.5	-	8.3/10.0	-	-	-	-	-	-	
V11483.6	-	7.8/9.8	8.3/9.0	-	-	-	-	-	
V11483.8	-	-	-	-	-	-	-	12.6/6.2	
V11483.9	-	-	-	-	-	-	-	13.5/6.1	
V11483.12	-	-	-	-	-	-	8.5/5.2	-	
V11483.13	-	-	-	-	-	7.1/4.7	-	-	
V11483.14	-	-	-	-	-	7.7/4.9	-	-	
V11483.15	-	-	-	-	-	7.0/5.0	8.0/5.3	-	
V11483.16	-	-	-	-	-	-	8.5/5.5	-	
V11483.17	-	-	-	-	-	-	8.3/5.5	-	
V11483.18	-	-	-	-	-	-	8.2/5.7	-	
V11483.19	-	-	-	-	-	-	8.0/6.0	-	
V11483.20	-	-	8.2/10.0	-	-	-	-	-	
V11483.21	7.3/9.2	-	-	-	-	-	-	-	
V11485.1	-	-	-	-	-	-	8.7/5.9	-	
V11485.2	-	-	-	-	-	-	7.9/5.3	-	
V11485.3	7.4/7.6	-	-	-	-	-	-	-	
V11485.4	-	8.3/10.0	-	-	-	-	-	-	
V11485.6	7.3/8.6	-	-	-	-	-	-	-	
V11485.7	7.2/9.4	-	-	-	-	-	-	-	
V11485.8	-	-	-	-	-	-	7.9/4.9	-	

比较与讨论 邱铸鼎(1978)根据下列特征在 *Indomeryx* 属中订了一个新种 *I. youjiangensis*: “与 *Indomeryx cotteri* 相似,但下颌水平支较为粗壮;牙齿的个体大;p4 内侧

的尖发育, 其主尖后内嵴短且与后外嵴分离。”同时, 他又将一些上颌骨及上臼齿和一些没有保留 p4 的下颌骨及一些下臼齿订为新属新种 *Notomeryx besensis*, 其根据如下: “个体较大。下颌水平支粗厚。上臼齿低冠, 具四尖, 丘~脊型齿; 次尖(实际应为后小尖, 笔者注)发育, 前尖外侧的肋粗壮, 后尖外侧的肋明显。下臼齿四尖, 由新月形的外尖和侧扁状的内尖组成; 齿尖收缩, 齿谷开阔; 下内尖后方具明显的双嵴。齿缘和附尖发育, 珐琅质粗糙。”

80 年代和 90 年代的野外工作使我们得到了更多、更完整的材料, 这些材料证明上述被分属于两属两种的动物实际上应为同属同种, 即 *N. besensis*。依据如下:

1) 更为完整的材料如 V11483.1 号标本(一存有 p3~m3 的残破的右下颌骨)显示出现在 p4 上具有原订的 *I. youjiangensis* 的特征, 即“主尖后内嵴短且与后外嵴分离”; 但在下臼齿形态上却具有 *N. besensis* 的特征, 即“下臼齿四尖, 由新月形的外尖和侧扁状的内尖组成; 下内尖后方具明显的双嵴, 齿带和附尖发育。”

2) 观察所有的 *N. besensis* 和原订的 *I. youjiangensis* 标本, 下内尖后方的双嵴现象实际上存在于上述所有的标本上, 但在程度上具有从雏形到较为发达再到很发达这样一系列过渡的情况。

同时, 笔者认为下颌水平支粗壮是与个体较大相关的性状; 珐琅质粗糙在 *I. cotteri* 的一些标本中也有出现, 而且这一性状的强弱存在个体差异; 齿尖收缩并不明显。因此, 这三项不能作为 *N. besensis* 的鉴定特征。

此外, 我们重新研究的标本包括有童永生等采于 80 年代初期、现存于古脊椎所标本馆内的所有材料, 其中一件存有 m1~3 的残破的左下颌骨(V11483.4)标本盒上的标签为 *Notomeryx youjiangensis*, 据我们观察, 其形态特征完全符合上面描述的 *N. besensis* 的特征。因此, 原订的 *Notomeryx youjiangensis* 实际上与 *N. besensis* 也是同物异名。

大南方麋鹿(新种) *Notomeryx major* sp. nov.

(图 3)

正型标本 一左 M2(V11484.1)。

副型标本 一三角座缺损的 m3(V11484.2)以及一三角座缺损的 m2(V11484.3)。

归入材料 一右 M3(V11484.4)。

地点和层位 广西百色福禄(83083)和广西田东塘烧; 晚始新世那读组上部(汤英俊等, 1974, 1979; 童永生等, 1995)。

名称来源 根据其个体大的特征命名。

特征 个体大的 *Notomeryx*。上臼齿近四方形。下臼齿齿尖壁收缩, 但齿谷仍开阔; 下内尖特别侧扁。

描述 个体显著大于 *N. besensis*(表 3)。

上臼齿低冠, 近四方形, 前缘略宽于后缘, 唇侧缘略宽于舌侧缘。唇侧主尖(前尖和后尖)丘形; 舌侧主尖(原尖和后小尖)新月形。原尖最大; 其前棱长, 几乎横向地延伸至牙齿的唇侧, 汇于前尖前棱与前附尖的连接处; 其后棱较短, 向后~唇侧方伸出不久即止于后

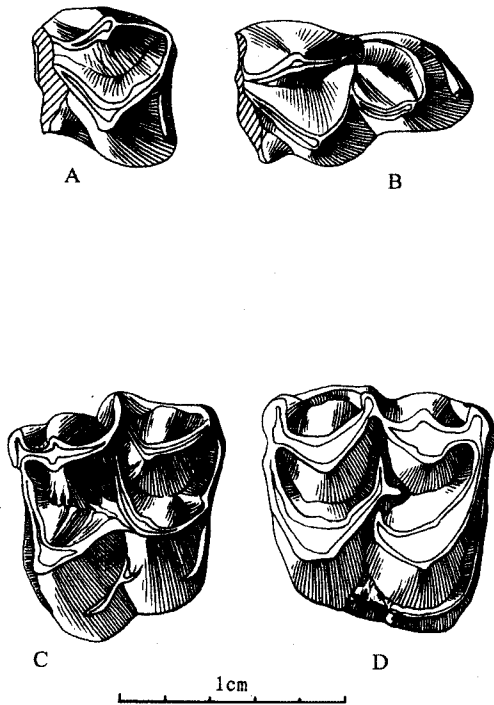


图3 大南方麝鹿(新种)

Fig.3 *Notomeryx major* sp. nov. (A. V11484.3; B. V11484.2; C. V11484.1; D. V11484.4)

小尖前棱上。后小尖前棱伸入前尖后棱与后尖前棱之间,但与二者均未相交。在牙齿中央由前尖的后舌侧面、原尖齿谷和后小尖前棱围成的区域内或多或少有珐琅质褶发育。后小尖后棱伸向牙齿唇侧与后尖后棱相连。前尖唇侧中肋很发达。后尖唇侧中肋较弱但很显著。前附尖和中附尖相当发育,内附尖较弱;M2 无后附尖,M3 具后附尖。前、后齿带长;内齿带在 M2 上仅存于舌侧两主尖之间,与前、后齿带均不相连,但在 M3 上则与前齿带连接,围绕原尖的前、内侧;外齿带在 M2 上存于后尖外侧、中附尖和后尖后棱末端之间,而在 M3 上则显著发育于后尖外侧。

下臼齿齿尖壁收缩,但齿谷仍开阔;下内尖特别侧扁。下内尖后棱后端未伸达齿后缘,而下次尖后棱延伸到牙齿后舌侧,因此后齿谷在牙齿的后~内侧角有一很小的开口。m3 第三叶仅有下次小尖;具后齿带。

比较与讨论 上臼齿低冠,唇侧主尖(前尖和后尖)丘形;舌侧主尖(原尖和后小尖)新月形。原尖最大;其前棱长,几乎横向地延伸

至牙齿的唇侧,汇于前尖前棱与前附尖的连接处;其后棱较短,向后~唇侧方伸出不久即止于后小尖前棱上。后小尖前棱伸入前尖后棱与后尖前棱之间,但与二者均未相交。在牙

表3 大南方麝鹿(新种)牙齿测量(长/宽)

Table 3 Measurements of the teeth of *N. major* sp. nov. (Length/Width) (mm)

	M2	M3	m2	m3
V11484.1	9.5/11.3	-	-	-
V11484.2	-	-	-	/6.6
V11484.3	-	-	/6.6	-
V11484.4	-	10.3/10.9	-	-

齿中央由前尖的后舌侧面、原尖齿谷和后小尖前棱围成的区域内或多或少有珐琅质褶发育。后小尖后棱伸向牙齿唇侧与后尖后棱相连。前尖唇侧中肋很发达。后尖唇侧中肋较弱但很显著。前附尖和中附尖相当发育,内附尖较弱;M2 无后附尖,M3 具后附尖。前、后齿带长;内齿带在 M2 上仅存于舌侧两主尖之间,与前、后齿带均不相连,但在 M3 上则与前齿带连接,围绕原尖的前、内侧;外齿带在 M2 上存于后尖外侧、中附尖和后尖后棱末端之间,而在 M3 上则显著发育于后尖外侧。下臼齿上,下内尖后棱后端未伸达齿后缘,而下次尖后棱延伸到牙齿后舌侧,因此后齿谷在牙齿的后~内侧角有一很小的开口。m3 第三叶仅有下次小尖;具后齿带。上述这一系列性状说明,发现于百色盆地的这些较大型的反

刍类无疑属于 *Notomeryx*。

另一方面, 它们又因下列特征而与 *N. besensis* 有别: 体形大; 上臼齿近方形; 下臼齿齿尖壁收缩, 但齿谷仍开阔, 下内尖特别侧扁。因此, 它们无疑代表了 *Notomeryx* 属内的一个新种。

戈壁原驰鹿属 *Gobiomeryx* Trofimov, 1957

戈壁原驰鹿(未订种) *Gobiomeryx* sp.

(图 4)

材料 一左 m3 (V11481)。

地点和层位 广西田东却林北 (74067)。

描述 V11481 号标本大小与 *I. cotteri* 相当。舌侧主尖(下后尖和下内尖)侧扁, 唇侧主尖(下原尖和下次尖)呈简单的新月形; 下原尖的前、后棱分别与下后尖的前、后棱相连, 无古鹿褶和“*Dorcatherium* 褶”; 下次尖后棱以单嵴与下内尖连接, 但斜棱以单嵴汇于下原尖而不是下内尖。锥形的下后附尖开始出现于下后尖后棱末端舌侧。小的下外附尖出现于下原尖与下次尖之间的牙齿基部。下内尖后部在其后棱唇侧向前方缩入呈很浅的凹沟。前齿带发育, 不具后齿带。第三叶上下次小尖两侧的环状嵴前伸并迅速并拢后与下次尖连接, 连接处的舌侧有一附加的小尖; 该小尖横向上正好处于下次尖后棱终端的位置上。

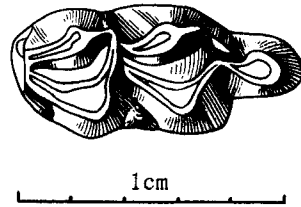


图4 戈壁原驰鹿(未订种)
Fig.4 *Gobiomeryx* sp. (V11481)

比较与讨论 V11481 号标本舌侧主尖(下后尖和下内尖)侧扁, 唇侧主尖(下原尖和下次尖)呈简单的新月形; 下原尖的前、后棱分别与下后尖的前、后棱相连, 无古鹿褶和“*Dorcatherium* 褶”; 下次尖后棱以单嵴与下内尖连接, 但斜棱以单嵴汇于下原尖而不是下

表4 戈壁原驰鹿(未订种)牙齿测量及其与属型种 *G. dubius* (据 Sudre, 1984) 的比较(长/宽)

Table 4 Measurements of the teeth of *Gobiomeryx* sp. and comparison with *G. dubius* (by Sudre, 1984) (Length/Width) (mm)

	<i>G. sp.</i>	<i>G. dubius</i>
m3	10.8/5.1	13.0/5.5

内尖。锥形的下后附尖开始出现于下后尖后棱末端舌侧。下内尖后部在其后棱唇侧向前方缩入呈很浅的凹沟。前齿带发育, 不具后齿带。第三叶上下次小尖与下内尖连接处的舌侧有一附加的小尖。这些性状与 *Gobiomeryx dubius* 非常接近。

但是, 在下列特征上与 *G. dubius* 又有所不同:

- 1) V11481 号标本仅具特别弱的锥形下后附尖, 而 *G. dubius* 下后附尖相当发育。
- 2) 在 m3 第三叶上, V11481 号标本下次小尖两侧的环状嵴前伸并迅速并拢后与下内尖连接, 附加的小尖横向上正好处于下次尖后棱终端的位置上; 而 *G. dubius* 环状嵴并不并拢, 两侧的嵴分别与下内尖相连, 附加的小尖横向上处于下次尖后棱终端之后的位置上。
- 3) 百色标本个体较小(表 4), m3 长度只有 *G. dubius* m3 长度的 81.5%。

因此, V11481 号标本很可能代表 *Gobiomeryx* 属中的一个新种。但由于材料仅有一

m3, 而早期反刍类 m3 常存在个体变异, 因此新种的确定尚需发现更多、更完整的材料。

3 *Indomeryx*、*Notomeryx*、*Gobiomeryx* 以及与之相关的 *Prodremotherium* 的系统位置的讨论

Pilgrim (1928) 指出, 确定原始的具有新月型齿的始新世偶蹄类的关系是很困难的。基于此, 他将 *Indomeryx* 暂时归入 *Tragulidae* 科中。随后, 他讨论指出, *Indomeryx* 与 *Gelocus* 在 p4 形态上或多或少具有一些相似性; 同时, *Indomeryx* 与 *Archaeomeryx* 在 m3 座上也有相似性。

Colbert (1938) 注意到, *Indomeryx* 不具备 *Tragulidae* 科下原尖后面具双嵴 (通常在下后尖后面也具双嵴) 这一显著特征。同时他认为, *Indomeryx* 显示出在某些方面与 *Gelocus* 相似, 但又较后者原始; 在另外一些方面与 *Archaeomeryx* 相似, 但又较后者进步。但总的来说, *Indomeryx* 与 *Archaeomeryx* 更为接近, 因此他将 *Indomeryx* 放在 *Hypertragulidae* 科中。

遵循 Colbert (1938) 的分类, 邱铸鼎 (1978) 也将 *Indomeryx* 及与之关系密切的 *Notomeryx* 归入 *Hypertragulidae* 科。

近来, 随着材料的积累和研究的深入, 对早期反刍类的系统关系有了新的认识。*Indomeryx* 和 *Notomeryx* 与 *Pseudogelocus*、*Paragelocus*、*Gelocus*、*Gobiomeryx* 以及 *Prodremotherium* 一起被纳入 *Gelocidae* 科的分类方法已被许多学者接受 (Sudre, 1984; Sudre *et al.*, 1996; Janis, 1987; Janis *et al.*, 1987), 而该科被认为是保留了许多原始的麋鹿次目 (*Tragulina*) 特征的有角次目 (*Pecora*) 的基础类群 (Simpson, 1945; Viret, 1961; Romer, 1966; Webb *et al.*, 1980)。

但同时, 所谓的 *Gelocidae* 科内部各属之间却存在着许多无法调和的矛盾性差异。其中最显著的矛盾性差异就是, 作为科型属的 *Gelocus* 具有如下麋鹿次目的原始特征: 下臼齿下后尖前棱不发育 (因而下后尖显得较为圆钝而不是侧扁), 同时, 具有“*Dorcatherium* 褶”但没有下后附尖; 而 *Indomeryx*、*Notomeryx*、*Gobiomeryx* 和 *Prodremotherium* 在相关性状上却都表现出有角次目的衍生特征: 下臼齿下后尖侧扁, 同时, 没有“*Dorcatherium* 褶”但具有下后附尖。因此, *Gelocidae* 科被认为并不是一个单系的自然类群, 而是一个多系的集合体; 其中, *Gelocus* 又是所有有角次目的姊妹群 (Janis, 1987)。

Gelocidae 科的这种混杂状况是不能令人满意的。如果考虑到地质年代, 则矛盾更加不可调和: 性状原始的 *Gelocus* 均为欧洲渐新世动物群的分子, 而具有进步特征的 *Indomeryx*、*Notomeryx* 和 *Gobiomeryx* 在亚洲却在中始新世最晚期业已出现。

此外, 欧洲渐新世的 *Pseudogelocus* 和 *Paragelocus* 显示出与 *Gelocus* 密切的系统关系, 其相关性状包括下臼齿具“*Dorcatherium* 褶”, 无下后附尖, 下后尖与下内尖较圆钝等 (Sudre *et al.*, 1996)。另一方面, 欧洲渐新世的 *Prodremotherium* 与上述欧洲类群差别很大, 却表现出与亚洲始新世的 *Indomeryx* 和 *Notomeryx* (尤其是 *Notomeryx*) 更为密切的系统关系, 相关性状包括下臼齿内侧齿尖侧扁, 无“*Dorcatherium* 褶”, 具下后附尖等。同时, *Prodremotherium* 在下后附尖更为发达以及体型更大等方面显示出比 *Indomeryx* 和 *Notomeryx* 更为进步, 这与它们地质年代上的前后关系是一致的。

综上所述我们认为, 原来被归入一个多系集合体——所谓的 Gelocidae 科中的早期反刍类应分为两个显著不同的谱系: *Pseudogelocus*, *Paragelocus* 和 *Gelocus* 自成一个欧洲渐新世类群, 仍统以 Gelocidae 科; *Indomeryx*, *Notomeryx*, *Gobiomeryx* 和 *Prodremotherium* 代表一个在中始新世起源于亚洲、并在渐新世散布到欧洲的科, 我们以这一类群中最早定名的属来命名这一新科, 即 Prodremotheridae Fam. nov.。

致谢 参加野外工作的人员还有古脊椎所的李岩先生和广西壮族自治区地质研究所的梁保华先生; 在研究中曾与古脊椎所高等室王景文研究员、童永生研究员、王原助理研究员以及美国匹兹堡卡内基自然历史博物馆罗哲西博士交换意见; 古脊椎所高等室原老第三纪组同仁给予指正; 杨明婉女士绘制插图。在此谨表谢意。

A RESTUDY OF THE EOCENE RUMINANTS FROM BAISE AND YONGLE BASINS, GUANGXI, CHINA, WITH A DISCUSSION OF THE SYSTEMATIC POSITIONS OF *INDOMERYX*, *NOTOMERYX*, *GOMIOMERYX* AND *PRODREMOTHERIUM*

GUO Jian-Wei¹ QI Tao¹ SHENG Hong-Jie²

¹ Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044

² Department of Biology, Beijing Institute of Education Beijing 100044

Key words Baise and Yongle basins, Guangxi, Eocene, ruminant

Summary

Some Eocene ruminant fossils were collected by the authors and some colleagues¹⁾ in 1995 from Baise and Yongle basins in Guangxi, China. When the new found fossils were identified and compared with *Indomeryx* and *Notomeryx*, which were excavated from Baise Basin in 1970's and studied by Qiu (1978), and with the unpublished Eocene ruminant materials collected from Baise Basin by Savage D. E., Zhai Renjie, Tong Yongsheng *et al.*, the authors of this paper find that the systematic positions of *Indomeryx* and *Notomeryx* were in great debate (Pilgrim, 1928; Colbert, 1938; Qiu, 1978; Sudre, 1984; Janis, 1987; Janis and Scott, 1987; Russell and Zhai, 1987). Although it was commonly accepted by the recent scholars that the above genera could be referred to the family Gelocidae, the relationship of the two genera

1) The scholars who took part in the field work include Prof. Kuang Guodun, Dr. Christophor Beard, Dr. Daniel Gebo, Mr. Li Yan and Mr. Liang Baohua.

was still unclear. Even the family Gelocidae itself was considered to have polyphyletic affinities within the Pecora rather than a natural group that could be united by the unique characters (Janis, 1987; Janis and Scott, 1987).

The above facts lead to a restudy of all Eocene ruminant materials from Baise and Yongle basins in this paper. In result, 4 species in 3 genera of ruminants, *Indomeryx cotteri* Pilgrim, 1928, *Notomeryx besensis* Qiu, 1978, *Notomeryx major* sp. nov. and *Gobiomeryx* sp. are described. Further more, *Indomeryx*, *Notomeryx* and *Gobiomeryx*, together with *Prodremotherium*, are referred to a new family, Prodremotheridae Fam. nov.

1 Description

Order Artiodactyla Owen, 1848

Suborder Ruminantia Scopoli, 1777

Infraorder Pecora Linnaeus, 1758

Family Prodremotheridae Fam. nov.

Diagnosis of the family As for the type genus.

Type genus *Prodremotherium* Filhol, 1877.

Included genera *Indomeryx* Pilgrim, 1928; *Notomeryx* Qiu, 1978; *Gobiomeryx* Trofimov, 1957.

Diagnosis of the type genus (Revised from Viret, 1961; Bouvrian and Geraads, 1985; Janis, 1987; Janis and Scott, 1987) The upper molars, with mesostyle and incipient entostyle, not very developed transversally; the cingula not continuous. P3 quite developed on the inner part and not reduced on the anterior lobe. The lower molars with crescent outer cusps (the protoconid and the hypoconid) and transversely compressed inner cusps (the metaconid and the entoconid); neither "*Dorcatherium* fold" nor "*Palaeomeryx* fold" existing; metastylid and pre-cingulum present; the rear of the labial face of the entoconid weakly depressed beside the postentocristid; the postentocristid not extending to the rear margin of the tooth and the posthypoconid reaching the lingual margin of the tooth; therefore, the posterior fossette of the tooth slightly opened posterior-lingually. The metatarsals fused to form a cervoid-like closed gully.

Genus *Indomeryx* Pilgrim, 1928

Indomeryx cotteri Pilgrim, 1928

(fig. 1)

1978 *Indomeryx* sp. Qiu, p.7~12

Materials A broken right M2 (V4954.1); a left mandibular ramus with p3~m3

(V4954.2); two left mandibular rami with m2~3(V4954.3 & V4954.4); a left p4 and a left m3 of an individual (V4954.5); a right mandibular ramus with m1~3 (V4956.1); a right mandibular ramus with m1 and m3 (V4956.2); a left m2 (V4956.3); a right m1 (V11482.1); a left m1 (11482.2) and a right M2 (V11482.3).

Locality and horizon Tangshao (73081), Northern Futang (73080), Quelin (73086) and Northern Quelin (74067) in Tiandong County; Nonglu (74-1-古-13) in Lianxiong County, Guangxi. Nadu Formation, latest Middle Eocene (Tong *et al.*, 1995).

Revised diagnosis M2 without metastyle and its inner-cingulum separated from both the pre-cingulum and the post-cingulum. The lower molars with an incipient metastylid and a small ectostylid. The third lobe of m3, without the post-cingulum, consisting of a single loop, only with a hypoconulid, containing a forwardly directed shallow valley joining with the entoconid where varied folds formed by the end of the postentocristid. The protoconid of p4 with two prominent ridges running steeply down to the rear and forming prominent rims encircling a basin-shaped heel and a weak and small metoconid existing just on the lingual side of the beginning of the innermost ridge.

Remarks The included fossils show identical characters with the *I. cotteri* defined by Pilgrim (1928) and maintained by Colbert (1938) and Qiu (1978) as follows:

1) The size of the molars studied by both Pilgrim (1928) and Colbert (1938) fall in the variation of the molar sizes of the above materials (see Table 1).

2) The lower molars show crescent outer cusps and laterally compressed inner cusps. The protoconid, without the *Palaeomeryx* fold and the *Dorcatherium* fold, joins the metaconid by the single preprotocristid anteriorly and the single postprotocristid posteriorly. The postentocristid does not extend to the rear margin of the tooth and the single posthypocristid reaches the lingual margin of the tooth. Therefore, the posterior fossette of the tooth slightly opens posterior-lingually. The single cristid obliqua joins the protoconid rather than the entoconid.

3) The third lobe of m3 consists of a single loop, with a hypoconulid which contains a forwardly directed shallow valley and joins with the entoconid without any intervention of accessory small cusps. The end of the postentocristid forms varied folds where the entoconid joins with the third lobe.

4) The protoconid of p4 contains two prominent ridges which run steeply down to the rear and form prominent rims encircling a basin-shaped heel. A weak and small metoconid exists just on the lingual side of the beginning of the innermost ridge.

The above characters form the basic appearance of the specimens. Therefore, the included fossils should be referred to *I. cotteri*, as Qiu (1978) has suggested.

Meantime the new found materials give some revised characters, which also can

be seen, even though not very clearly, on the figures of both the Pilgrim's specimens and Colbert's specimens but were not emphasized by them (Pilgrim, 1928; Colbert, 1938), as follows:

1) An incipient metastylid can be traced as a bulge on the lingual side of the end of the postmetacristid and a small ectostylid, varied in developing degree on different individuals, is present just on the very base of the crown between the protoconid and the hypoconid.

2) Beside the postentocristid, the rear of the labial face of the entoconid is weakly depressed. A weak fold can be seen beside the postentocristid labially in some individuals as the rear of the labial face of the entoconid is depressed a little bit deeper than others.

3) The postentocristid does not extend to the rear margin of the tooth and the posthypoconid reaches the lingual margin of the tooth. Therefore, the posterior fossette of the tooth is slightly opened posterior-lingually.

4) The pre-cingulum is present on m1, m2 and m3 but the post-cingulum exists only on m1 and m2.

5) p3 is slender with a middle located main cusp.

6) The anterior part of the preprotocristid of p4 turns to anterior-lingual direction and then joins the paraconid, which differs from the straight forward directive preprotocristid drawn by Pilgrim (1928) according to an uncompleted material. Consequently, the length of p4 is less than what was estimated by Pilgrim (1928).

7) M2 is brachyodont and bunoselenodont. An extremely prominent labial rib exists on the paracone and the labial rib of the metacone is less developed than the former. Both the parastyle and the mesostyle are developed but the metastyle is absent. The pre-cingulum, the post-cingulum and the inner-cingulum are present while the last, without any continuity with the others, exists only between the protocone and the metaconule.

Specimens V4956.1, V4956.2 and V4956.3 were treated as *Indomeryx* sp., other than *I. cotteri* by Qiu (1978) according to the characters of the lower molars with more developed labial cingulum and rugose enamel, and m3 with a shorter and smaller post-loop. However, the authors of this paper find that specimens V4954.3 and V4954.5, which were referred to *I. cotteri* by Qiu (1978), also show rugose enamel. Meanwhile, the lower molars of the *I. cotteri* collected from Pondang show more developed labial cingulum too (Pilgrim, 1928; Colbert, 1938). On the other hand, the character of post loop of m3 shows some individual variety on some specimens of *I. cotteri* (e.g. V4954.2~5). And the character of the post loop of m3 on specimen V4956.2, the only specimen of so-called *Indomeryx* sp. with a post loop of m3, is not so clear because it was damaged to some extent. In this case, it is too hard to say that the so called *Indomeryx* sp. shows any clearly distinguished characters

different from *I. cotteri*.

Genus *Notomeryx* Qiu, 1978

Notomeryx besensis (Qiu, 1978)

(fig. 2)

1978 *Indomeryx youjiangensis* Qiu, p.7~12

1985 *Notomeryx youjiangensis* Tong (according to Russell and Zhai, 1987)

Materials A right mandibular ramus with p4~m3 (V4955.1); two broken right M3 (V4955.3 and V11485.4); three broken left m3 (V4955.4 and V11483.11); a right mandibular ramus with m1~3 (V4955.5); a left mandibular ramus with p3~m3 (V11480); a piece of left maxilla with M1~3 (V4957.1); a right mandibular ramus with m2~3 (V4957.2); a left M2 (V4957.3); a right mandibular ramus with p3 and m1~2 (V4957.4); two left mandibular rami with dp4~m1 (V4957.5 and V11483.14); three left m2 (V4957.6a, V11483.17 and V11483.19); a right m1 (V4957.6b); five right m2 (V4957.6c, V11483.18, V11483.21, V11485.1 and V11485.2); a broken right p3 (V11479); a right mandibular ramus with p3~m3 (V11483.1); a right mandibular ramus with dp4~m2 (V11483.2); related right M1, M2 and left m2 (V11483.3); two left mandibular rami with m1~3 (V11483.4 and V11483.16); a right M2 (V11483.5); related right M2 and M3 (V11483.6); a broken left m2 (V11483.7); two right m3 (V11483.8 and V11483.9); a broken right m3 (V11483.10); two left mandibular rami with m1~2 (V11483.12 and V11483.15); a right mandibular ramus with m1~2 (V11483.13); a left M3 (V11483.20); a right M1 (V11485.3); a broken left M2 (V11485.5); two left M1 (V11485.6 and V11485.7); a left m1 (V11485.8) and a broken right m2 (V11485.9).

Locality and horizon Quelin (73086), Northern Quelin (74067), Nasang (73078) and Futang in Tiandong County; Dongsun (74-1-古-18) and Liutang (73072) in Baise City; Wanjiang and Dongyu in Yongle County, Guangxi. Nadu Formation, latest Middle Eocene (Tong *et al.*, 1995).

Revised diagnosis The metastyle absent on M1 and M2 but present on some M3; the inner-cingulum separated from both the pre-cingulum and the post-cingulum on M1 and M2 but joining with the pre-cingulum on M3; the outer-cingulum absent on M1, weakly present outside the metacone of M2 and developed outside the metacone of M3. On the lower molars, the metastylid more developed than *I. cotteri*; the rear of the labial face of the entoconid depressed in various degree beside the postentocristid so that the entoconid of some specimens with posterior double-ridges. The third lobe of m3 with a single hypoconulid and with post-cingulum. p4 without the basin-shaped heel as the protoconid only with a prominent labial ridge running

steeply down to the rear and only a short enamel fold present on the lingual side. p3 with a longitudinal ridge formed by the combination of the labial crests of the cusps and both the protoconid and the hypoconid with lingual crests; the rear of the tooth with a slightly post-lingual opened and triangular-shaped fossette encircled by the lingual crest of the hypoconid, the longitudinal ridge and the posterior transversal ridge which linked with the longitudinal ridge.

Remarks Qiu (1978) described *Indomeryx youjiangensis* as "similar to *I. cotteri*, but differs from that in being larger in size and having more robust and deeper ramus and more progressive p4 (the inner crest short and separated from the outer crest)" and *N. besensis* by the characters of "its larger size, its robustness of mandibular ramus and the rugosity of molar enamel, lower molar with double-ridges or crested-entoconid posterior face."

The more complete and more abundant materials collected in 1980's and 1990's indicate that the so-called *I. youjiangensis* and *N. besensis* are in fact an identical species in a single genus with the following reasons:

1) The *N. besensis* defined by Qiu (1978) bears no characters of p4 as no formerly collected specimens preserve any p4. The more complete materials, such as the specimen V11483 which contains the teeth of p3~m3, show that the character of so-called *I. youjiangensis* (more progressive p4) and the character of *N. besensis* (lower molar with double-ridges or crested-entoconid posterior face) exist on some specimens at the same time.

2) The more abundant materials show that the character of the double-ridged posterior face of the entoconid exists in *N. besensis* in various degree and also exists in so-called *I. youjiangensis* in various degree, from incipient to very developed.

Therefore, it is reasonable to refine the above materials in *N. besensis*, different from *I. cotteri* on the generic level, by the characters of "p4 without the basin-shaped heel because the protoconid with only one prominent labial ridge running steeply down to the rear and only a short enamel fold present on the lingual side; the lower molar with more developed metastylid and more remarkable double-ridged posterior face of the entoconid; and m3 with post-cingulum".

Moreover, the more complete and more abundant materials give some other additional characters, which were not described by Qiu (1978), as follows:

1) The metastyle is absent on M1 and M2 but is present on some M3. The inner-cingulum is separated from both the pre-cingulum and the post-cingulum on M1 and M2 but joins with the pre-cingulum on M3. The outer-cingulum is absent on M1, but can be seen between the mesostyle and the end of the postmetacrista outside the metacone of M2 and develops outside the metacone of M3.

2) On p3, the labial crests of the cusps connect and form a longitudinal ridge of

the tooth. Additionally, both the protoconid and the hypoconid have lingual crests. The longitudinal ridge joins with the posterior transversal ridge of the tooth. The lingual crest of the hypoconid does not contact with the posterior transversal ridge. Therefore, the rear of the tooth is encircled into a slightly post-lingual opened and triangular-shaped fossette.

Meanwhile, "the more robust and deeper mandibular ramus" is probably a correlative character with the larger size of the individual.

The so-called *Notomeryx youjiangensis* should be the synonymous of *Notomeryx besensis* because the specimen V11483.4, which was collected in 1980's and was originally labeled as "*Notomeryx youjiangensis*" before this study, shows no difference from the characters of *Notomeryx besensis* described above.

Notomeryx major sp. nov.

(fig. 3)

Holotype A left M2 (V11484.1).

Paratypes A broken left m3 preserving talonid (V11484.2); a broken left m2 preserving talonid (V11484.3).

Other material A right M3 (V11484.4).

Locality and horizon Tangshao in Tiandong County; Fulu in Baise City, Guangxi. Upper part of Nadu Formation (Gongkang Formation in past, Tang *et al.*, 1974, 1979), early Late Eocene (Tong *et al.*, 1995).

Etymology Named after the character of the larger size.

Diagnosis *Notomeryx* with a larger size. The upper molar nearly squareshaped. The lower molar with more compressed cusps but the fossettes of the teeth still quite wide; the entoconid extremely compressed transversely.

Remarks The specimens V11484.1~4 are referred to the genus *Notomeryx* by the following characters: the upper molars brachyodont and bunoselenodont; the paracone with an extremely prominent labial rib while the labial rib of the metacone less developed than the former; both the parastyle and the mesostyle developed but the metastyle absent on M2 and present on M3; the inner-cingulum without any touch with the pre-cingulum and post-cingulum on M2 but connecting to the pre-cingulum on M3; the outer-cingulum faintly existing between the mesostyle and the rear of the postmetacrista on M2 but strong on M3 in the same position as on M2; the lower molar with crescent outer cusps and transversely compressed inner cusps; m3 with the post-cingulum; the third lobe of m3 consisting of a single hypoconulid.

The specimens V11484.1~4 differ from *N. besensis* by the following characters: larger size (Table 3); lower molar with transversely more compressed cusps, especially entoconid. Hence, it is reasonable to define these large fossils to a new species,

Notomeryx major sp. nov.

Genus *Gobiomeryx* Trofimov, 1957

***Gobiomeryx* sp.**

(fig. 4)

Material A left m3 (V11481).

Locality and horizon Northern Quelin (74067) in Tiandong County, Guangxi. Nadu Formation, latest Middle Eocene (Tong *et al.*, 1995).

Remarks On V11481, the lower molars show crescent outer cusps and laterally compressed inner cusps. The protoconid, without the *Palaeomeryx* fold and the *Dorcatherium* fold, joins the metaconid by the single preprotocristid anteriorly and the single postprotocristid posteriorly. The single cristid obliqua joins the protoconid rather than the entoconid. An incipient metastylid can be traced as a bulge to the lingual side of the end of the postmetacristid and a small ectostylid presents just on the very base of the crown between the protoconid and the hypoconid. Beside the postentocristid, the rear of the labial face of the entoconid is weakly depressed. The third lobe has a lingual accessory small cusp beside the hypoconulid. The pre-cingulum exists, but the post-cingulum is absent. Therefore, V11481 can be referred to *Gobiomeryx* because the above characters are quite similar to *G. dubius*.

V11481 is identified as a new species of *Gobiomeryx* by the following characters:

1) The metastylid is incipient on V11481 but quite developed on *G. dubius*.

2) On V11481, the circle-shaped crests of the hypoconulid run forwardly, close up rapidly and then join with the entoconid. The accessory lingual cusp on the third lobe is located where the posthypocristid, the postentocristid and the third lobe join together. But on the third lobe of m3 of *G. dubius*, the circle-shaped crests of the hypoconulid do not close up, and join with the entoconid separately. The accessory lingual cusp is located at a level behind the joint point of the second lobe and the third lobe.

3) V11481 is remarkably smaller than the m3 of *G. dubius* (see Table 4).

The difference between V11481 and *G. dubius* indicates that V11481 is probably a new species of *Gobiomeryx*. There is every reason to erect a new specific name for the specimen of V11481, however, the extreme scarcity of material prevents us from doing so.

2 Discussion about the systematic position of *Indomeryx*, *Notomeryx*, *Gobiomeryx* and *Prodremotherium*

Indomeryx was originally defined in the family Tragulidae by Pilgrim (1928) with

two species, *Indomeryx cotteri* and *Indomeryx arenae*, which were collected from the Pondanug beds in Burma. Colbert (1938) referred two specimens from the same beds into *I. cotteri*, and indicated that *I. arenae* is possibly synonymous with *I. cotteri*, and referred the genus to the family Hypertragulidae. Besides agreeing with Colbert's idea and referring some specimens from upper Middle Eocene of Baise Basin in Southwestern China into the *I. cotteri*, Qiu (1978) defined a new species, *Indomeryx youjiangensis*, and a new species in a new genus, *Notomeryx besensis*, to the family Hypertragulidae. *N. besensis* and *I. youjiangensis* were mentioned with Tragulidae or Hypertragulidae in some Upper Eocene mammal faunas of Asia (Russell and Zhai, 1987). And both of the two forms were thought to be a single species, *Notomeryx youjiangensis*, with the family Gelocidae by Savage and Tong Yongsheng in some unpublished papers which are mentioned by Sudre (1984), Janis (1987) or Russell and Zhai (1987) but hardly referred by now. By the characters of the molars, Sudre (1984) thought that *Notomeryx* has no reason to be referred to Tragulidae and the reference to Hypertragulidae is also doubtful. He listed both the *Indomeryx* and the *Notomeryx*, together with the *Gobiomeryx*, to Gelocidae in his classification. According to Savage, Janis (1987) mentioned "*Indomeryx* (= *Notomeryx*)" with Gelocidae, however, without any discussion. By her view, it seems certain that *Notomeryx* should be a genus of the family Gelocidae, although Gelocidae itself was considered to be a polyphyletic assemblage, rather than a natural group that could be united by any unique character, composed of taxa of various phylogenetic affinities within the Pecora (Janis, 1987; Janis and Scott, 1987).

The condition of the family Gelocidae as a polyphyletic assemblage is far from satisfying when the phylogenetic study about the ruminants is taken. The reason bringing this immethodical condition is that the genus *Gelocus*, together with the genera *Pseudogelocus* and *Paragelocus* (Sudre *et al.*, 1996), is in fact dentally more primitive than other genera inside the family in the following characters: absence of metastylid on the lower molars, a small remnant of the "*Dorcatherium* fold" retained in some individuals, and absence of a premetacristid on the lower molars (interrelated the character of the inner cusps of the lower molar more or less round rather than transversely compressed). Meanwhile, these primitive genera occurred only in the Oligocene (MP21~MP23) in Europe. On the other hand, all other genera which were originally assembled in the family may be united with higher ruminants by the possession of the metastylid, the absence of the "*Dorcatherium* fold", and the transversely compressed inner cusps on the lower molar. At the same time, most of these "derived genera", such as *Indomeryx*, *Notomeryx* and *Gobiomeryx*, occurred in Eocene, an earlier time, in Asia.

The contradiction between the genera mentioned above already sheds light on the

way to resolve the problem in fact. When the original family Gelocidae was derived into two groups (families), *Gelocus*, *Pseudogelocus* and *Paragelocus* in one group and *Indomeryx*, *Notomeryx*, *Gobiomeryx* and *Prodremothrium* in another, the phylogenetic relationships of them are clear. The former represents a special Oligocene branch of the infraorder Tragulina only limited in Europe. The latter represents the earliest group of the infraorder Pecora in which *Indomeryx*, *Notomeryx* and *Gobiomeryx* occurred in the latest Middle Eocene in Asia and *Prodremothrium* represents a more derived genus occurred in Oligocene in Europe with some ancestor which dispersed from Asia in Oligocene.

Hence, the authors of this paper suggest that the genera *Gelocus*, *Pseudogelocus* and *Paragelocus* should be still referred to the family Gelocidae and the genera *Indomeryx*, *Notomeryx*, *Gobiomeryx* and *Prodremothrium* should be referred to a new family Prodremotheridae, named after the first genus found in the family.

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