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pp. 11～23
fig. 1

云南禄丰古猿化石地点的豪猪化石[1)]

王伴月 祁国琴
(中国科学院古脊椎动物与古人类研究所 北京 100044)

摘要: 描述了产自云南禄丰古猿化石地点的豪猪化石禄丰豪猪(新种)(*Hystrix lufengensis* sp. nov.)。这是一种较原始的豪猪。它的个体中等;两上颊齿列往前靠近;下颌骨骨体较低,齿隙稍凹,其前端高于下颊齿冠面;颊齿齿冠较低;上颊齿舌侧沟横向较短;P4 大,前尖通常孤立,中附尖很发达,不与中脊连;M3 较少退化;上颊齿具 3 齿根,大的内侧齿根具明显纵沟;下颊齿通常具 4 齿根等。形态结构分析表明, *H. lufengensis* 仅比 *H. parvae* 进步,比 *H. primigenia* 和 *H. sivalensis* 及其他种都原始。它可能代表亚洲目前已知最早、最原始的豪猪。其产出时代为晚中新世保德期(狭义)的较早期(距今约 8 Ma)。

关键词: 云南禄丰,晚中新世,豪猪科
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云南禄丰石灰坝禄丰古猿化石地点是 1975 年发现的。从 1975 年开始,中国科学院古脊椎动物与古人类研究所和云南省博物馆联合组队对该地点进行了 5 年(1975、1976、1980、1981、1983)的考察。在该地点除发现了古猿化石外,还发现了大量的其他脊椎动物化石,尤其以哺乳动物化石最为丰富,并采集到一些豪猪化石。新近纪的豪猪化石在亚洲发现得很少。禄丰的豪猪化石是我国目前已知最早的豪猪化石,这对了解亚洲豪猪的起源和与已知的豪猪的关系都很有意义。邱铸鼎等(1985)曾将禄丰的豪猪初步鉴定为 *Hystrix* sp.。对该批豪猪化石标本的进一步研究比较表明,它们应代表 *Hystrix* 属的一新种。本文是对这些豪猪化石详细的研究报道。

描述所用术语主要依王伴月、邱占祥(2002),个别依 Sen (2001)。文中缩写: IVPP,中国科学院古脊椎动物与古人类研究所; IVPP Loc.,中国科学院古脊椎动物与古人类研究所化石地点编号; IVPP V 中国科学院古脊椎动物与古人类研究所脊椎动物化石编号。

豪猪科 Hystricidae Fischer de Waldheim, 1817
豪猪属 Hystrix **Linnaeus, 1758**
禄丰豪猪(新种) Hystrix lufengensis **sp. nov.**
(图 1;表 1～3)

Hystrix sp. Qiu et al., p. 21

正型标本 可能属同一个体的压扁而破碎的头骨具左 I2、P4～M3、右 P4～M3 的印痕、左下颌骨具 i2、p4～m3 和一段右下颌骨具 m3 和 i2(IVPP V 13823)。

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正型标本产出层位 禄丰县石灰坝禄丰古猿化石地点(IVPP Loc. 75033)剖面 D 第 3 层(见祁国琴,1985,图 5);晚中新世。

归入标本 右下颌骨前部具 i2 和 p4～m1(V 14151.1);28 枚颊齿[可能为同一个体的左 P4～M3、右 M1 和 M3 各 1 枚(V 14152.1～6);1 枚 P4(V 14153.1);4 枚 M1/2(V 14153.2～5);4 枚 M3(V 14147.1～2, V 14153.6～7);4 枚 p4(V 14147.3～4, V 14148.1, V 14153.8);2 枚 dp4(V 14148.2, V 14153.9);4 枚 m1/2(V 14147.5～6, V 14151.2, V 14153.10);3 枚 m3(V 14148.3, V 14151.3～4)]和 4 枚 i2(V 14147.7, V 14149, 14150.1～2)。

归入标本产出层位 V 14147～V 14151 分别产自禄丰县石灰坝禄丰古猿化石地点剖面 D 的第 2～6 层,V 14152 和 V 14153 产出层位不清;晚中新世。

特征 个体中等、较原始的豪猪。两上颊齿列往前靠近。下颌骨水平支较低;齿隙长,上缘稍凹,其前端明显上翘,高于下颊齿冠面。颊齿齿冠较低;上颊齿舌侧沟横向较短,在成年个体不与颊侧褶相通,也不重叠;P4 大,前尖在成年时仍孤立,中附尖很发达,不与中脊连,颊侧褶 III 和 IV 相连成 U 形谷;M3 较少退化;上颊齿具 3 齿根,内侧齿根大,具明显纵沟;下颊齿通常具 4 齿根。

描述 V 13823 的头骨极度压扁破碎,无法判断它的形态结构,保存较好的部分为左上颌骨具 P4～M3,左 I2 和右鼓泡,还有右 P4～M3 的印痕。与头骨挤压在一起的还有一保存较好的左下颌骨具 i2、p4～m3 和右下颌骨的后半部具 m3 和较完整的左 i2。从颊齿的大小、形态结构和磨蚀程度判断,它们很可能属同一个体。依 van Weers(1990)对豪猪年龄所划分的阶段,V 13823 可能为成年个体(代表第 VI 年龄段)。V 14151.1 和 V 14152.1～6可能属 VII 年龄段的老年个体。V 14153.1 的磨蚀程度与 V 13823 的相近,可能也属第 VI 年龄段。V 14153.1 右 P4 的冠面形态结构与 V 13823 的左 P4 和右 P4 的印痕很像,有可能就是 V 13823 个体的右 P4。但由于右 P4 的印痕保存不完整,而且 V 14135.1的原始资料记录不全,层位不清楚,暂不将它归入 V 13823 个体。

V 13823 左上颌骨保存有部分腭面和中缝。M1 和 M2 舌缘至上颌骨中缝间的距离为 8 cm。如将该中缝延长,所测得 P4 和 M3 距中缝的距离分别为 7cm 和 9cm。如果这一测量是合理的话,V 13823 在 P4 和 M3 间的距离则分别为 14 cm 和 18 cm。这似乎表明 V 13823的腭面较宽,而且左、右两牙列是向前靠近的。鼓泡为卵圆球形,外耳道大,稍向外凸。茎乳孔很大。颈动脉孔很小,位于鼓泡内侧中部。鼓泡前端有欧氏管的痕迹。岩骨颅面有 2 个大而深的窝坑:下方的可能为弓形窝;上方的窝较大,其中的面神经管和内耳道被一约呈垂向延伸的隔板分开。

V 13823 的左下颌骨保存较好,但缺下颌角部分。下颌骨水平支较低,其下缘在 m1 及其以前的部分为向下凸的圆弧形,在 p4 的下方最厚;在 m2 的下方明显向上凹入。下颌骨前端上抬,下门齿齿槽后缘明显高于下颊齿的冠面。i2 与 p4 间齿隙很长(长约 41 mm,稍长于下齿列长),上缘稍凹。下颌联合后端约达 p4 下方。颏孔位于 p4 前下方。咬肌窝很发达,但受压变形,其前缘达 m1 的下方。咬肌嵴很发达。下颌角未保存,但其基部明显从 m2 下方、下门齿齿槽外侧伸出。下颌骨上升支受压破裂变形,但左、右下颌髁保存较好。其上的关节面为窄长的卵圆形球面。下门齿很长,向后伸达 m3 后缘下方。

上门齿仅保存有左侧门齿的前端一小部分。其横切面为横向较窄的卵圆形。门齿的

唇面较平缓,与外侧面圆缓过渡,无明显的界线,与内侧有明显的纵棱为界。釉质层覆盖在齿的唇面、外侧面唇侧的 1/3 和内侧面唇侧的 1/4 处。釉质层表面光滑,无明显的纹饰。下门齿与上门齿很相似,所不同的是釉质层覆盖面稍宽些,在内侧面约达唇侧的 1/3 处,在外侧面约达唇侧的 2/5～1/2 处。釉质层表面光滑,无明显的纹饰;但有的 i2 (V 14147.7、V 14149 和 V 14150.1～2) 在唇面中央有微弱的纵沟。

颊齿齿冠较低,尺寸由前往后逐渐减小。上颊齿的舌侧齿冠高于颊侧齿冠。从侧面看,颊侧诸褶向下延伸很少,仅褶 III 稍深;而舌侧沟较颊侧褶深得多。P4 为卵圆形,长大于宽,前边宽于后边。在第 VI 年龄段的 V 13823 和 V 14153.1 的颊侧褶 I～III 均向颊侧开口,仅褶 Ⅳ 封闭。前边脊与原尖形成连续的脊,中无前边沟的痕迹。前尖孤立,不与原脊连。前尖与中脊间的尖依 Sen (2001) 暂被称为中附尖。中附尖比前尖还要大些,与前尖连或不连,但不与中脊[依 Sen (2001), = 王伴月和邱占祥(2002) 的中脊 + 中附尖]连。中脊完全,与次尖和后边脊连,形成 U 形脊。后脊与后边脊在颊端连,封闭颊侧褶 Ⅳ。后脊舌部增大,或分叉,或为封闭的釉质坑;但其舌端均游离,不与次尖或后边脊连,因而颊侧褶 III 和 Ⅳ 相连成 U 形谷。短的舌侧沟向前颊侧斜伸,其颊端与原脊相对,既不与颊侧褶 I 或褶 II 相通,也不与颊侧褶重叠。老年个体(V 14152.1) 的 P4 的颊侧褶 I 为 2 个封闭的盆。后尖不与后边脊连。颊侧褶 II、III 和 Ⅳ 仍开口。后脊中间中断,使颊侧褶 III 与 Ⅳ 相通;后脊颊部游离;后脊舌部与中脊和后边脊连,将其舌侧的褶封闭成孤立的盆。舌侧沟为斜的封闭的盆。P4 通常具 3 齿根,内侧单齿根大,其舌侧有明显的纵沟,颊侧 2 齿根小。在 V 14153.1 P4 后缘,在后颊侧齿根和舌侧齿根间还有一小的附加的齿根。

M1 冠面为四边形,前缘宽于后缘。颊侧褶 I 通常被分成两部分:其舌部为封闭的坑;其颊部在 V 13823 的 M1 在颊侧开口处留有弱沟的痕迹;而在 V 14152.2 和 V 14152.5 仍为封闭的坑。M1 后部的形态结构与 P4 的相似,所不同的是后脊舌部向后弯,并与后边脊连,使褶 III 成为 L 形,而将褶 Ⅳ 封闭成坑。因 M1 相对磨蚀较深,舌侧沟通常已封闭成盆,其颊端仍不与褶 I 或 II 通。M1 齿根与 P4 的相似。

M2 和 M1 的冠面形态结构很相似,只是磨蚀程度不同。在属第 VI 阶段的正型标本 (V 13823) 中,M2 磨蚀程度较轻,很发达的中附尖仍孤立,颊侧褶 II 和 III 均向颊侧开口。褶 I 横向延伸得虽比 M1 的长,但颊端已被封闭。舌侧沟仍向舌侧开口。但在老年个体 V 14152的 M2 (V 14152.3) 的前半部似乎比 M1 (V 14152.2 和 V 14152.5) 的磨蚀还深些:其颊侧褶 I 的颊部仅为痕迹,褶 II 颊端几乎被封闭。

单个的 M1 和 M2 无法区别,我们暂称其为 M1/2。V 14153.2 与上述的 M1 和 M2 的形态结构上有明显区别:如其颊侧具 6 条横脊和 5 个颊侧褶(褶 Ⅰ～Ⅳ和后脊间褶),即在中脊和后边脊之间有 2 条后脊(Ⅰ和 Ⅱ)。它们的舌端彼此相连,并与中脊和后边脊连,与次尖一起形成封闭的坑,它们间的褶的颊端仍开口,后脊 II 颊端与后边脊连,封闭颊侧褶 Ⅳ;前尖与原脊连,无中附尖等。因这些区别在禄丰的另一些 M1/2 上显出是连续变化的(详见下),我们将上述区别暂作种内变异。V 14153.5 比 V 13823 年轻些,磨蚀较浅,其中附尖仍孤立,不与原脊连。但在中脊和后尖间有一附加的小尖,几乎封闭褶 III。在后脊向后转弯处有一向外伸的突起与上述附加的小尖相对。V 14153.4 较 V 14153.5 更年轻些,磨蚀更少,仍可见各脊顶端的串珠状结构。前边脊与原脊中部连,将褶 I 分成 2 部分。无明显的中附尖。但在中脊和后尖间的附加的孤立小尖很发育。在褶 III 中由后脊拐弯

处向外伸的突起已发育成脊,几乎与中脊和后尖间的附尖连(如果相连形成一横脊,就出现了 2 个后脊,也就是我们在 V 14153.2 所见到的情况)。

M3 的冠面的基本形态和结构与 M2 的很相似,舌侧沟均不与颊侧褶通,只是 M3 的后部更窄些,变异更大些。V 13823 的褶 Ⅳ 未完全封闭。V 14152.6 的褶 Ⅳ 为一封闭的盆,而 V 14152.4 的褶 Ⅳ 被斜脊分成 2 个坑。其余的 4 枚 M3 (V 14147.1～2, V 14153.6～7) 均较年幼些,磨蚀较少或未磨蚀。各个脊的顶端均为串珠状,其中以原脊的串珠最发育,其前还有附属的小尖,经磨蚀后,原脊形成褶曲状。这一结构在 V 14153.6 和 V 14153.7 中最为发育。在这一阶段,舌侧沟与颊侧褶相通。中附尖和中脊与后尖之间的小尖在 V 14147.1和 V 14147.2 均存在,而在 V 14153.6 和 V 14153.7 均无。

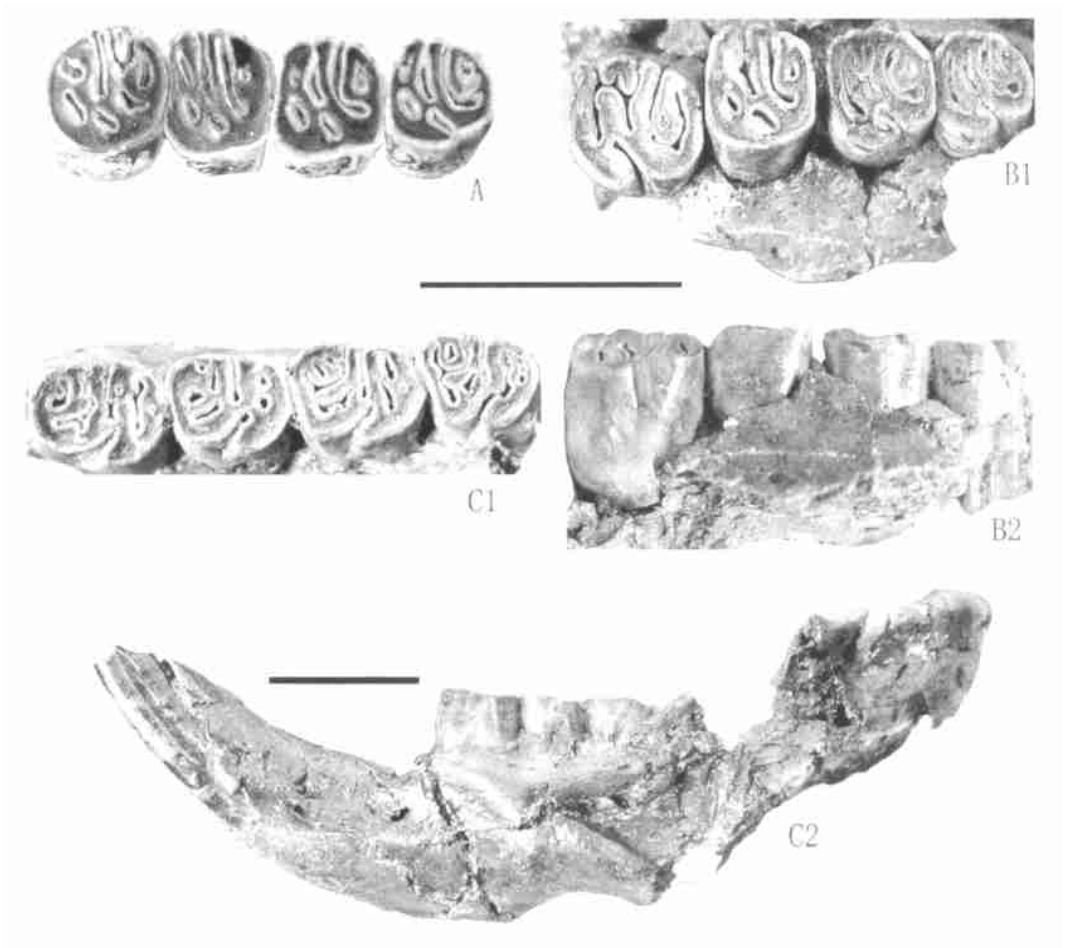

图 1 禄丰豪猪(新种),标尺 = 2 cm

Fig. 1 *Hystrix lufengensis* sp. nov., scale = 2 cm

A. 左 left P4～M3 (V 14152.1～4) 冠面 occlusal view; B～C. V 13823 (正型标本 holotype),
B. 左上颌骨 left upper jaw with P4～M3, B1. 冠面观 occlusal view; B2. 舌面观 lingual view;
C. 左下颌骨 left lower jaw with i2, p4～m3, C1. p4～m3 冠面观 occlusal view;
C2. 下颌骨外侧面 lateral view of lower jaw

下颊齿的颊侧齿冠稍高于舌侧齿冠。在侧面舌侧诸褶向下延伸很浅,仅褶 III 稍深;而下颊侧沟较舌侧褶深得多,距齿根较近。p4 冠面约为前窄后宽的卵圆形,下三角座明显窄于下跟座。V 13823 的 p4 的下后脊前弯,其颊端与下前边脊连,舌端与下后附尖连,使下舌侧褶 I 为封闭的坑。在该褶中从下前边脊向后还伸出一小的突起。下中脊与下原尖和下前边脊连接成 U 形脊。舌侧褶 II 成前弯的 L 形,其颊部被从下原尖伸出一小刺分叉。下中附尖与下中脊连,在连接处的前面有一突起,几乎伸达下后附尖。下舌侧褶 IV 封闭。下内尖大而明显,在与下次脊连接处有一封闭的坑。下次小尖处稍宽,其中有一小的坑。下舌侧褶 II 和 III 均开口。下颊侧沟向后舌侧斜,其颊侧开口,舌端不与舌侧褶相通。4 个单个的 p4 (V 14147.3～4, V 14148.1 和 V 14153.8) 的磨蚀程度均较 V 13823 的浅。其中以 V 14147.3 的磨蚀稍深些,其下颊侧沟不与下舌侧褶相通;但它的下三角座与 V 13823 不同,其下后脊与下中脊之间有附加的、几乎连成脊的 3 个尖。其余 3 枚 p4 除了颊侧沟均与舌侧褶相通外(可能是磨蚀少或无的缘故),冠面的基本特征均与 V 13823 的相同。老年个体的 V 14151.1 的 p4 前缘已破损,冠面磨蚀很深,褶和沟均为封闭的坑:下舌侧褶 I 和 II 为双坑,下舌侧褶 III、IV 和下颊侧沟为单坑。P4 或具 4 个分开的齿根,后颊侧齿根较大;或前 2 齿根相连,但其前侧仍留有划分 2 齿根的明显的纵沟。

在 V 13823 的齿列中 m1 和 m2 的冠面形态结构很相似,只是 m2 比 m1 磨蚀较浅些,形态结构较清楚些。孤立的 m1 和 m2 很难区分,我们将其笼统称为 m1/2。m1 和 m2 的冠面为前缘较平的卵圆形,下三角座与下跟座的宽度相近。V 13823 的 m2 的下前边脊、下原尖和下中脊相连成 U 形脊。下后尖处有一封闭的环形脊,可能是由弯曲的下后脊组成;其前面与下前边脊的舌端相连,后面与下后附尖连。下中央尖(依 Sen, 2001) 连接下前边脊和下中脊,将下舌侧褶 II 分成 2 部分:其颊部为封闭的盆,在该盆中从下原尖伸出的小刺几乎伸达下中央尖;其舌部为向前弯的弧形。舌侧褶 II 和 III 颊侧均开口。下中附尖与下中脊连。舌侧褶 IV 被封闭,并被分为内、外两个盆。下次小尖处稍宽,其中有一小的坑。下颊侧沟向后舌侧斜伸,不与舌侧褶相通。V 13823 的 m1 的下后尖处的坑已消失,但其后部分别与下后附尖和下中央尖相连;而下后附尖也与下中附尖连,使下舌侧褶 II 舌部成为两个封闭的坑,未见从下原尖向下中央尖伸出的小刺。下舌侧褶 IV 的两个盆缩小成卵形坑。在 4 枚孤立的 m1/2 中,V 14147.5 磨蚀较 V 13823 的 m1 还深些。其下三角座与 V 13823 的不同,下后脊为向前弯的弧形,与下前边脊连。其颊侧无中央尖。下后附尖很发达,并与从下中脊伸出的脊连。下舌侧褶 IV 单一,横向伸长。其余的 3 枚 m1/2 为较年轻的个体,磨蚀较轻,形态与 V 13823 的较相似。下后尖处的环还未形成,下中央尖与下前边脊和下中脊连或几乎连。下后附尖存在,弱或很发育。下颊侧沟与下舌侧褶 IV 通(2/3) 或不通(1/3)。V 14151.1 的 m1 磨蚀很深,其舌侧褶 I、II 和 III 各成 2 个坑,下舌侧褶 IV 和下颊侧沟各成单一的坑。m1/2 具 4 齿根,后颊侧齿根较大。

m3 冠面约为前宽后窄的三角形。m3 的下三角座与 m1/2 的相似。下后尖处的环在 V 13823 的已形成,只是左、右者大小形状上有些差异;而在其他的较少磨蚀的 m3 上,下后尖处的环还未形成。另外,在 V 13823 和 V 14148.3 的下三角座中,由下原尖向舌侧伸出的小刺已达下中央尖。m3 的后部稍缩小,下跟座稍窄于下三角座。下中脊完全,或中间稍中断。下次脊舌端与下后边脊连,封闭下颊侧褶 IV;下次脊颊端在 V 13823 的右 m3 与下次尖连,而在左 m3 和另外 3 枚 m3 中不连。因此,下颊侧沟在前者不与下舌侧褶通,

而在后 4 枚 m3 中与下舌侧褶 Ⅳ 相通。下舌侧褶 Ⅳ 的变化较大:在 V 13823 被横脊分成前、后 2 个坑,其后坑在右侧是扁的长圆形,而在左侧则为串珠状;其余的 3 枚 m3 中,舌侧褶 Ⅳ 被数量、大小和形状不同的尖或突起充填。在 5 枚可见齿根的 m3 中有 4 枚具分开的 4 齿根,仅 V 14148.3 的后 2 齿根开始相连,但该 2 齿根间仍有显著的纵沟相隔。

dp4 冠面的形态结构与 p4 相似,也为前窄后宽的卵圆形,但比 p4 稍小,较窄长些,齿冠也低些。具前 1 后 2 共 3 齿根。

测量(见表 1 和表 2)

比较 禄丰的标本在齿冠的高低、颊齿的冠面形态结构和个体较大等特征上均与 *Hystrix* 属的一致,而与 *Trichys*、*Atherrurus* 和 *Thecurus* 明显不同。与 *Hystrix* 属的已知种比较,禄丰的标本的齿冠比第四纪和现生的种要低得多。

Hystrix 属目前已知有 11 种化石出现在新近纪,它们是:*H. parvae*、*H. primigenia*、*H. sivalensis*、*H. leakeyi*、*H. etrusca*、*H. refossa*、*H. zhengi*、*H. depereti*、*H. aryaenesis*、*H. gansuensis* 和 *H. caucasica*。在这些种中,禄丰标本在齿冠较低的特点上与 *H. parvae*、*P. primigenia* 和 *H. sivalensis* 的相近而比其余的 8 种的齿冠都低(见表 3)。在颊齿的尺寸大小上,禄丰的标本比 *P. parvae* 和 *H. leakeyi* 的大,而小于 *H. primigenia*、*H. zhengi*、*H. depereti* 和 *H. caucasica*。此外,禄丰的标本与 *H. parvae* 的不同还在于上臼齿舌侧褶较短,其颊端约与颊侧褶的舌端在同一水平,不与颊侧褶舌部相重叠(而 *H. parvae* 的较长,其颊端超过颊侧褶 I 舌端,彼此部分重叠);与 *H. primigenia* 的区别还有:禄丰标本的上颌骨腭面较宽,左、右上颊齿列往前靠近(而 *H. primigenia* 的往前分开),下颌骨齿隙较长,前端较高,比颊齿冠面还高(而后者的约与颊齿齿槽缘在同一水平),上颊齿的舌侧沟横向较短,其颊端约与颊侧褶的舌端在同一水平(而后者的较长,其颊端往外通常超过颊侧褶 I 舌端,彼此部分重叠),M3 较少退化,p4 和 m3 通常具 4 齿根;与 *H. sivalensis* 的区别还在于禄丰标本的 p4 和 m3 具 4 齿根(而 *H. sivalensis* 的 p4 和 m3 均具 3 齿根,前齿根无纵沟);与 *H. gansuensis* 的区别还在于上颊齿通常具发达的中附尖,上臼齿颊侧褶 I 通常开口,P4 前尖通常孤立等;与 *H. aryanensis* 的区别还有:上颌骨腭面较宽,2 颊齿列往前靠近;上颊齿舌侧沟不与颊侧褶相通,具 3 齿根;与 *H. depereti* 的区别还在于上颊齿内侧齿根具明显的纵沟;与 *H. etrusca* 的区别还在于后者的两上颊齿列彼此近于平行,下颌骨水平支较高,较厚;与 *H. refossa* 的区别还在于下颌骨较浅,厚度较少;与 *H. caucasica* 的区别还在于 p4 缺下前褶(anteroflexid,见 Lopatin et al., 2003,图 2)等。由上面的比较可以看出,禄丰标本代表不同于 *Hystrix* 属目前已知种的新种,我们称其为禄丰豪猪 *Hystrix lufengensis* sp. nov.。

关于禄丰古猿地点产化石层位的时代 邱铸鼎等(1985)认为禄丰古猿地点产化石层位的时代属最晚中新世保德期,相当欧洲陆相哺乳动物分期的土洛里期(Turolian)。个体由小到大被认为是 *Hystrix* 的一种演化趋势(Sen, 1999)。而 *H. lufengensis* 的个体较 *H. parvae* 的大,有可能比 *H. parvae* 稍进步些。另一方面,*H. lufengensis* 具有一些比 *H. primigenia* 较原始的特征,如个体稍小,M3 较少退化,p4 和 m3 通常具 4 齿根等。*H. lufengensis* 在进化程度上有可能比 *H. primigenia* 还稍原始些。*H. parvae* 目前已知时代分布为欧洲陆相哺乳动物群分期的 MN10～MN11,而 *H. primigenia* 的时代分布为 MN12～MN16。如果上面关于 *H. lufengensis* 的进化程度在 *H. parvae* 和 *H. primigenia* 之间的分析

表1 禄丰豪猪(新种)上牙测量

Table 1 Measurements of upper teeth of *Hystrix lufengensis* sp. nov. (in mm)

		V13823 正型(holotype)		V14152.1~6		V14153.1	V14153.2	V14153.3	V14153.4	V14153.5	V14153.6	V14153.7	V14147.1	V14147.2
		left	right	left	right									
P4~M3 L		37.2	36.8*	34.6										
M1~3 L		26.2	21.9*	24.6										
P4	L	11.2		10.5		11.5								
	Wc	10.6		9.9		10.2								
	Wm	11.4		11.2		11.7								
	Hl	9		7.2		9.2								
	Hb	5		4.1		5.4								
	Hs	5.2				5.2								
	Hl/Hb	1.8		1.76		1.7								
	Hl/L	0.8		0.69		0.8								
M1	L	9.1		8.5	8.7		10							
	Wc	9.6		9.8	9.6		8.6	8						
	Wm	10		10.4			9.1							
	Hl	7e		4.9	5.1		9.6							
	Hb	4.6		4.2	4		5.5							
	Hs						6.1							
	Hl/Hb	1.52		1.17	1.28		1.75							
	Hl/L	0.77		0.58	0.59		0.96							
M2	L	8.7		8.8					8.8	8.1				
	Wc	9.3		9.3					7.2	6.7				
	Wm	9.4		10.1					8.5	8				
	Hl			5.6					11	8.2				
	Hb	4.4		4					4.6	3.7				
	Hs								6.5	6				
	Hl/Hb			1.4					2.39	2.22				
	Hl/L			0.64					1.25	1.01				
M3	L	8.4		8.5	8.6						9.3	8.7	8.5	9.2
	Wc	8.4		9	9.1						7	7.6	6.7	7.5
	Wm	8.7		9.5							9.2	8.8	8	8.4
	Hl	8.6		6	6						10.5	11.2	9	12.7
	Hb	4e		3.7	4						5.7	5	3.7	5.6
	Hs	6.6		5.5	4.5						5.5	3.1	4.4	8.2
	Hl/Hb	2.15		1.62	1.5						1.84	2.24	2.43	2.27
	Hl/L	1.02		0.71	0.7						1.13	1.29	1.06	1.38
I2	T	9.1												
	W	6.5												

缩写 Abbreviations: L. 长 length; Wc. 冠面宽 width of occlusal surface; Wm. 最大宽 maximum width; Hl. 舌侧釉质层高 enamel height of lingual side; Hb. 颊侧釉质层高 enamel height of buccal side; Hs. 舌(颊)侧沟基部到釉质层底的高 enamel height from base of sinus (sinusid) to base of enamel..

* 根据颊齿印痕测量 Based on prints of cheek teeth.

表 2　禄丰豪猪(新种)下牙测量

Table 2　Measurements of lower teeth of *Hystrix lufengensis* sp. nov.　(in mm)

	V13823 正型(holotype)		V14151.1	V14147.3	V14147.4	V14153.8	V14148.1	V14153.9	V14148.2	V14147.5	V14151.2	V14153.10	V14147.6	V14151.3	V14151.4	V14148.3	V14150.1	V14150.2	V14149	V14147.7
p4～m3 L	39																			
m1～3 L	28.5																			
L	11		10.3	10.5	11.1	10	10.7													
Wc	9.3		9.7	8.6	8.8	7.4	8.2													
p4 Wm	10			8.8	9.2	8.3	9.3													
Hl	6.5		5.5	4.7	8	6.1	8													
Hb	7.5		5.2	5.4	9.8	7.4	9.2													
Hs	3.5			5	3	2	2													
Hb/L	0.68		0.5	0.51	0.88	0.74	0.86													
L	10		9.6							9		9.9								
Wc	9		9.5							8.2		7.2								
m1 Wm	9.3									8.3		8.3								
Hl	4		3.9							4.1		6.5								
Hb	5		2.5							4.1		7								
Hs										2		3.2								
Hb/L	0.5		0.26							0.46		0.71								
L	10.3										9.8		9.6							
Wc	9.6										8.3		8.4							
m2 Wm	10.1										9.2		9.1							
Hl	5										5.4		5.3							
Hb	5.5										5.4		6.5							
Hs											2.1		2.5							
Hb/L	0.49										0.55		0.68							
L	9.7	9.7												9	9.7	8.3				
Wc	8.4	8.6												7.1	6.3	6.9				
m3 Wm	8.6	8.9												8.3	8	7.8				
Hl	6	5.6												6	5.6	5.8				
Hb		5												6	7.5	6				
Hs														2.5	2.8	2				
Hb/L		0.52												0.67	0.77	0.72				
L								10.1	10.1											
Wc								6.4	6.4											
dp4 Wm								7.4	7.2											
Hl								4.5	4.6											
Hb								7	5.7											
Hb/L								0.69	0.56											
i2 T	8.9	8.9	8.5														8.2	8.4	9.3	8.2
W	6.3	6.2	6.2														5.9	5.9	6.2	5.2

缩写同表 1 Abbreviations same as in table 1.

表 3　几种豪猪 M1/2、p4 和 m1/2 的釉质层高度*与齿冠长之比值比较

Table 3 Comparison of ration of the enamel height*/ occlusal length of M1/2, p4 and m1/2

Species	M1/2			p4			m1/2		
	N	Range	Mean	N	Range	Mean	N	Range	Mean
H. lufengensis	7	0.58～1.25	0.83	6	0.44～0.88	0.69	7	0.26～0.71	0.53
H. parvae[1)]	8	0.72～1.39	1.07				4	0.41～0.82	0.68
H. primigenia[1),4)]	2	0.7～0.9	0.8	4	0.86～0.92		4	0.39～0.75	0.56
H. primigenia[2)]	9	0.56～1.366	0.82				12	0.23～0.70	0.46
H. gansuensis[3)]	3	1.39～1.52	1.43						
H. brachyura[1)]	28	1.1～2.5	2				22	1.2～2.2	1.8
H. cristata[1)]	16	1.2～2.2	1.8				10	1.5～1.9	1.8
H. refossa[1)]	13	1.6～2.4	2.1				7	1.5～2.2	1.8
H. depereti[4)]				1		1.11			
H. zhengi[5)]				4	0.9～1	0.96			
H. caucasica[6)]				1		1.06			
H. sivalensis[7)]							1	0.64	

*M1/2 为舌侧釉质层高 lingual enamel height on M1/2, p4 和 m1/2 为颊侧釉质层高 buccal enamel height on p4 and m1/2; 1)～6) After Sen (1999), van Weers and Montoya (1996), Wang and Qiu (2002), Sen (2001), van Weers and Zhang (1999), Lopatin et al. (2003) respectively; 7) After Lydekker (1884), length of m1 is taken by senior author based on fig. 4.

是合理的话,它的时代有可能相当欧洲陆相哺乳动物群分期的 MN11 和 MN12 之间。李传夔等(1984)将中国的晚中新世划分为灞河和保德两个期。邱占祥和邱铸鼎(1990,1995)认为划分灞河期和保德期的化石证据还不够充分,建议将该两期合并,统称为保德期(广义)。张兆群等(2002)根据陕西蓝田地区晚中新世地层和哺乳动物化石的研究,认为灞河期和保德期的哺乳动物群有明显的区别,建议仍将中国的晚中新世划分为灞河期和保德期(狭义)。我们赞同张兆群等(2002)将灞河期和保德期划分开的意见。这样,云南禄丰古猿动物群的时代应为距今约 8 Ma 的晚中新世保德期(狭义)的较早期,与欧洲 Turolian 期的较早期的时代大致相当。

亚洲中新世的豪猪已知包括 3 种: *H. lufengensis*、*H. sivalensi* 和 *H. gansuensis*。*H. lufengensis* 的齿冠明显比 *H. gansuensis* 的低,显然要比后者原始得多。*H. lufengensis* 与 *H. sivalensis* 的区别特征(如 p4 和 m3 具 4 齿根等)也为较原始的特征,*H. lufengensis* 显然也要比 *H. sivalensis* 原始些。*H. gansuensis* 的产出时代为晚中新世或更晚些。*H. sivalensis* 的时代距今约 7.3～8 Ma (Barry et al., 2002)。这样,*H. lufengensis* 代表亚洲目前已知最早、最原始的豪猪。Van Weers & Zheng (1998)认为 *H. primigenia*、*H. sivalensis*、禄丰的豪猪(即 *H. lufengensis*)和龙骨坡的豪猪(即 *H. zhengi*)可能有共同的起源。*H. sivalensis* 和 *H. lufengensis* 的形态结构的确很相似,只是稍进步些,它有可能是由类似 *H. lufengensis* 的种类演化来的。至于 *H. lufengensis* 与欧洲的 *H. parvae* 和 *H. primigenia* 的关系,因材料太少还难作判断,这有待发现更多更好的材料。

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A PORCUPINE (RODENTIA, MAMMALIA) FROM LUFENGPITHECUS SITE, LUFENG, YUNNAN

WANG Ban-Yue QI Guo-Qin

(*Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences* Beijing 100044)

Key words Lufeng of Yunnan, late Miocene, Hystricidae

Summary

The porcupine fossils from the *Lufengpithecus* site in Lufeng, Yunnan, were collected in the period from 1975 to 1983. They were preliminarily identified as *Hystrix* sp. (Qiu et al., 1985). Further study of these fossils indicates that they represent a new species of *Hystrix*. All the specimens were collected from *Lufengpithecus* site, IVPP Loc. 75033, at Shihuiba, Lufeng, Yunnan.

Hystricidae Fischer de Waldheim, 1817

Hystrix **Linnaeus, 1758**

Hystrix lufengensis **sp. nov.**

(Fig. 1; Tables 1～3)

Hystrix sp. Qiu et al., p. 21

Holotype A badly crushed skull with left I2, P4～M3, imprints of right P4～M3, left mandible with i2, p4～m3, posterior part of right mandible with m3, and an i2, all of which may belong to one and the same individual (IVPP V 13823).

Horizon of holotype Level 3 of the *Lufengpithecus* site section D (See Qi, 1985, fig. 5); late Miocene.

Referred specimens Anterior part of a right mandible with i2 and p4～m1 (V 14151.1); 28 isolated cheek teeth and 4 i2 (V 14147～14153).

Horizons of referred specimens V 14147～14151, from Level 2 to 6 of *Lufengpithecus* site section D respectively; the levels of V 14152 and V 14153 are unclear; late Miocene.

Diagnosis A mid-sized and more primitive *Hystrix*. Upper cheek tooth rows convergent anteriorly; horizontal ramus of mandible low, long diastema with slightly concave upper border and high anterior end, higher than the occlusal surface of cheek teeth. Cheek teeth moderately brachyodont; lingual sinus in upper cheek teeth transversely short, neither communicating nor overlapping with buccal folds; P4 large, with isolated paracone in adult individuals, well-developed mesostyle, not joining with mesoloph, Fold III and IV forming U-shaped valley; M3 slightly reduced. Upper cheek teeth with 3 roots, large lingual root with distinct longitudinal groove; lower cheek teeth usually 4-rooted.

Description IVPP V 13823 and 14153.1 are of adult individuals (equivalent to age-class VI of van Weers in 1990), and V 14151.1 and V 14152.1～6 may be of old individuals (age-class VII of van Weers).

The skull of V 13823 is badly crushed and compressed. The only preserved parts are the left maxillary with P4～M3 and part of palate, and the right auditory bulla. The distances from central palate suture to P4, M1/M2, and M3 are 7 cm, 8 cm and 9 cm respectively. The two upper cheek tooth rows are convergent anteriorly. The horizontal ramus of the mandible is low and its lower border is convex anterior to the m1. The i2～p3 diastema is long, with a slightly concave upper border and a high anterior end, which is higher than the upper surface of the lower cheek teeth. The

mental foramen is located anterior to the p4. The anterior end of the well-developed masseteric fossa extends below m1. The masseteric ridges are strong. The angular process extends outside the posterior end of the i2 alveolus.

The I2 is oval in cross section with a flatter labial side. The enamel covers the labial side, 1/3 of the lateral side and 1/4 of the medial side. No distinct groove is present on the enamel surface. The i2 is similar to the I2, but less curved. The enamel covers slightly wider: covering the labial side, 2/5～1/2 of lateral side and 1/3 of medial side.

The cheek teeth decrease posteriorly in size, and are moderately brachyodont. The lingual side of the upper cheek tooth crown is higher than the buccal one, and has a deep sinus. The P4 is oval in occlusal view, longer than wide. The anteroloph joins with the protocone to form a continuous ridge. The isolated paracone connects neither with protoloph, nor anteroloph. The mesostyle (after Sen, 2001) is well developed and larger than the paracone, may or may not meet the paracone, but never joins with the mesoloph. The hypocone joins with the mesoloph (after Sen, 2001 = mesostyle + mesoloph of Wang and Qiu in 2002) and posteroloph to form a U-shaped crest. The lingual part of the metaloph is free and complex in form. It may be forked, or may form a closed basin. On the occlusal surface the sinus is short and extends antero-buccally. It does not meet Fold I or Fold II, nor overlapped the latters in adult stage, but forms a closed basin in old stage. P4 is 3-rooted, the large lingual root has a distinct longitudinal groove.

The M1 is trapezoid in occlusal view, with a longer anterior side than the posterior one. Fold I is usually separated into two small basins; the buccal one is open buccally in slightly worn specimens, but closed in heavier worn ones. The metaloph bends posteriorly to meet the posteroloph. Fold III is L-shaped and Fold IV forms a closed basin. The sinus is usually closed into a basin on heavier worn specimens. The other features of M1 are similar to those of P4. The M2 is similar to M1 in basic features. The M1 and M2 are difficult to be distinguished when they are isolated. In such cases we call them M1/2.

The M3 is similar to M1/2 in basic features, but its posterior part is narrower and more variable. Fold IV may be open or closed buccally, and when closed may form one basin or two separated by an oblique crest. When more accessory cupids are present before the protoloph (for example, V 14153.6 and V 14153.7), the protoloph usually has more folds when worn. There is an accessory cusp between the mesostyle and the metacone in V 14147.1～2.

In the lower cheek teeth the buccal side of the crown is slightly higher than the lingual one. The sinusid on the buccal side extends deeply, almost to the base of the crown. The p4 is oval in occlusal view, with a narrower trigonid. The metalophid bends anteriorly to meet the anterolophid and metastylid. Fold I is a closed basin. A "crist" extends from the anterolophid into Fold I. The protoconid joins anterolophid and mesolophid to form a U-shaped lophid. L-shaped Fold II bends anteriorly, and has a forked buccal end. There is also a "crist" extending from the joining point of the mesolophid and mesostylid towards the metastylid. Fold IV is closed.

m1 and m2 are similar to each other in occlusal features. We could not distinguish them when they are isolated. We call them m1/2 here. The m1/2 is oval in occlusal view, with a straighter anterior side. In V 13823 the m2 is less worn than the m1. The anterolophid, protoconid and mesolophid form a U-shaped lophid. On the anterolingual corner of the m2 the ring-shaped lophid may be formed of metalophid, which joins anterolophid and metastylid. Fold II is separated by the central conid (after Sen, 2001) into two parts: the lingual one is L-shaped and open lingually; the buccal one is a closed basin, in which a "crist" extends from the protoconid towards the central conid. The mesostylid joins the mesolophid. Fold IV is separated into two closed basins. There is a small closed basin in the wide area of the hypoconulid. The sinusid extends posterolingually and does not communicate with the lingual fold. In V 13823 the m1 is worn heavier than the m2. The basins in the anterolingual corner and the hypoconulid area disappear. The lingual part of Fold II is separated into two parts in worn m1. In some slightly worn m1/2 the ring at the anterolingual corner is incompletely formed. In some heavier worn m1/2 (V 14147.5) the metalophid bends anteriorly to

join the anterolophid. The central conid is absent and the metastylid is well developed to join the mesolophid. Fold IV is a single long basin. In heavily worn m1 of V 14151.1, Fold I, II and III form 2 closed basins each, but Fold IV and sinusid form only single basins. The m1/2 has four roots.

The trigonid of m3 is similar to that of m1/2 in basic features. The "crist" from the protoconid is more developed, reaching the central conid. The talonid is narrower than the trigonid and variable. The mesolophid is either complete or interrupted at middle part. The hypolophid joins the posterolophid to close Fold IV lingually. The buccal end of the hypolophid joins the hypoconid in right m3 of V 13823 to separate Fold IV and sinusid. In left m3 of V 13823 and other three m3 it does not meet the hypoconid, and the sinusid communicates with Fold IV. Fold IV is variable: it may be separated by a transverse crest into two basins or beaded in form. The m3 usually have four roots (in four of five). In V 14148.3 the two posterior roots coalesced into one, leaving still a distinct longitudinal groove. The dp4 is similar to p4 in basic features, but is slightly smaller and narrower, and lower crowned than the p4.

Comparison The assignment of the Lufeng specimens to the genus *Hystrix* is based on the large size, crown height and occlusal morphology of the teeth. They are different from the Pleistocene and Recent species of *Hystrix* in having much lower crown.

The Neogene fossil *Hystrix* are known to include 11 species. The cheek tooth crown of the Lufeng specimens is similar to that of *H. parvae*, *H. primigenia* and *H. sivalensis* in height, but lower than in the other eight species. In addition, the Lufeng specimens are larger than *H. parvae* and *H. leakeyi*, but smaller than *H. primigenia*, *H. zhengi*, *H. depereti* and *H. caucasica*.

The Lufeng specimens are further different from those of *H. parvae* in having transversely shorter sinus in upper molars; from those of *H. primigenia* in having a wider palate, anteriorly convergent upper cheek tooth rows, longer i2～p4 diastema with its higher anterior end, transversely shorter sinus in upper cheek teeth, less reduced m3 and four roots in p4 and m3; from *H. sivalensis* in having four roots on p4 and m3; from *H. gansuensis* in having a well-developed mesostyle in upper cheek teeth, a usually open Fold I on upper molars and an isolated paracone in P4; from *H. aryanensis* in having wider palate, anteriorly convergent upper cheek tooth rows, sinus not communicating with buccal folds and three roots in the upper cheek teeth; from *H. depereti* in having distinct longitudinal groove on the lingual side of the lingual root of upper cheek teeth; from *H. etrusca* in having anteriorly convergent upper cheek tooth rows and lower and narrower horizontal ramus of mandible; from *H. refossa* in having lower and narrower horizontal ramus of mandible; from *H. caucasica* in lacking anteroflexid on p4. It seems that the Lufeng specimens represent a new species of *Hystrix*, named as *H. lufengensis* here.

Age of deposits bearing fossil of the Lufengpithecus **site** The age of the deposits yielding *Lufengpithecus* fauna was formerly considered as Baodean, latest Miocene, about equivalent to the Turolian in Europe Mammalian Ages (Qiu et al., 1985). *Hystrix lufengensis* seems more advanced than *H. parvae* because of its larger size, if Sen's (1999) suggestion that "the increase of the size may be considered as a derived feature" is tenable. On the other hand, *H. lufengensis* seems slightly more primitive than *H. primigenia* because of its primitive features than in the latter: smaller in size, less reduced M3, p4 and m3 with four roots, etc. Thus, *H. lufengensis* is more advanced than *H. parvae*, but more primitive than *P. primigenia*. *Hystrix parvae* is known to range from MN10 to MN11 in Europe Mammalian Ages, and *H. primigenia* from MN 12 to MN16. The age of the deposits bearing *H. lufengensis* thus may well be equivalent to the period between MN 11 and MN 12 in European Mammalian Age. In the Chinese Mammalian Ages the late Miocene was subdivided into two periods: Bahean and Baodean (Li et al., 1984). However, Qiu and Qiu (1990, 1995) thought that the differences between the Bahean and Baodean faunas were obscure, and suggested that the Chinese late Miocene would be represented by a single Baodean (s. l.), which included both Bahean and Baodean (s. s.). Recently, Zhang et al. (2002), based on distinct turnover event occurred between the Bahe Fauna and the Baode Fauna in the Lantian Basin,

suggested to reinstate Li et al.'s subdivision, with which we agree. The *Lufengpithecus* fauna is thus early Baodean (s. s.) in age, late Miocene (about 8 Ma), roughly equivalent to early Turolian in Europe.

The Miocene *Hystrix* in Asia is so far known to include three species: *H. lufengensis*, *H. sivalensis* and *H. gansuensis*. As above comparison shows, the former seems to be more primitive than the two latters in having more primitive features. The age of *Hystrix sivalensis* has been considered about 7.3～8 Ma (Barry et al.,2002). *Hystrix lufengensis* is perhaps the earliest and most primitive *Hystrix* so far found in Asia. Van Weers and Zheng (1998) suggested that *H. primigenia*, *H. sivalensis*, *Hystrix* from Lufeng (= *H. lufengensis*) and from Longgupo (= *H. zhengi*) might have a common origin. *Hystrix sivalensis* is very similar to *H. lufengensis* in basic features, probably only slightly advanced than the latter. *Hystrix sivalensis* could be derived from *H. lufengensis*-like forms. For a better understanding of the relationships among *H. lufengensis*, *H. parvae* and *H. primigenis*, more material is needed.

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后记:本文三校后,笔者收到了 van Weers 博士关于云南禄丰豪猪化石的文章(Beaufortia, **54**(5):75～80)。文中提到他的研究乃受本文后一作者和邱铸鼎博士的委托。van Weers 博士在访问我所时曾观察过这批豪猪化石,并多次表示希望与本文后一作者共同研究。不论是本文后一作者,还是邱铸鼎都没有表示过同意。不意 van Weers 博士已将文章发表了。

好在 van Weers 博士只记述了禄丰豪猪的牙齿。在对禄丰豪猪全部化石(包括头骨、下颌骨等)作了全面研究后,本文作者得出了和 van Weers 博士不同的结论:禄丰的豪猪化石不应该归入 *H. primigenia*,而应该是一个新种。