

Allacerops (奇蹄目、犀超科)化石在我国的发现及其分类地位的讨论¹⁾

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摘要 记述了一段属于 *Allacerops* cf. *A. turgaica* 幼年个体的下颌骨。化石采自甘肃兰州盆地渐新世地层中。*Allacerops* 是亚洲一类较原始的犀。在基本特征上,特别是在门齿和犬齿构造上,它和欧洲的 *Eggysodon* 最为接近,有人把它们合为一属。研究表明,它们在门齿的数目和颊齿的形态上有比较明显的差异,应是跑犀科内不同的属。文中主要根据犀类门齿、犬齿的分异,对犀超科内科一级的现行划分提出质疑,认为 Indricotheriidae 科的地位应予恢复,跑犀科只应包括那些门齿、犬齿未特化,也不急剧退化的中、小型犀类。这样,除两栖犀外,犀超科包括三科: Hyracodontidae, Indricotheriidae 和 Rhinocerotidae。

关键词 兰州盆地, 渐新世, 犀类, 分类

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Allacerops 是生活于亚洲大陆渐新世的一类犀牛。由于化石发现不多,古生物学家对它还不十分了解,对它在犀超科中的分类地位的见解分歧较大。在我国的渐新世地层中过去一直没有发现过这个属的化石。1996年9月,我们在兰州盆地大红沟一带考察时,在 GL9605 地点咸水河组下段第二层黄砂岩中发现了这类犀的一段幼年个体的下颌骨 (IVPP V9964)。这件标本的发现不但进一步证实了兰州盆地西北部产 *Allacerops* 的咸水河组下段黄砂岩层的地质时代为渐新世,使其与兰州盆地东部产南坡坪渐新世哺乳动物群的地层能够互相对比 (邱占祥等, 1997), 更重要的是,它为我们进一步了解这个属的性质和分类地位提供了新的重要信息。

GL 为甘肃省博物馆野外地点编号, IVPP V 为中国科学院古脊椎动物与古人类研究所化石编号。

1 *Allacerops* 属的研究历史及问题

Allacerops 这个属名是 H. E. Wood 于 1932 年提出的,用以代替 Borissiak 所使用的 *Epiaceratherium (turgaicum)* 和 Roman 的 *Eggysodon*。古生物学家对上述三个属的含义和

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使用有很大的分歧。为了弄清这些分歧,我们对 *Allacerops turgaica* 和 *Eggysodon* 的研究历史作一简单回顾。

Eggysodon 这个属名是 Roman 于 1910 年所创,属名的含义是犬齿离前臼齿很近。关于该属的详细记述和讨论发表于 1911 年。Roman 在建属时指定 Schlosser 于 1902 年所建的“*Ronzotherium*” *osborni* 为属型种。属型种的正型标本是发现于德国 Verigenstadt 地点 Bohnerz 层中一个左 M2。Schlosser 在建立该种时曾指出, Filhol (1886) 和 Osborn (1900) 所提到过的产自法国 Quercy 的一些零散牙齿也应该归入该种。Roman 在创建 *Eggysodon* 时记述了产自 Quercy 的很完整的上齿列,标本共三件(两件保存在法国 Montauban 博物馆,一件在瑞士巴塞尔博物馆)。他把它们都归入到 *Eggysodon osborni* 种中。同时 Roman 把 Rames 于 1886 年定为 *Acerotherium gaudryi* 的一件下颌骨(产于 Auvergne 地区 Brons 地点的 Cantal 粘土中)也归入了他的新属: *Eggysodon gaudryi*。此外,他把瑞士巴塞尔博物馆的一件保存得很好的下颌骨(产自 Lot-et-Garonne 的 Latou 地点)也归入了 *Eggysodon gaudryi*。Roman 还自创了一个新种: *Eggysodon pomeli*, 材料是采自 Allier 地区 Gannat 的上颌。应该说,上述这些材料已经相当丰富,足以对 *Eggysodon* 属的牙齿特征作出比较全面的概括,但 Roman 给 *Eggysodon* 属下的定义却十分简单:“小个体犀类,上牙有连续生长的三个臼齿,四个前臼齿,犬齿和数目不详的门齿”(Roman, 1911, p. 7)。实际上我们通过 Roman 的描述可以把这个属的特征更清楚地概括为:上前臼齿为异型齿, M3 三角形,犬齿粗壮,近于垂直生长,距离颊齿很近。其中具有大的犬齿这一点,和当时已知所有的真犀都有鲜明的差别:在真犀中只有第二对下门齿加大并向前伸。

Borissiak (1915) 根据在哈萨克斯坦 Chelkar-Tenis 湖边采到的不完整头骨、下颌和颅后骨骼定了一个新种: *Epiaceratherium turgaicum*。这个种的详细描述发表于 1918 年。这件化石也是有近于垂直生长的犬齿,但门齿的情况不知。Borissiak 没有把它和 Roman 的 *Eggysodon* 联系在一起,而归入了 Abel 于 1910 年所创建的 *Epiaceratherium* 属。这主要是由于它们的上前臼齿在进化水平上比较接近的缘故。这一归属是错误的,因为 *Epiaceratherium* 的属型种, *E. bolcense*, 无下犬齿,而有加大的第二下门齿。Dal Piaz (1930) 首先发现了这个错误。Wood (1932) 同意 Dal Piaz 的看法,但是,不知什么原因,他认为 *Eggysodon* 不是一个有效属名,因而以 *turgaicum* 作为属型种另创了一个新的属名: *Allacerops*。他同时也把欧洲 *Eggysodon* 的三个种: *E. gaudryi*, *E. osborni* (Wood 将其改名为 *osborniana*) 和 *E. pomeli*, 都归入了 *Allacerops* 这个属,并为它们创造了一个新亚科 *Allaceropinae*。

Roman 和 Borissiak 之后比较重要的发现是 Stehlin (1930) 记述的采自法国 Tarn 省 Puylaurens 地点的一个下颌骨。它使我们第一次了解到这类犀牛除了有较粗壮的犬齿外,还有两对没有加大的下门齿(根据齿槽判断)。Stehlin 还指出 Roman 的 *Eggysodon* 在语源上有毛病,建议更改为 *Engyodon*。不过这一点没有充分的命名法规则的依据,因此没有为后人所接受。

此后的半个多世纪中关于这类犀牛的报道甚少。Beliajeva (1954) 记述了少量采自蒙古 Tatal-Gol 的材料,定了一个新亚种: *Allacerops turgaica minor*。Brunet (1979) 记述了若干采自法国阿奎丹盆地 Villebramar 地点的 *Eggysodon* 牙齿和肢骨化石。Dashzeveg (1991)

曾把若干蒙古 Khoer-Dzan 地区 Ergilin 组的一些化石鉴定为 *Allacerops* sp.。但这一鉴定的可靠性很值得怀疑,一方面是因为化石保存很差,另一方面是标本的尺寸都明显地小于这类犀。Reshetov 等(1993)在哈萨克斯坦离 Chelkar-Tenis 不远的 Tort-Mola 地点发现了属于同一个体的上、下颌,认为它和 Borissiak 的“*Epiaceratherium*” *turgaicum* 完全一样,应为同一种犀。他们没有采纳 Wood 的属名 *Allacerops*,而是为它另起了一个新属名 *Tenisia*。后来由于发现这个名称已先被一腕足类占有,1994 年又改名为 *Teniseggsodon*。这件标本虽然保存得很不理想,但第一次提供了亚洲这类犀牛的准确的下门齿的信息。De Bonis 等(1995)记述了若干采自法国 Garouillas 的 *Eggsodon* 的材料,使我们对欧洲这类吻端构造特殊的犀牛有了更多的了解。

目前对这一类犀牛在属一级的分类上有三种不同的意见:一是沿用 Wood 的意见,使用 *Allacerops*,把 *Eggsodon* 看作 *Allacerops* 的同物异名,例如 Beliajeva(1954)和 Dashzeveg(1991)。二是以 *Eggsodon* 取代 *Allacerops*。Brunet(1979)首先提出,*Allacerops* 与 *Eggsodon* 应为同属,而后者具有优先权。这一意见获得大多数古生物学家的赞同(Heissig, 1989a; Prothero 等, 1989)。三是认为这两者应为不同的属。Reshetov 等(1993)承认欧洲的 *Eggsodon* 为有效属,而为 *turgaicum* 另创一新属名: *Teniseggsodon*。Dashzeveg(1996)表示赞同这一意见。

在属以上的分类上,最早明确提出为这类具粗壮犬齿的犀类建立亚科的是 Breuning。1924 年他以 *Eggsodon* 为模式属建立了 *Eggsodon tinae* 亚科,包括 *Eggsodon*, *Prohyracodon*, *Meninatherium* 和 *Praeaceratherium*。Wood(1932)以 *Allacerops* 为模式属提出了另一个亚科名称 *Allaceropinae*,只包括 *Allacerops* 一个属。此后这两个名称被不同的学者分别沿用。由于一般都错误地认为 *Eggsodontinae* 是 Viret 于 1958 年首次提出的,晚于 Wood 的 *Allaceropinae*,所以目前大多数人都使用 *Allaceropinae*。在这一亚科究竟应该包括哪些属的问题上仍然有不同的意见。Heissig(1989a)提出该亚科包括三个属: *Eggsodon*, *Prohyracodon* 和 *Illianodon*。这一意见为大部分古生物学家所接受(Prothero 等, 1989 和 Reshetov 等, 1993)。但是 Dashzeveg(1996)把 *Forstercooperia*, *Juxia* 和 *Armania*(应归两栖犀?)也包括在内。至于这一亚科在科一级的归属,在 1966 年之前它一直被归入真犀科。Radinsky(1966)提出把它改归跑犀科。现在这一意见已被古生物学家所普遍接受。可能唯一的例外是 Dashzeveg(1991)所表示的意见,当时他仍然把 *Allaceropinae* 归入真犀科。不过 1996 年他已经改变了看法,把它放入了跑犀科。

从以上的叙述我们可以看出,围绕 *Allacerops* 的主要问题在于:1)欧洲的和亚洲的种究竟应该归入一个属,还是分属不同的属? 2)它们和目前归入跑犀科中其他形态接近的属的关系又是如何?

2 标本描述与鉴定

IVPP V9964(图版 I)为一幼年个体的下颌骨的前半部,左水平支只保留 dp4 中部以前的部分,右水平支保留到 m2 后端齿槽缘开始上升处。牙齿中保存有左 di3, dp2, dp3 和 dp4 的前半段,第一、二门齿,犬齿和 dp1 只保留齿槽;右侧 dp1 的齿根、dp2~m1(m2 完全

在齿槽内)保存,门、犬齿仅齿槽保留。

下颌联合部短而窄,其后缘在 dp2 前半部;自顶面看(图版 I, A),中央为斜向前上方的纵向凹槽,dp1 和犬齿之间的齿隙很短,仅长 15mm,齿槽中部向内收缩,左右两峰间最短距离为 26mm,门齿区在 di3 处最宽;自侧面看(图版 I, B),联合部的唇缘与下颌长轴形成大约 45°角,它和下颌下缘的转折处在犬齿下方稍后;自腹面看,左、右两下颌支间的骨缝还可以看出,唇面的上半部较平,但下半部则可见微弱中棱,在中棱的两侧有一对滋养孔,中棱的下后方有清楚的二腹肌的附着痕迹。水平支很粗壮结实,下缘只在 dp3~4 的下方稍稍隆凸,两侧颞孔形状和位置稍有不同,左侧者位于 dp1 的下方,距水平支下缘 15mm;右侧者在 dp1~2 之间的下方(图版 I, B),距下颌下缘约 12mm。下颌骨在齿隙处的高 40mm,在 dp4 和 m1 之间的高 52mm,此处的厚 32mm。

根据齿槽判断,第二门齿可能最大,第一门齿次之,而第三门齿最小。di3 外缘稍破损,自舌面看高接近于宽:牙齿为扁铲状,舌面平,唇面隆,顶缘为不对称弧形,在近中缘稍高,舌侧基部有明显的齿带,在唇侧近中部也可看到微弱的齿带。犬齿没有保存,但从齿槽判断,比门齿大。dp1 只保留单一的齿根。dp2 磨蚀厉害,冠面为扁长形,在形态上很象鹿类的前臼齿:外壁较平,具四个横脊。下前尖近一圆形,它的前方还有一个很小的突起;下原尖膨大,它和下前尖在舌侧以沟相分,自下原尖向内后方伸出一斜脊,它的末端几乎达到牙齿的后缘,使跟座变得很小,下内尖不发育,所以跟座的后横脊只在外半部发育;齿带在前半部的内、外侧都发育,斜向前上方,在唇侧面,在牙齿的中部齿带微弱可见,在后端有一不规则的突起,应为外后齿带的残迹;在舌侧面,除了前端的齿带之外,再无齿带痕迹。dp3 比 dp2 大很多,三角座和跟座的外壁都很圆隆,中间隔以很深的沟,下前脊粗壮,向内伸达舌侧,下前尖之前的突起比 dp2 者明显得多,使牙齿呈锥形三叶齿,下原尖和下后尖组成的横脊,和 dp2 的一样,也是强烈后斜,几乎将跟座凹封闭,和 dp2 不同的是,dp3 的跟座大,下内尖和下次尖组成的横脊很长,使跟座的宽度大于三角座者;齿带的发育情况和 dp2 者相同。dp4 已臼齿化,和 m1 相比,它的三角座由于前脊更斜而接近 V 形;从舌侧看,它的三角座和跟座在高度上大体相同,而在臼齿中跟座的冠高大于三角座者。齿带发育的情况仍然和 dp3 者相近,但更弱些。m1 刚刚开始磨蚀,它的齿冠显著地高于前面的乳齿,跟座的位置低于三角座,微弱弯曲的下次脊的前端,在和三角座外后壁相接的地方突然降低,形成一个深的切迹(图版 I, B)。

测量(mm): di3: 前后厚 6.4,横宽(破)约 10,冠高 9; dp1(齿根): 11×6.3; dp2: 19×10.3; dp3: 28×17.4; dp4: 27×20; m1: 31×22.8×24.5(舌侧下后尖处冠高); dp1~dp4: 85; dp2~dp4: 73.5; dp1~m1: 118; dp2~m1: 107。

在第三纪中期犀类化石中和 IVPPV9964 在形态和大小上最接近的是 Reshetov 等最近记载的 *Teniseggyson turgaicus* 的一个下颌骨。遗憾的是 V9964 为一幼年个体,而 Reshetov 等记述的下颌骨则是成年个体,在牙齿上除 m1 外无法直接对比。但两者仍共有在分类上十分重要的特征。这表现在: 1) 两者都具有接近垂直向上的三对铲形下门齿和一对较门齿粗壮的犬齿; 2) 下颌联合部短而高, c~dp1 之间的齿隙短; 3) 有四个前臼齿, dp1 为单根齿; 4) 在大小上两者接近: Tort-Mola 标本的 p1~p4 长 82.3mm, 兰州标本的 dp1~dp4 长为 85mm。前者的 m1 为 29.9×26.4, 后者的为 31×22.8。Reshetov 等认为他

们记述的 Tort-Mola 的标本和 Borissiak 的正型标本完全一样。这两件标本在上述几点上确实很接近,只是正型标本的下犬齿比 Tort-Mola 者更大些。这可能是性别差异。V9964 和上述两件标本相比似乎整个下颌都更粗壮些,下颌联合部和水平支下缘之间的转角也更尖锐。

另一个和 V9964 较为接近的属则是欧洲的 *Eggysodon*。De Bonis 等最近(1995)发现的材料表明,这个属也有接近垂直向上的下门齿和一对较粗壮的犬齿,其下颌联合也是短而高,c~dp1 之间的齿隙也短,水平支下缘较平直,两者在大小上也接近(见测量)。但是 *Eggysodon* 只有两对下门齿,而不是三对,它的下颌联合的唇侧缘不如 V9964 中那样陡直。*Eggysodon* 的材料中有乳齿,可以和 V9964 直接对比。这就是 Brunet(1979)记述的 Villebramar 的一段带 dp2~m1 的下颌骨。两者在形态上,虽然 dp2~3 都是三叶形,三角座横脊明显斜向内后方,但在 V9964 中下前尖以前的部分很小,亦即三叶形构造不明显,而在欧洲的标本上它们的三叶形构造都很明显。此外,*Eggysodon* 的牙齿显然窄于兰州的标本(见测量,括号内为兰州标本;单位:mm): dp2~dp4: 79(73.5); dp2: 20×8(19×10.3); dp3: 30×14(28×17.4); dp4: 29×16(27×20); m1: 30×19(31×22.8)。

综上所述,我们可以得出以下几点结论:1) V9964 和 Tort-Mola 的标本最为接近,很可能是同一种犀。2) 如果将来的材料能够证明, Tort-Mola 的标本和 Borissiak 记述的 *Epiaceratherium turgaicum* 的区别仅在犬齿的大小上,而且这只是性别差异,那么它们也应为同种。3) 在属名上,我们主张恢复使用 *Allacerops* 这个属名。理由是 Wood(1932, p. 170)在建属时就明确指定 *Allacerops turgaica* 为属型种,而不是如 Reshetov 等(1993, p. 716)所说, *E. osborniana* (或 *osborni*) 是 *Allacerops* 的属型种。因此 *Allacerops* 为有效属名。4) V9964 似乎比上述两件标本都更粗壮,而且下颌联合部和水平支下缘之间的转角也更尖锐。但由于 V9964 为一幼年个体,和 *Allacerops turgaica* 可以直接对比的部分很少,我们暂将它定为 *Allacerops* cf. *A. turgaica*。5) *Eggysodon* 和 *Allacerops* 虽然在形态和大小上相当接近,但两者仍有明显差别。Reshetov 等曾指出两属之间只有两点差别: *Eggysodon* 有两对下门齿, p1 (应为 dp1) 退失; *Allacerops* 有三对下门齿,有 dp1。De Bonis 等新发现的材料表明, *Eggysodon* 也可以有 dp1。这样一来, Reshetov 等所指出的两个差别中就只剩下一个了。我们在对比了这两类犀牛目前已知的材料之后发现,它们之间还有以下一些差别:1) *Eggysodon* 的所有下颊齿都明显比亚洲者更细长,它的 dp2 和 dp3 的三叶状结构也更长而明显;2) 在所有已知 *Eggysodon* 的材料中,下颊齿外壁上的齿带连续而显著,而在亚洲的材料中则发育很弱。考虑到上述这些差别的稳定性,我们认为把欧洲和亚洲的种分为不同的属更为符合实际情况。

3 *Eggysodontinae* 的系统地位

关于这个亚科的名称、组成以及它在犀超科中的地位,还有许多不同的意见。目前的材料也还不足以比较彻底地解决这些问题。但近几年来 *Allacerops* 和 *Eggysodon* 的新材料,特别是吻部的发现,使我们对现行的分类方案的合理性产生了一些疑问。这首先涉及到它的亚科名究竟应该是 *Allaceropinae* 还是 *Eggysodontinae* 的问题。如前所述,

Eggysodon 和 *Allacerops* 在形态上非常接近。遗憾的是, 到目前为止我们还不确切地知道 *Eggysodon* 的下门齿究竟是什么样子。虽然如此, 考虑到它们在整体进化水平和特征上的一致, 把它们归入同一亚科显然更为合理。这样, 亚科名就应为 *Eggysodontinae*, 而不是 *Allaceropinae*。前者是 Breuning (1924) 根据 *Eggysodon* 建立的, 先于 Wood (1932) 创建的 *Allaceropinae*, 因此具有优先权。

其次是关于 Radinsky 的除真犀外几乎无所不包的跑犀科的内涵。1966 年之前大多数古生物学家都同意犀超科包含五个科, 即: *Hyrachyidae*, *Hyracodontidae*, *Amynodontidae*, *Indricotheriidae* 和 *Rhinocerotidae*。1966 年 Radinsky 把 *Hyrachyidae* 改归獬超科, 把除两栖犀科以外的所有犀类重新划分为两个科: 真犀科和跑犀科。真犀科只包括那些 I1/i2 变大的属, 而把所有剩下的属, 包括所有的巨犀, 和当时一般都认为是真犀的 *Allaceropinae* (应为 *Eggysodontinae*) 的成员都归入了跑犀科。这一分类无疑使真犀科变得界限十分分明, 成为一个真正的单系分类单元, 但代价却是使跑犀科又变成一个异常庞杂的复杂分类单元。这一点连 Radinsky 本人也直言不讳。虽然有这样的缺憾, 这一分类还是为大多数古生物学家, 特别是美国的古生物学家所接受。不过也有不同的意见。Heissig (1989b) 认为巨犀仍然应该归入真犀科, Spassov (1989) 和 Dashzeveg (1996) 则认为巨犀应该是一个单独的科。

就目前的资料来看, 如果把两栖犀科排除在外, 所有的犀类在颊齿的进化上都沿着非常近似的路径前进。颊齿, 特别是前臼齿的特征所反映的更多地是进化水平的不同, 而不是支系的分异。相反, 犀类在门齿、犬齿的形态上却沿着十分不同的方向进化。根据现有的资料, 它们可以分成以下三个方向: 1) 在三对门齿和一对犬齿中仅 I1/i2 变大, I1 齿冠变为纵长侧扁, i2 变为高冠, 断面三角形, 包括其余门齿和犬齿退失和 I1/i2 本身后期也退失的类型。属于这一类的是所有目前已知的真犀科。其最早的代表是早始新世的 *Teletaceras*。2) 在不互相密接的锥形的三对门齿和一对犬齿中仅 I1/i1 变大, i1 保持低冠, 向前平伸, 包括其余门齿和犬齿完全退失的类型。属于这一类的是所有目前已知的, 包括 *Juxia* 在内的巨犀类。Forstercooperinae (*Forstercooperia*, *Pappaceras* 等) 具有同样不互相密接的锥形的三对门齿和一对大的犬齿, 但是它们并没有向巨犀的方向发展。它们可以作为巨犀的姊妹组(亚科)归入巨犀科中。3) 犬齿门齿化, 并与门齿组成连续齿列。这一类又可分为二支。以 *Hyracodon* 为代表的北美的类型代表一支, 其门齿、犬齿紧密相连, 门齿和犬齿逐渐演化为细棒状。这一支系可以归入一个亚科, *Hyracodontinae*。以 *Ardynia*, *Parahyracodon* 和 *Allacerops* 等为代表的亚洲的类型代表另一支, 它们的门齿保留铲形, 可以归入另一个亚科, *Eggysodontinae*。 *Ardynia*, *Parahyracodon* 等是早期特化的小型跑犀类, 其犬齿变小, 前臼齿变短, 数目减少。 *Allacerops* 的犬齿仍然保留较大, 前臼齿不退缩。欧洲的 *Eggysodon* 和 *Allacerops* 最为接近。根据上述分析, 我们建议, 除两栖犀外, 犀超科划分为三个科, 即 *Rhinocerotidae*, *Indricotheriidae* 和 *Hyracodontidae*。 *Indricotheriidae* 包括两个亚科: *Forstercooperinae* 和 *Indricotheriinae*。 *Hyracodontidae* 也包括两个亚科: 北美的 *Hyracodontinae* 和亚(欧?) 洲的 *Eggysodontinae*。

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ALLACEROPS (RHINOCEROTOIDEA, PERISSODACTYLA), ITS DISCOVERY IN CHINA AND ITS SYSTEMATIC POSITION

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Key words Lanzhou Basin, Oligocene, rhinoceros, classification

Summary

Allacerops is a comparatively poorly known Asian Oligocene rhinoceros genus. Paleontologists differ widely concerning its systematic position. It had not been found in China until 1996, when the lower jaw (IVPP V9964) was unearthed from the second layer of the yellow sandstone of the Lower Member of the Xianshuihe Formation at GL 9605 in the Dahonggou area of the Lanzhou Basin, Gansu Province (vide Qiu *et al.*, 1997). The discovery not only verified our previous dating of the yellow sandstone of the Lanzhou Basin as of Oligocene, but also provided us with important new information as to the affinity of the poorly known genus *Allacerops*.

1 Brief history of investigation of *Allacerops*

The generic name *Allacerops*, created by H. E. Wood in 1932, was given to the specimens described by Borissiak as *Epiaceratherium turgaicum* to substitute *Eggysodon* erected by Roman in 1910. The name *Eggysodon* was used to allude to the short distance between the canine and the premolars. *Ronzotherium osborni* was designated as the type species of *Eggysodon*, and the type specimen was a left M2. Roman transferred the lower jaw of *Acerotherium gaudryi* described by Rames (1886) in *Eggysodon*, i.e. *E. gaudryi*. Roman also erected a new species, *Eggysodon pomeli*. Although the material known to him was pretty good, the diagnosis of the genus given by Roman was rather simple (Roman, 1911, p.7). In fact, Roman stated the diagnostic features of *Eggysodon* more clearly in the descriptive part of his paper: the upper premolars were heterodont, M3 triangular in form, canine robust, almost vertically implanted, close to the premolars, with almost no diastema between them, etc. The presence of a big canine in this genus clearly separated it from the true rhinoceroses (s.s.), where the 2nd pair of lower incisors are enlarged and the canines

are atrophied.

Boriassiak described an incomplete skeleton of "*Epiaceratherium*" *turgaicum* from Chelkar-Tenis, Kazakhstan, in 1918. This form has also a vertically implanted canine. However, Boriassiak did not associate it with *Eggysodon*, but linked it with *Epiaceratherium* of Abel (1910). This was evidently wrong, since the type of the latter genus, *E. bolcense*, was provided with a pair of enlarged i2, but no lower canine, and the upper canine was also strongly reduced. The error was first pointed out by Dal Piaz in 1930, then by H. E. Wood in 1932. Wood was right in finding out the close affinity between Boriassiak's specimen and the European *Eggysodon*. Unfortunately, he lumped all these forms in one genus, and for some unknown reasons coined a new name: *Allacerops*. For the single genus *Allacerops* Wood also created a new subfamily Allaceropinae. Later, Stehlin (1930) described a lower jaw from Puy-laurens, Tarn, France. This material made it clear that *Eggysodon* had only two pairs of lower incisors.

Since then only a few specimens were referred to this group of rhinoceros. Beliajeva (1954) described a new subspecies from Tatal-Gol, Mongolia: *Allacerops turgaica minor*. Brunet (1979) reported a few specimens of *Eggysodon* from Villebramar, Aquitan, France. Dashzeveg (1991) mentioned some specimens of *Allacerops* sp. from Ergilin Formation, Khoer-Dzan, Mongolia. The referral is doubtful, because the specimens are not only very poorly preserved, but also much smaller in size. Reshetov *et al.* (1993) described a specimen composed of upper and lower jaws of one individual from Tort-Mola, a locality not far from Chelkar-Tenis. This specimen was thought by Reshetov *et al.* as belonging to the same species as Boriassiak's "*Epiaceratherium*" *turgaicum*. Reshetov *et al.* created a new genus for this form: *Tenisia turgaica*. Later the generic name was found to be preoccupied, and renamed as *Teniseggysodon*. Although not ideal in preservation, this material provided us with sure information of the lower incisors (three pairs) of the genus *Allacerops*.

So far there are three different opinions as to the naming of this group of rhinoceroses: 1) To use *Allacerops* instead of *Eggysodon*, as Wood did, and followed by Beliajeva (1954) and Dashzeveg (1991). 2) To use *Eggysodon* instead of *Allacerops*, as Brunet maintained (1979). This was currently accepted by most of the paleontologists (Heissig, 1989a; Prothero *et al.*, 1989). 3) To consider the two as separate genera, as Reshetov *et al.* proposed (1993). Dashzeveg supported this view-point lately (1996).

Breuning was the first to establish a new subfamily: Eggysodontinae, including four genera: *Eggysodon*, *Prohyracodon*, *Meninatherium* and *Praeaceratherium*. H. E. Wood was the second to propose the subfamily name: Allaceropinae, which included only *Allacerops*. Eggysodontinae was often wrongly thought to have been proposed by

Viret in 1958, thus, later than Allaceropinae of Wood (1932). This is the reason why Allaceropinae is currently more widely accepted than Eggysodontinae. Heissig (1989a) included three genera in this subfamily: *Eggysodon*, *Prohyracodon* and *Illianodon*, a view-point widely accepted now (Prothero *et al.*, 1989). Dashzeveg (1996) added *Forstercooperia*, *Juxia* and *Armania* (an amynodont?) to this subfamily. As to its family rank, opinion has changed radically since 1966, when Radinsky transferred it to Hyracodontidae. Prior to 1966, it was referred to Rhinocerotidae without exception.

From the above discussion it becomes clear that there are two main questions in classification of this group of rhinoceroses: 1) Whether the European *Eggysodon* and the Asian *Allacerops* belong to one genus, or represent two separate genera? 2) What is the relationship between this group of rhinoceroses and the other members of the Hyracodontidae?

2 Description of the material

V9964 (pl. I) is the anterior half of a lower jaw of juvenile individual. Of the left branch the part anterior to the middle part of the dp4 is preserved, while of the right branch the part anterior to the ramus ascendens is preserved. Of the teeth the left di3, dp2, dp3 and the anterior part of the dp4 are preserved, and the i1, i2, c, and dp1 are represented only by their alveoli. Of the right side the root of the dp1, the dp2~m1 (m2 is totally in its crypt), and the alveoli of the incisors and canine are preserved.

The symphysis is short and narrow, with its posterior border situated at the level of the anterior half of the dp2. The dorsal (lingual) surface is trough-like. The dp1~c diastema is short, only 15mm long. The alveolar crests are curved, converging lingually at their middle. The shortest distance between the two alveolar crests of the dp1~c diastema is 26mm. The width of the symphysis at the level of the i3 is slightly smaller than that between the two dp2. In lateral view (pl. I, B), the lower border of the symphysis is oblique in direction, forming an angle of about 45° with the alveolar border. On the lower half of the ventral (labial) surface of the symphysis there is a weak sagittal ridge, accompanied bilaterally by a pair of nutrition foramina. The horizontal rami are stout, with their lower border slightly convex below the dp3~dp4. The mental foramen on the left side is located below the dp1, 15mm above the lower border of the jaw, while that of the right side is located between the dp1 and dp2 (pl. I, B). The height of the lower jaw at the diastema is 40mm, at the dp4~m1 is 52mm, and the thickness of this part is 32mm.

Judging from their alveoli, the di2 seems to be the largest of the incisors, the di1 is next large, and the di3 is the smallest. The di3 is slightly damaged. Seen from

the lingual side, the width of the crown approximately equals the crown's height. It is spatulate, with its lingual surface flat, bordered by basal cingulum, and labial surface convex with very weak cingulum. The dp2 is heavily worn. In crown view it is somewhat similar to the lower premolars of a deer: with more or less flat labial wall and four transverse lophids. The paraconid is rounded in shape, with a small tubercle anterior to it. The protoconid is bulky, clearly separated from the paraconid by a deep lingual groove. The ridge connecting the protoconid and metaconid is thick and strongly backward shifted and obliquely extended, with its lingual end reaching almost the posterior end of the tooth and closing the talonid. The entoconid can hardly be considered present, and, therefore, the posterior-most transverse lophid is very short, being formed by the single hypoconid. The cingulum is developed in the anterior half of the tooth on both lingual and labial sides, ascending anteriorly. The posterior cingulum is represented by a small tubercle of irregular form. The dp3 is much larger than the dp2. The labial walls of the trigonid and talonid are strongly convex, separated by a deep valley. The paralophid is robust, extending lingually, with a tubercle in front of the paraconid more prominent than in the dp2. This makes the dp3 more tri-lobed in pattern than the dp2. The cingulum of the dp3 is similarly developed as in the dp2. The dp4 is almost fully molarized. Compared with the molars, its trigonid is more V-shaped than U-shaped, and the trigonid and talonid basins are equally deep, while in the molars the talonid basin is definitely deeper than the trigonid one. The m1 is in its initial stage of wear. It is evidently more high-crowned than all the deciduous premolars. The highest part of the talonid is situated lower than that of the trigonid. The anterior end of the hypolophid descends sharply before reaching the posterior wall of the trigonid, leaving a prominent cleft between the trigonid and talonid, more clearly seen from the labial side. The labial cingulum is well developed in the anterior part of the trigonid, strongly ascending anteriorly (pl. I, B).

Except the measurements of the cheek teeth, which are given in the Chinese text, the few measurements of value are (mm): di3: Thickness: 6.4, Width (broken): 10, Height of crown: 9; The root of the dp1: 11 × 6.3.

Among the mid-Tertiary rhinoceroses the specimen referred to "*Teniseggysodon turgaicum*" (Reshetov *et al.* 1996) is without doubt closest to the above described V9964. Although different in age and difficult in direct comparison, the two samples show the following similarities: 1) Both lower jaws have complete number of anterior teeth (incisors and canine), disposed in a continuous series and rather vertically implanted; 2) The symphysis is short, stout and high, with short c~dp1 diastema; and 3) They are close in size. Next close to V9964 is the European genus *Eggysodon* in sharing similarly common features. However, *Eggysodon* has only two pairs of

lower incisors, as pointed out by Stehlin (1930) and verified recently by de Bonis *et al.* (1995). The lower jaw with dp2~m1 from Villebramar (Brunet, 1979) makes the comparison of the Asian and European forms possible. The measurements show clearly that the Asian form has generally wider cheek teeth than the European form. Furthermore, the tri-lobed pattern is more clearly shown in the dp2~dp3 in the European form than in the Asian form. From the foregoing comparison the following conclusions can be drawn: 1) V9964 is very close to "*Teniseggyodon*" *turgaicum*, and may be conspecific. 2) So far as we can judge, the major difference between Borissiak's "*Epiaceratherium*" *turgaicum* and Reshetov *et al.*'s "*Teniseggyodon*" *turgaicum* lays only in the size of the canine. In the first specimen it is evidently larger than in the latter one. If this can prove as merely sexual difference, the two specimens should be considered conspecific as well. 3) It seems inappropriate to create another name, *Teniseggyodon*, to substitute *Allacerops*. Reshetov *et al.* were wrong when they stated that *A. osborniana* was the type species of the genus *Allacerops* (Reshetov *et al.*, 1993, p. 716). In fact, Wood himself made an unequivocal designation of "*Epiaceratherium*" *turgaicum* as the type species of his *Allacerops* (Wood, 1932, p. 170). 4) V9964 seems to be more robust in general structure and has a clear angle between the lower borders of the symphysis and the horizontal ramus. However, since there are few parts that can be directly compared between V9964 and the other *Allacerops* specimens, we tentatively identified V9964 as *Allacerops* cf. *A. turgaica*. 5) Although very close in general morphology, *Allacerops* and *Eggysodon* differ in a number of points. First, *Eggysodon* has only two pairs of lower incisors. Second, all the lower cheek teeth of *Eggysodon* are proportionally narrower than in *Allacerops*, with very pronounced, continuous labial cingula, and the tri-lobed pattern is more clearly expressed in the lower premolars of *Eggysodon* than in the Asian form. As a result, the European and Asian forms should be considered as belonging to different genera.

3 Systematic position of Eggysodontinae

As stated above, the subfamily Eggysodontinae (Breuning, 1924) has the year priority over Allaceropinae (Wood, 1932). As regards its composition and its position within Hyracodontidae or Rhinocerotoida, the material now available seems inadequate to solve this problem thoroughly. However, the new material of both *Allacerops* and *Eggysodon* accumulated during the last years, especially the finding of the anterior parts of the jaws, casts some doubt on the rationality of the current high-rank classification of the Rhinocerotoida, in particular, the all-embracing Hyracodontidae defined by Radinsky (1966).

Prior to 1966, the majority of the paleontologists agreed that the Rhinoceroidea included Hyrachyidae, Hyracodontidae, Arynodontidae, Indricotheriidae and Rhinocerotidae. In 1966 Radinsky transferred the Hyrachyidae to the Tapiroidea, and re-grouped all the others, except for the Arynodontidae, into two families: Hyracodontidae and Rhinocerotidae. He referred only the forms with enlarged I1 / I2 to the latter, and lumped all the others in the Hyracodontidae. In so doing he succeeded in making the Rhinocerotidae strictly monophyletic and clear-cut in definition. Unfortunately, this was achieved at the cost of turning the Hyracodontidae into a new waste-paper basket. Regardless of this shortcoming, Radinsky's procedure has been highly evaluated. Although disagreements were expressed from time to time with regard to the ranking of the giant rhinoceroses (Heissig, 1989b, Spassov, 1989, Dashzeveg, 1996, etc.), this classification was widely accepted, especially by the Americans.

It seems to the authors of the present paper that the cheek teeth of all the rhinoceroses evolved along extremely similar paths. Their differences, especially those of the premolars, reflect rather the evolutionary grade than phylogenetic clade. Thus, they are more useful in grade assessment than in clade discrimination. On the contrary, the evolutionary trends of the anterior teeth (incisors and canines) were highly divergent. At least three major directions can be recognized: 1) The rhinocerotid direction. The I1 / I2 become increasingly enlarged and the other incisors and canines atrophied. All the anterior teeth, including the once enlarged I1 / I2, can be secondarily atrophied. The earliest form of this evolutionary trend so far known is the Early Eocene *Teletaceras*. 2) The giant rhinocerotid direction. The anterior teeth are conic in form, sparsely situated, of which only I1 / I1 become enlarged. *Juxia* is to be included in this group, since it has already enlarged I1 / I1. The members of the Forstercooperinae (*Forstercooperia*, *Pappaceras* etc.) have the same basic type of the anterior teeth, without evident tendency of enlargement of I1 / I1. They could be considered sister group of the true giant rhinoceroses. 3) The hyracodontid direction. The canines become incisiformed and all the anterior teeth are closely implanted, forming a continuous series. The American true hyracodonts with weakly spatulate to pointed anterior teeth can be grouped under the subfamily Hyracodontinae. The Asian forms, *Ardynia*, *Parahyracodon*, *Allacerops* etc. with complete number of spatulate incisors and large canines can be grouped under the subfamily Eggysodontinae.

Based on the above discussion the following three families are proposed to be included in the Rhinoceroidea (in addition to Arynodontidae): Rhinocerotidae, Indricotheriidae (including Forstercooperinae and Indricotheriinae), and Hyracodontidae (including Hyracodontinae and Eggysodontinae).

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图版 I 说明 (Explanations of Plate I)

Allacerops cf. *A. turgaica* V9964, 下颌骨 (mandible) 带左 (left) di3, dp2~dp4, 右 (right) dp2~m1, $\times 4/5$, A. 冠面 (crown view); B. 外侧面 (lateral view)

