

新疆准噶尔盆地北缘中中新世食肉类¹⁾

王晓鸣

(美国自然历史博物馆 纽约 10024)

中国科学院古脊椎动物与古人类研究所 北京 100044)

叶捷 孟津 吴文裕 刘丽萍 毕顺东

(中国科学院古脊椎动物与古人类研究所 北京 100044)

摘要 1995年和1996年在新疆准噶尔盆地北缘乌伦古河沿岸中中新世地层中新发现的食肉类,经研究有8属9种,包括一新种:*Nimravus* sp.、*Pseudaelurus cuspidatus* sp. nov.、*Protictitherium intermedium*、*Protictitherium*小种、*Thalassictis chinjiensis*、*Gobicyon* sp.、*Oligobunis?* sp.、*Alopecocyon goeriachensis*和*Simocyon*小种。新材料虽较破碎,但其发现扩大了一些已知属种的地层和地理分布范围。通过对标本的观察和对比,对各属种的系统发育作了讨论。各属种与通古尔、丁家二沟、下草湾等动物群以及欧洲、南亚相关动物群的食肉类分子的比较结果尚不能肯定含化石地层的确切时代,但有可能早于通古尔组。

关键词 准噶尔盆地,中中新世,食肉类,系统发育,动物群对比

中图法分类号 Q915.874

1 前言

八十年代初期中国科学院古脊椎动物与古人类研究所在新疆准噶尔盆地进行古生物考察时,在盆地北缘乌伦古河北岸发现了丰富的脊椎动物化石。1987年童永生等发表“新疆准噶尔盆地北缘第三纪地层古生物”一文²⁾,其中简短地描述了该动物群中的食肉类:*Amphicyon*一新种和*Ictitherium* cf. *I. gaudryi*。此后,齐陶又于1989年正式命名了新种*Amphicyon ulungurensis*。1995和1996年我们又赴该地区进一步考察中中新世地层和动物群,发现了较多的食肉类化石。虽然这些化石仍较破碎,但大部分材料或者是代表了新的分类单元,或者是扩大了原有已知属种的地层和地理分布范围。本文是对1995年以来采集的食肉类化石新材料的研究报告。文中涉及的化石地点及其层位请参阅童永生等(1987)及吴文裕等(1998)。标本测量单位为毫米。标本保存在中国科学院古脊椎动物与古人类研究所。

1)本课题获中国科学院古生物学与古人类学科基础研究特别支持基金(95602)、中国国家自然科学基金(批准号49572080)、中国科学院王宽诚科研基金和国家自然科学基金委员会资助留学人员短期回国工作讲学专项基金资助。

2)载于《新疆古脊椎动物化石及地层》。北京:中国科学院古脊椎动物与古人类研究所(内部刊物),36—57

收稿日期:1997-08-25

2 分类描述

食肉目 *Carnivora* Bowdich, 1821

猫形亚目 *Feliformia* Kretzoi, 1945

Nimravidae Trouessart, 1885

Nimravus Cope, 1879

Nimravus ? sp.

(图1)

材料 V11490, 左下颌残支带 c、p2 及部分 m1 的齿槽和 p3-p4。

地点与层位 铁尔斯哈巴合, 哈拉玛盖组下部。

测量数据 p2(齿槽) 2.3×1.9 ;
p3 9.9×4.6 ; p4 13.5×6.0 。

描述 下颌支在 c 齿根处破损。下颌唇侧在犬齿部位没有垂直的凹槽, 表明上颌不具有剑齿。此外, 与具有剑齿的 *Nimravus* 不同, 在犬齿之下的颊部不具凸缘。下颌短, 在 p3 前下方有一大颊孔, p3 之下有三个小颊孔。p2 齿槽小, 其前后均有一齿隙(约 3mm)。p3 的高度约为 p4 的 $3/4$, 并且不如大部分北美的 *Nimravus* 的 p3 齿冠高。p3 的前齿带尖退化为小隆起, 后附加尖基部破损, 附加尖之后有一很发育的齿带。p4 具有明显的前、后附加尖, 前附加尖小于后附加尖; p4 不具后齿带。据保留在齿槽内的 m1 的前齿根判断, m1 与 p4 略有叠复。

讨论 见英文。

猫科 *Felidae* Gray, 1821

Pseudaelurus Gervais, 1948-52

Pseudaelurus cuspidatus sp. nov.

(图2A-B)

正型标本 V11491, 右下颌残段带有 c-p1 的齿槽和颊齿 p3-m1。

模式地点 铁尔斯哈巴合。

层位与时代 哈拉玛盖组下部, 中中新世。

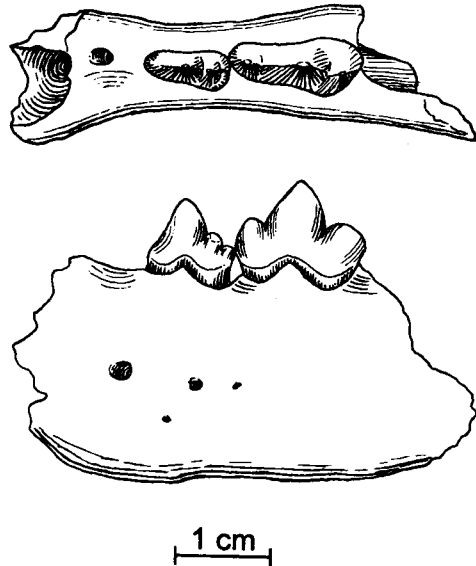


图1 *Nimravus*? sp. 左下颌残支带 p3-p4、c、p2 及部分 m1 的齿槽, V11490 嚼面视(上)和唇侧视(下)
Fig.1 *Nimravus*? sp. Left ramal fragment with c and p2 alveoli, p3-p4 and m1 alveolus (V11490), occlusal (upper) and labial (lower) views

归入标本 V11492, 残破右 P4, 铁尔斯哈巴合, 哈拉玛盖组下部。

测量数据 V11491 p3 8.5×4.0 ; p4 10.6×4.9 ; m1 12.6×5.6
V11492 P4 17.0×6.5 。

鉴别特征 *Pseudaelurus* 属内最小的种之一。以下列特征区别于该属其它的种: p4 窄, 原尖与前附尖接近; 下颌腹缘拱形, p1 前置, 无 p2, 前臼齿上有发育的前齿带尖; m1 三角座的后边缘垂直, 下后尖高。

命名由来 *cuspidatus* 指该种发育的齿尖。

描述 下犬齿齿槽后方紧挨着 p1 的单齿根齿槽, 无 p2, p1 齿槽与 p3 间的齿隙为 10mm。p3、p4 的主齿尖稍向后倾, 并有一个明显的前齿带尖和一个后附加尖, 后附加尖之后是一低的后齿带。m1 的裂叶高耸, 其下前尖叶稍弯向唇侧; 下原尖的后缘垂直, 下原尖的后脊之后有一 4mm 高的小齿尖, 该齿尖较高位, 可能是下后尖; 下后尖之后基部有一不明显的隆起, 相当于残余跟座。m2 不存在。

V11492 很可能是稍大于正型标本的个体。V11491 的 m1 的长度几乎与 *Proailurus lemanensis* 的正型标本 (MNHN1903-20) 一样, V11492 的 P4 长度 (17.0mm) 则较

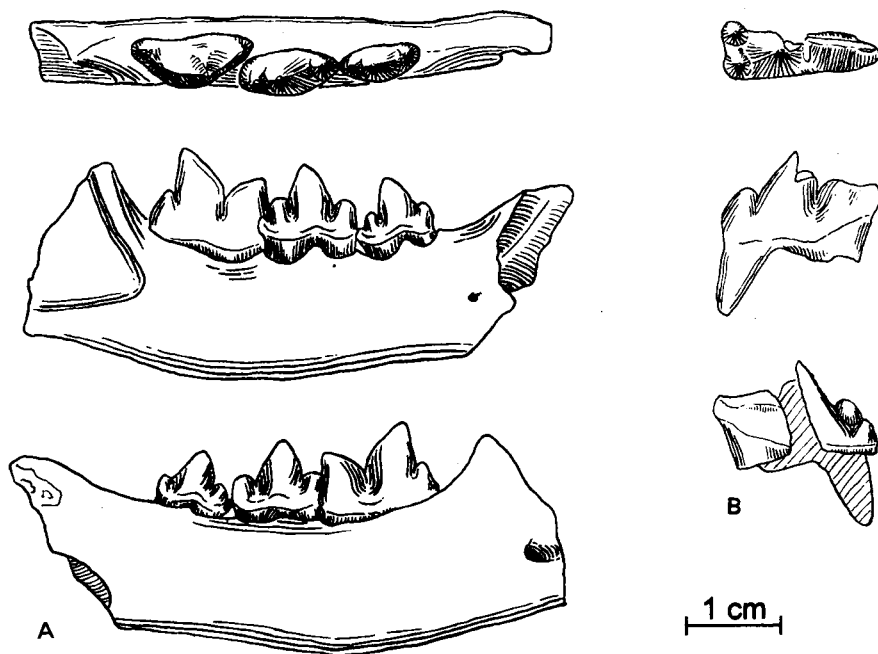


图 2 *Pseudaelurus cuspidatus* (新种)

A. 右下颌残段带有 c-p1 的齿槽和 p3-m1, 正型标本 (V11491), 嚼面视 (上)、唇侧视 (中) 和舌侧视 (下)
B. 残破右 P4 (V11492), 嚼面视 (上)、唇侧视 (中) 和舌侧视 (下)

Fig. 2 *Pseudaelurus cuspidatus* sp. nov.

A. Partial right ramus with c-p1 alveoli and p3-m1, Holotype (V11491), Occlusal (upper), labial (middle) and lingual (lower) views B. Right broken P4 (V11492), occlusal (upper), labial (middle) and lingual (lower) views

MNHN1903—20 的长 2mm。假设其上、下裂齿的长度比与 *Proailurus* 的一样,那么, V11492 较 V11491 约大 13%, 其变化量落入 *Pseudaelurus* 各已知种的变异范围内 (Heizmann, 1973: 图 16)。如果 P4 归入该新种是正确的,那么,这个种的上裂齿在 *Pseudaelurus* 属内同样是独特的,它的最明显的特征是其前端远比该属其它种侧扁,原尖几乎就位于前附尖的旁边,而在其它种内原尖位于近舌侧。与齿尖发育的下前臼齿相适应, P4 的前附尖较在其它种内高而明显。

比较和讨论 见英文。

鬣狗科 Hyaenidae Gray, 1869

Protictitherium Kretzoi, 1938

Protictitherium intermedium Schmidt-Kittler, 1976

(图 3A-B)

材料 V11493, 左下颌残段带 i3 齿槽, 残破 c, p1 齿槽, p2-m1, 及 m2 的齿槽 (图 3A); V11494, 左下颌残段带 p3 齿槽和 p4-m1 (图 3B); V11495, 右下颌残段, 仅带有 c-p4 的齿槽; V11496, 部分右下颌带有残破的 p1-m1。

地点与层位 所有材料产自铁尔斯哈巴合, 哈拉玛盖组下部层位。

测量数据 V11493: p1-m1 (齿槽) 长 33.0, p2 6.0 × 2.3, p3 (近似值) 7.7 × 2.7, p4 8.2 × 3.7, m1 (近似值) 9.5 × 4.5。V11494: p4 9.0 × 4.0, m1 10.4 × 5.0。

描述 本种的主要材料是两支下颌残段, 带有保存较好的牙齿。两者很相似, 仅在尺寸上稍有差别。p1 (仅保留齿槽) 单根。p2 简单, 具有一高的主尖和不明显的前后齿带尖。p3 破损, 残留的前半部与 p2 的很相似。p4 有一粗壮的后附加尖和一中等发育的前齿带尖, 附加尖周围有发育的齿带。m1 三角座相当高, 下原尖最发育, 下后尖小, 其高度不及下原尖的一半, 下前尖具有一条微弱的、由其顶端向下伸至基部的舌侧脊。与 *Plioviverrops* 相比, m1 的跟座小, 下内尖和下次尖大致等高, 下内尖向舌侧突出, 并由一深槽与三角座分开, 下次小尖缩小成为一远低于下内尖和下次尖的横脊, 因此跟座凹向后敞开。

讨论 见英文。

Protictitherium 小种

(图 3C)

材料 V11497, 带 m1 和 m2 齿槽的左下颌残段 (图 3C), 播塔莫音。V11498, 左下颌残段, 带 i1-m2 齿槽和 p2 的后半截, 铁尔斯哈巴合。

层位 哈拉玛盖组下部。

测量数据 V11497: m1 8.0 × 3.7。V11498: p1-m2 (齿槽) 长 33.5mm, p1 齿槽长 2.1, p2 齿槽长 4.6, p3 齿槽长 5.4, p4 齿槽长 6.4, m1 齿槽长 8.9, m2 齿槽长 2.4。

描述 下颌水平支长而纤细, 具有两个颊孔, 大孔位于 p1 和 p2 之间, 小孔位于 p3 之下。从 V11498 的 p2 后段来看, p2 有单一主尖和不明显的后齿带尖。m1 的三角座较长, 下原尖最发育, 下后尖小, 不及下原尖高度的二分之一。跟座由三尖组成, 下次尖和下内尖

大,下次小尖小。下内尖和下次尖大致等高,两者以一不明显的横脊相连。下次小尖呈齿带状,因受磨蚀其高度不明。

讨论 见英文。

Thalassictis Gervais, 1850

Thalassictis chinjiensis(Pilgrim, 1932)

(图 3 D-E)

Ictitherium cf. *I. Gaudryi* (Zdansky, 1924): Tong *et al.*, 1987:48, figs. 18.2, 18.3 (in part)

Ictitherium cf. *I. Gaudryi* (Zdansky, 1924): Qi, 1989:135, figs. 2.2, 2.3 (in part)

Miohyaena: Qiu *et al.*, 1995: 50

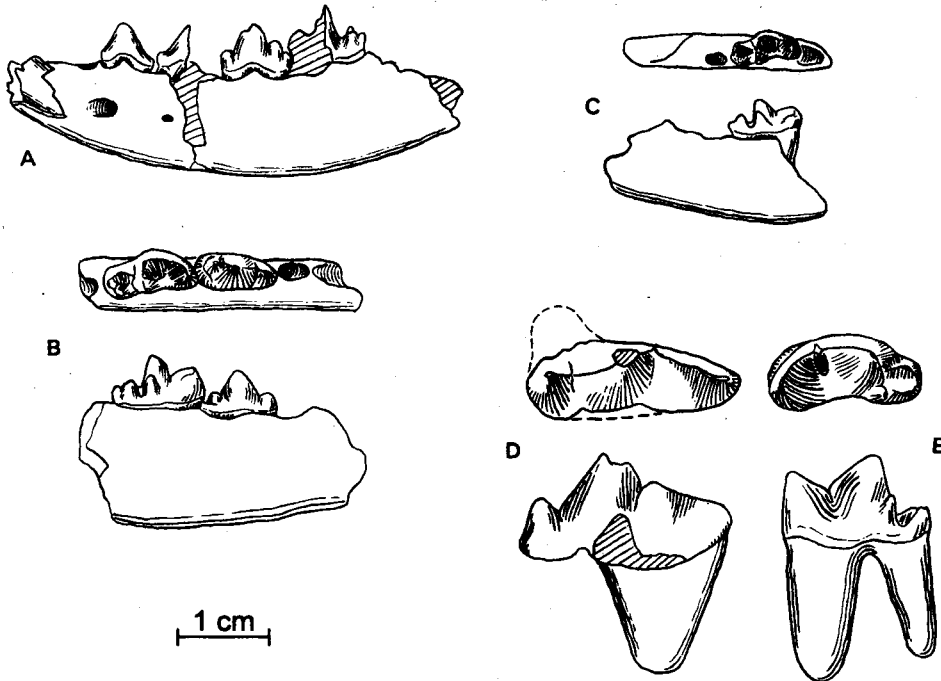


图 3 A-B. *Protictitherium intermedium* Schmidt-Kittler, 1976

A. 左下颌残段带 i3 齿槽, 残破 c, p1 齿槽, p2-m1, 及 m2 的齿槽 (V11493), 唇侧视 B. 左下颌残段带 p3 齿槽和 p4-m1 (V11494), 嚼面视(上)及舌侧视(下) C. *Protictitherium* 小种 左下颌残段带 m1 和 m2 的齿槽 (V11497), 嚼面视(上)及舌侧视(下) D-E. *Thalassictis chinjiensis* (Pilgrim, 1932) D. 部分右 P4 (V11500), 嚼面视(上)及舌侧视(下) E. 右 m1 (V11499), 嚼面视(上)及舌侧视(下)

Fig.3 A-B. *Protictitherium intermedium* Schmidt-Kittler, 1976

A. Partial left ramus with i3 alveolus, broken c, p1 alveolus, p2-m1 and m2 alveolus (V11493), labial view B. Left ramal fragment with p3 alveolus and p4-m1 (V11494), occlusal (upper) and lingual (lower) views C. *Protictitherium* small sp. Left ramal fragment with m1 and m2 alveolus (V11497), occlusal (upper) and lingual (lower) views D-E. *Thalassictis chinjiensis* (Pilgrim, 1932) D. Partial right P4 (V11500), occlusal (upper) and lingual (lower) views E. Isolated right m1 (V11499), occlusal (upper) and lingual (lower) views

材料 V7733, 左下颌残段, 带 p2-4 (童永生等, 1987; 图 18.2; 齐陶, 1989; 图 2.2)。播塔莫音, 哈拉玛盖组下部。

V7734, 单个右 m1 (童永生等, 1987, 图 18.3; 齐陶, 1989; 图 2.3)。干奇开日希, 哈拉玛盖组下部。

V11499, 单个右 m1 (图 3E); V11500, 部分右 P4 (图 3D)。夺勒布勒津, 索索泉组顶部上部砂岩夹层。

测量数据 (V7733 和 V7734 的数据引自齐陶, 1989)

V7733: p2 9.8×5.0 ; p3 12.1×6.2 ; p4 14.0×6.7

V7734: m1 13.8×7.5

V11499: m1 16.6×8.1

V11500: P4 长 23.3

描述 我们未能见到齐陶 (1989) 描述的标本, 因此本文的记述来源于对其图版的观察。P4 (V11500) 的前附尖大, 是中等食肉型的鬣狗类的特征。相对于前尖叶, 后附尖叶长, 这是衍生特征。下颌具两个颊孔, 大孔位于 p2 之下, 小孔位于 p3 之下 (齐陶, 1989; 图 2.2b)。齐陶 (1989) 认为 V7733 标本上很可能没有 p1。残破的 p2 上有一很小的后附加尖, 该尖在 p3-4 上渐次增大。从 p3 开始发育有一小的后齿带, 齿带进一步增大并扩展至附加尖的舌侧。保存完整的几枚 m1 具有延长的三角座和缩短的跟座; 唇侧齿带中等发育, 仅限于三角座的下前尖部分; 下原尖裂叶与下前尖裂叶近乎等长, 并仅稍高于后者; 下后尖大大缩小, 仅稍高于下内尖; 下次小尖缩小成为一联结下内尖和下次尖的低齿带, 封闭跟盆; 下内尖与下次尖等高。

讨论 见英文。

犬形亚目 Carniformia Kretzoi, 1945

熊次目 Arctoidea Flower, 1869

半犬科 Amphicyonidae, Trouessart, 1885

Gobicyon Colbert, 1939

Gobicyon? sp.

材料 V11501, 一枚右 p4 的前部残块; V11502, 一枚左 P4 的前部残块。

地点与层位 铁尔斯哈巴合, 哈拉玛盖组下部。

讨论 见英文。

鼬超科 Musteloidea Schmidt-Kittler, 1981

Oligobunis Cope, 1881

Oligobunis? sp.

(图4A)

材料 V11503, 一年轻个体的右下颌残段, 带有 dp4, p2-p4 以及 m1 的齿槽 (图 4A)。

地点和层位 铁尔斯哈巴合, 哈拉玛盖组下部。

测量数据 V11503, dp4 9.4×4.3 ; p2 7.1×3.6 ; p3 7.5×4.0 ; p4 9.1×5.0 。

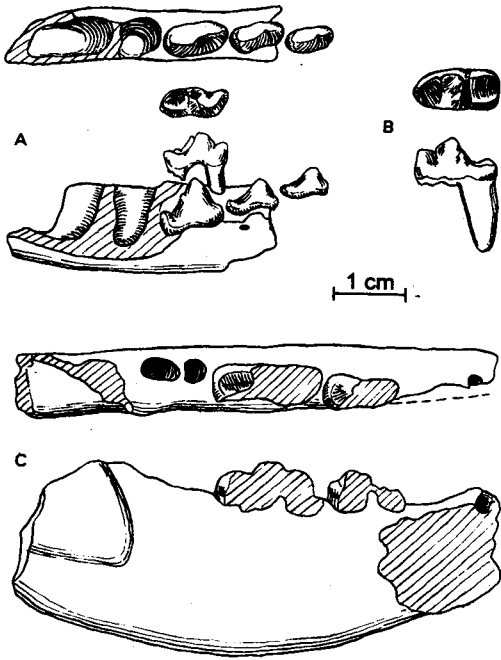


图4 A. *Oligobunis?* sp.

一年轻个体的右下颌支残段,带 dp4, p2-p4 和 m1 的齿槽 (V11503)

下颌及齿列顶面视(上), dp4 嚼面视(中), 下颌及齿列唇侧视(下)

B. *Alopecocyon goeriachensis* (Toula, 1884)

右下第一臼齿 m1 (V11504)

嚼面视(上)和舌侧视(下)

C. *Simocyon* 小种

右下颌支残段带 p1 齿槽、残破的 p4-m1、m2 的齿槽 (V11505)

下颌顶面视(上)及唇侧视(下)

Fig. 4 A. *Oligobunis?* sp.

Right ramal fragment of a young individual, with dp4, p2-p4 and alveolus of m1 (V11503)

Top view of ramus and dentition (upper) and dp4 (middle), labial view (lower)

B. *Alopecocyon goeriachensis* (Toula, 1884)

Right m1 (V11504); occlusal (upper) and lingual (lower) views

C. *Simocyon* small sp.

Right ramal fragment with p1 alveolus, broken p4-m1 and m2 alveolus (V11505)

Top (upper) and labial (lower) views

描述 前臼齿的尺寸和形态与 *Oligobunis* 很一致。dp4(乳裂齿)的三角座低,其下后尖大,跟座上的下次尖大,下内尖小,位于舌侧。p2 具一低冠主尖,主尖位置靠前,其后为一长跟。p3 与 p2 很相似,只是尺寸稍大。p4 几乎全埋于下颌骨内,其齿尖刚刚露出下颌水平支上缘,并具有一小的后附加尖。

讨论 见英文。

浣熊科 Procyonidae Gray, 1825

***Alopecocyon* Viret, 1951**

***Alopecocyon goeriachensis* (Toula, 1884)**

(图4B)

材料 V11504, 单个右 m1 (图 4b)。

地点与层位 夺勒布勒津; 索索泉组顶部上砂层。

测量数据 m1, 11.9 × 5.7。

描述 m1 的尺寸与 La Grive 的标本 (Viret, 1951: 图版 I, 图 8-9) 差不多, 而稍长于 Sansan (Ginsburg, 1961: m1 长 10.7mm) 的标本。在形态上准噶尔的 m1 的稍高的三角座和下次尖也更接近于 La Grive 标本。除这些微小变化外, 准噶尔的材料与欧洲种是很相似的。

讨论 由于材料有限, 将 m1 归入 *Alopecocyon goeriachensis* 是暂时的。

***Simocyon* Wagner, 1858**

***Simocyon* 小种**

(图 4c)

Ictitherium cf. *I. Gaudryi* (Zdansky, 1924): Tong et al., 1987: 48, 图 18.1

Ictitherium cf. *I. Gaudryi* (Zdansky, 1924): Qi, 1989: 135, 图 2. 1a, b. (in part)

Gobicyon: Qiu et al., 1995: 50

材料 V7732, 右下颌残段带 m1-2 (童永生等, 1987: 图 18.1; 齐陶, 1989: 图 2.1a, b);

V11505, 右下颌残段带 p1 齿槽, 残破的 p4-m1, m2 的齿槽(图 4c)。

产地和层位 播塔莫音; 哈拉玛盖组下部。

测量数据 V7732: m1 16.6 × 7.4; m2 8.9 × 5.0(依据齐陶, 1989)。

V11505(均为齿槽长度): p1 2.2; p4 10.1; m1 16.0; m2 8.8。

描述 我们未能见到齐陶(1989)描述的标本, 本文的观察源自他的图版。

p1 的齿槽小, 位于下颌(V11505)的前端, 紧挨在犬齿齿槽的后面。p1 齿槽与 p4 间的齿虚长, 在残破的 p4 上仅有一个部分保存的后附加尖。p4 相对于 m1 相当大, 这是 *Simocyon* 的特点。m1 的三角座在 V7732 上磨蚀很深, 在 V11505 上残破, 在齐陶的插图(1989: 图 2.1a)上没见有下后尖。两块标本上都保留有 m1 的跟座, 其下次尖大而低, 下内尖呈小而窄的脊状。m2 具有典型的 *Simocyonine* 的特点: 三角座短, 跟座相对延长。m2 的下原尖为一低尖, 后方与低矮的下次尖脊相连。无 m3。

讨论 见英文。

3 关于系统发育与地层时代的讨论

通常人们将哈拉玛盖组的哺乳动物与内蒙古通古尔组的哺乳动物对比, 并认为其时代为陆相哺乳动物分期的通古尔期(如童永生等, 1987; 齐陶, 1989; Qiu, 1990)。邱占祥等(Qiu and Qiu, 1995)将通古尔期分为在时间上顺序排列的几个地方哺乳动物群, 以宁夏的丁家二沟动物群作为通古尔期内最早的动物群, 而通古尔动物群是通古尔期的最后一个动物群。通古尔组内有丰富的食肉类化石, 然而大部分通古尔期的其他动物群中只有少数食肉类可与通古尔组的比较。

尽管哈拉玛盖动物群中的化石保存不完整, 却具有通古尔动物群中的一些典型的成员, 如 *Platybelodon*, *Anchitherium*, *Stephanocemas* 和 *Anchitheriomys*。在食肉类方面, 总的来说也是相似的: *Protictitherium*(包括 *Tungurictis*), *Gobicyon*, *Amphicyon* 和 *Oligobunis*。进一步的对比则表明, 两地还没有一个共有的种。

只有 *Protictitherium* 属(包括 Hunt 和 Solounias 1991 年建立的亚属 *Tungurictis*), 在这两个地区具有关系较密切的种, 可以比较其进化阶段, 用以推测它们的相对地层时代。*P. intermedium* 较 *P. (Tungurictis) spocki* 尺寸稍小, 看来较原始。另外, 李传夔等(1983)曾报道过江苏泗洪中新世早期下草湾组的 *Protictitherium* sp., 可能会对进一步了解这一支系提供信息。

还有两个属对于通古尔和准噶尔两个动物群之间的对比可能有用。一是 *Oligobunis*, 但在通古尔和准噶尔的材料都太少, 尚不能进行很有意义的对比。根据北美这一属的进化趋势判断, 哈拉玛盖动物群中 *Oligobunis* 的尺寸较小, 可能较原始。另一个属是 *Gobicyon*, 哈拉玛盖的材料太残破, 连其归属都不肯定, 更不能做种一级的比较。这类稀有的半犬也在同心丁家二沟(Qiu and Qiu, 1995)和欧洲塞尔维亚的 *Prebreza*(MN6, Pavlovic et al., 1959)发现过, 因此其地史分布较过去认为的要长一些。

准噶尔和通古尔的 *Amphicyon* 虽然归入同一属中, 二者差别相当大, 可能属于不同的分支。*A. tairumensis* 大小如狼, 而 *A. ulungurensis* 是巨型的熊犬, 与山旺早中新世的 *A.*

confucianus Young, 1937 和欧洲的几个大种如, *A. giganteus* (MN3-5), *A. major* (MN5-9)等相似(Viranta, 1996)。由于准噶尔和通古尔的 *Amphicyon* 之间无紧密关系, 该属不大可能提供生物年代方面的依据。

Thalassictis 在欧洲出现于 Astaracian 至 Vallesian 期, 准噶尔材料的发现, 在东亚通古尔期中乃属首次。总的来说, 准噶尔的 *Thalassictis* 的 P4 的后附尖长, 与欧洲种比较是衍生特征。更有趣的是, *T. chinjiensis* 在准噶尔的出现说明了准噶尔的动物群与西藏高原以南的南亚的动物群的直接联系。 *Pseudaelurus* 也可能是这种情况。

鉴定为 *Simocyon* 的下颌残块与已知各种的差别很大。该属通常是三趾马动物群的成员(欧洲 Vallesian 至 Turolian 期, 亚洲保德期至榆社期, 北美的 Hemphillian 期)。在对准噶尔 *Simocyon* 有更多的了解之前, 其地层意义是有限的。它可能代表了该支系的早期祖先。 *Alopecocyon goeriachensis* 的出现也证明了这一点。该种在欧洲发现于 Göriach, Neudorf, Sansan 和 La Grive。

致谢 作者感谢 Richard Tedford 在标本鉴定过程中的讨论与切磋。

参 考 文 献

- 齐陶, 1989. 新疆阿尔泰地区中中新世肉食类动物. 古脊椎动物学报, 27(2): 133—139
- 李传夔, 林一璞, 顾玉珉等, 1983. 江苏泗洪下草湾中中新世脊椎动物群-1, 化石地点暨近年发现的新材料简介. 古脊椎动物与古人类, 21(4): 313—327
- 邱占祥, 顾玉珉, 1986. 江苏泗洪下草湾中中新世脊椎动物群-3, 两种肉食类化石 *Semigenetta* 和 *Pseudaelurus*. 古脊椎动物学报, 24(1): 20—31
- 吴文裕, 叶捷, 孟津等, 1998. 新疆准噶尔盆地北缘第三纪地层古生物研究新进展. 古脊椎动物学报, 36(1): 24—31
- 曹忠祥, 杜恒俭, 赵其强等, 1990. 甘肃广河地区中中新世哺乳动物化石的发现及其地层学意义. 现代地质, 4(2): 16—29
- Andrews C W, 1914. On the lower Miocene vertebrates from British East Africa, collected by Dr. Felix Oswald. *Quart. Jour. Geol. Soc. London*, 70: 163—186
- Beaumont de G, 1967. Observations sur les Herpestinae (Viverridae, Carnivora) de l'Oligocène supérieur avec quelques remarques sur des Hyaenidae du Néogène. *Arch. des Sci. Genève*, 20: 79—108
- Beaumont de G, Mein P, 1972. Recherches sur le genre *Plioviverrops* Kretzoi (Carnivora, ? Hyaenidae). *C. R. des Séances, SPHN Genève, NS*, 25: 383—394
- Blainville H M D de, 1843. Ostéographie ou description iconographique comparée du squelette et du système dentaire des mammifères Récents et fossiles, II, O, Félics. Paris: J. B. Baillièrre et Fils. 1—196
- Colbert E H, 1939. Carnivora of the Tung Gur Formation of Mongolia. *Bull. Am. Mus. Nat. Hist.*, 76: 47—81
- Crusafont-Pairó M, Petter G, 1969. Contribution a l'Étude des Hyaenidae, la sous-famille des Ictitheriinae. *Ann. Paléontol.*, 55: 89—127
- Dashzeveg D, 1996. Some carnivorous mammals from the Paleogene of the eastern Gobi Desert, Mongolia, and the application of Oligocene carnivores to stratigraphic correlation. *Am. Mus. Novit.*, 3179: 1—14
- Dehm R, 1950. Die Raubtiere aus dem Mittel-Miocen (Burdigalium) von Wintershof-West bei Eichstatt in Bayern. *Abh. Bayer. Akad. Wiss. Math.-naturw. Kl.*, 58: 1—141
- Depéret C, 1892. La faune de mammifères Miocènes de la Grive-Saint-Alban-Isère. *Arch. Mus. Hist. Natur. Lyon*, 5: 1—89
- Forsyth Major C I, 1903. New Carnivora from the middle Miocene of La Grive St-Alban. *Geol. Magaz. N. S.*,

1: 534—538

- Gaillard C, 1899. Mammifère Miocènes de Sansan (Gers). *Mém. Mus. Natl. Hist. Nat., Sér. C, Sci. Terre (Paris)*, 9:1—190
- Gervais P, 1850. Zoologie et Paléontologie Francaises. Paris: Arthus Bertrand. 1—136
- Ginsburg L, 1961. La faune des carnivores Miocenes de Sansan (Gers). *Mém. Mus. Natl. Hist. Nat. N. S.*, 9:1—187
- Ginsburg L, 1982. Sur les modalites d'evolution du genre Néogène *Pseudaelurus* Gervais (Felidae, Carnivora, Mammalia). *Coll. intern. du C. N. R. S.*, 330:131—136
- Heizmann E P J, 1973. Die Carnivoren des Steinheimer Beckens, B. Ursidae, Felidae, Viverridae sowie Ergänzungen und Nachtrage zu den Mustelidae. *Palaeontogr. Suppl.*, 8:1—95
- Hibbard C W, 1934. Two new genera of Felidae from the middle Pliocene of Kansas. *Trans. Kans. Acad. Sci.*, 37:239—255
- Hoernes R, 1882. Säugetier-Reste aus der Braunkohle von Görjach bei Turnau in Steiermark. *Jahrb. D. K. K. Geol. Reichsanstalt*, 32:153—164
- Hunt R M Jr, Solounias N, 1991. Evolution of the aeluroid Carnivora: hyaenid affinities of the Miocene carnivoran *Tungurictis spocki* from Inner Mongolia. *Amer. Mus. Novit.*, 3030:1—25
- Kretzoi N, 1929. Materialien zur phylogenetischen Klassifikation der Aeluroideen. *X Congr. Internat. Zool. Budapest*, 2: 1293—1355
- Kurtén B, 1982. Status of the fossil hyaenids *Ictitherium viverrinum* and *Thalassictis robusta* (Mammalia). *Z. Geol. Wiss. Berlin*, 10:1009—1018
- Leidy J, 1858. Notice of remains of extinct vertebrata, from the valley of the Niobrara River, collected during the exploring expedition of 1857, in Nebraska, under the command of Lieut. G K Warren, U. S. Top. Eng., by Dr. F V Hayden, Geologist to the expedition. *Proc. Acad. Nat. Sci. Philadelphia*, 20—29
- Macdonald J R, 1948a. A new species of *Pseudaelurus* from the lower Pliocene of Nebraska. *Univ. Calif. Publ. Bull. Geol. Sci.*, 28:45—52
- Macdonald J R, 1948b. The Pliocene carnivores of the Black Hawk Ranch Fauna. *Univ. Calif. Publ. Bull. Geol. Sci.*, 28:53—80
- Macdonald J R, 1954. A new *Pseudaelurus* from the Lower Snake Creek Fauna of Nebraska. *J. Paleontol.*, 28: 67—69
- Pavlovic M, Thenius E, 1959. *Gobicyon macrognathus*(Canidae, Mammalia) aus dem Miozän Jugoslawiens. *Anz. Akad. Wiss. Wien.*, 96:214—222
- Pavlov M, 1908. Quelques carnivores fossils du gouvernement de Kherson et de Bessarabie. *Mém. Soc. Natur. Nouvelle-Russie, Odessa*, 32:27—48
- Pilgrim G, 1910. Notices of new mammalian genera and species from the Tertiaries of India. *Rec. Geol. Surv. India*, 60:65
- Pilgrim G, 1915. Note on the new feline genera *Sivaelurus* and *Paramachaerodus* and on the possible survival of the subphylum in modern times. *Rec. Geol. Surv. India*, 65:138—155
- Pilgrim G, 1932. The fossil Carnivora of India. *Palaeontol. Indica*, 18:1—232
- Qiu Z X, 1990. The Chinese Neogene mammalian biochronology—its correlation with the European Neogene mammalian zonation. In: Lindsay E H *et al.* eds. *European Neogene Mammal Chronology*. New York: Plenum Press. 527—556
- Qiu Z X, Qiu Z D, 1995. Chronological sequence and subdivision of Chinese Neogene mammalian faunas. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 116:41—70
- Roman F, Viret J, 1934. La faune des Mammifère du Burdigalien de La Romieu (Gers). *Mém. S. G. F., N S*, 21:5—67

- Schmidt-Kittler N, 1976. Raubtiere aus dem Jungtertiär Kleinasiens. *Palaeontogr. Abt. A.*, **155**:1—131
- Schmidt-Kittler N, 1987. The Carnivora (Fissipedia) from the lower Miocene of east Africa. *Palaeontogr. Abt. A.* **197**: 85—126
- Semenov Y A, 1988. *Ictitherium spelaeum* sp. n. (Carnivora, Viverridae) from middle Sarmat of the Ukraine. *Vestnik Zoologii*, **1988**: 45—49 (In Russian, English abstract)
- Semenov Y A, 1989. Ictitheres and morphologically related hyaenas from the Neogene of the USSR. *Naukova Dumka*, Kiev. 1—178 [in Russian with English summary]
- Tedford R H, Galusha T, Skinner M F *et al.*, 1987. Faunal succession and biochronology of the Arikareean through Hemphillian interval (Late Oligocene through Earliest Miocene epochs) in North America. In: Woodburne M O ed. *Cenozoic Mammals of North America, Geochronology and Biostratigraphy*. Berkeley: Univ. Calif. Press. 153—210
- Thorpe M R, 1921. Two new fossil Carnivora. *Am. J. Sci.*, **1**:477—483
- Thorpe M R, 1922a. *Araeocyon*, a probable Old World migrant. *Am. J. Sci.* **3**:371—377
- Thorpe M R, 1922b. Some Tertiary Carnivora in the Marsh Collection, with descriptions of new forms. *Am. J. Sci.*, **3**:432—455
- Toohy L, 1959. The species of *Nimravus* (Carnivora, Felidae). *Bull. Am. Mus. Nat. Hist.*, **118**:77—112
- Villalta Comella J F de, Crusafont-Pairo' M, 1943. Nuevas aportaciones al conocimiento de los carnívoros pontienses del Vallés-Panadés. *Bol. Geol. Min.*, **65**:1—192
- Viranta S, 1996. European Miocene Amphicyonidae—taxonomy, systematics and ecology. *Acta Zool. Fenn.*, **204**:1—61
- Viret J, 1951. Catalogue critique de la faune des mammifères Miocènes de la Grive Saint-Alban (Isère). *Nouv. Arch. Mus. Hist. Nat. Lyon*, **3**:7—104
- Wang X, 1997. New cranial material of *Simocyon* from China, and implications for phylogenetic relationship of the red panda (*Ailurus*). *J. Vertebr. Paleontol.*, **17**:184—198
- Werdlin L, Solounias N, 1991. The Hyaenidae: taxonomy, systematics and evolution. *Fossils and Strata*, **30**:1—104
- Young C C, 1937. On a Miocene mammalian fauna from Shantung. *Bull. Geol. Soc. China*, **17**:209—245
- Zdansky O, 1924. Jungtertiäre Carnivoren Chinas. *Palaeontol. Sin.*, Ser. C, **2**(1):1—149

CARNIVORA FROM MIDDLE MIOCENE OF NORTHERN JUNGGAR BASIN, XINJIANG AUTONOMOUS REGION, CHINA

WANG Xiaoming

(Department of Vertebrate Paleontology, American Museum of Natural History, New York New York 10024)

YE Jie MENG Jin WU Wenyu LIU Liping BI Shundong

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

Key words Junggar Basin, middle Miocene, Carnivora, Systematics, fauna, correlation

1 Introduction

Extensive paleontological explorations in the early 1980s by the Institute of Vertebrate Paleontology and Paleoanthropology in Junggar (Dzungar) Basin, Xinjiang Autonomous Region, have led to the discovery of rich vertebrate fossils from the middle Miocene Halamagai Formation just north of the Ulungur River. A preliminary summary of the stratigraphy and paleontology was published (Tong *et al.*, 1987), in which a new *Amphicyon* and an *Ictitherium* cf. *I. gaudryi* were figured and briefly mentioned as the carnivoran components of the vertebrate fauna. Qi (1989) later named the new amphicyonid *Amphicyon ulungurensis*. After a hiatus of more than 10 years, a renewed effort in the 1995 and 1996 field seasons has resulted in a larger sample of carnivorans. Although still fragmentary, most of the new materials represent either new taxa or new stratigraphic or geographic occurrences of known taxa. This is a progress report on the new carnivoran materials collected since 1995. Future collections will surely shed further light in this still poorly known fauna.

We thank Richard Tedford for stimulating discussions during the writing of this paper.

Abbreviations for Institutions

AMNH American Museum of Natural History, New York

CUGS GV China University of Geoscience, Beijing (formerly Geological College of Beijing)

F:AM Frick Collection, American Museum of Natural History

IVPP Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing

MCZ Museum of Comparative Zoology, Harvard University, Cambridge

MNHN Museum National d'Histoire Naturelle, Paris

2 Systematic paleontology

Order Carnivora Bowdich, 1821

Suborder Feliformia Kretzoi, 1945

Family Nimravidae Trouessart, 1885

Nimravus Cope, 1879

Nimravus? sp.

(Fig. 1)

Material IVPP V11490, left ramal fragment with c and p2 alveoli, p3-p4, and m1 alveolus (Fig. 1), from lower part of Halamagai Formation, Teiersihabahe.

Measurement (in millimetre): p2(alveolus), 2.3×1.9 ; p3, 9.9×4.6 ; and p4, $13.5 \times$

6.0.

Description The ramus is broken at the root of c. The ramal remains on the buccal side of the lower canine suggest no trace of a vertical groove to indicate a saber-tooth. Similarly, a chin just below the c root is only vaguely indicated, lacking a flange as seen in saber-toothed *Nimravus*. The ramus is short with one large mental foramen just in front of the p3 and three small foramina below the p3. There is a short diastemata (approximately 3 mm) both in front and behind a tiny p2 alveolus. The p3, approximately 3 / 4 of the height of p4, is not as tall-crowned as most North American species of *Nimravus*. The p3 essentially lacks an anterior cingular cusp, which is reduced to a weak bulge. There is a small posterior accessory cusp, which is broken at the base. Behind the accessory cusp is a well-developed cingulum. The p4 has prominent anterior and posterior accessory cusps; the anterior cusp is smaller than the posterior one. There is no trace of a cingulum on the p4. The anterior root of the m1 is preserved, which indicates a slightly imbricated m1 with the p4.

Discussion Poor preservation of this individual makes its identification difficult. Presence of a single posterior accessory cusp on p4 without a posterior cingulum is not known among existing species of *Pseudaelurus*. Such a premolar morphology, on the other hand, is present in all known species of *Nimravus*. One is thus faced with the difficult choice of accepting this individual as a peculiar *Pseudaelurus* that lost the p4 posterior cingulum or a very late lineage of *Nimravus*. The latter is preferred in absence of any evidence that the unique premolar morphology of this specimen is independently developed in the pseudaelurines.

IVPP V11490 differs from most North American forms (see Toohey, 1959 for a summary) in its relatively low-crowned p3, a primitive feature found in *Nimravus intermedius* from the Phosphorite de Quercy and other primitive feliform carnivorans. Toohey (1959) identified a left ramal fragment with m1 from the Hsanda Gol Formation of Mongolia as "*Nimravus* sp." (AMNH21638). This specimen is identical in size and morphology to a referred specimen of *N. intermedius* from Caylux, France (MCZ8938). Toohey, however, was unwilling to refer AMNH 21638 to *N. intermedius*, partly because of their wide geographic distance. Regardless the taxonomic status of AMNH 21638, it probably has much longer premolars than in IVPP V11490 assuming the premolar proportions in the Quercy specimen are the same as in the Hsanda Gol form. Another Asiatic species is *N. mongoliensis* from the late Eocene / early Oligocene Ergilin Dzo Formation of Mongolia (Dashzeveg, 1996). This Paleogene species differs from IVPP V11490 in its long ramus, presence of a p1, and slender premolars.

If the reference of IVPP V11490 to *Nimravus* is correct, IVPP V11490 probably represents an undescribed species in a very late occurrence. The combination of a

short ramus, lack of a well-developed flange, and presence of small p2 are not known in other species of *Nimravus*. The latest previous record of *Nimravus* in Asia is from the Hsanda Gol Formation of Mongolia. In Europe, the status of *N. jourdani?* (Kretzoi, 1929), based on an isolated upper canine from La Grive, is still unresolved. If confirmed, the La Grive and Junggar *Nimravus* represent the latest occurrences in the middle Miocene of Eurasia.

Family Felidae Gray, 1821

Pseudaelurus Gervais 1948-52

Pseudaelurus cuspidatus sp. nov.

(Fig. 2A-B)

Holotype IVPP V11491, partial right ramus with c-p1 alveoli and p3-m1 (Fig. 2A).

Type locality Tiersihabahe, northern Junggar Basin, Xinjiang Autonomous Region.

Stratigraphic range Lower Halamagai Formation, early middle Miocene.

Referred specimen IVPP V11492, right broken P4 (Fig. 2B), from Tiersihabahe, lower Halamagai Formation.

Measurements IVPP V11491: p3, 8.5 × 4.0; p4, 10.6 × 4.9; m1, 12.6 × 5.6. IVPP V11492: P4, 17.0 × 6.5.

Diagnosis One of the smallest species of *Pseudaelurus* with the following combination of characters that can be distinguished from other known species of the genus: narrow P4, P4 protocone close to parastyle, ventrally arched ramus, an anteriorly positioned p1, p2 absent, well-developed anterior cingular cusps on premolars, vertical posterior edge of m1 trigonid, and high metaconid on m1.

Etymology In allusion to the cuspidate nature of its dental morphology.

Description Immediately behind the c alveolus is a single-rooted alveolus for p1. Between the p1 alveolus and p3 is a 10 mm diastema—p2 is lost. The principal cusps of p3-4 are tilted slightly posteriorly. The p3-4 have a conspicuous anterior cingular cusp and a posterior accessory cusp. Behind the posterior accessory cusp is a low posterior cingulum. The m1 shearing blade is tall and the paraconid blade is slightly bent toward the buccal side. The posterior border of the protoconid is vertical. There is a small but distinct metaconid, 4 mm in height, behind the posterior ridge of the protoconid, followed behind near the base of the crown by a vague bulge representing the remnant of a talonid. The relatively high crowned metaconid is consistent with the cuspidate nature of the premolars. There is no m2.

IVPP V11492 probably represents a slightly larger individual than the holotype. Whereas the m1 length of IVPP V11491 is nearly identical to that of the holotype of *Proailurus lemanensis* (MNHN 1903-20), the P4 length of IVPP V11492 (17.0 mm)

is 2 mm longer than that of MNHN 1903-20. Assuming similar upper and lower carnassial proportions as the *Proailurus*, IVPP V11492 is approximately 13% larger than IVPP V11491, an amount of variation within the normal range of known species of *Pseudaelurus* (Heizmann, 1973:fig.16). If the P4 is correctly referred to this species, the upper carnassial is equally unique among *Pseudaelurus*. The most striking feature of this carnassial is its far more mediolaterally compressed outline than any known *Pseudaelurus*, particularly at its anterior end. The protocone is almost right next to the parastyle instead of the far more medially positioned protocones in all other *Pseudaelurus*. Consistent with the cuspidate morphology of lower teeth, the P4 parastyle is also higher and more distinct than other species of the genus.

Comparison Two middle Miocene *Pseudaelurus* have been reported from China: *P. cf. lorteti* from Xiacaowan, Jiangsu Province (Qiu and Gu, 1986), and *P. guangheensis* from Guanghe, Gansu Province (Cao *et al.*, 1990). Materials from Xiacaowan consist of a ramal fragment with broken p3-m1, a partial P3, and a complete p4. Dental dimensions from the broken mandible are close to those of the Junggar specimen. The stage of reduction in m1 metaconid is also comparable to that in *P. cuspidatus*. The premolars, on the other hand, are quite different between the two forms. Both p2 and p3 from Xiacaowan are much less cuspidate than is seen in *P. cuspidatus*. The presence of a prominent anterior cingular cusp in the premolars of *P. cuspidatus* is in sharp contrast to those from Xiacaowan (Qiu and Gu, 1986: figs. 2,3A,B) and seems to leave little doubt that the Junggar specimen belongs to a different species.

Pseudaelurus guangheensis, on the other hand, was established on a maxillary fragment with P2-4. The only comparable part between materials from Guanghe and Junggar is their P4s. In addition to the much smaller size, the holotype of *P. guangheensis* (CUGS GV 87037, P3 length, 7.7 and P4 length, 12.0) has a normal proportioned upper carnassial of *Pseudaelurus*, in contrast to the more slender P4 in IVPP V11492. An even smaller individual (CUGS GV 87038, left ramus with broken p3, p4, and broken m1) from a higher bed relative to the holotype of *P. guangheensis* was listed as *Pseudaelurus* sp. by Cao *et al.* (1990). CUGS GV 87038, however, is probably not a *Pseudaelurus* because of its short trigonid of m1 with a transverse posterior surface on the protoconid (primitive condition for carnivorans) in contrast to a sharp posterior edge in all pseudaelurines.

In south Asia, Pilgrim (1910) recorded a small *Pseudaelurus*, *P.* (= *Sivaelurus*) *chinjiensis*, from the Chinji Formation of the Siwalik Group, Salt Range, Pakistan, based on a maxillary fragment. A ramal fragment from Chinji was later referred to this species (Pilgrim, 1915) and then became the holotype of a new genus and species, *Sivasmilus copei* Kretzoi, 1929, with a weak chin and crenulated p3, characters for

saber-toothed cats. That left the holotype of *P. chinjiensis* as the only known material of this species, which differs from IVPP V11492 in its broader P4 and more medially positioned protocone. There is, however, another ramal fragment with a broken m1 from Chinji in the collection of the American Museum of Natural History (AMNH96594). This undescribed m1 is of the same size as *P. cuspidatus* (m1, 12.3×5.4) and with similar morphology (with a distinct metaconid). AMNH 96594, however, has a deeper ramus (17.5 mm below m1) than that in the Junggar lower jaw (14.7mm). Being in the same general size category as the holotype, this Chinji ramus may properly be referred to *P. chinjiensis* pending additional materials.

In Europe, Heizmann (1973) recognized four species of *Pseudaelurus*. In order of increasing size, these are: *P. turnauensis* (Hoernes, 1882; equal to *P. transitorius* Depéret, 1892), *P. (Schizailurus) lorteti* (Gaillard, 1899), *P. romieviensis* (Roman and Viret, 1934), and *P. quadridentatus* (Blainville, 1843). All are distinguishable from *P. cuspidatus* by their wide upper carnassial, lack of or much weaker cusplets on premolars, more reduced metaconid on m1, and more anteriorly inclined posterior border of m1 trigonid. In terms of size, however, *P. cuspidatus* falls within the overlapping ranges of *P. turnauensis* and *P. lorteti* (Heizmann, 1973: fig. 16). *P. turnauensis* is well represented by a large sample from the Wintershof-West, which displays a certain amount of variations in the shape of m1 talonid and in the presence or absence of a p1 and m2 (Dehm, 1950: figs. 230—239, table 29). None, however, possesses the combination of morphology shown in *P. cuspidatus*.

In North America, *Pseudaelurus* is known to occur in Hemingfordian through Hemphillian (Tedford *et al.*, 1987). No systematic revision is available for the several species previously proposed: *P. intrepidus* (Leidy, 1858), *P. marshi* (Thorpe, 1922b), *P. (Pratifelis) martini* (Hibbard, 1934), *P. (Adelphailurus) kansensis* (Hibbard, 1934), *P. pedionomus* (Macdonald, 1948a), *P. thinobates* (Macdonald, 1948b), and *P. aeluroides* (Macdonald, 1954). As in the case of European *Pseudaelurus*, the North American species consistently differ from the Junggar form in their less compressed P4, less well developed accessory and cingular cusps in premolars and their less conspicuous metaconid of m1. In terms of size, the Junggar form is closest to *P. aeluroides*, whose m1, however, is still 24% longer than the former but whose premolars are only 7—10% longer.

There is an undescribed small *Pseudaelurus* in the Sheep Creek Formation (late Hemingfordian) in the Frick Collection (F: AM 61812-4, 61816, 61818). Represented by mostly jaw fragments, these individuals are about the same size as the Junggar form and tend to have more ventrally arched ramus. Two of these lower jaws have identical premolar / molar proportions, whereas two others have relatively shorter premolars (their m1s are equal to IVPP V11491). As in other known species

of *Pseudaelurus*, the Sheep Creek materials have less well-developed anterior cingular cusps on premolars compared to *P. cuspidatus*.

Finally, Andrews (1914) described a small cat, *Pseudaelurus africanus*, from east Africa. This species begins to have a downward extension of symphysis and erect canine, characters that signal machairodont trends, and was included in a new genus *Afrosmilus* by Kretzoi (1929), a conclusion followed by Schmidt-Kittler (1987) but contradicted by Ginsburg (1982). In any case, the African species is morphologically distinguishable from the Junggar form in its lack of an anterior cingular cusp on p3 and less pointed metaconid on m1.

Discussion The vertical posterior border of m1 trigonid and well-developed accessory and cingular cusps are general tendencies of saber-toothed cats. However, the ventrally bowed horizontal ramus of *Pseudaelurus cuspidatus* suggests that it lacks a chin in the anterior end and the ventral border of masseteric fossa is not dropped to the level of ventral border of the ramus, characters that are associated with saber-toothed cats. The Junggar lower jaw is thus more likely a peculiar *Pseudaelurus* rather than a saber cat.

As a stem genus of the felids, *Pseudaelurus* is likely paraphyletic, often defined by its transitional stage of dental reduction, such as a small p2, loss of m2, and a small talonid of m1, between the primitive *Proailurus* and more derived lineages. By these characters, the Junggar specimen generally belongs to *Pseudaelurus*. The reduction of its anterior premolars, however, is peculiar in that the p2, instead of p1, is lost, leaving a long diastema between p1 and p3. In all *Pseudaelurus*, the p2, when present, is always in the middle of the diastema or close to the p3. A p1 is absent in most *Pseudaelurus*.

Except some regional revisions, such as that by Heizmann (1973) and Schmidt-Kittler (1987), no comprehensive review of *Pseudaelurus* exists and relationships among species of the genus are not well understood. The present new material from the Junggar Basin is sufficient to demonstrate its morphological differences from other species but can contribute very little to a better understanding of its phylogenetic relationship. In its peculiar morphology, even the generic assignment of this new species may be questionable.

Hyaenidae Gray, 1869

***Protictitherium* Kretzoi, 1938**

***Protictitherium intermedium* Schmidt-Kittler, 1976**

(Fig. 3A-B)

Material IVPP V11493, partial left ramus with i3 alveolus, broken c, p1 alveolus, p2-m1, and m2 alveolus (Fig. 3A); IVPP V11494, left ramal fragment with

p3 alveolus and p4-m1 (Fig. 3B); IVPP V11495, edentulous right ramal fragment with c-p4 alveoli; and IVPP V11496, right partial ramus with p1-m1 all broken. All from Tiersihabahe, Halamagai Formation.

Measurements IVPP V11493: m1-p1 (alveolus), 33.0; p2, 6.0×2.3 ; p3*, 7.7×2.7 ; p4, 8.2×3.7 ; m1*, 9.5×4.5 ("*" indicates estimates). IVPP V11494: p4, 9.0×4.0 ; m1, 10.4×5.0 .

Description Two individuals that have well-preserved lower teeth are the main materials of this species. They differ slightly in size but is otherwise quite similar. The p1(missing) is single-rooted. The p2 is simple with a high principal cusp and only vague remnants of anterior and posterior cingular cusps. The p3 is broken and the remaining anterior half is very similar to that of the p2. The p4 has a strong posterior accessory cusp and a moderate anterior cingular cusp. Surrounding the accessory cusp is a well-developed cingulum. The m1 trigonid is rather high-crowned with a dominant protoconid and a small metaconid which is less than half the height of the protoconid. The paraconid has a weak lingual ridge extending from its apex down toward its base. The talonid is small compared to those in *Plioviverrops*. The entoconid and hypoconid is about equal in height. The entoconid projects lingually and is separated from the trigonid by a deep notch. The hypoconulid is reduced to a low, transverse ridge that is considerably lower than the hypoconid and entoconid—the talonid basin is rather open posteriorly.

Discussion Great emphasis was placed on the morphology of m1 talonid in the interpretation of phylogenetic relationships of primitive hyaenids(e.g., Schmidt-Kittler, 1976; Werdlin and Solounias, 1991; Hunt and Solounias, 1991). In particular, the development of a hypoconulid and relative sizes of metaconid and entoconids are characters commonly used to chart different lineages. Two genera, *Plioviverrops* and *Protictitherium*, are in the same general size class and have similar morphology as the Junggar form. Both lineages start with a talonid that have a small hypoconulid, in contrast to the general lack of this cusp in *Herpestides* (Beaumont, 1967), and exhibit a common tendency toward hypocarnivory with increasing developments of the m1 metaconids, entoconids, and hypoconulids (Beaumont and Mein, 1972; Schmidt-Kittler, 1976). *Plioviverrops* represents a more hypocarnivorous clade with higher-crowned metaconid, entoconids, and hypoconulids, and shorter trigonid relative to the elongated talonid. Lacking these features, the Junggar form seems best placed within *Protictitherium*.

Schmidt-Kittler (1976) recognized four species of *Protictitherium* from western Europe and Turkey: *P. crassum* (Depéret, 1892), *P. gaillardi* (Forsyth-Major, 1903), *P. intermedium* Schmidt-Kittler, 1976, and *P. cingulatum* Schmidt-Kittler, 1976(see Werdlin and Solounias, 1991 for a different content of the genus). Except the much

larger and more derived *P. crassum*, the rest three species are more or less comparable in size to the Junggar form (see Schmidt-Kittler, 1976; fig. 83). Of these, *P. cingulatum* is easily ruled out because of its prominent developments of buccal cingula in p4 and m1 that are absent in the Junggar materials. Referred specimens of *P. gaillardi* from Turkey (Schmidt-Kittler, 1976) and Spain (Crusafont-Pairó and Petter, 1969) seem to give this species a slightly more hypocarnivorous appearance with lower trigonid and higher entoconid on m1 than is the holotype from La Grive (Hunt and Solounias, 1991). *P. intermedium* from Candir of Turkey, on the other hand, is oldest, smallest, and least hypocarnivorous among species of *Protictitherium* (Werdlin and Solounias, 1991). The Junggar materials fall within the size range of *P. intermedium* (m1 length 9.4–10.5mm) and are morphologically indistinguishable from those illustrated by Schmidt-Kittler (1976: figs. 60–62).

***Protictitherium* small sp.**

(Fig. 3C)

Materials IVPP V11497, left ramal fragment with m1 and m2 alveolus (Fig. 3C), from Botamoyin; and IVPP V11498, left ramus with i1–m2 alveoli and posterior half of p2, from Tiersihabahe. All from Lower Halamagai Formation.

Measurements IVPP V11497: m1, 8.0×3.7 . IVPP V11498: p1–m2 (alveoli), 33.5; p1 alveolar length, 2.1; p2 alveolar length, 4.6; p3 alveolar length, 5.4; p4 alveolar length, 6.4; m1 alveolar length, 8.9; and m2 alveolar length, 2.4.

Description The long, slender horizontal ramus has two mental foramina, a larger one between p1 and p2 and a smaller one below p3. The half p2 in IVPP V11498 indicates a single main cusp and a vestigial posterior cingular cusp. The m1 has a relatively elongated trigonid with a dominate protoconid and a much smaller metaconid, which is less than half the height of the protoconid. The talonid is tricuspid with large hypoconid and entoconid, and a small hypoconulid. The entoconid is about equal height as the hypoconid and is connected to the hypoconid through a vague, transverse cristid. The hypoconulid is cingular-like and its original height is unknown due to wear.

Discussion Except a 20% smaller size, this small *Protictitherium* is indistinguishable from *P. intermedium* described above. Yet, its elongated m1 trigonid and presence of a small hypoconulid preclude possibility of *Herpestides antiquus*, a similar-sized carnivoran considered by some authors to be a basal hyaenid (e. g., Beaumont, 1967). If the present assignment to *Protictitherium* is correct, the Junggar form most likely represents the smallest and most primitive species of the genus. The fragmentary materials, however, is not adequate to establish a new species. The co-occurrence of this small form and *P. intermedium* in the lower part of the

Halamagai Formation seems to suggest a local cladogenetic event between these two species. Such an event would have interesting implications about the origin of the hyaenid clade based on the phylogenetic framework by Werdlin and Solounias (1991), in which *Protictitherium* was interpreted to be the most basal hyaenid and *P. intermedium* the most primitive *Protictitherium*.

***Thalassictis* Gervais, 1850**

***Thalassictis chinjiensis* (Pilgrim, 1932)**

(Fig. 3D-E)

Ictitherium cf. *I. gaudryi* (Zdansky, 1924): Tong *et al.*, 1987: 48, figs. 18.2, 18.3(in part). Qi, 1989: 135, figs. 2.2, 2.3 (in part).

Material IVPP V7733, left ramal fragment with p2-4 (Tong *et al.*, 1987: fig. 18.2; Qi, 1989: fig. 2.2), Botamoyin; IVPP V7734, isolated right m1(Tong *et al.*, 1987: fig. 18.3; Qi, 1989: fig. 2.3), Ganqikair; IVPP V11499, isolated right m1(Fig. 3E), and IVPP V11500, partial right P4 (Fig. 3D), from Duolebulejin, "upper sands" of uppermost Suosuoquan Formation.

Measurements(those for IVPP V7733 and V7734 are adopted from Qi, 1989: table 2) IVPP V7733: p2, 9.8×5.0 ; p3, 12.1×6.2 ; p4, 14.0×6.7 . IVPP V7734: m1, 13.8×7.5 . IVPP V11499: m1, 16.6×8.1 . IVPP V11500: P4, 23.3 (length).

Description We were unable to locate specimens described by Qi (1989) and the following observation is based on his illustrations. The isolated P4 of IVPP V11500 has a large parastyle, as is characteristic of mesocarnivorous hyaenids. Signalling its derived status, the P4 has a long metastyle blade relative to the paracone blade. There are two mental foramina, a larger one below p2 and a smaller one below p3 (Qi, 1989: fig. 2.2b). Qi (1989) remarked that there is probably no p1 on IVPP V7733. The broken p2 has a very small posterior accessory cusp, which is progressively enlarged in p3-4. Starting in p3 there developed a small posterior cingulum, which is further enlarged and expanded to lingual side of the accessory cusp. The perfectly preserved m1s have an elongated trigonid and shortened talonid. A moderate buccal cingulum is restricted to the paraconid part of the trigonid. The protoconid blade is approximately equal in length to the paraconid blade and is only slightly higher than the latter. The metaconid is very reduced and only slightly higher than the entoconid. The hypoconulid is reduced to a low cingulum connecting between entoconid and hypoconid, closing off the talonid basin posteriorly. The entoconid is of the same height as the hypoconid.

Discussion Suspicious of the original identification of *Ictitherium*, which is not known before the *Hipparion* faunas in north China, Qiu and Qiu (1995:50) suggested

that the Junggar hyaenid probably belongs to *Miohyaena* (here equals *Thalassictis*, see below). Furthermore, Tong *et al.*'s (1987) and Qi's (1989) hypodigm of *Ictitherium* cf. *I. gaudryi* apparently included some nonhyaenid materials (see discussion under *Simocyon*). In addition to the partial jaw referred to *Simocyon* (IVPP V7732), an isolated p4 illustrated by Qi (1989: fig. 2.4) is also inconsistent with that in IVPP V7733 and not included in the present hypodigm.

It is beyond the present purpose to tackle the intricate systematic problems of primitive hyaenids, and we follow Werdlin and Solounias' (1991) usage of taxonomy derived from their phylogenetic analysis. The Junggar form is more derived than *Ictitherium* in its more hypercarnivorous morphology: long P4 metastyle, reduced m1 metaconid, high m1 trigonid and small talonid. On the other hand, presence of two mental foramina indicates its more primitive status relative to *Hyaenotherium wongii*, which possesses one mental foramen. The Junggar materials thus seem to fall within the loosely defined paraphyletic grade *Thalassictis* (including *Miohyaena* of other authors) between *Ictitherium* and *Hyaenotherium*. Werdlin and Solounias (1991) recognized six middle to late Miocene species that generally fit in this grade: *T. robusta* Gervais, 1850, *T. certa* (Forsyth Major, 1903), *T. sarmatica* (Pavlov, 1908), *T. proava* (Pilgrim, 1910) = *T. chinjiensis* (Pilgrim, 1932), *T. montadai* (Villalta Comella and Crusafont-Pairó, 1943), and *T. spelaea* (Semenov, 1988).

European species of *Thalassictis* are generally more primitive in their less hypercarnivorous dentitions. The Junggar form is about the same size as the La Grive *Thalassictis certa* (Viret, 1951: pl. I, figs. 12–15, pl II, fig. 1) but differs from it by a longer P4 metastyle blade and more reduced m1 metaconid and talonid. Similarly, the Junggar *Thalassictis* falls within the size range and relative trigonid length of the genotypic species *T. robusta* from Kishinev (see Kurtén, 1982: fig. 2) but is more derived in its longer P4 metastyle blade and lower m1 metaconid. Another species from Kishinev is *T. sarmatica*, which was synonymized to *T. robusta* by Semenov (1989) but retained as a distinct species by Werdlin and Solounias (1991), who pointed out its more reduced premolars. The only comparable part between *T. sarmatica* and the Junggar form is the P4, which, as in other European species, has a relatively shorter metastyle blade than the latter. A fourth species, *T. montadai* from late Astaracian to early Vallesian localities of Spain, is distinguished from the Junggar species in its shorter metastyle blade of P4 and much more robust (broad) premolars. Finally, the Vallesian *T. spelaea* from Gritsev is similar to other European species in its relatively high m1 metaconid and short P4 metastyle.

The closest match for the Junggar form is the Siwalik species *Thalassictis chinjiensis* (Pilgrim, 1932) from Chinji. IVPP V11499 is almost identical in size to the holotype of *T. chinjiensis* and matches well in terms of reduction of m1 metaconid.

Another Siwalik species, *T. proava* (Pilgrim, 1910), was often regarded conspecific with *T. chinjiensis* and if so, has priority (see Werdlin and Solounias, 1991). The holotype of *T. proava*, however, seems to exhibit more primitive features of less reduced m1 talonid and metaconid than is seen in the holotype of *T. chinjiensis* (compare pl.5, fig.6 with pl.6, fig.6 in Pilgrim, 1932). In these features, the Junggar form is much closer to the holotype of *T. chinjiensis*. Obviously, secure reference of this form to the Siwalik species can only come after more complete materials become available from both places. Until then, it is more precise to refer the Junggar materials to *T. chinjiensis* and to leave *T. proava* as possibly distinct.

Suborder Caniformia Kretzoi, 1945

Infraorder Arctoidea Flower, 1869

Family Amphicyonidae, Trouessart, 1885

***Gobicyon* Colbert, 1939**

***Gobicyon?* sp.**

Materials IVPP V11501, anterior fragment of a right p4; IVPP V11502, anterior fragment of a left P4. All from Tiersihabahe, lower Halamagai Formation.

Discussion The high-crowned p4 principal cusp with a very erect anterior face is characteristic of *Gobicyon*, in contrast to much lower crowned and less erect premolars in *Amphicyon*, known to occur in the Junggar Basin (Qi, 1989). This partial p4 compares well with AMNH 26601, a referred specimen of *Gobicyon macrognathus* (Colbert, 1939). IVPP V11501 may also be compared with premolars of a medium-sized *Hyaenodon*, which, however, is mostly extinct in the Miocene of north China and seems less likely a candidate for the Xinjiang materials.

The P4 fragment, IVPP V11502, most likely belongs to that of an amphicyonid. It is probably not that of an *Amphicyon* because of its primitively anteriorly positioned protocone in contrast to a more reduced protocone that is behind the anterior border of the paracone in *Amphicyon*. Although no upper teeth is known for *Gobicyon*, the P4 from Xinjiang is tentatively referred to it for lack of a better alternative.

Qiu and Qiu (1995:50) re-identified a jaw fragment as *Gobicyon* that was formerly included in *Ictitherium* by Tong *et al.* (1987) and Qi (1989). This specimen is presently regarded as a *Simocyon* (see below).

Superfamily Musteloidea Schmidt-Kittler, 1981

***Oligobunis* Cope, 1881**

***Oligobunis?* sp.**

(Fig.4A)

Material IVPP V11503, right ramal fragment of a young individual, with dp4,

p2-p4, and alveolus of m1 (Fig. 4A), from Tieersihabahe, lower part of Halamagai Formation.

Measurement IVPP V11503: dp4, 9.4×4.3 ; p2, 7.1×3.6 ; p3, 7.5×4.0 ; and p4, 9.1×5.0 .

Description The preserved premolars match well with the size and morphology of *Oligobunis*. The dp4 (deciduous carnassial) has a low trigonid which has a large metaconid. Its talonid has a large hypoconid and a small, lingually positioned entoconid. The p2 has a low-crowned main cusp which is anteriorly located and followed by a long heel. The p3 is very similar to p2 except its slightly larger size. The p4 is nearly entirely embedded within the ramus and its tip is barely erupted out of the top edge of the ramus. It has a small posterior accessory cusp.

Discussion Recent discovery in the Tunggur Formation of Nei Mongol of materials belonging the *Oligobunis-Aelurocyon* lineage establishes its presence in the middle Miocene of north China (unpublished materials). The overall robust construction with their simple main cusps on p2-p3 and very reduced posterior accessory cusp on p4 are characteristic of this early lineage of musteloids so far known only in North America. The poor condition of preservation in the Junggar materials obviously call for caution about this identification. In particular, the lack of m1 prevents observation of its state of reduction in metaconid, an important characteristic in the evolution of this lineage.

Procyonidae Gray, 1825

***Alopecocyon* Viret, 1951**

***Alopecocyon goeriachensis* (Toula, 1884)**

(Fig. 4B)

Material IVPP V11504, isolated right m1 (Fig. 4B), from Duolebulejin, upper sands of uppermost Suosuoquan Formation.

Measurement m1, 11.9×5.7 .

Description The isolated m1 from Junggar is about the same size as that from La Grive (Viret, 1951: pl.1, figs. 8-9) and is slightly longer than that from the Sansan (Ginsburg, 1961: m1 length = 10.7). Morphologically, the Junggar form seems also closer to the La Grive material in its slightly higher trigonid and hypoconid. Other than such subtle variations, the limited Junggar material offers a reasonably good match to the European specimens.

Discussion Under the limitation of a single m1, the present identification can only be tentative pending further discovery about this species.

***Simocyon* Wagner, 1858**

***Simocyon* small sp.**

(Fig. 4C)

Ictitherium cf. *I. gaudryi* (Zdansky, 1924): Tong *et al.*, 1987: 48, fig. 18.1. Qi, 1989: 135, figs. 2.1a, b (in part).

Gobicyon: Qiu *et al.*, 1995: 50.

Material IVPP V7732, right ramal fragment with m1-2 (Tong *et al.*, 1987: fig. 18.1; Qi, 1989: figs. 2.1a, b), IVPP V11505, right ramal fragment with p1 alveolus, p4 broken, m1 broken, and m2 alveolus (Fig. 4C). All from Botamoyin, lower Halamagai Formation.

Measurement IVPP V7732: m1, 16.6×7.4 ; m2, 8.9×5.0 (from Qi, 1989: table 2). IVPP V11505 (all alveolar length): p1, 2.2; p4, 10.1; m1, 16.0; m2, 8.8.

Description We were unable to locate the specimen described by Qi (1989) and the following observation is based on his illustrations. On IVPP V11505, a small alveolus of p1 at the anterior tip of the ramus is closely behind the alveolus for c. There is a long diastema between the p1 alveolus and p4. Only a posterior accessory cusp is partially preserved on the broken p4. The p4 is quite large relative to m1, a characteristic of *Simocyon*. The m1 trigonid is heavily worn in IVPP V7732 and is broken in IVPP V11505, and a metaconid cannot be seen in Qi's (1989: fig. 2.1a) illustration. The talonid of m1 is preserved on both specimens that show a large, low-crowned hypoconid and a small, narrow entoconid ridge. The m2 has a typical simocyonine elongation of talonid relative to a short trigonid. The m2 protoconid is a low cusp connected posteriorly to a low hypoconid ridge. There is no m3.

Discussion The ramal fragment (IVPP V7732) described as *Ictitherium* cf. *I. gaudryi* by Tong *et al.* (1987) and Qi (1989) shows no resemblance to a primitive hyaenid, as first commented by Qiu and Qiu (1995) who identified it as *Gobicyon*. Indeed, the m1 talonid lacks a conical entoconid separated from trigonid by a deep notch that is present in all primitive hyaenids, and the m2 trigonid is that of an arctoid carnivoran rather than that of a hyaenid which has marginally located protoconid and metaconid. Instead, IVPP V7732 has the same ramal and dental proportions as IVPP V11505 and they do not seem to be *Gobicyon* either. Beside the much smaller size than the specimens referred to *Gobicyon* above, the following characters can be cited to indicate its affinity with *Simocyon*: robust ramus, loss of p2-p3, a long diastema between p1 and p4, enlarged p4, reduced m1 metaconid, large but low-crowned m1 hypoconid, narrow and ridge-like entoconid, and elongated m2 talonid.

If correctly identified as *Simocyon*, the Junggar form probably represents an undescribed species of the genus. Its degree of premolar reduction (loss of p2-p3) is

comparable to an individual of *S. (Araeocyon) primigenius* from the early Hemphillian of Rattlesnake Formation (Thorpe, 1921, 1922a), although loss of premolars are subject to variations in the species (Wang, 1997). On the other hand, its small size, less elongated m2 talonid, and less reduced m1 entoconid ridge are closer to *S. (Metarctos) diaphorus* from Eppelsheim (Vallesian), Germany, the earliest occurrence of this genus in Europe.

3 Phylogenetic and stratigraphic remarks

Mammals from the Halamagai Formation have generally been compared with those from the Tunggur Formation in Nei Mongol and believed to belong to the Tunggurian land mammal age (e.g., Tong *et al.*, 1987; Qi, 1989; Qiu, 1990). Within the Tunggurian age, Qiu and Qiu (1995) recognize a series of "local faunas" spanning the entire age, ranging from the Dingjiaergou fauna in Ningxia as the earliest Tunggurian to the Tunggur fauna in Nei Mongol as the late Tunggurian. Unfortunately, most of these Tunggurian faunas have few carnivorans in common and the Tunggur Formation offers the richest carnivorans for comparison.

Despite the incomplete nature of its fossil record, the Halamagai fauna possesses some typical taxa of the Tunggurian chronofauna, such as *Platybelodon*, *Anchitherium*, *Stephanocemas*, and *Anchitheriomys*. In carnivorans, there is also a general similarity in these faunas: *Protictitherium* (including *Tungurictis*), *Gobicyon*, *Amphicyon*, and *Oligobunis*. More detailed comparison, however, reveals that a single species is yet to be recognized that is shared by these two regions.

Only one genus, *Protictitherium* (including *Tungurictis* as a subgenus, as suggested by Hunt and Solounias, 1991), has species from the two regions that are closely enough related to offer evaluations of their stage of evolutions useful for stratigraphic inference. *P. intermedium* appears to be slightly more primitive than *P. (Tungurictis) spocki* in its smaller size. For a geologically earlier occurrence, a *Protictitherium* sp. was listed by Li *et al.* (1983) in the early Miocene Xiacaowan Formation at Sihong, Jiangsu Province, and may shed further light in this lineage.

Two other genera may be potentially useful in comparisons between faunas from Tunggur and Junggar. One is *Oligobunis*, whose records in both Junggar and Tunggur are still too poor to make much meaningful comparisons. Based on what is known, *Oligobunis* from the Halamagai is smaller and possibly more primitive, judging from similar trends seen in its North American relatives. Another genus is *Gobicyon*, whose materials from the Halamagai is still too fragmentary to be sure of its generic assignment, let alone its species comparison. This rare amphicyonid is also known in Dingjiaergou in Tongxin (Qiu and Qiu, 1995) and Prebreza (Serbia) in the MN 6 of Europe (Pavlovic and Thenius, 1959), making its stratigraphic range longer than what

has been previously thought.

Despite their common generic name *Amphicyon*, species from Junggar and Tunggur are quite different and likely belong to different clades. *A. teirumensis* is a wolf-sized predator, whereas *A. ulungurensis* is a giant bear-dog comparable in size to *A. confucianus* Young, 1937 in the early Miocene of Shanwang and European giants such as *A. giganteus* (MN3-5), *A. major* (MN5-9) and others (Viranta, 1996). Lacking a close relationship, the *Amphicyon* from Junggar and Tunggur is unlikely to yield clues about their chronological relationship.

Thalassictis in Junggar is the first record in the Tunggurian of east Asia, as contrasted to its Astaracian to Vallesian occurrence in Europe. In general, the Junggar *Thalassictis* seems more derived than the European species in its long P4 metastyle. More intriguingly, the identification of *T. chinjiensis* in Junggar provides another direct link to south Asia south of the Tibetan Plateau, as may also be hinted in *Pseudaelurus* from both of these regions.

Jaw fragments identified as *Simocyon* are significantly different from known species of *Simocyon*, which are often associated with *Hipparion faunas* (Vallesian-Turolian of Europe, Baodean-Yushean of Asia, and Hemphillian of North America). Until the Junggar *Simocyon* becomes better known, its stratigraphic value is very limited beyond the general recognition that it may represent an early precursor of the lineage, as also hinted by the co-occurrence of *Alopecocyon goeriachensis* (known from Goriach, Neudorf, Sansan, and La Grive of Europe).