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甘肃结沟保德期 *Agriotherium* 的发现及其意义

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关键词　甘肃　保德期　郊熊

内　容　提　要

本文记述了郊熊的一个新种： *Agriotherium inexpetans* sp. nov.。这是 *Agriotherium* 与保德期三趾马动物群共生的首次可靠记录。新种个体小，下臼齿具有若干近祖性状：如 M_2 的下前尖和 M_3 各主尖尚可辨认等。 *A. inexpetans* 在形态上与内蒙古通古尔中中新统发现的 *Dinocyon* (=*Hemicyon*) *teilhardi* 有许多相近之处。它们很可能有最直接的系统关系。作者还就这一发现对熊科分类的含义进行了讨论。

Indarctos（印度熊）和 *Agriotherium*（郊熊）的化石在我国发现不多，特别是 *Agriotherium*，可靠的记录至今只有一次（Qiu et Schmidt-Kittler, 1983）。*Indarctos* 和 *Agriotherium* 形态上很接近，这早已为古生物学家所认识，但对它们之间的系统关系，则有相当大的分歧意见。Hendey 强烈主张 *Agriotherium* 是由 *Indarctos* 直接进化而来的，其主要依据是 *Indarctos* 和 *Agriotherium* 出现的时序是连续的，亦即 *Indarctos* 只发现于晚中新世，而 *Agriotherium* 则仅出现于上新世。他把 *Agriotherium* 中的某些原始特征（比 *Indarctos* 还原始）解释为从杂食至肉食习性的再适应，即反向进化的结果。这种系统关系的解释在分类上的反映则是为这两个属建立一个单独的亚科（现称 Agriotheriinae）。邱占祥和 N. Schmidt-Kittler, 1983 则认为 *Agriotherium* 所具有的原始特征是残存的近祖性状。这就意味着 *Indarctos* 和 *Agriotherium* 各有一段独自发展的历史。但是，他们发表这种观点的时候还没有找到化石依据。

1987年谢骏义在东乡族自治县结沟收集到一些零散的熊牙。当时并没引起特别的注意。1990 年秋，本文作者仔细地观察了这几件标本，发现其中肯定有属于 *Agriotherium* 的牙齿。

东乡族自治县的结沟是著名的"龙骨"产地之一。所产化石以三趾马和大唇犀最多，上述熊类化石就是和它们一起发现的，化石保存情况也完全一致。这样，结沟的 *Agriotherium* 就成了该属在晚中新世三趾马动物群中第一批有可靠记录的化石。

本文蒙沈文龙先生绘图，张杰先生照相，在此一并致谢。

一、化石产地地层简记

结沟位于甘肃省东乡族自治县(锁南镇)城南约五公里，隶属平庄乡。化石产自结沟西糊淌沟之红山(甘肃省博物馆野外化石地点编号：8909)。

含化石的地层为褐红色粘土与淡褐红色泥灰岩(钙质富集层)互层所组成的一套红色岩系(厚逾 50 米)，底部有一层厚 2—3 米的含钙质团块，夹含砾粗砂透镜体的灰白色泥灰岩。化石集中于这套红色岩系的中部。除上述 *Agriotherium* 化石外，经初步观察还有：*Chilotherium* sp.、*Hipparion* sp.、*Honanotherium* sp.、*Cervocerus* sp.。

这套红色岩系相当于临夏组第四岩性段的上部，其时代一直归入保德期。

上伏第四系黄土，下覆灰白一灰褐色含砾中细砂岩(厚约 6 米)。

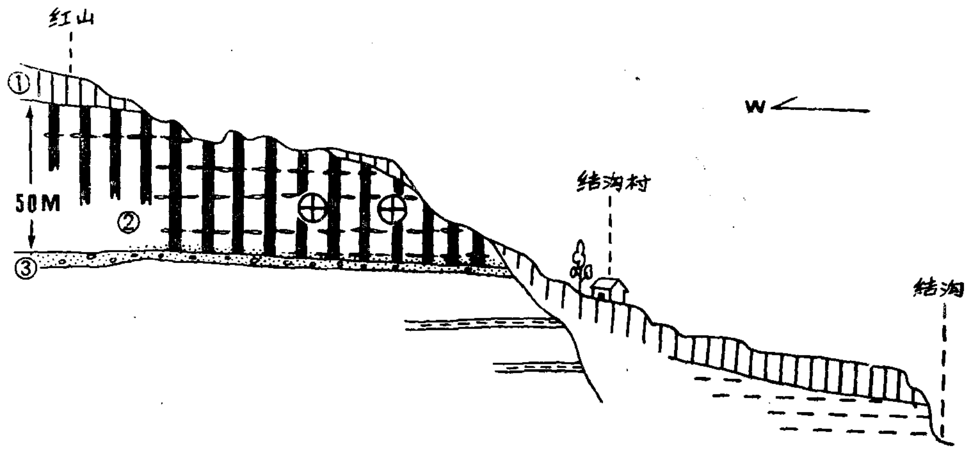

图 1　化石产地剖面图
(Section of fossil locality)

二、化 石 记 述

熊科 Ursidae Gray, 1825

半熊亚科 Hemicyoniinae Frick, 1926

意外郊熊(新种) *Agriotherium inexpetans* sp. nov.

正型标本　属于同一个体的左 P_4，左、右 M_1 的跟座(具下后尖)，左、右 M_2 和左 M_3。一右下犬齿顶端断块，可能也属于同一个体。甘肃省博物馆标本编号：GVJ 87001。

特征　一种小而原始的郊熊，M_1 的下内尖比下后尖低很多，且位置靠后，与下后尖以

一凹槽相隔。M_2 具分离出来的下前尖，整体轮廓较细长，三角座不特别加宽；M_3 也相对较窄长，冠面构造与 M_2 各尖大体对应。

描述 除犬齿外，牙齿保存状况完全一样：珐琅质局部受风化（植物浸蚀?），表面粗糙，呈淡黄(白)色，偶现灰黑色细斑纹。牙齿刚有一点磨蚀的痕迹。齿根破损，显然皆来自同一下颌。下犬齿顶端颜色更浅些，但带有更多的灰黑色斑纹。很可能与上述牙齿也属同一个体。

下犬齿顶端具三嵴：前内嵴粗而高耸，其后方有深沟；后嵴细锐，仍很明显；外后方的嵴钝平，但仍能触摸出来。P_4 具有小的前边附尖。主尖前嵴伸向正前方，接近前边附尖时，嵴变锐。后嵴与前嵴在同一线上，比前嵴更锐，向下至下 1/3 处突然变缓，这可能代表了后边的附尖的部分。这一部分显著地长于前边的附尖，所以自侧面看牙齿前后不对称，主尖偏向前半部。P_4 的内缘在基部有一很明显的隆突的部分，它位于内壁的后 1/3 处，这使牙齿的轮廓自顶面看近一底长的不等边三角形。自最隆凸处向主尖顶端方向伸出一斜嵴，但此斜嵴只在下半部分清楚，至主尖顶端逐渐消失。齿带在内后角最发育，在前边附尖的内侧也有一小段，在外侧的后半部较清楚，前半部则很模糊。

M_1 的下后尖呈孤立锥状，比下次尖高大。尖的中央有嵴，嵴的前半段斜向前外方，后半段则伸向后方，与下原尖以一浅沟相隔。下后尖的前嵴下降相对较缓，而后嵴近于陡直。下次尖锥状，位于牙齿外壁的后端。下次尖的前嵴很长，斜向前内方，其后半段缓缓向前下降，其前半段向前又稍上升，因此自侧面看呈浅 V 字形。此嵴前端显然达原尖后壁中央。下次尖后嵴向后平伸的部分很短，然后转向内方，甚至稍稍斜向前方，与下内尖的后外嵴相接。此处嵴很微弱，所以跟座在此处并不形成封闭。下内尖很小，左侧者前嵴明显，与下后尖后嵴相连；右侧者前嵴不显，在下内尖和下后尖之间有一光滑的凹面，成为跟座向内侧的开口。下内尖的后嵴呈弧形转向外方，与下次尖的后外嵴相接。下内尖的后嵴的嵴形程度高于下次尖后嵴者。由于下后尖和下次尖膨大而位置交错，跟凹呈一 S 形。齿冠的内壁圆隆，下后尖和下内尖之间以明显的凹沟相隔；外壁较平，但倾斜厉害；跟座外壁的齿带的前、后端升高并逐渐消失。

M_2 轮廓近长方形，其外壁在中部稍后处稍稍向内凹入。外壁冠高，倾斜；牙齿冠面由各尖前、后嵴相连而形成一封闭的长椭圆形、下原尖最高，下后尖稍低，其位置稍后于下原尖。两尖相向伸出的嵴约在中部相会，以纵沟相隔。此嵴自前、后看呈 V 形，并将冠面分成三角凹和跟凹两大部分。下原尖的前嵴向前伸至牙齿最前端，然后以一圆弧转向内后方，与相当大而分离出来的下前尖相连，后者位于下后尖前方，与之以沟相隔。下原尖的后嵴长，向后伸达锥形下内尖的中部水平，并与下次尖前嵴相接，此处是外壁最低处，此处嵴上有若干横沟，使嵴呈连续锥状。下内尖是主尖中最低的尖，分前、后两部分：前者锥状，后者嵴状，与下次尖后内嵴相连将跟凹封闭。齿带不发育，仅在外壁中凹处隐约可见。

M_3 为前宽后窄的圆三角形。冠面有由各主尖前、后嵴相连形成的封闭椭圆形嵴，原尖是各尖中最高的，其外壁强烈倾斜，向内伸出一相当粗大的嵴，此嵴的末端内后方连接着一个圆锥形突，这应当是下后尖。与 M_2 不同的是此尖不位于冠面周围嵴之上，而是被其包围。下前尖分辨不出来。下次尖较明显，构成牙齿后外端的最高处。下内尖不大明

显，但此处嵴变得粗而高。齿带不发育，仅外壁中凹处多少隐约可见。

表 1　几种郊熊下颊齿(长×宽)的比较　　单位：毫米 (in mm)

	P_4	M_2	M_3
A. inexpetans sp. nov. GVJ 67001	19.7×13.5	26.2×20.0	18.7×16.4
A. cf *intermedium* Qiu et Schmidt-Kittler, 1983	18.8×10.7		
A. insignis Viret, 1939	20.5×13.6	30.2×23.2	17×—
A. africanum Hendey, 1980	21.8—25.4×14.0—16.8	28.6—33.5×21.9—26.0	16.2—19.8×16.0—19.0

三、比较与鉴定

上述标本应归属于郊熊而不为印度熊是毫无疑义的。这两属在 M_1 跟座上的差别最为明显。前者的下后尖大，位置较靠后，与下原尖分隔较远；下内尖一个，短小，显著低于下次尖。而后者的下后尖较小，且与下原尖靠得较近；下内尖分成前、后两个，它们和下后尖在高度和大小上差别不那么显著，形成自前向后逐渐变小的三个连续的尖，其中至少前两个尖是高于下次尖的，所以自外侧可以看到下内尖。郊熊和印度熊的 P_4 也有区别：前者内壁后半部有明显的隆凸，并伴之以嵴形突起；而在印度熊中则没有这一嵴形突起，隆凸也不那么明显。结沟标本的 P_4 和 M_1 在构造上完全和郊熊者一致。

结沟的标本大概是目前已知各种郊熊中个体最小而构造最原始的一个种。由于郊熊中其它种都远为粗大而进步，实际上只有 *A. intermedium* 一种可以进行对比，但遗憾的是，至今我们对 *A. intermedium* 这个种仍所知甚少。结沟的材料也很可怜，两者可资对比的部分太少了。*A. intermedium* 的正型标本中下牙只有 M_1。而结沟材料中的 M_1 又只保存了跟座，单就跟座而言，两者大小和构造又都很接近，但前者的下内尖较高大，靠下后尖近，而后者的下内尖比下后尖低很多，位于牙齿后端，和下后尖之间以一凹槽相分隔。1983 年邱占祥和 N. Schmidt-Kittler 曾根据大小将安徽萧县的一件标本归入 *A.* cf. *intermedium*。其中下牙有 P_4 和 M_1，可和结沟的标本进行对比。二者 P_4 的差别较大。萧县者内壁虽有嵴形突起，但隆凸不明显；另一方面其后边的附尖和主尖之间以一沟槽相隔，这是结沟标本所没有的。

结沟的标本和 *A. intermedium* 的正型只有 M_1 的跟座可以对比，两者区别不大。它和萧县的标本在 P_4 的构造上差别较明显，但萧县标本是否一定是 *A. intermedium* 也还不能十分肯定。所以上述区别不一定表示结沟的标本应为一新种，使其构成新种的倒是它的 M_2 和 M_3 的一些独特的性状，这对郊熊属来说是很少见的。这主要是指其 M_2 具分离出来的下前尖，整个轮廓显得较细长，前半部不特别加宽；M_3 相对较窄长，冠面上仍保留着大体上能和 M_2 对应的各尖的构造。郊熊中已知各种的 M_2 和 M_3 都比结沟者进步得多。*A. intermedium* 至今未发现 M_2 和 M_3。但是如果它们确实都是出现在上新世的话，

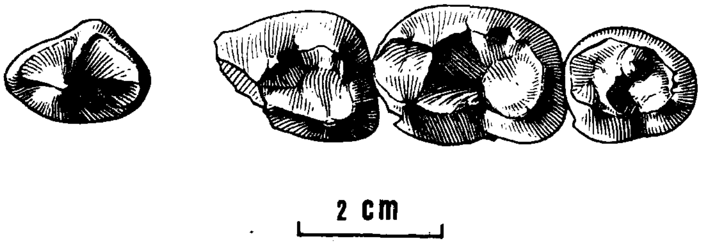

图 2 *Agriotherium inexpetans* sp. nov.
(GVJ 87001) 左 Left P_4、M_1—M_3 冠面观 (occlusal view)

很可能它的 M_2 和 M_3 也和其它各种大体一样，只是个体更小些。基于上述考虑，虽然结沟的材料还不够多，我们仍然认为将其作为一个新种是合适的。由于这次发现多少有些意外，故将其命名为意外郊熊——*Agriotherium inexpetans* sp. nov.。

四、讨 论

结沟材料的发现至少在以下两个方面是很有意义的：首先，它是晚中新世郊熊的首次可靠记录；其次，它在形态上比已知各种都原始，它的许多特征和内蒙古中中新世的 *Dinocyon* (=*Hemicyon*) *teilhardi* 很接近。

在欧亚大陆，过去在晚中新世地层中发现的郊熊化石只有两次记录：一是印度西瓦里克据称是发现于 Dhok-Pathan 中的 *A. palaeindicum*；一是发现于西班牙 Venta del Moro 地点的 *A. roblesi*。前者的时代，根据最近的研究（Barry *et al.*, 1982）大约应为距今 7.4 至 5.3 百万年之间。但是没有人能肯定 *A. palaeindicum* 这个种确实产自这一层位。西班牙的 Venta del Moro 化石点，目前西班牙的古生物学家都把它归入 MN 13，亦即晚中新世的最末期。但是，这一动物群包括了犬科、骆驼科等欧亚大陆典型的上新世分子（Morales, 1984）。结沟的郊熊则是典型的和三趾马动物群共生的动物。

Thenius 早在 1949 年就曾指出过，内蒙古通古尔的"*Hemicyon*" *teilhardi* 和欧洲典型的 *Hemicyon* 都不同，而更接近 *Dinocyon*。他指出在下牙上它和后者共同的特点是 M_1 跟座上只有一个下内尖和 M_2 的下前尖呈分离状态。有趣的是在这两点上它和结沟的标本也是相同的，而且它们两个还有更多的相近之处。它们的 M_2 在长宽比例和前、后宽度的差别程度很接近，而区别于典型郊熊的短宽而前部很宽的 M_2。它们的 M_3 在大小、形态以及具有大体可辨的三角座和跟座以及各尖的形态等方面也都很接近（Colbert, 1939, fig. 4）。"*Hemicyon*" *teilhardi* 在其它方面，例如前臼齿和上牙等也和 *Dinocyon* 很接近。所以，我们同意把它改归入 *Dinocyon* 这个属中。*Dinocyon* 这个属过去从来没有人把它直接和郊熊或印度熊从系统关系上联系起来。这个属在欧洲只有一个种，即：*D. thenardi*。它个体极大，已很特化，它不大可能是郊熊或印度熊的祖先。还有一个最大的障碍就是这个属的 M^1 也和其它典型的 hemicyonines 一样，也具有很宽大的内齿带，内齿带和原尖及其后嵴之间以深沟相隔，特别是在"次尖"的位置上齿带更为发育。在

郊熊和印度熊中“次尖”处反而是没有齿带的。*Dinocyon teilhardi* 个体远小于欧洲的属型种，在下臼齿的构造上又和在结沟发现的原始的郊熊化石如此相似，这使我们不能不想到，它或与它很接近的类型可能正是郊熊的祖先。至于说到两者在 M^1 上的区别这唯一的障碍，我们可以设想，位于“次尖”处的内齿带，逐渐与原尖后嵴靠近，其间的沟，逐渐变浅并且消失，这样“次尖”就和后小尖合而为一了(图 3)。

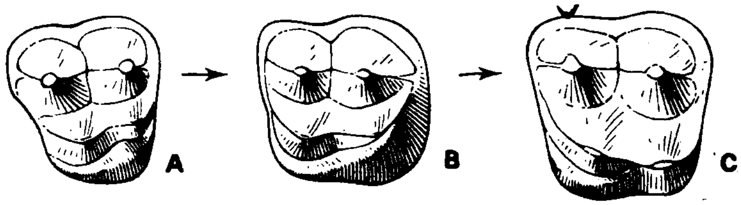

图 3　M^1 演化过程假想图

A. *Dinocyon*; B. 假想的过渡类型; C. *Agriotherium*

(A conjecture of evolution of M^1 for A. B. and C)

如果郊熊是从 *D. teilhardi* 类型的动物中产生的，那么印度熊就可能是从某种 *Hemicyon* 中演化出来。*Hemicyon* 和 *Dinocyon* 的不同很像印度熊和郊熊之间的不同：前者 M_1 具较长的跟座，跟座上常有两个下内尖，上臼齿也比较长而窄。如果单从牙齿的形态来看，*Ursavus* 也有可能是印度熊的祖先。它比 *Hemicyon* 似乎更接近印度熊，但从化石记录来看，它似乎一直是一个小个体熊类的支系，而且延续的时间较长，不单是和印度熊共生，而且还从中分出了大猫熊类(邱占祥、祁国琴，1989)。*Ursavus* 作为郊熊祖先的可能性更小，这是因为 *Ursavus* 从一开始 M_1 就有两个下内尖和比较长的跟座，这一特征一直保持没变。

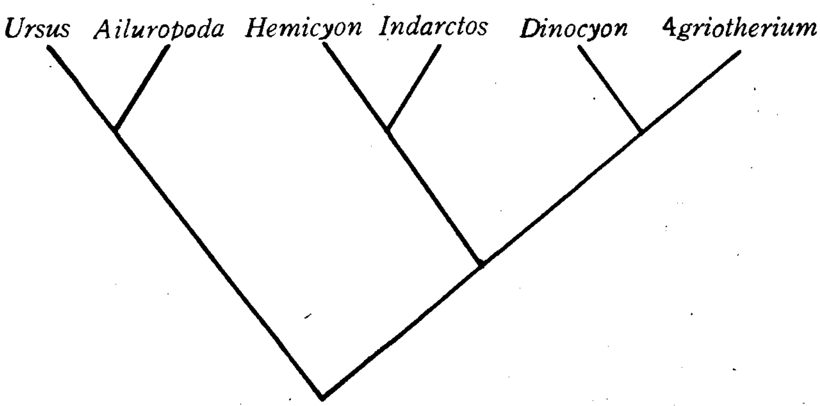

图 4　晚新生代熊类分支系统关系设想

(A tentative cladogram showing interrelationships of concerned genera)

如果上述的分析是正确的话，亦即印度熊是从 *Hemicyon* 这一支系中产生，而郊熊则是从 *Dinocyon teilhardi* 这一支系中产生，那么在分类上，根据分支系统学的基本观点，最直接的一个结果就是应该废弃 Agriotheriinae 这一分类单元。Agriotheriinae 亚

科是 Kretzoi 1942 年建立的，开始时包括了 *Agriotherium*、*Indarctos*、*Ursavus* 和 *Agriarctos* 四个属。最后一个属已被归入了大猫熊亚科(邱占祥、祁国琴，1989)。*Ursavus* 和大猫熊及广义的真熊系统关系更为密切,已如前述。而前两个属既不为祖裔关系，也不是从共同的祖先中直接发展出来的。因此把这两个属从 Hemicyoniinae 中分出单独作为一个亚科的作法也是不足取的，因为这样的分类明显地包含了并系发生。如果把熊类动物更早期的成员，如 amphicyonines 等暂不考虑在内，那么上述各属关系大体应如图 4 所示。从这个分支图上可以看到,晚第三纪以来,熊类的发展主要有两大支系：一支是祖熊、真熊和大猫熊;另一支则是 hemicyonines，它主要包括两个小分支（还有别的属，这里不予讨论）：一支为 *Hemicyon* 和 *Indarctos*，而另一支则包括 *Dinocyon* 和 *Agriotherium*。

熊科的分类一直是一个争论问题。自发现大猫熊和祖熊的关系密切后，这一分类问题变得更为引人注目了。而结沟材料的发现又为人们提出了一些新的问题。本文作者并没有对这些问题作出结论,但很愿意就上述的一些设想求教于同行们。

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DISCOVERY OF LATE MIOCENE *AGRIOTHERIUM* FROM JIEGOU, GANSU, AND ITS TAXONOMIC IMPLICATIONS

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Summary

Few *Indarctos* and *Agriotherium* fossils, especially the latter, have been found in China since 1920s. The only reliable record of *Agriotherium* is that described by Z.-x. Qiu and Schmidt-Kittler in 1983. It is a well known fact that the two genera are very close morphologically. However, as far as their relationship is concerned, opinions differ widely. Hendey (1972 etc.) ardently advocated his hypothesis that *Agriotherium* derived directly from *Indarctos*. One of his arguments was the successive occurrences of the two genera: *Indarctos* was found exclusively, from late Miocene, while *Agriotherium* only from Pliocene. Based primarily on analysis of dental morphology, Qiu and Schmidt-Kittler inclined to consider that the two had probably rather different origins, although then without material support from the side of fossils.

In 1987, the junior author of the present paper found some isolated large ursine teeth from Jiegou, Dongxiang Autonomous County, Gansu Province. Unfortunately, the discovery slipped special attention then. Having closely observed these specimens, the authors of the present paper concluded that they belong to *Agriotherium*. What is more important is the fact that they were found together with typical hipparion fauna elements. Jiegou is a well known "dragon-bone" site of Gansu Province. The fossil bearing deposits, red clay with calcareous nodules about 50m thick, have been correlated with the 4th member of the Linxia Formation by the local geologists. Based on lithology and the hipparion fauna fossils they found during the 70s, the local geologists always assigned the above mentioned 4th member of the formation to Baodean stage. Our own finds include *Hipparion, Chilotherium, Honanotherium, Cervocerus* etc. Therefore, this is the first discovery of *Agriotherium* together with typical hipparion fauna elements in China. The discovery thus considerably shook the foundation of Hendey's arguments, but is in favor of the 2nd viewpoint.

Ursidae Gray, 1825

Hemicyoniinae Frick, 1926

***Agriotherium inexpetans* sp. nov.**

Type Left P_4, talonids of left and right M_1, left and right M_2 and left M_3, all belonging to the same individual. A broken right lower canine, probably belonging to the same individual as the cheek teeth. All the specimens are housed in Gansu Provincial Museum. GVJ 87001.

Diagnosis The most primitive *Agriotherium* of small size. Entoconid of M_1 reduced in size, posteriorly located, separated by a wide notch from the much higher metaconid. M_2 long and narrow, trigonid not wider than talonid, with recognizable paraconid. M_3 long, with recognizable para-, meta- and hypoconid.

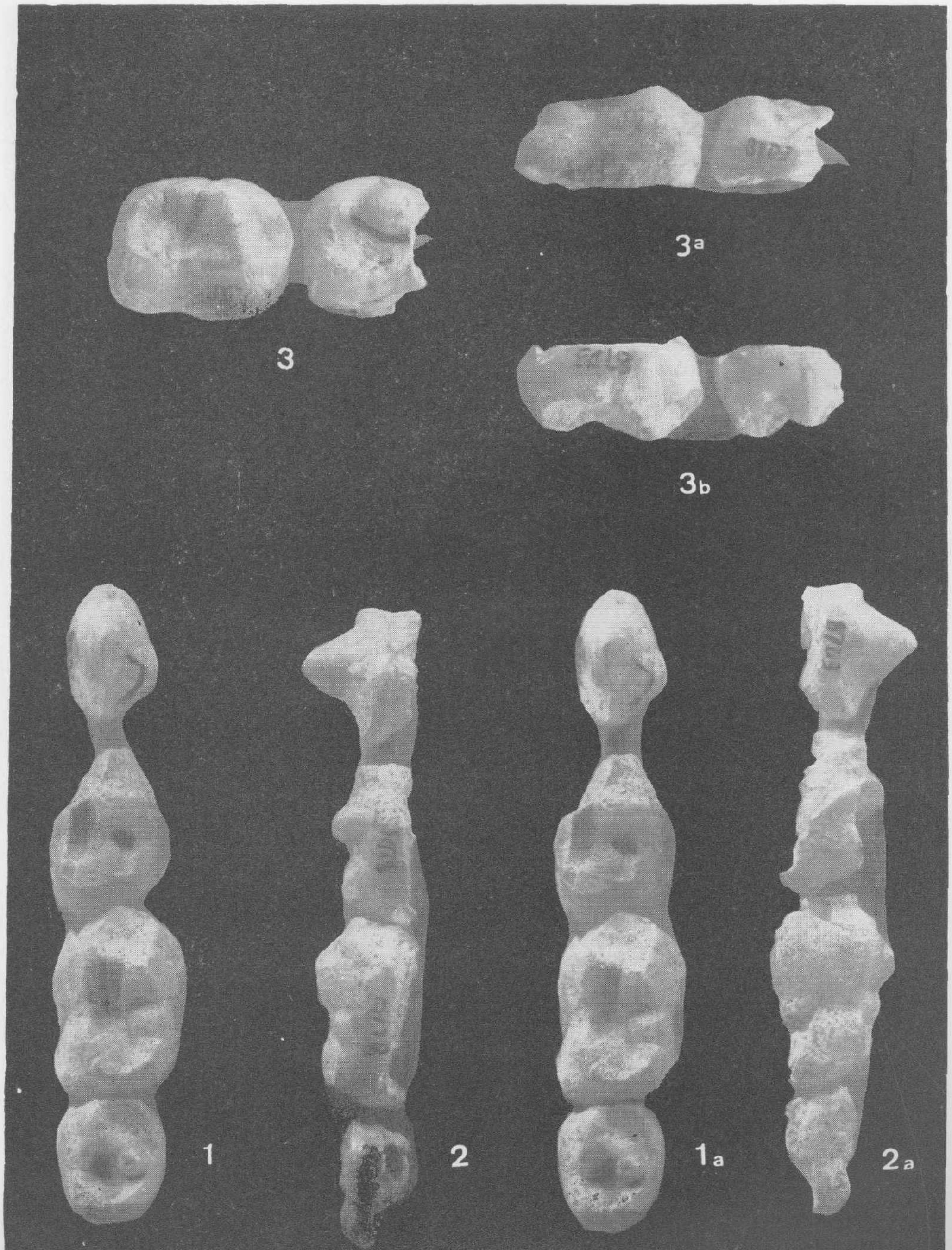
Description There are three ridges on the top portion of the lower canine: comparatively heavy antero-internal one, bordered posteriorly by a deep groove; fine but sharp posterior one and an obtuse postero-external one. P_4 has a tiny anterior accessory cusp. A sharp crest stretches longitudinally across the whole tooth. The posterior 1/3 of the posterior half of the crest slopes much less steeply than its anterior 2/3, representing the enlarged posterior accessory cusp. Labially, at its posterior 1/3, P_4 possesses a pronounced bulge at the crown base. From the bulge a ridge stretches upwards, but fades out before reaching the top of the main cusp. Cingulum is better developed on the posterior halves of the tooth labially, especially lingually.

The metaconid of M_1 is conic in shape, higher than hypoconid, separated from the protoconid by a shallow notch. The hypoconid has a form of compressed cone, situated at the postero-external corner of the talonid. A ridge stretches from its top to the middle of the posterior wall of the trigonid. Posteriorly the talonid is open. The entoconid is very small, separated from the metaconid by a U-shaped groove serving as the lingual outlet of the talonid. The external cingulum of the talonid turns upwards both anteriorly and posteriorly. M_3 is rounded triangular in shape. Its crown is sur ounded by a marginal ridge connecting the main cusps. The protoconid is the highest among the cusps, with strongly inclined external wall. A prominent ridge stretches postero-lingually and connects the metaconid, which lies labial to the lingual part of the marginal ridge. The paraconid is hardly discernible. The hypoconid comprises the highest point of the talonid. The entoconid is not well differentiated from the postero-lingual ridge of the talonid. Cingulum is weak, discernible at the base of the external valley.

Comparison and identification There is no doubt that the above described specimens should belong to the genus *Agriotherium*. The distinction between *Agriotherium* and *Indarctos* is particularly well demonstrated in the structue of the M_1 talonid. In the former the entoconid is single-cuspid and lower than the hypoconid, while in the latter the entoconid is double-cuspid and higher than the hypoconid. The above described specimens show clearly the first type of M_1 talonid. The two genera differ also in the configuration and structure of P_4. In this regard, the new specimens again conform with those of the first type.

In comparison with known species of *Agriotherium*, the new specimens resemble only *A. intermedium*, as far as size and morphology are concerned. All the other species are much larger and morphologically more advanced than the above described specimens. Unfortunately, the material of *A. intermedium* so far known is so poor, that little direct comparison could be made. From the type specimens, the only part allowing direct comparison with ours is the talonid of M_1. The endoconid in the new specimens is smaller than that in the type specimen of *A. intermedium*. But in general the two are very close in morphology. In comparison with those described as *A.* cf. *intermedium* by Qiu and Schmidt-Kittler, the P_4 of the new material differs by lacking the notch between the protoconid and the posterior accessory cusp characteristic of the latter material. What makes us feel convincing that the new specimens represent a new species is the unusual structure of the M_2 and M_3. As indicated in the description, the presence of a paraconid on M_2 and the possible recognition of the main cusps on the comparatively large M_3 are quite unique for the genus *Agriotherium*. Although we do not know exactly the structure of these two teeth in *A. intermedium*, we presume it is not far away from the common pattern of that genus. Therefore, we erected a new species for the material described above, Agriotherium inexpetans.

Comments It is worthy of special note that what makes our new species different from the other species of *Agriotherium* is the structure linking it with the middle Miocene "*Hemicyon*" *teilhardi* from Tungur, Nei Mongol. In the latter the talonid of M_1 possesses a single-cuspid entoconid, M_2 has a discernible paraconid and its M_3 is comparatively large and long, with all the main cusps still recognizable (see Colbert, 1939, fig. 4), just as in our new species. Primarily based on these and some other features of the upper teeth, Thenius (1949) transferred the Tungur species in *Dinocyon*. We concur with Thenius' referral. This led us to think hat *Agriotherium* might derive from a group of animals similar to *Dinocyon teilhardi*. The European species, *Dinocyon thenardi* is too specialized to be the ancestor of *Agriotherium*. It is true that *Agriotherium* and the hemicyonines including *Dinocyon* have different basic patterns of upper molars and this has been considered the major threshold hindering the derivation of *Agriotherium* from the hemicyonines. However, if we assume, the enlarged "hypocone" cingular shelf in the hemicyonines gradually approximated the posterior ridge of the protocone in the course of evolution and finally united with the latter, this would result in the formation of the basic pattern of the upper molars of *Agriotherium* (fig.3). On the other hand, *Indarctos* might well originate from some group of the hemicyonines other than *Dinocyon*. After the close relationships between the ursavines and the ailuropodines were recently recognized (Qiu and Qi, 1989, and others), it becomes more and more evident that there were two major lineages in the evolution of the late Neogene ursine animals. One was the *Ursavus* group and its derivatives: ailuropodines and the true ursines. The other is the lineage of hemicyonines. Apart from the early forms which were recently split into several genera, it comprises two subbranches: hemicyonines s.s. with their derivative *Indarctos* on the one hand, and *Dinocyon* and *Agriotherium* on the other. A tentative cladogram showing the interrelationships of these concerned genera is given in figure 4.



Agriotherium inexpetans 1. 1a. sp. nov. 左 P_4—M_3 立体照片 (stereoscopic), 冠面观 (occlusal view); 2. 左 P_4—M_3 唇侧观 (labial view); 2a. 左 P_4—M_3 舌侧观 (lingual view); 3. 右 M_1 跟座, M_2 冠面观 (occlusal view) 3a. 右 M_1 跟座, M_2 唇侧观 (labial view); 3b. 右 M_1 跟座, M_2 舌侧观 (lingual view)