第 27 卷 第 2 期　　古 脊 椎 动 物 学 报　　pp. 77—86
1989 年 4 月　　VERTEBRATA PALASIATICA　　pl. I

关于 *Interogale* 和 *Anchilestes* 属分类位置的讨论

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关键词　裂齿目　中间狪　安琪掠兽[1)]

内　容　提　要

Interogale 和 *Anchilestes* 属原被归入狪目(哺乳纲)。本文根据属型种 *Interogale datangensis* 的吻区结构及 *Anchilestes impolitus* 的颊齿特征，对两属的分类位置进行了讨论，认为它们代表裂齿目的两个古老类型。

Interogale 原是哺乳纲狪目 (Anagalida, Mammalia) 的一个属；属型种 *I. datangensis* Huang et Zheng, 1983 是依据一段保存完好的下颌骨 (正型标本，V6861) 建立的。该属归入狪目的主要理由：下颊齿与狪科及假古蜻科某些类型的牙齿形态相似。原作者在讨论中，同时指出了该属与狪目各科的明显区别，特别是缺少 P_1 (仅有三个前臼齿、齿式/3.1.3.3)，与狪目已知类型均不相同，因而未将它归入任何一科。

根据该属第二门齿增大这一特点，我们重新修理了正型标本的前面部分，发现除齿式外，它的吻区结构也与狪目各科完全不同：

门齿。*Interogale* 的三个门齿彼此以小间隙分开，齿冠均为薄釉质层覆盖。I_2 增大 (形态类似啮齿类门齿)，齿冠横切面椭圆形，齿根至少伸至 P_2 下方。I_1 比 I_2 小，两者形态相似，左右 I_1 紧靠下颌联合缝。I_3 比 I_1 和 I_2 小得多，以小间隙与后面犬齿分开，齿根向下约伸至下颌深度的一半。在狪目中，狪科、假古蜻科及丽狪科的门齿不增大；宽臼齿兽科门齿增大，但退化为一个，与啮齿类情况相同；重菱齿兽科的某些属第一门齿增大。

犬齿。*Interogale* 的犬齿大小与 I_2 相近，比 I_1 和 I_3 大。在狪目中，狪科、假古蜻科及丽狪科的犬齿比所有门齿都大；重菱臼齿科的某些属犬齿比增大的门齿小很多。

上述 *Interogale* 吻区与狪目各科不同的特点 (I_2 增大；I_3 非常小，夹在大 I_2 和犬齿之间；左右 I_1 紧靠下颌联合缝)，恰恰是它与裂齿目早期类型 (*Esthonyx*, *Megalesthonyx*) 的吻区相同之点。此外，*Interogale* 的齿式也与裂齿目 (/3—1?.1.3.3) 相同，两者都只有三个前臼齿。如前所述，齿式不同曾是妨碍该属归入狪目各科的主要障碍，如果将该属视为裂齿类，它的齿式则是完全正常的了。

Interogale 颊齿的形态结构 (特别是 M_3) 与裂齿目较原始的属种 (*Esthonyx xeni-*

1) 安琪掠兽：*Anchilestes*.

cus, *E. ancylion*) 亦十分相似。甚至在某些细节上,如 P_2 双根、两根与齿列不在同一直线上(约以 30° 角向唇面斜)的特点都与后者相同 (Rose, 1972)。

根据齿式及吻区与裂齿目相同的特征,我们认为 *Interogale* 代表一裂齿类动物,并建议将其归入裂齿目 (Tillodontia)。

Gingerich 和 Gunnell (1979) 在研究北美最原始的裂齿类 *Esthonyx* 属时,依据下颌联合愈合情况及颊齿形态特征,提出该属的两个进化支系。原始的一支 (*E. xenicus-E. ancylion-E. grangeri*),下颌联合不愈合,最早出现于 Clarkforkian 初期,延续到 Wasatchian 早期;另一支 (*E. spatularius-E. bisulcatus-E. acutidens*),下颌联合愈合,最早出现于 Wasatchian 早期,延至 Bridgerian 早期。*Interogale* 的下颌联合不愈合,它与北美最原始的属种 (*E. xenicus* 和 *E. ancylion*) 相比,仍有如下区别: 1) 个体比最小的 *E. xenicus* 约小一半左右; 2) 下颌联合伸至 C—P_2 之间 (*E. xenicus* 下颌联合伸至 P_3 前缘); 3) I_2 齿冠表面均覆盖薄釉质层 (*E. xenicus* 的 I_2 仅前表面覆盖釉质层); 4) P_{3-4} 臼齿化程度低; 5) M_{1-3} 无下后附尖。这些区别表明,*Interogale* 具有比 *Esthonyx* 更为原始的性质。

本文要讨论的另一属 *Anchilestes*, 原被归入狍目重菱齿兽科 (Zalambdalestidae, Anagalida)。属型种 *A. impolitus* Chiu et Li, 1977, 是依据属同一个体的不完整左上下颌(正型标本, V4315) 建立的。该属归入重菱齿兽科的主要理由: 与这一科的典型代表 *Zalambdalestes* 牙齿特征基本一致。特别是与 *Kennalestes* 属,在牙齿脊形程度、上臼齿宽扁、次尖架发育、下臼齿三角座形状、下前尖位置、P_4^1 臼齿化程度、M_2^2 在齿列中为最壮者、以及 M_3 的下次小尖向后延伸等特点最接近。

将 *Anchilestes* 的下颊齿与 *Interogale* 相比,可以看出,除前者下三角座V形脊在原尖处略窄,舌侧开口较宽外,二者形态结构基本相同。另外,将该属的上臼齿与我国较原始的裂齿类 *Meiostylodon* 相比,前者除前后长度短、外架及外中凹稍发育、舌侧单面高冠不显著外,与后者的形态结构也基本相同(从 M^2 后脊中间的膨大看, *Anchilestes* 应是有小尖的)。尽管我们目前还不了解 *Anchilestes* 属的吻区特征,但从它的上下颊齿(特别是上臼齿)与特征清楚的裂齿类 *Interogale* 和*Meiostylodon* 非常接近看,它应代表一裂齿类。*Anchilestes* 的 P_4 比 *Interogale* 相应牙齿臼齿化程度低,个体比 *Meiostylodon* 小,说明在形态上它比这两属要原始。该属的产出层位——安徽潜山望虎墩组下段(早—中古新世),是目前我国产有裂齿类化石层位最低的一个。看来,它代表了已知裂齿类中最古老、原始的种类。

值得提到的是,原作者在讨论中曾指出, *Anchilestes* 在 1) 上颊齿的外架大、外中凹深、外齿带粗壮; 2) 上颊齿齿列外缘弧形转折点在 M^{1-2} 之间; 3) 次尖架大; 4)下三角座不高; 5) 个体大等方面与 *Kennalestes* 不同,显得"相当特化"(邱、李, 1977)。上述五点如与裂齿类相比,可以看出,它们恰好是相同的。因此,若视 *Anchilestes* 为裂齿类,这些特征不仅不显得特化,反而是完全正常的。原作者的这段分析从另一侧面支持了 *Anchilestes* 代表裂齿类的看法。

与 *Anchilestes* 产于同一层位的 *Wanogale* 属,它的下颊齿下前尖低,靠近舌侧、跟座较宽等特点,显得比狍类更近于裂齿类。蒙古格夏托的 *Kashanagale* 颊齿结构与

Interogale 和 *Anchilestes* 非常接近 (Chiu et Li, 1977; Huang et Zheng, 1983)。但这两属的材料过于欠缺，分类位置尚难确定。

在我国已报道的裂齿类中，*Meiostylodon* 的个体大小及形态，与北美 *Esthonyx* 属中早期类型最为接近。它与该属较原始的两个种 *E. xenicus* 和 *E. ancylion* 相比，除牙齿前后较短、外架略宽、外中凹较明显、小尖位置稍靠舌侧外（这些同样是它与 *Anchilestes* 属共同区别于北美 *Esthonyx* 属的特征），几乎很难找出其他区别。*Meiostylodon* 在形态上曾被认为是处于 *Esthonyx* 和 *Lofochaius* 的中间类型 (Chow et Wang, 1979; Gingerich et Gunnell, 1979; Stucky et Krishtalka, 1983)。遗憾的是，这一属的材料至今仍只有两个上臼齿，许多特征还不十分清楚（原定为门齿的标本，经切片观察，未见齿质小管，有可能不是牙齿）。因此，目前尚难通过它研究亚洲与北美早期裂齿类的关系。

另一原始的属 *Lofochaius*，标本保存较差，从 M^{2-3} 看，上臼齿齿脊特点与裂齿类 (*Anchilestes*, *Meiostylodon*, *Esthonyx*) 不同。前者上臼齿原脊和后脊分别与前、后尖相连，前后齿带分别从前、后附尖向舌侧延伸（这些特点与全齿目[1] *Harpyodus* 和 *Plethorodon* 属相似）；后者原脊和后脊分别与前、后附尖联结，前后齿带分别起自牙齿前后壁的中部。与 *Lofochaius* 产于同一层位的 *Dysnoetodon* (Zhang, 1980) 属，其正 (V5837)、副 (V5838) 型标本的形态是不同的。V5837 号标本与 *Anchilestes* 区别明显。V5838 号标本与某些食虫类有类似的地方，但与发现于南美的 *Alcidedorbignya inopinata* 属 M^2 (YPFR PAL 6122 号标本)的个体大小及形态特征更为接近。这两属的分类位置看来是有问题的，但需更多的材料进一步证实。

裂齿目是一类古老、绝灭的哺乳动物。它的系统位置及起源问题一直是研究哺乳动物早期分化的重要议题之一。

长时期来，对裂齿目起源的研究主要依据北美最原始的属 *Esthonyx*。Gazin (1953) 在对北美裂齿类作系统研究时，首先注意到这一目与全齿类的关系，认为二者可能通过中古新世前的祖先发生联系。Van Valen (1963) 进而提出裂齿类起源于踝节目的假设，并将其作为亚目归入该目。

近十多年来，在我国古新统中发现了裂齿目的一些新属种，国内外学者研究裂齿目起源的注意力逐渐转移到亚洲，认为裂齿目的祖先应在亚洲，而不是北美（周、王，1979; Gingerich et Gunnell, 1979; Stucky et Krishtalka, 1983)。周、王 (1979) 根据我国发现的新材料进一步支持了 Gazin 的观点。他们指出，裂齿类颊齿的主要特征与全齿类基本相同。Gazin 曾提到的一些差异点（如裂齿类上臼齿的中附尖、大的次尖架、单侧高冠等），由于新材料的发现而变得不明显了。此外，*Lofochaius* 和结构较原始的全齿类 *Harpyodus* 十分相似，这些都表明裂齿目与全齿目有较近的亲缘关系。但认为裂齿类的大门齿、臼齿前、后尖为丘形等特征在早期类型中不显著，因而未将其作为讨论系统位置及起源等问题的依据。

根据前述 *Interogale* 及 *Anchilestes* 属的齿系特征，我们对裂齿目的亲缘关系提出如下意见：

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1) 全齿目 Pantodonta（见周、王，1978)。

1. 裂齿类头骨形态的主要特点之一，表现在吻区伸长。这一特点是与 I_2 强烈增大有关的。因此，吻区特化（I_2 增大、I_3 退化、P_1 消失可能与此有关）应是反映裂齿类头骨进化趋势的重要特征；我们将其考虑为衍生特征。这些特征很早就出现在裂齿目的原始类型中（如 *Interogale*）。但全齿类的所有类型不具这些特征。

2. 已知最原始的裂齿类 *Anchilestes* 和最原始的全齿类 *Bemalambda* 上臼齿的基本结构是不同的。前者前后尖呈锥状、原尖前棱及原尖后棱分别通过原小尖、后小尖向外伸至前、后附尖处，有次尖、次尖架及前齿缘。后者前后尖侧扁、原尖的“V”形脊分别伸达前尖和后尖基部，有内齿缘，无次尖及次尖架。因此，裂齿类和全齿类某些晚期类型颊齿的相似（如中附尖、次尖架、单侧高冠等），看来更可能是趋同特征。

3. *Interogale* 和 *Anchilestes* 的下臼齿与全齿类 *Bemalambda* 区别明显，而与猬目某些类型（如 *Pseudictops*）相似，这些相似反映两者具有的原始性状。

4. *Lofochaius* 和 *Harpyodus* 的臼齿结构相似，但它们又共同区别于已知的裂齿类。因此，它们的相似性，有可能说明 *Lofochaius* 不属裂齿类，但不足以作为支持裂齿类和全齿类有亲缘关系的证据。

从前述对 *Interogale* 和 *Anchilestes* 分类位置的讨论，推测裂齿类祖先类型牙齿的形态结构应该是与这两属接近的。*Interogale* 和 *Anchilestes* 曾先后被归入过猬目，说明它们的颊齿形态的确是与猬类的某些类型接近的。*Anchilestes* 原被归入的重菱齿兽科是猬目中唯一的晚白垩纪类型，其中不只一属有门齿增大现象，这表明吻区特化（尽管特化情况不一样，早在白垩纪的猬类中就已存在。根据亚洲目前已有资料看来，猬目似乎比其他类群在形态上更接近裂齿类，它应与裂齿类有较近的祖先关系。

本文撰写过程中，得到周明镇先生的鼓励；翟人杰、李传夔、邱占祥、黄学诗同志与笔者讨论有关分类方面的问题，并对文章内容提出宝贵意见。童永生、王伴月、齐陶、王景文同志帮助审核文稿。美国自然历史博物馆 M. C. McKenna 教授帮助修改英文摘要，并对文章提出修改建议。杜治同志摄制照片。笔者在此向他们深表谢意。

（1988 年 4 月 19 日收稿）

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THE AFFINITIES OF *INTEROGALE* AND *ANCHILESTES* AND THE ORIGIN OF TILLODONTIA

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Key words　Tillodontia; *Interogale*; *Anchilestes*

Summary

The Genus *Interogale* was originally assigned to the order Anagalida. The genotype, *I. datangensis* Huang et Zheng, 1983, was erected based on a well-preserved mandible (V6861) from the late Paleocene, Nanxiong, Guangdong.

After the original description we reprepared the snout of the specimen and found that the snout of *I. datangensis*, especially, I_2 is specialized in a very different way from that of any known anagalids. It represents a late Paleocene tillodont with a distinct derived feature. Another genus assigned to the Order Anagalida, *Anchilestes* Chiu et Li, 1977 from early-middle Paleocene, Qian-shan, Anhui, is very close to *Interogale* and *Meiostylodon* in morphology. It

represents the oldest tillodont known from China.

This paper will focus mainly on the revision of the systematics of the two genera, giving more details on the morphology. It is hoped that the revision will be a significant addition to the knowledge of the early radiation of the tillodonts and throw new light on the understanding of the origin of the Order Tillodontia.

We thank Prof. Chow Minzhen for his support and encouragement in the study, Profs. Zhai Renjie, Li Chuankuei, Qiu Zhanxiang, and Huang Xueshi for their valuable discussion on the systematics and critical reading of the manuscript, and Profs. Tong Yongsheng, Wang Banyue, Qi Tao, and Wan Jingwen for their suggestions for the improvement of the paper. We are grateful to Dr. M. C. McKenna of the American Museum of Natural History for his valuable comments and for correcting the English summary. We thank Drs. W. A. Clemens, D. E. Savage, and G. Shkurkin of the University of California at Berkeley, and Dr. J. A. Schiebout of Louisiana State University for their discussion of the systematics and critcal reading of the manuscript. The photographs were taken by Mr. Du Zhi. We thank him.

Systematic Revision

Order Tillodontia Marsh, 1875

Family Esthonychidae Cope, 1883

?Subfamily Esthonychinae Zittel and Schlosser, 1911

Genus *Interogale*, Huang et Zheng, 1983, new assignment

Type species *I. datangensis* Huang et Zheng, 1983 (V6861).

Diagnosis A tillodont smaller than any other known genus.

Dental formula /3. 1. 3. 3. I_2 enlarged, rooted, with enamel covering all the surfaces of the crown. I_3 much reduced. P_2 with two roots. P_4 with a distinct talonid. M_{1-3} without metastylids.

Description This is the smallest tillodont known. The three incisors are separated from each other by short diastemas, and have enamel covering on all surfaces of the crown, which differs from those of both *Esthonyx* and *Trogosus*. I_2 is enlarged, with the roots extending to a point below the anterior part of p_2. It is laterally compressed and oval in cross section. I_1 is slightly smaller than I_2, with long roots, and is oval in cross section. Both left and right I_1 are close to the symphysis. The size of I_1 relative to I_2 of *Interogale* contrasts with the much greater size difference seen in *Esthonyx* and *Trogosus*. I_3 is very small, roughly less than half the size of I_1 and round in cross section, which shows that reduction of I_3 in tillodonts began as early as late Paleocene.

The canine is separated from I_3 and P_2 by a short diastema and is intermediate between I_3 and P_2 in size. Unlike the condition in *Megalesthonyx* and *Trogosus*, the canine is robust and oval in cross section, which is similar to that of *Esthonyx*.

P_2 is separated from P_3 by a short diastema. It is smaller than P_3, but not so reduced as those in the later forms. In *Megalesthonyx* and *Trogosus*, P_2 is much smaller reletive to P_3. Both roots of P_2 are very robust and not directly in line with the tooth row, whereas the anterior roots are situated labially from the line of the tooth row, which is the same condition as that in *Esthonyx* and differs from that in *Megalesthonyx*, *Trogosus*, and *Tillodon*. P_2 bears a single major cusp extending anteroposteriorly and has no talonid.

P_3 is closely appressed to P_4 as in other tillodonts. It has a prominent single cusp on the

trigonid and only a rudimentary talonid, differing from those of the other known forms, in which the talonid is basined.

The nonmolariform P_4 differs from P_4 of *Esthonyx* in its incompletely basined talonid. Its talonid is composed of a simple ridge. There is no metastylid.

The lower molars are mostly similar to those of *Esthonyx*. The molar trigonids of *Esthonyx* and *Interogale* are compressed anteroposteriorly. The metaconid is the highest of the three cusps. The paraconid is reduced. There is no distinct metastylid on the lower molars, which differs from those in the other known forms, but there is an ambiguous ridge slightly projecting medioposteriorly behind the metaconid. The entocristid extending through the entoconid forms the lingual edge of the talonid. The entoconid is well developed and roundshaped, and separated from the oblique crest of the talonid basin by a small notch. There is a distinct round wear facet on the entoconid of each molar. The cristid obliqua originates from the middle point of the posterior wall of the trigonid, This condition is closer to that in *Esthonyx* than in *Megalesthonyx* and the later forms, in which the cristid obliqua originates from a point near the metaconid.

M_1 and M_2 are almost identical, the latter being slightly larger than the former. M_3 is much larger than M_1 and M_2. The hypoconulid of M_3 is elongated to become a third lobe, the typical condition among the tillodonts.

The horizontal ramus is rather shallow and the depth of the ramus increases posteriorly as in *Esthonyx*. The deepest part is below M_3. The symphysis is not fused and extends to a point below the anterior ridge of P_2. It is the shortest among the known tillodonts. Two mental foramina are situated beneath P_2 and between P_{3-4} respectively. The ascending ramus has a strong ridge originating from beneath the posterior part of M_3 and limiting the deep masseteric fossa anteriorly.

Discussion *Interogale* was originally assigned to the Order Anagalide based mainly on the similarities of the lower molars to those of anagalids, especially *Pseudictops* and *Kashanagale*. However, the similar features are primitive ones occurring in many placental mammals.

After repreparing the type specimen of *Interogale datangensis*, we find that its snout differs significantly from that of any known anagalids. It differs from anagalids in having an enlarged I_2, much reduced I_3, P_1/dP_1 lost, and elongated hypoconulid of M_3. These are derived features shared with the tillodonts (see following discussion), therefore, we would assign *Interogale* to the Order Tillodontia.

Interogale differs from the trogosine tillodonts in having rooted, enlarged second incisors with the enamel on all the surfaces of the crown, a relatively large canine, double-rooted second premolars, and less reduced anterior cheek-teeth. It is much smaller than any known tillodonts and about half the size of *Esthonyx xenicus*, the most primitive North American species. It differs from *Esthonyx* in having the enamel of the second incisors covering all the surfaces of the crown, in having P_{3-4} with relatively weak talonids, and M_{1-3} without distinct metastylids. This indicates that *Interogale* represents a more primitive form of tillodonts than *Esthonyx*.

Genus *Anchilestes* Chiu et Li, 1977, new assignment

Type species *Anchilestes impolitus* Chiu et Li, 1977 (V4315)

Diagnosis A tillodont slightly laptr than *Interogale*. Upper molars shortest and widest of the known forms of tillodonts and relatively wider than in *Esthonyx*. P_{3-4} having protocone and paracone cusps without a metacone. M_{1-2} with a distinct hypocone shelf. P_4 with a

well-developed talonid. M_{1-3} without a metastylid.

Description P_3 is triangular, It has a prominent buccal cusp. The lingual cusp is present, but the specimen is demaged at that point and it is difficult to discern in detail. It is more similar to that of *Esthonyx* than to that of *Megalesthonyx,* in which is present a smaller crest-like metacone posterior to the paracone cusp. The parastyle and metastyle of P_3 are not as well developed as in either *Esthonyx* or the later forms.

P_4 is nonmolariform, transversely wider than P_3, and differs from the other known forms in being shorter antero-posteriorly, lacking a distinct metacone, having a well-developed parastyle and metastyle, and a weak antero-posterior cingula.

M_{1-2} are tritubercular, with a broad buccal shelf-cingulum, a distinct antero-lingual cingulum, and a prominent postero-lingual cingulum, but they are closer to those of *Meiostylodon* than to those of *Esthonyx* in morphology (especially in having the paracone and metacone lingually placed and relatively shorter anteroposteriorly). Besides the small size, M_{1-2} of *A. impolitus* differ from those of *Meiostylodon* in being much shorter anteroposteriorly, and having a weak paraconule and metaconule, weak anterior cingulum, and hypocone shelf.

The lower teeth are very similar to those of *Interogale.* P_4 is nonmolariform. The trigonid is relatively shorter anteroposteriorly than that of *Interogale,* but the talonid is not so well-developed as in the latter.

M_{1-3} are similar to each other in morphology and increase in length posteriorly. M_2 is the widest lower molar. The trigonid is V-shaped, with an acute angle at the protoconid and at the paraconid and metaconid, which is the only difference between *Anchilestes* and *Interogale.* The metaconid is the highest cusp of the trigonid. The talonid of M_3 is elongated and longer than those of M_{1-2}. The Hypoconulid of M_3 is enlarged and separated from the hypoconid by a small notch, of which becomes a third lobe like that of other tillodonts, but it is not as long as in *Interogale.* The entoconid can not be seen clearly because it is deeply worn.

Discussion *Anchilestes* was compared extensively with other mammalian orders by the original authors. The major evidence for assigning it to the Zalambdalestidae (Anagalida) is the similarities of the upper and lower molars between *Anchilestes* and *Kennalestes* (such as upper molars being transeversely wider and anteroposteriorly shorter, and having a well-developed hypocone shelf; M_3 having a transversely wider trigonid and an elongated hypoconulid; M_2 being the largest of all the cheek teeth, etc,). The original authors also pointed out that *Anchilestes* obviously differs from *Kennalestes* in having a well-developed shelf-like external cingula, a pronounced hypocone, less height difference between trigonid and talonid, and in being much larger in size. These differences between *Anchilestes* and *Kennalestes* are just the features shared by *Anchilestes* and tillodonts. Besides, as mentioned above, the upper and lower molars of *Anchilestes* are very close to those of *Meiostylodon* and *Interogale* respectively. We reassign it to the Order Tillontia. It represents the oldest tillodont known.

Among the known Chinese tillodonts, *Meiostylodon* is the form most similar to the primitive North American species, *Esthonyx xenicus* and *E. ancylion,* in both size and morphology. It differs from them in having a stronger external cingulum and ectoflexus, lingually located conules, and teeth shorter antero-posteriorly. It is more primitive than *Esthonyx.* Unfortunately, this genus has been known only from two upper molars. Its relationship to North American genera remains an open question.

Another genus, *Lofochaius,* was previously considered the most primitive tillodont known. Teeth of known specimens are deeply worn. Based on M_{2-3} it differs from the later form in

having the preprotocrista and postprotocrista connecting with the paracone and metacone, and in having the anterior and posterior cingula originating from the parastyle and metastyle, which are similar to those of *Harpyodus* and *Plethorodon*. Judged from *Esthonyx* and other forms, tillodonts have the preprotocrista and postprotocrista elongating to the direction to parastyle and metastyle, the anterior and posterior cingula originating from half way on the anterior and posterior wall of the teeth. The molars of *Lofochaius* thus differ slightly from those of true tillodonts and, therefore, the systematic position of *Lofochaius* is questionable.

The Genus *Dysnoetodon* occurs in the same location as *Lofochaius*. As originally described, it resembles several mammalian orders in various respects. However, the holotype (V5837) of the genus is different morphologically from the paratype (V5838). V5838 is closest morphologically to M_2 of the newly published *Alcidedorbignya inopinata* (YPFB PAL 6124) than to those of other forms, based on the comparison with the stereophoto. It is apparent that V5838 is not a tillodont and more materials are needed to determine its systematic position.

The Origin of Tillodontia

The origin of the Order Tillodontia is an important subject for those who are interested in the early radiation and differentiation of the mammals, because, in some points, this short lived archaic offshoot of the placental mammals is near the base of the placental stem.

Discussion of the phylogenetic relationships and the hypotheses of the origin of the tillodonts have long been based on the North American early Eocene genus *Esthonyx*, which was for a long time the oldest tillodont known.

Gazin (1953) first called attention to the relationship of tillodonts and pantodonts. He mentioned "there is a basic cheekteeth pattern suggesting relationships through a pre-Torrejonian ancestry". The hypotheses of condylarthra origin of tillodonts was proposed by Van Valen (1963) later on.

During the last ten years, great attention in the discussion concerning tillodont phylogeny and origin has been generated by the newly discovered Chinese Paleocene tillodonts (mainly based on the genera *Lofochaius* and *Meiostylodon*) (Chow et Wang, 1979; Gingerich et Gennell, 1979; Stucky et Krishtalka, 1983). Gazin's opinion on the relationship of tillodonts and pantodonts was strengthened by Chow and Wang (1979). Their major arguments supporting the pantodont-tillodont relationship: 1) not only that similarities of the molars occurred in pantodont and tillodont, but intermediate morphology was demonstrated by the new Chinese discovery; 2) the similarities of *Lofochaius* and *Harpyodus* (a primitive pantodont) also indicates the close relationship of pantodonts and tillodonts.

Based on the systematic revision in this paper, new evidence questioning on the relationship of pantodonts and tillodonts can be discussed as follows:

1. The specialization of the snout is one of the significant changes of the skull of the tillodonts during their evolutionary history, which was related to the enlargement of I_2. The enlarged I_2, much reduced I_3, and the loss of P_1 schould be considered as the derived features (autapomorphy) for the Order Tillodontia. These features occurred also in *Interogale*, and did not occur in any pantodont.

2. The basic pattern of upper molars of *Anchilestes* and *Bemalambda* (the oldest tillodont and pantodont) are different (the former has the preprotocrista and the postprotocrista elongating in the direction of parastyle and metastyle; the latter has the preprotocrista and

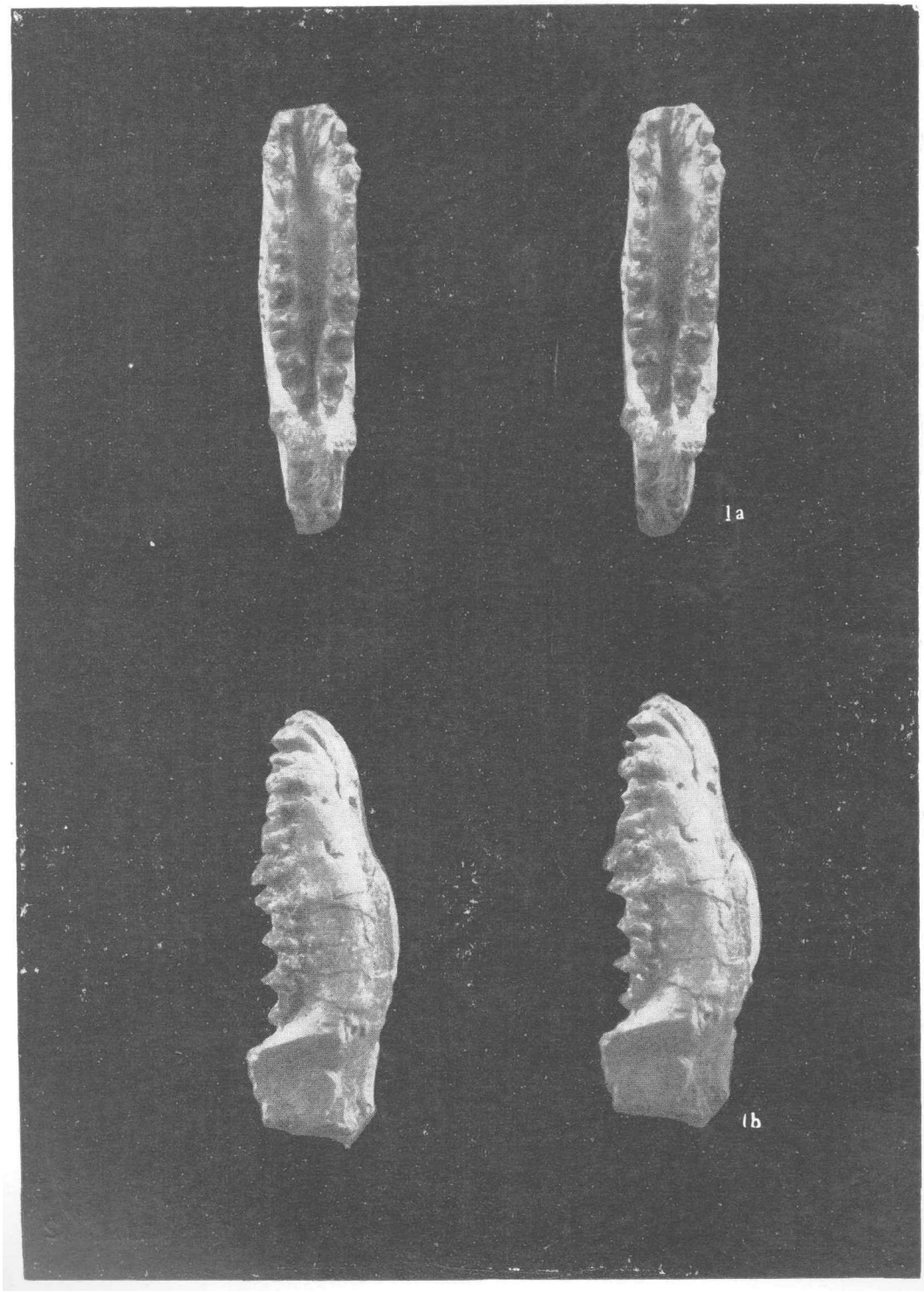
postprotocrista connecting the paracone and metacone). The similarities in some later forms of pantodont and tillodont might be interpreted as convergence.

3. The lower molars of *Interogale* and *Anchilestes* are different from those of *Bemalambda,* but are close to those of anagalids (especially pseudictopids). These similarities are interpreted as primitive features.

4. The upper molars of *Lofochaius* are similar to those of *Harpyodus* in overall pattern, but both of them differ from those of *Anchilestes, Meiostylodon,* and other tillodonts. This indicates that the similarities of *Lofochaius* and *Harpyodus* are not evidence supporting a pantodont-tillodont relationship, but instead, might indicate that *Lofochaius* is not a tillodont.

Based on the above analysis, we suppose that the basic pattern of the cheek-teeth of thte ancestral tillodonts is similar to those of *Interogale* and *Anchilestes*. Among the known Asian Cretaceous and Paleocene mammals, Zalambdalistids (such as *Zalambdalestes, Kennalestes*) and *Anchilestes* have similar cheek teeth patterns as mentioned by Chiu and Li (1977). There are some forms with enlarged incisors in the family Zalambdalestidae, which indicates that the specialization of the snout in the anagalids (although the specialization in a different way) had occurred as early as the Cretaceous. We consider that the Order Anagalida is the form most closely related to the Order Tillodontia and the best candidate for understanding the origin of tillodonts.

The order Anagalida, an Asian endemic mammalian group, was originally thought to be most closely related to the Order Lagomorpha (Szalay et McKenna, 1971). Recently, several hypotheses on the origin of different mammalian orders deals with the Order Anagalida (Li, 1977; Li et al., 1987; Szalay et Li, 1987; present paper). This throws the order into confusion and complication. Review of the anagalids is necessary.



大塘中间狸 *Interogale datangensis* (Huang et Zheng, 1983) (V 6861)

1a. 下颌嚼面 Occlusal view of mandible; 1b. 下颌唇面 Labial view of mandible
均为立体照片 All stereophotographs ×1.5