AGRIOTHERIUM INTERMEDIUM (STACH 1957) FROM A PLIOCENE FISSURE FILLING OF XIAOXIAN COUNTY (ANHUEI PROVINCE, CHINA) AND THE PHYLOGENETIC POSITION OF THE GENUS

by

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SUMMARY

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Palaeovertebrata, Montpellier, **13** (3) : 65-81, 1 fig., 1 pl.
(Accepté le 30 Mai 1983, publié le 30 Septembre 1983)

摘要

本文记述了採自中国安徽省萧县的一幼年小个体郊熊化石。根据牙齿的形态和大小可以定为郊熊中间种。享地博士曾提出郊熊由印度熊产生的观点，本文根据新材料对此进行了讨论，结论是：1.所谓的从印度熊至郊熊个体增大的论点是站不住脚的。

2.没有正面的证据可以说明两者间系统上的直接过渡。

3.认为郊熊在进化中发生反向适应的论点证据不足，享地提出的许多特征只是近祖特征，

4.享地的观点从方法论上看也是行不通的。

新资料表明，印度熊和郊熊很可能是分别发生的。较进步的郊熊与印度熊有适应相似性，但原始的郊熊则与印度熊不同。后者可能产生于祖熊一类的祖先，而前者则可能源于介于祖熊和半熊类之间的某一类别。

ABSTRACT

A fragmentary mandible and maxilla of a small sized *Agriotherium* of a young individual discovered from a Pliocene fissure filling in Xiaoxian county (Anhuei Province, China) are described. Judging from the morphology of the dentition and its dimensions the new material can be identified as *Agriotherium intermedium* (STACH 1957). Hendey's proposition (1980) that the *Agriotherium* species are derived from *Indarctos* is reconsidered on the basis of the new documents. As a result of a more general phylogenetic discussion it can be stated, that:

1. the supposed size increase as well as other trends, leading from *Indarctos* to *Agriotherium* are untenable ;
2. there are no positive indications to assume a phylogenetic transition of these two genera.
3. there are no real arguments in favor of an adaptational reversal in the evolution of *Agriotherium*. Hence, many features of that genus supposed by Hendey to be derived are plesiomorphic ;
4. regardless of the previous points it is methodologically impossible to establish direct ancestor — descendant relationships between *Indarctos* and *Agriotherium* species, as Hendey did.

Based on the data available and especially on the characters of the new material from China it is more likely that *Agriotherium* and *Indarctos* are two genera which developed independently. While advanced *Agriotherium* species, *e.g. A. africanum*, resemble in some respects *Indarctos* by adaptational analogies, more primitive species, *e.g. Agriotherium intermedium*, are quite dissimilar to *Indarctos*.

While *Indarctos* might be derived from an *Ursavus* like forerunner, *Agriotherium* has its roots more likely somewhere in between *Ursavus* and the *Hemicyon*-group.

1. INTRODUCTION

In comparison with the closely related genus *Indarctos*, the genus *Agriotherium* is rather poorly known. In fact, all the classic species referable to the latter genus, according to Pilgrim (1931) have been based either on upper or on lower dentitions separately. The diagnosis of *Agriotherium*, proposed chiefly by Pilgrim is therefore rather speculative and based partly upon indirect deduction from the better known teeth material of *Indarctos* and partly upon the assumption of ecological incompatibility of more than one closely related species of the same adaptation in one habitate. Associated upper and lower teeth material to improve Pilgrim's original diagnosis of *Agriotherium* therefore have been eagerly expected. The recent discovery in Langebaanweg (South Africa) of a rather rich sample of that genus and its final publication in 1980 by Hendey is the first case to meet such an expectation. The discovery of the present material, a well preserved snout of a juvenile animal with some unexpected peculiarities for an *Agriotherium* species, might as well be of considerable importance to the understanding of the nature of the genus, and deserves to be reported.

It is rather astonishing that, although *Agriotherium* proved a wide spread genus with fossil documents reported from Europe, South Asia, North America and Africa, no reliable material has been found in China up to now. The «*Hyaenarctos*» remains mentioned by Lydekker (1885) and by Schlosser (1903) were too scanty to be identified generically. Zdansky's (1924) ?*Hyaenarctos* sp., judging from the enlarged talon of its M2, as pointed out by Erdbrink (1953), seems more probably to belong to *Indarctos*. Licent and Trassaert (1935) mentioned *Hyaenarctos* sp. in their faunal list of the first "zone" of the Yushe series, but no description has ever been published. Therefore the present material is to be considered the first record of the genus in China. Since mammalian fossils of Ruscinian age are very rare in China, the remains are of considerable importance stratigraphically as well.

The characters of the new material are not in accordance with Hendey's phylogenetical interpretation of *Indarctos* and *Agriotherium*, which, after this author, are linked together as successive stages of phylogenetical lineages as a case of parallel evolution. This is the reason, why the position of these genera and also Hendey's methodology are to be reconsidered.

2. DESCRIPTION OF THE NEW MATERIAL

The new fossil documents consist of an upper and lower jaw belonging to a juvenile individual (pl. 1). Both, the maxilla and the mandible are broken behind the first molars. The material was first collected by a farmer working at one of the fissure fillings exploited as a phosphorite pit in Xiaoxian county Anhuei Province (fig. 1). From the upper dentition the right Cd, P3/-M1/ and the left I1-2/, Cd and P1/P4/ are preserved. The I3/ of both sides are in eruption. The right I3/ is intentionally exposed on its lingual side. From the lower dentition the right Cd, P/4-M/1 and the left I/1-3, P/4-M/1 are preserved. Both permanent canines are still in their sockets, but the right one is labially exposed. The left lower Cd was evidently broken before deposition. The upper right P1-2/ and the lower P1-3/ of both sides seem to have been dropped away before burrying as well.

Owing to the state of preservation and the juvenile age, little can be said about the anterior parts of the skull and the lower jaw themselves.

The fossa palatina is better seen on the left side of the upper jaw. It is elongated and oval in form, with its length 19,5 mm and width 5,5 mm. The foramen palatinum anterior is located at the posterior end of the fossa palatina. The premaxilla-maxilla suture on the palate is situated far back with respect to the fossa palatina, making a curve and ending labially to the anterior border of Cd.

Though the animal must have been very young in age, the mandible is considerably massive. The symphyseal margin of each hemimandible is anteroventrally averted, forming a keeled "chin" together with its counterpart. As a result, together with the

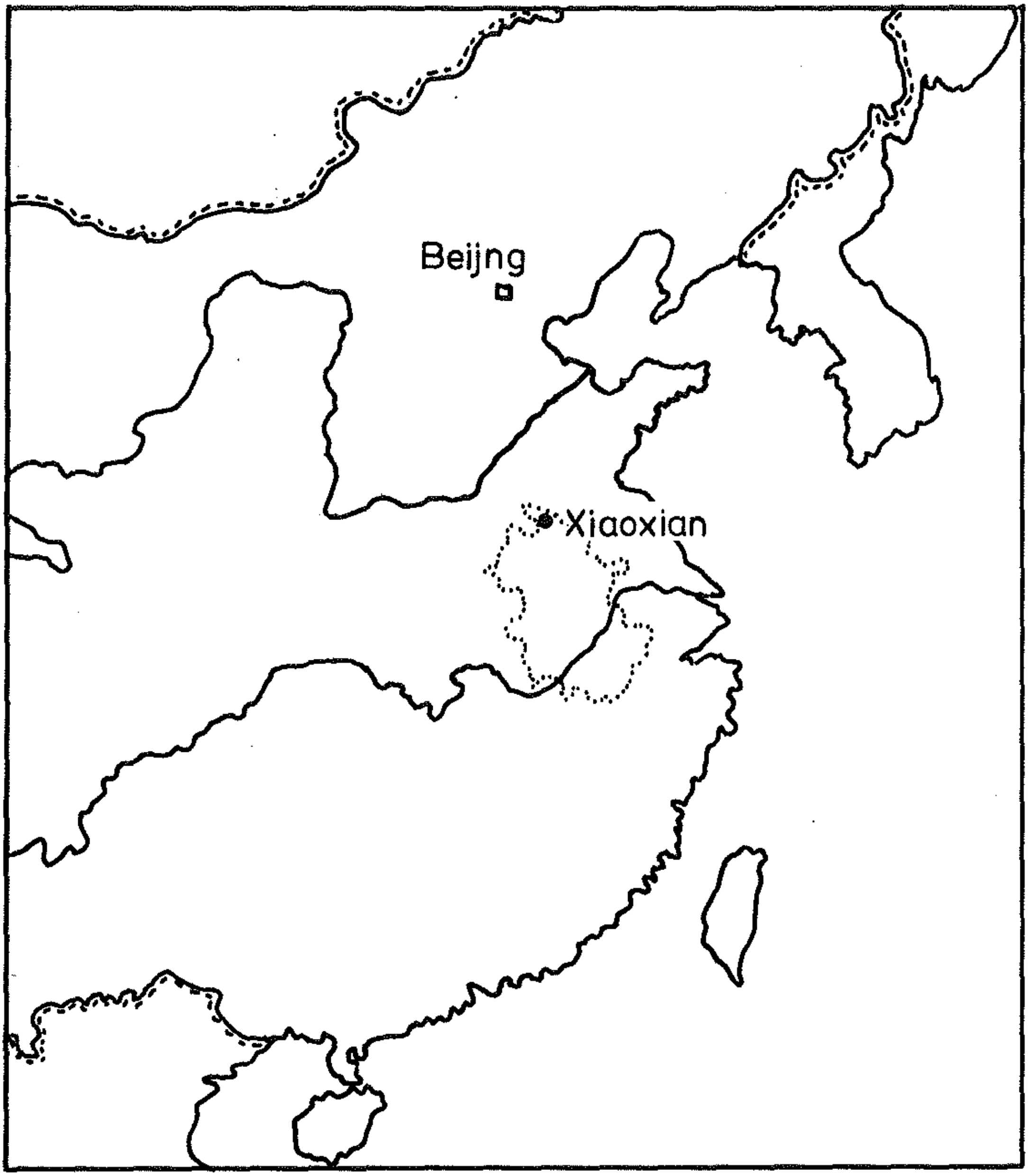

Fig. 1. — Geographic position of the Pliocene fissure filling of Xiaoxian (Anhuei Province, P.R. China).

straight lower border of the mandible, the ramus horizontalis in its anterior part is as high as in its posterior part (pl. 1, fig. 2). There are 4 mental foramina. The posterior one is the largest. It is oval in form and lies below the anterior root of P/4. The three others are smaller and situated below P/2, the posterior half of P/1 and the deciduous canine respectively. On the external surface of the mandible a depression below P/1-3 can be seen more or less clearly. I1/ and I2/ are rather similar in form. I2/ is somewhat larger and more asymmetrical. Their labial surfaces are well rounded and marked by a central vertical furrow. Their main cusps are spatulate in form. On the lingual side of I1/ and I2/ there are two cingulum cusps of about the same size, separated by a groove. Between the main cusp and the cingulum cusps there is a central pit which in I2/ is more deeply carved than in I1/. I3/ is very robust. Its principal cusp is like that of I1/ and I2/, but more enlarged. The lingual cingulum is well developed on the medial half. Towards the external half it takes the form of a vague swelling without clear demarcation. There are no cingulum cusps.

The root of the upper deciduous canine (Cd is stouter than its crown. On each of the antero-internal and posterior surface of the tooth a vertical keel is developed. The internal surface is roughly flat, possessing a central vertical ridge.

P1/-P3/ are low-crowned and similar in morphology. The height of their crown is less than the crown-length. A low, approximately centrally situated crest divides the crown into a convex labial and a concave lingual surfaces. From P1/ to P3/ the labial surfaces increase in size at the cost of the lingual surfaces. There is a basal swelling on the lingual side of the teeth. The central crest is sagittal on P1/. On P2/ it is stretching from the antero-lingual — to the posterolabial edge of the tooth forming an angle of about 45° with the sagittal axis. P3/ is similar to P2/, but with an angle of about 60°.

The parastyle of P4/ (pl. 1, fig. 5) is smaller, and very low, when compared to *Agriotherium africanum* from Langebaanweg (Hendey, 1980, fig. 7 and 9). Its length is no more than one third of the paracone length. Paracone and metacone are subequal in length. The protocone is clearly separated from the shearing blade of the tooth by a deep grove and is smaller than the corresponding element in *Agriotherium africanum*. It stands directly opposite the notch between paracone and metacone. There is no indication of accessory cusp anterior or posterior to the protocone. The cingulum of the tooth is rather weak and only clearly developed in the vicinity of the parastyle, encircling it from both the labial and lingual sides, as well as on the lingual wall of the metacone.

M1/ is preserved only on the right side (pl. 1, fig. 4). Paracone and metacone are subequal in size, the former being a little larger and higher. The tooth is trapezoid in outline. Each cusp bears sharp anterior and posterior keels. There are also small parastyle and metastyle cusps. The latter is only a little larger and higher than the former. On the lingual half of the tooth a strong longitudinal crest is developed, which is usually homologized to the protocone in its anterior part and to the hypocone in its posterior part. However, from a comparison with primitive members of the Ursidae like *Chephalogale* and *Ursavus* it becomes evident, that this identification can only be right in respect to the protocne, whereas the posterior part of the mentioned crest can only be homologized with the posterior ridge of the primitive trigonstructure and thus to metaconule. The protocone and metaconule ridges are separated by a shallow notch. On the buccal wall of the tooth a very distinct cingulum is visible. The lingual cingulum is less clearly developed. It descends from the postero-lingual side of the tooth down to the lingual base of the protocone and then ascends again to meet the keel stretching from the protocone to the parastyle.

I/1 is bilobate. In the middle of its labial wall a vertical grove is developed. The lingual side consists of a shallow central depression and two bordering ridges which form a V — pattern converging towards the base of the crown.

I/2 is much larger than I/1. Seen from the labial side, the tooth is similar to I/1, but more asymmetrical, with the vertical groove more laterally situated. The lingual side consists of a more or less flattened central surface bordered by a pair of lateral ridges, which likewise converge downwards.

The principal cusp of I/3 is very large, with a prominent accessory cusp on its lateral side. The vertical groove on the labial wall is even more laterally situated. The ridges bordering the lingual side of the tooth are well marked and form an approximately right angle at the base of the crown.

Both lower Cd were broken. The right lower permanent canine exposed during the preparation is of the usual ursine type, with the height of the total crown about 40 mm.

P/1-P/3, according to their alveoli, must be small and one- rooted, the middle one being the smallest.

P/4 (pl. 1, fig. 3), owing to the absence of a postero-lingual bulge (present in the P/4 of *Agriotherium africanum*, see Hendey 1980, fig. 4 and 5), is roughly oval in outline. The main cusp bears a blunt anterior keel and a somewhat more accentuated and steeper posterior ridge. At the middle of the lingual wall another vertical ridge is visible near the base of the crown. The anterior accessory cusp is small and crest-like. Behind the main cusp there is a well developed talonid consisting of a longitudinal keel descending slightly towards the posterior border of the tooth. It is separated from the main cusp by a shallow notch. The cingulum is only lacking on the anterior part of the labial wall.

In the M/1 (pl. 1, fig. 3) the trigonid is longer, but narrower than the talonid. Besides the sharp anterior ridge forming part of the shearing blade the protoconid is provided with two posterior keels among which the lingual one is leading to the metaconid and the buccal one is descending more postero-externally. The metaconid is large and has the same position in respect of the protoconid as it is found in the other *Agriotherium* species. It is clearly higher than the hypoconid and entoconid. The hypoconid is a rather low cusp bearing an anterior and a posterior ridge: the anterior one stretches to the base of the protoconid in between the above mentioned two posterior keels of the protoconid. There is no intermediate cusp between the protoconid and hypoconid, as described by Zdansky for *Indarctos lagrelli* (1924, pl. 4). However in the left M/1 a very faint furrow, which could be observed only after careful examination, may well be homologous to the groove which separates Zdansky's intermediate cusp from the hypoconid. The posterior keel of the hypoconid is directed posterolingually, continuing into the posterior border of the talonid. The entoconid is the smallest cusp of the tooth and is situated somewhat anteriorly to the posterior

MEASUREMENTS

	I1/	I2/	I3/	Cd	P1/	P2/	P3/	P4/	M1/
				(L × W)					
Agriotherium intermedium (STACH, 1957)									25 × 25
Agriotherium intermedium (this paper)	12.6×9.0	12.1×9.9	12.0	8.3×6.6	8.8×6.8	7.2×6.4	8.4×7.1	25.9×18.1	25.5×19.5[1)]×24.5
Agriotherium paleoindicus (mesured from Lydekker 1884, pl. 30, fig. 1)								27.7×20.0	27.2×26.6
Agriotherium sivalensis (FRICK, 1926)								32 × 22	29 × 29.9
Agriotherium insignis (meas. from Bale mat.)							12.2×7.5	30 × 22.6	
Agriotherium schnéideri (FRICK, 1926)									29.8×30.2
Agriotherium africanum (HENDEY, 1980, Mean)							9.6×7.6	32.8×24.2	29.1×29.5

	I/1	I/2	I/3	P/4	M/1
			(L × W)		
Agriotherium intermedium (STACH, 1957)					37 × 20.5
Agriotherium intermedium (this paper)	7.8×5.6	11.3×6.2	11.4×11.3	18.8×10.7	33.7×15.8[1)]×19.8
Agriotherium insignis (VIRET, 1939)				20.5×13.6	38 × 21.2 40 × 22.5
Agriotherium schneideri (FRICK, 1926)				23 ×	41 × 23.5
Agriotherium africanum (HENDEY, 1980)				23.6×15.2	41.7×20.2[1)]×22.9

1) anterior width.

margin of the talonid. A cingulum is developed only on the buccal side of the talonid and the lingual wall of the paraconid.

3. THE GEOLOGICAL AGE

The only accompagnying animal, several mandibles of which were gathered together with the present specimen, is a preliminarily identified gazelle, *Gazella* cf. *blacki*. *Gazella blacki* is a form characteristic for Jinlo stage of China, which is equivalent in age to the European Ruscinian in age. If the determination is tenable, the species tends to indicate that the age of the fissure-filling which yielded the fossils, is approximately Ruscinian. It is thus in full accordance with the present state of our knowledge concerning the geological age of the genus *Agriotherium*. According to Hendey (1980), except the doubtful *Agriotherium paleoindicus, Agriotherium* is to be restricted to the time-span of Ruscinian. This should be also the age of our form.

4. COMPARISON

4.1 THE DISTINCTION BETWEEN *AGRIOTHERIUM* AND *INDARCTOS*

Indarctos was first separated from *Hyaenarctos* by Pilgrim in 1913 chiefly by its enlarged talon of M2/. Owing to the absence of veritable association of upper and lower dentitions, in the ensuing 20 years the discussion had been mainly restricted to the characters of the upper dentition. Zdansky's adoption of the differentiation of the two genera was based exactly on the characters of M2/, as proposed by Pilgrim in 1913. Frick, while considering *Indarctos* one of this three subgenera of the genus *Hyaenarctos*, dwelt on P4/-M1/ in 1926. Matthew's correct summary of the differences of the two genera in 1929 was based also on P4/-M1/. Pilgrim was the first to combine the lower dentition, namely M/1 with the upper ones in his diagnostic characters for the two genera and his viewpoints have been subsquently widely accepted. According to this author, the most important characters, by which *Agriotherium* differs from *Indarctos*, with exception of the less important position of the zygomatic arch, are:

1. P1 to P3 are small, single-rooted teeth; one lower premolar is missing.
2. Inner border of the upper molars shorter than the outer border.
3. M2/ without talon.
4. P4/ with antero-posterior diameter greater than that of M1/; parastyle prominent.
5. M/1 relatively short, with talonid much shorter than trigonid, and hypoconid higher than entoconid.

In 1939, Viret reintroduced the exact observations of Stehlin (1907) on the differences in the structure of M/1 of «*Hyaenarctos*» (=*Indarctos*) *punjabiensis* and *Hyaenarctos* (=*Agriotherium*) *insignis*, and thus made an important addition to the diagnoses of the genera: "chez *Indarctos*, le métaconide est plus haut et plus accolé à la pointe principale", while "le métaconide d'*Hyaenarctos insignis*, quoique bas, et assez volumineux et notablement plus saillant que les pointes du talon". Viret further pointed out that, in *Indarctos* "suite au métaconide", there is "une pointe interne un peu plus basse que celui-ci (métaconide) et suivie immédiatement d'une pointe accessoire postéro-interne bien nette, chez *H. insignis* la muraille interne se soulève en un léger denticule comprimé".

Erdbrink (1953) and Stach (1957) laid their emphasis on the differences of the upper dentition, while Tobien (1955) took Viret's viewpoints into serious consideration.

The rich material of Langebaanweg, South Africa, enabled Hendey to give a thorough review of the problem. Though obscured by his emphasis on the linkage of the two genera, the differences in one way or another indicated by Hendey concerning those teeth, which are also present in our material, can be summarized as follows:

1. The incisors and canines are of little use in distinguishing the two genera, except for accessory cusp or the cusp is very small.
2. The anterior premolars, P 1-3, of *Agriotherium* are more reduced and one-rooted. their number can be reduced to only one in one tooth row.
3. All the teeth posterior to P3 are comparatively high-crowned in *Agriotherium*.
4. P4/ of *Agriotherium* has an enlarged parastyle, but a reduced protocone without accessory cusp or the cusp is very small.
5. M1/ of *Agriotherium* has a very weakly developed metastyle. Hence, no clear talon behind the metacone and "hypocone" can be distinguished (it has to be repeated here, that in this paper the hypocone of earlier authors is interpreted as metaconulus). There is no connecting ridge between the metacone and the "hypocone".
6. M2/ of *Agriotherium* without or with very short talon.
7. M/1, as described by Viret and Pilgrim.

Some other features, which were mentioned by different authors in their description, but were not duly considered as important in distinguishing the two genera, may prove in the future no less diagnostic as the above listed, according to our observation and comparison of the related forms:

1. The "chin" of the mandible of *Agriotherium*. In fact, all the available pictures of lower jaws of that genus (*Agriotherium schneideri*: Frick, 1926, fig. 36; *Agriotherium insignis*: Viret, 1939, fig. 6; *Agriotherium africanum*: Hendey, fig. 4, 5) show a prominent "chin", while those of *Indarctos* (*Indarctos lagrelii*: Zdansky, 1924, pl. VI, fig. 3; *Indarctos* sp. (= *atticus*?): Helbing 1932, fig. 5; *Indarctos arctoides*: Thenius, 1959, fig. 1 & 7; *Indarctos vireti*: Crusafont-Pairo and Kurtén, 1976, fig. 2 & 4) are characterized by a smooth curvature of that part. A close comparison of our specimen with the picture of Zdansky's *Indarctos lagrelii* mandible of similarly juvenile age shows the contrast strikingly.
2. The anterior ridge of the hypoconid of M/1 in *Agriotherium* seems more lingually directed, with its anterior end reaching the middle of the base of the protoconid, while the same part in *Indarctos* directs more labially and links with the labial side of the protoconid. This character can hardly be testified on every M/1 described or figured in literature, since in most cases the description or the figures concerning

this part of the tooth were inadequately represented. But several of these pictures, for example, fig. 32 in Frick (1936), fig. 3 in Helbing (1932) show clearly the *Indarctos* type of protoconid.

3. The number of the foramina of the mandible may also be a distinctive character of the two genera. There seems to be a tendency to increase the number of the mental foramen in *Agriotherium* in comparison with *Indarctos*. Zdansky mentioned two mental foramen for *Indarctos lagrelii*, Thenius described 2 or 3 for *Indarctos arctoides*. *Agriotherium insignis* may have only 3, as indicated by Viret's vague picture, but all the other species have 4 - 5 foramen.

4.2. THE IDENTIFICATION OF THE CHINESE MATERIAL AS *AGRIOTHERIUM INTERMEDIUM*

From the fore-going discussion it can be safely concluded that all characters listed above as diagnostic of *Agriotherium*, except the prominent parastyle of P4/, coincide with those of our specimen. It differs from all the other species, except *Agriotherium intermedium*, which we will discuss at the end of this paragraph, by its smaller size, smaller parastyle and protocone of P4/ and the trenchant enlarged posterior cusp on P/4. Furthermore, it differs from *Agriotherium insignis* by its weak development of cingulum on P4/, M1/ and M/1, the comparatively posterior position of the protocone of P4/ and the truncate, rather than convex posterior margin of M/1. *Agriotherium africanum* has a more square-formed M1/, more reduced anterior premolars (in size and in number) and seemingly more prominent protocone of P4/ (sometimes even subdivided into two cusps). Among the Siwalik forms, *Agriotherium sivalensis* is widely different from our species in the upper dentition by the especially prominent and lingually situated parastyle of P4/ and wider M1/. It is, at least at present, meaningless to compare our specimen with the only lower jaw, referred originally by Lydekker to *Agriotherium sivalensis*, but doubted later by many other authors as a correct reference. However, it is interesting to note that the large posterior cusp of P/4 is the only case similar to our specimen among all the teeth of either *Agriotherium* or *Indarctos* that we have compared. Unfortunately, further comparison is excluded by the fact that its M/1 is completely worn down. Perhaps, *Agriotherium paleoindicus* is morphologically more similar to our specimen in comparison with other forms. The antero-posterior diameter of M1/ is greater than its width (27,2 × 26,6), an uncommon character for *Agriotherium*. In this respect, our species approximates to *Agriotherium paleoindicus* rather than to the other species. The length and width of M1/ in our form are 25.5 : 24.5. The cingulum on M1/ of both forms is also very similar. But P4/ of these two species are quite different. Except *Agriotherium paleoindicus*, all the other lower jaws, from Siwalik whichever genus or species they might be attributed, are different from ours by the presence of two cusps behind the metaconid in M/1. Both of the North American species are very advanced and can easily be separated from our species.

Agriotherium intermedium is the smallest species among the genus. Its overall size is almost the same as ours. The only comparable M/1 of both forms are also very similar. The only distinction may be, that there is an entoconulid on M/1 of the first form, as described by Stach (1957). However the accompanying figures show that the named cusp is not so clearly developed (pl. fig. 5b), and is very small in size. Unfortunately, the preserved material of the holotype of *Agriotherium intermedium* from Weze is too scanty to permit a more detailed comparison and therefore it can not be excluded that they represent specifically different forms. However, as far as there are no definite indications against their specific identity (*e.g.* by new material from the type region and of the same age as the holotype) the Chinese remains can be considered conspecific with *Agriotherium intermedium*.

If this view is right, *Agriotherium intermedium* can be characterized (besides the features of the holotype) as a species with very peculiar fourth premolar, being provided with only a small parastyle and P/4 exhibiting a keeled talonid.

5. PHYLOGENETIC DISCUSSION

5.1. METHODOLOGICAL PROBLEMS

Hendey in his paper on *Agriotherium africanum* (1980) gave a philogenetic view within which he not only proposed a dendrogramm of Vallesian and Turolian Indarctos species, but also indicated the Ruscinian *Agriotherium* species as the direct descendants of these former species and integrated them (with question marks in some cases) into the same phylogenetic tree. In his opinion the phylogenetic transition from *Indarctos* to *Agriotherium* took place at least twice and perhaps even four times independently, and in each case was accompanied by a complete reversal of the direction of adaptation.

Many of Hendey's arguments are based upon the large sample of the Langebaanweg *Agriotherium* which, in fact, at that time was the first case of associated upper and lower dentitions of this genus coming from the same locality. In order to support his view, Hendey took also the trouble to give an extensive discussion of the features of the two mentioned genera. It seems, however, that his arguments are not sufficient to maintain his interpretation and to sustain all the implications he imperceptibly made.

The new documents of *Agriotherium intermedium* from Xiaoxian county described in this paper represent another case of associated upper and lower teeth (belonging to one individual) and by its many differences from the South African species in size and morphology enable us to improve the comprehension of the genus *Agriotherium*. There are several problems involved with Hendey's interpretation.

First: are we able to state direct ancestor - descendant relationships on the basis of morphologic similarities? Engelmann & Wiley (1977) and other authors demonstrated that this is not possible on principal grounds. In fact, this kind of relationship can only be established with sufficient probability by a sequence of fossil "populations" documented within a geologic section and mammalogists are normally not in the condition to benefit from such a completeness of fossil documentation.

The relatively few remains of *Indarctos* and *Agriotherium* scattered over different continents and which — with few exceptions — have been described as independent species from nearly each locality are not suitable to defend theories of direct ancestor-descendant relationships. Our ignorance of the phylogeny of these animals is also caused by the fact, that — up to now — we do not know anything about their paleo-zoogeographic relationships. Hendey's supposed direct phyletic transition from different *Indarctos* species to *Agriotherium* species is therefore only based on stratigraphic occurrence and on the argument that the features of the first mentioned form are more primitive. But even supposing that the features of a considered species of *Indarctos* are really plesiomorphic in respect to a certain species of *Agriotherium*, as presumed by Hendey (and which is very doubtful, see below), this would not be an argument in favor of his supposition: to possess only plesiomorphic characters compared to his descendant is exactly what we expect from a direct phylogenetic forerunner. But this does not enable us to indicate the forerunner among different species (either documented or possibly existing) fulfilling the same conditions of plesiomorphy. It is true, that all remains of *Indarctos*, found up to now, are of Vallesian and Turolian age, whereas *Agriotherium* does not emerge earlier than in the Ruscinian and this fact has been taken by Hendey as a strong argument in favor of his view. However, a great number of examples could be cited, dealing with taxa which suddenly emerge in geologic history without a known immediate ancestor. *Agriotherium* is a member of the post-Turolian faunal assemblages which were formed as the result of a major biogeographic event. These assemblages are characterized by a lot of new elements (*e.g. Nyctereutes, Meles*) which in turn are also not known from earlier stratigraphic levels simply by reasons of incompleteness of documentation or immigration from elsewhere.

Another important question is, how to determine the direction of evolutionary processes with only fossil documents at hand? Peters & Gutmann (1971) argued that this is only possible on the basis of morphofunctional and adaptational phenomena in so far as they can be interpreted as economizing developments. It must however be stated that together with rather complete stratigraphic documentation, it is well possible in many cases to determine the direction of evolution in the fossil record.

In this respect also the history of the Ursidae contains good examples. For instance, it is very likely that *Cephalogale*-species of the Oligocene led in the course of phylogeny to more omnivorous Middle Miocene descendants of the type of *Ursavus* and *Hemicyon*, and that evolution in this case has not to be read in the opposite direction. This can be concluded with reasonable likelyhood from the existence of transitional morphotypes in the Lower Miocene together with the supposition that ecologic diversity in carnivores was still increasing. In the same way a transition from *Ursavus* - like to *Indarctos* - like ursid carnivores is probable.

Contrary to that, Hendey's supposed *Indarctos* - *Agriotherium* transition is based on the assumption of a complete reversal of the former adaptive direction. Of course there are examples to substantiate comparable processes as trands within major taxonomic groups and stratigraphic evidence is playing an important role in these cases. However, in order to state reversals on the genus and species level either a very complete documentation of transitional stages is needed or that assumption has to be based on other convincing arguments, like optimizing and economization of morpho-functional structures.

5.2. ALTERNATIVE INTERPRETATION

Hendey discussed a number of trends in his opinion leading from *Indarctos* to *Agriotherium* which cannot stand closer examination. For instance, the pretended trend of size increasing from *Indarctos* to *Agriotherium* cannot be claimed on the base of Hendey's table 17 and 18 because in the M/1's and M/2's we find two none overlapping size classes, the one including the Vallesian *Indarctos vireti* and arctoides, the other comprising the Turolian *Indarctos atticus* and *punjabiensis* together with many *Agriotherium* species but there are no transitions in the dimensions. Are there really stratigraphic indications to arrange the *Agriotherium* species like they are grouped in the mentioned tabels or is it rather in order to suggest a convincing sequence of length: breadth ratios?

In the same way the new *Agriotherium* material from China is clearly in contradiction to the supposed view of a transition from *Indarctos* to *Agriotherium* together with an increase of size, because it is by far smaller than other *Agriotherium* species and in this respect is only comparable to the Vallesian *Indarctos* forms.

Also the assumed progressive reduction in size and number of the premolars can hardly be recognized, given Turolian species like *Indarctos lagrelii*, with P3/3/-P1/1/ which are even stronger than those of *Indarctos vireti* and *atticus* (compare Zdansky 1924, pl. 4 with Crusafont & Kurtén 1976, fig. 1-4 and Thenius 1959, fig. 1, 2, 6 and 7). As the mentioned figures show, there is also a considerable variation, and it is therefore impossible to notice any significant change.

Further trends assumed by Hendey and in his opinion leading from *Indarctos* to *Agriotherium* can as well be understood in an alternative way as results of parallel evolution. This is for instance the case in the development of a parastyle in P4/ or in the emergence of a supplementary cusp anterior to the P4/ - protocon, the latter being known also from other groups as an element, which developed several times independently (*e.g.* in Mustelidae and Procyonidae). After all, there are *Agriotherium* species which lack this supplementary cusp completely as seen in the new material of *Agriotherium intermedium*.

Special discussion deserves the supposed reversal of the direction of adaptation (after Hendey), during which, descending from predominantly omnivorous *Indarctos* species, *Agriotherium* recovered a more carnivorous dentition. In order to sustain this view, it is necessary to interprete the dentition of *Agriotherium* as more primitive than that of *Indarctos*. However, there are characters *e.g.* in the M/1 of *Agriotherium*, which can hardly be interpreted as derived from *Indarctos*. As a consequence of this view the more carnivorous dentition of *Agriotherium* would have to be explained as a result of retrograde evolution in respect of both *Ursavus* and *Indarctos*. This interpretation, however, is in contradiction with other observations:

1. The strong metaconid in the M/1 (lower carnassial) of many *Agriotherium* species can hardly be explained as derived from the strongly reduced M/1 - metaconid

present in the omnivorous adapted *Ursavus* and *Indarctos*, because it can be demonstrated by a great number of examples from the evolution of other carnivore families that the metaconid of the lower carnassial is evidently inadaptive with progressive carnivore evolution. A shifting of the direction of adaptation from omnivorous to more carnivorous feeding habits could therefore result in a reinforcement of only the shearing blade of M/1 but not the metaconid (like in *Thaumastocyon* among the Amphicyonidae). This is the reason why the trigonid of the lower carnassial of *Agriotherium* has rather to be interpreted as a primitive feature.

In order to escape from this consequence and also to strengthen his view of a phyletic transition from *Indarctos* to *Agriotherium*, Hendey tried to interprete the trigonid cusp of the M/1 of *Agriotherium* (regarded as the metaconid by all earlier authors) as the entoconid. He explained this by the complete loss of the metaconid and the shifting of the entoconid right at its place and — irrespective of throwing some doubts on his own theorie — he is inclined to adopt it. But it would be difficult to substantiate, why the metaconid should be substituted by another cusp occupying the same position and growing to the same size without any functional necessity.

2. The anterior keel of the M/1 hypoconid in *Agriotherium* is not connected to the buccal wall of the protoconid but is directed antero-lingually, which can clearly be observed in the Chinese material of *Agriotherium intermedium* and also in *Agriotherium africanum* (Hendey 1980, fig. 10 A). This feature is characteristic of very early members of the Ursidae, *e.g.* the *Cephalogale*-species and it is very unlikely that in *Agriotherium* this feature would have been produced accidentally as a result of the reduction of the rather different talonid pattern of *Indarctos*.

3. The M1/ of *Agriotherium* is more trapezoidal than its counterparts in *Ursavus* and *Indarctos*. This cannot be explained by molar reduction in connection with a more carnivorous adaptation because such a development would more likely result in a uniforme shortening of the tooth. That means, the shape of M1/ of *Agriotherium* must be considered a retained plesiomorphic character.

4. The so-called shearing function of the molars, M1/ and M2/2/, (Hendey 1980: 1057 has nothing to do with carnivore specialization but is characteristic of many herbivorous adaptations. Therefore the molars of *Agriotherium* can more naturally be interpreted as a sign of different feeding habits in regard of *Indarctos*, the latter being characterized by more dominating crushing surfaces in his cheek teeth.

5. A reduction of the molars in the evolution to *Agriotherium*, as assumed by Hendey, is very unlikely, as in all carnivore examples we know molar reduction is caused by the need of more space on the jaws in connection with the enlargement of other teeth (the carnassials, or both the carnassials and premolars, *e.g.* hyaenids). Space problems in the dentition of *Agriotherium*, however, did hardly exist because of the strongly reduced premolars, which in turn have to be understood in connection with more herbivorous feeding habits.

Hendey emphasized the close similarities in the skull between *Indarctos atticus* and *Agriotherium africanum* but did not illustrate it by figures. A comparison of the restored skull from Langebaanweg with the well preserved skull of *Indarctos atticus* from Samos figured by Thenius 1959 (fig. 2-6) reveals, however, considerable differences in general proportions as the breadth of the zygomatic arches compared to the length of the skull, the breadth of the basicranium, strength of the mastoid process and the position of the anterior boarder of the orbita compared to the molars (in *Agriotherium africanum* situated above the anterior part of M2/, in *I. atticus* above the middle of M1/). The loss of the alisphenoid canal has been realized too frequently in the evolutionary history of carnivores to be used as an argument in favor of phylogenetic relationships and it has to be repeated on this occasion that morphologic similarities as such are not suitable to support theories of ancestor - descendant relationships.

6. CONCLUSION

As a whole, it has to be stated, that Hendey's arguments to suppose direct ancestor - descendant relationships between several *Indarctos* species and *Agriotherium* species are far from convincing. Irrespective of the methodological inconsistencies involved (see p. 75) there are no proper reasons in support of his opinion:

1. The various trends brought forward by Hendey as arguments in favor of a phyletic transition from *Indarctos* to *Agriotherium* cannot stand closer examination: As the new material of *Agriotherium intermedium* from China demonstrates, the plesiomorphic characters of this species are far from identical with, or closely comparable to, the features of advanced *Indarctos* species, which, however, should be expected. And if we take all known species of the two genera into consideration, there is no trend of size increase at all (see p. 77).

2. Among the resemblances between *Indarctos* and *Agriotherium* mentioned by Hendey, as arguments in favor of very close relationships, there are characters, which are highly suspect to be caused by similar omnivorous adaptation (*e.g.* the supplementary antero-internal cusp in the P4/ of *Indarctos* and *Agriotherium africanum*) but none which could be considered common derived characters of these two genera. Hence there are no reasons to lump these forms together generically and even not to consider them phylogenetically very close related.

3. The numerous morphologic differences in the dentition of both genera are interpreted by Hendey as result of a reversal in the adaptational direction of *Agriotherium* compared to *Ursavus* and *Indarctos*. However, as pointed out in the last paragraph several characteristic features indicate, that the evolution of *Agriotherium* has to be read in the opposite sense as Hendey did. As a consequence, the dentition of *Agriotherium* must be interpreted as more primitive than that of *Ursavus* and *Indarctos* and its similarities to the latter forms must be understood as a case of parallelism.

Following the arguments exposed in our discussion (5.2.) *Agriotherium* cannot be derived from *Ursavus* and *Indarctos* and therefore is less close related to them than these genera to each other. *Agriotherium* can be understood as a lineage retaining many primitive features and being less developed into the ursid adaptational direction than *Ursavus* and *Indarctos*. It is correct, that *Agriotherium africanum* exhibits more advanced characters than various other species of that genus and in this way shows more analogies to *Indarctos*. But on the other side there are more conservative forms of *Agriotherium* like the species intermedium which demonstrate very clearly the phylogenetic independence of this genus in regard of the *Ursavus-Indarctos* group. The origin of *Agriotherium* can still not be discerned in more detail but it seems likely, that this lineage has an independent root in between the *Ursavus-Indarctos* complex on one hand and the *Hemicyon*-group on the other. Though, at present, we have no definite indications in favor of closer relationships to the *Hemicyon*-group, there are no principal obstacles to derive *Agriotherium* somewhere from this stock. Hendey's objection against such a possibility is that the hemicyonids became extinct already in the Middle Miocene. But at the actual state of knowledge based on scattered documentation we can not infer this with reliability for the whole group.

ACKNOWLEDGEMENTS

This study was supported by the Alexander von Humboldt-Stiftung in West Germany, which is gratefully acknowledged.

We thank Mrs. Hella Lang, Mainz, for writing the manuscript and Mr. Manfred Schmicking for elaborating the fotographs.

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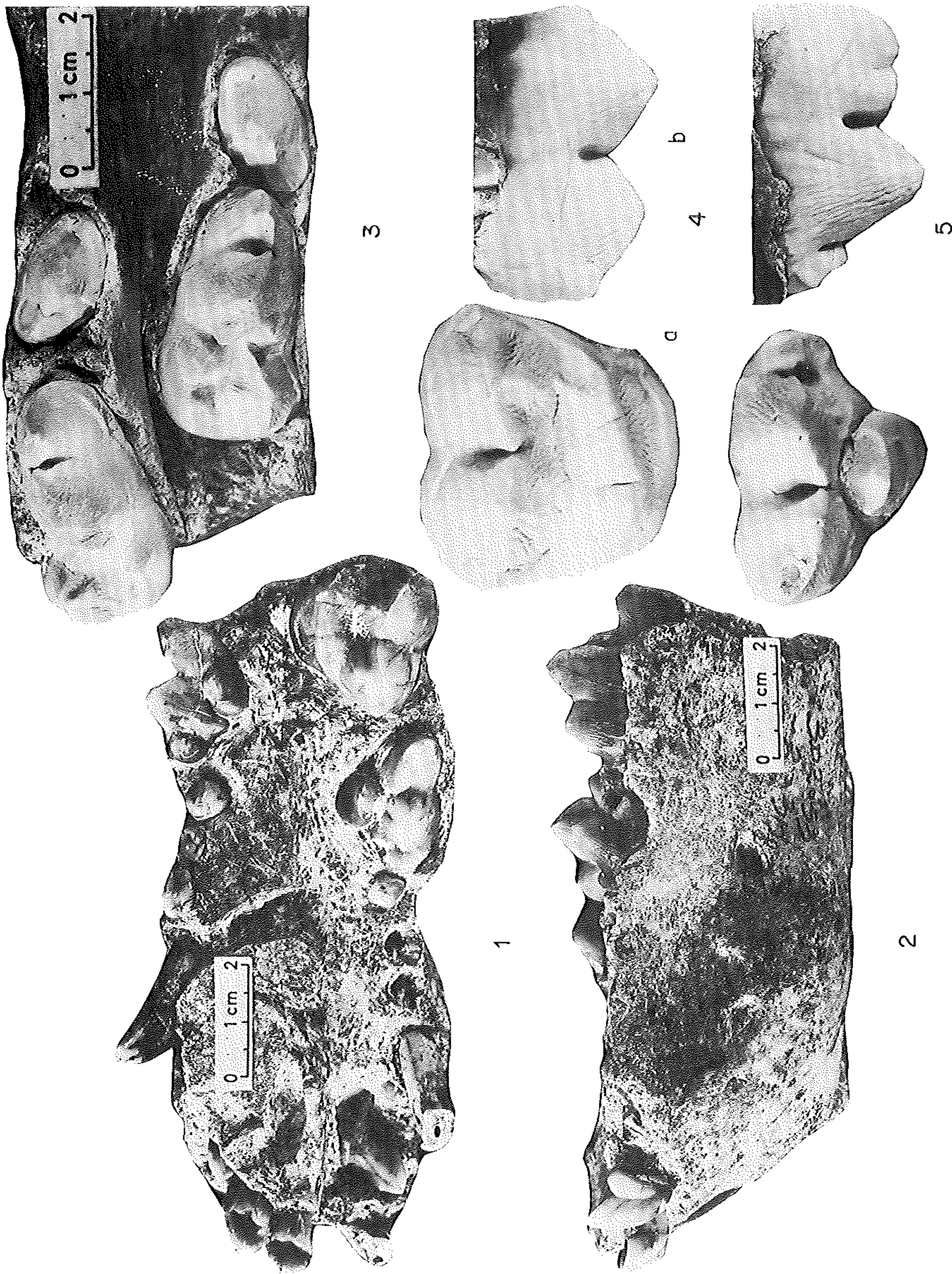
PLATE 1

Fig. 1 : *Agriotherium intermedium* (STACH), upper jaw, occlusal view.
Fig. 2 : *Agriotherium intermedium* (STACH), lower jaw, lateral view.
Fig. 3 : *Agriotherium intermedium* (STACH), lower jaw, occlusal view.
Fig. 4 : *Agriotherium intermedium* (STACH) M1/ dex., a/ occlusal view, b/ buccal view; × 2.
Fig. 5 : *Agriotherium intermedium* (STACH), P4/ dex., a/ occlusal view, b/ buccal view; × 2.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