Carnivora of the Tung Gur Formation of Mongolia

By Edwin H. Colbert

BULLETIN

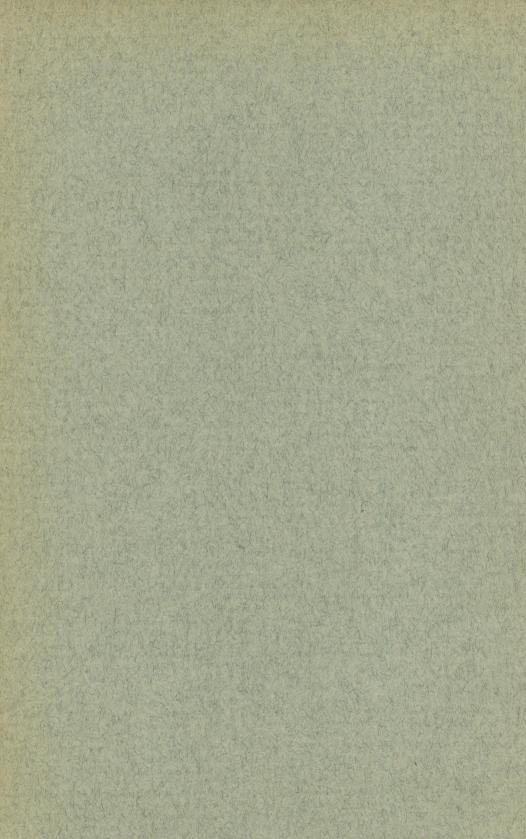
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Article II.—CARNIVORA OF THE TUNG GUR FORMATION OF MONGOLIA¹

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INTRODUCTION

The Tung Gur formation of Mongolia is a horizon of Upper Miocene age, discovered by the Asiatic Expeditions of The American Museum of Natural History in 1928 and named by Spock in 1929.2 This formation is particularly interesting because of the rich mammalian fauna contained within it, a fauna including the peculiar shoveltusked mastodon, Platybelodon, several rodents, a chalicothere, a Listriodon, at least three types of deer, of which the new genus Stephanocemas characterized by palmate antlers on long pedicles is the most noteworthy, a giraffid and several types of antelopes. These mammals have been described in a series of papers by various authors.

The carnivores, hitherto undescribed, constitute a large and varied element of the Tung Gur fauna. Not only is this group represented by well-preserved fossils, but it also contains a large variety of forms in comparison with the rest of the fauna. It is the purpose of this present paper to describe these Tung Gur carnivores, and to discuss their taxonomic and phylogenetic relationships.

The author is greatly indebted to Dr. Walter Granger for permission to study the Tung Gur carnivores. The illustrations for this paper were made by Louise Waller Germann and John C. Germann.

Ursidae

Hemicyon teilhardi,3 new species

Type.—Amer. Mus. No. 26594, an associated skull and mandible, virtually complete but somewhat crushed.

Paratypes.—Amer. Mus. No. 26595, left maxilla with P^3 — M^2 and right ramus with P_1 — M_3 . Amer. Mus. No. 26596, left ramus

with I_s, canine and cheek teeth. Amer. Mus. No. 26213, a very large right mandibular ramus with the root of the canine and the cheek teeth. Amer. Mus. No. 26544, portion of left ramus with roots of cheek teeth.

Horizon.—Tung Gur formation; Upper Miocene.

Locality.—"Wolf Camp" quarry, about five miles southwest of Gur Tung Khara Usu, Inner Mongolia (for 26594–26596). Tung Gur escarpment, about ten miles northeast of Gur Tung Khara Usu (for 26213). Escarpment, near "Wolf Camp" (for 26544).

Diagnosis.—A Hemicyon of medium size,

but with relatively large teeth. Dental formula $\frac{3}{3} - \frac{1}{1} - \frac{4}{3-4} - \frac{2}{3}$. Incisors very large, canine with oval cross-section. Premolars generally well developed; lower premolars varying in number from three to four. Upper carnassial with internal cusp medially placed. Upper molars more "canoid" than in other species of Hemicyon, that is, antero-posterior diameters are less as compared with the transverse diameters than in most of the other species; otherwise these teeth are typical of *Hemicyon*. Lower carnassial with a well-developed metaconid and a basined talonid. Second lower molar variable in size and shape; third lower molar rather large. Mandible with premasseteric fossa. Frontals expanded, particularly as compared with Hemicyon ursinus, and brain case likewise expanded. Bulla relatively large and oval, as in the canids, rather than being reduced and flattened as in Hemicyon ursinus and the bears. External auditory meatus tubular. Bulla separated from paroccipital process and mastoid expanded, as in Hemicyon ursinus and the bears. The expansion of the mastoid is, however, less than in these latter forms.

Seldom are mid-Tertiary carnivores so completely preserved as are the skull and jaw that constitute the type of this new species. Indeed, the material on which *Hemicyon teilhardi* is based, consisting as it does not only of the associated skull and jaw, but also of additional jaws and a maxilla, is so complete that it is worthy of a rather detailed description and full comparisons. Consequently the new species will be considered at some length in the following paragraphs.

The type skull and jaw indicate a *Hemi-cyon* of medium size, perhaps closely com-

¹Publications of the Asiatic Expeditions of the American Museum of Natural History. Contribution No. 139.

² Spock, L. E. 1929. Amer. Mus. Novitates,

No. 394.

No. 39



Fig. 1. Hemicyon teithardi, new species. Type, Amer. Mus. No. 26594, skull. Dorsal view, one-half natural size.

Fig. 2. Hemicyon teilhardi, new species. Type, Amer. Mus. No. 26594, skull and mandible. Lateral view of left side, one-half natural size. (Right mandibular ramus, reversed.)

parable in this respect to H. sansaniensis, the generic type, and to H. göriachensis; considerably larger than H. barstowensis of the North American Miocene, and somewhat smaller than H. ursinus of the Santa Fé beds. It is an interesting fact that the teeth of this species are unusually large as compared with the skull. For instance, although the skull of the form now under consideration is considerably smaller than the skull of H. ursinus, the teeth are actually larger than the teeth in the North American form. (The partial skull of H. göriachensis is so badly crushed and distorted that its use in a general comparison of size differences is not practicable.)

Although the skull of *Hemicyon teilhardi* has been distorted to a certain extent, nevertheless it is sufficiently well preserved that its characters may be readily seen without recourse to paper reconstructions or other methods of restoration. the striking characters of this species is the relatively great expansion of the frontals and the considerable size of the brain case. As a result of this development in the skull there is no postorbital constriction of the frontals, as in H. ursinus and other Mio-Pliocene related forms, but rather these expanded frontals continue back, maintaining an almost constant width, from the postorbital processes to the similarly expanded parietals. In a general way, the fronto-parietal region of Hemicyon teilhardi resembles that of the modern Canis, and it is evident that there must have been large frontal sinuses in the Mongolian form.

The brain case itself would also seem to be rather large as compared with the size of the skull.

The sagittal and lambdoidal crests are high, though the former is less developed than it is in *H. ursinus*, thereby affording attachments for strong temporal muscles. As is the case with the American species, the occiput extends far back, to overhang the occipital condyles. The occiput is narrow, and triangular as seen from the posterior view, and there is a central, vertical occipital ridge.

The orbit is situated above the anterior border of the second molar, while the intraorbital foramen is above the front portion of the upper carnassial. The anterior border of the posterior nasal choanae is opposite the posterior border of the second molar; in *H. ursinus* the choanae are somewhat more posterior in position. The pterygoids are, however, similar to those in the American species, being strongly developed and forming a long, deep trough extending back to the region of the glenoids. The zygomatic arches are not preserved, but undoubtedly were widely arched and strong.

The glenoid articular surface is truly intermediate in its form and structure between that of the dogs and that of the bears. It resembles the glenoid of the canids in general shape and in the lesser transverse expansion than is characteristic of the bears, and incidentally of H. ursinus, too. On the other hand, the glenoid of Hemicyon teilhardi is very ursoid in the ventral and forward extension of the postglenoid process, so that the articular surface faces forwardly, as in the bears, rather than down, as in the dogs. In fact, the forward direction of the glenoid surface is even more pronounced in the Mongolian species than it is in H. ursinus, in which latter species this character is developed as fully as it is in the bears.

Unfortunately the cranial foramina have been for the most part obliterated, but a few facts regarding them may be ascertained with certainty. On the whole their arrangement would seem to be similar to that in H. ursinus. The foramen lacerum anterius and the foramen rotundum were both probably large. The alisphenoid canal is seemingly fairly long, similar to the same structure in H. ursinus, longer than the canal in the Canidae and shorter than the canal in the Ursidae. The foramen ovale is close to the posterior opening of the alisphenoid canal and opposite the anterior border of the glenoid. The foramen lacerum medius is more or less hidden beneath the anterior end of the inflated bulla (of which more will be said in succeeding paragraphs), while the foramen lacerum posterius is seemingly located behind and somewhat separated from the bulla, and contiguous to the internal border of the paroccipital process. There is seemingly a stylomastoid foramen similar to that in the bears, in front of the paroccipital process and internal to the mastoid. The postglenoid foramen is not visible, and it would appear to be somewhat hidden beneath the expanded bulla. In the dogs the postglenoid foramen is near the outer border of the postglenoid process, in *H. ursinus* it occupies an intermediate position, while in the bears it is near the internal border of the postglenoid process. If the foramen in *Hemicyon teilhardi* occupied the same relative position that it does in *H. ursinus* it should be visible, even though the bulla

In the bears the bulla is very much flattened and extended, and there is a long bony tube for the external auditory meatus. In *Hemicyon ursinus* the bulla is rather small and flattened, though not to the degree typical of the bears, and there is a rather long tube for the meatus. In both the bears and *Hemicyon ursinus* the bulla is confined to the more anterior portion of the basicranial region and thus is separated from the paroccipital process. This confinement of the bulla has been accompanied by an enlargement of the mastoid process, which thrusts itself between the bulla and

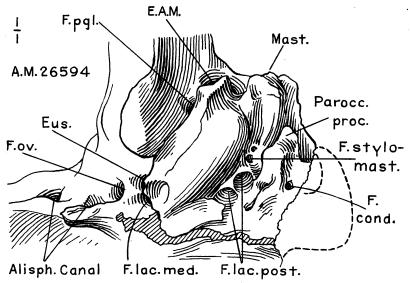


Fig. 3. Hemicyon teilhardi; new species. Basicranium of type skull, Amer. Mus. No. 26594, natural size.

is inflated to such a degree that it is contiguous to the internal portion of the posterior surface of the postglenoid process. Therefore it would seem likely that the foramen occupies a more medial position, as it does in the bears, and thus is hidden by the bulla.

Perhaps the most interesting single character of this skull is the auditory bulla. In the dogs the bulla is strongly inflated, and of ectotympanic origin. It occupies all of the space between the foramen ovale and the paroccipital process, and there is a short bony tube for the external auditory meatus.

the paroccipital. Hemicyon teilhardi shows the interesting condition of an inflated bulla, similar to that of the dogs, having a moderately long bony tube for the meatus, as in Hemicyon ursinus and being separated from the paroccipital process, though not to the same extent as is typical of H. ursinus and of the bears. As might be expected, the mastoid of Hemicyon teilhardi is smaller and thus more dog-like than the same structure in Hemicyon ursinus and in the bears.

It would seem that an inflated bulla is a primitive character in the Canidae. As Matthew has shown, the canids are essentially diphyletic, one branch, including all of the modern canids, having been derived from the Oligocene genus Cynodictis, the other branch, constituting the large "bear-dogs" and leading to the bears, having been derived from the Oligocene genus Daphaenodon. In Cynodictis the bulla is inflated and of large size, and obviously developed into the very large, inflated bulla of the modern canids. In Daphaenodon the bulla, though inflated to a certain extent, is relatively small. Now the small, rather flattened bulla of Hemicyon ursinus must have been derived from the small bulla of Daphaenodon. The process leading from the one to the other would involve merely a flattening of the Daphaenodon bulla and a certain extension of the tube of the meatus. By a further process of flattening and extension the bulla of the bears would have developed from a bulla like that of Hemicyon ursinus.

But in *Hemicyon teilhardi* the bulla is inflated, in which respect it shows a resemblance to the dog bulla and is quite different from the bulla in Hemicyon ursinus. the other characters of the bulla and the basicranium in this new Mongolian form are truly hemicyonine (confinement of the bulla, extension of tube, foramina, etc.), it must be presumed that this species is closely related to the other species of the genus in all but this one character. Consequently it would seem proper to interpret the inflated bulla of *Hemicuon teilhardi* as a secondary development, paralleling the enlarged bulla of the dogs, but independently derived from the small, typical Daphaenodon-Hemicyon bulla.

The mandible of *Hemicyon teilhardi* is characterized by its large premasseteric fossa, a feature typical of this genus. The lower border of the ramus beneath this fossa is strongly convex, a development correlative with the excavation of the fossa, and like it typical of the genus. The ascending ramus is long antero-posteriorly, with a deep masseteric fossa, and the coronoid process is high. The mandibular condyle is transverse, and on the inner side of the jaw it is curved ventrally, to articulate with the ventrally and forwardly projecting postglenoid process. On the internal sur-

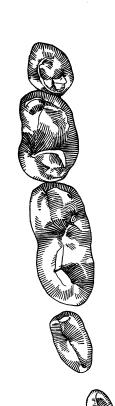
face of the angle of the mandible is a well-developed, longitudinal ridge, for the attachment of the internal pterygoid muscle. This ridge, a secondary development, is not seen in the dogs, nor is it present in *Hemicyon ursinus*, but it is well developed in the bears. The symphysis is rather long; there is no "chin" as in the bears.

Coming now to a consideration of the teeth, it may be well at the teginning to call attention to the variation in the dental formula. In the type specimen of *Hemicyon teilhardi* (No. 26594), there are but three lower premolars, while in three of the other specimens (Nos. 26595, 26213, 26544), there are four premolars. In the fifth jaw (No. 26596) the number of premolars cannot be accurately determined. The first premolar is probably the variable tooth in this species, although the actual determination of the tooth that is either present or absent cannot be made.

The incisors are large, as is usual in *Hemicyon*. The first and second upper incisors are distinguished by the strong development of the internal cingula to form shelves against which the lower incisors occluded. The third upper incisor, much larger than the other two, has a very large internal cingulum, to receive the elongated and sharpened edge of the third lower incisor. The upper canine is oval in cross-section, with a well-marked posterior keel.

The anterior three upper premolars are elongated teeth, each consisting essentially of a central cone, with ridges running anteriorly and posteriorly from it, and a slight internal cingulum. The upper carnassial is typically hemicyonine in that the internal cusp is situated in the middle of the internal border, and not anteriorly as in most of the This is an ursid character in Hemidogs. The tooth is dog-like, however, because of its large size, for it is somewhat longer than the first upper molar. metacone is sharp and high, the metastyle shear is well developed, and there is a small external cingulum.

The molars are perhaps somewhat more of the "canid" type than is the case in most species of *Hemicyon*. That is, the width of these teeth as compared to their length is somewhat greater than is the case with





H. ursinus, H. sansaniensis and other forms, and are in this respect more or less comparable to the molars of H. göriachensis. In the molars the external cingulum is well developed, while the internal cingulum is very heavy. There is a posterior swelling of the internal cingulum that forms what is essentially an additional cusp functioning as a hypocone. The protocone is ridgelike, directed antero-posteriorly, not a sharp V as in the more typical canids.

The lower incisors, though large, are relatively smaller than the upper incisors, as might be expected. They increase in size from the central to the lateral members of the series, and the third incisor is broad and rather spatulate, with a secondary external cusp connected to the main cusp by a sharp, transverse ridge.

The canine, like the upper canine, is rather oval in cross-section, with a posterior keel. There is in addition an antero-internal keel on this tooth, and the internal surface between the two keels is somewhat flattened.

The variation in number of the lower premolar teeth has been mentioned above. Not only are these teeth variable as to number, but also as to their size and form. In the type mandible they are very large, as contrasted with the same teeth in one of the paratypes (No. 26595). The three anterior premolars are elongated, each with a low central cusp and anterior and posterior ridges running from it. In the last lower premolar the central cusp is much higher than in the teeth preceding it, and the posterior border of the tooth is expanded, especially internally, to form a small heel.

The lower carnassial is long, with a high protoconid, a well-developed metaconid and a basined talonid. The strong metaconid and the basined heel are characteristic features of *Hemicyon*. In the heel of the tooth, the outer cusp or hypoconid is much higher than the inner cusp, or entoconid, so that the basin, which is very shallow, has a high ridge forming its external border. There is a faint external cingulum.

The second lower molar is of the typical *Hemicyon* form, in which the trigonid is

somewhat higher than the talonid, the former with a strong cross-crest at its summit and an anterior basin, the latter with a large hypoconid forming part of a high ridge on the external surface of a very shallow basin. This tooth is quite noticeably variable in size, as will be seen in the discussion and charts below.

The third lower molar is also very variable as to size. It has the essential characters of the tooth preceding it, but the trigonid is virtually no higher than the talonid. The inner portion of the talonid is compressed toward the outer surface, so that the tooth is pointed posteriorly. This tooth would seem to have distinct anterior and posterior roots.

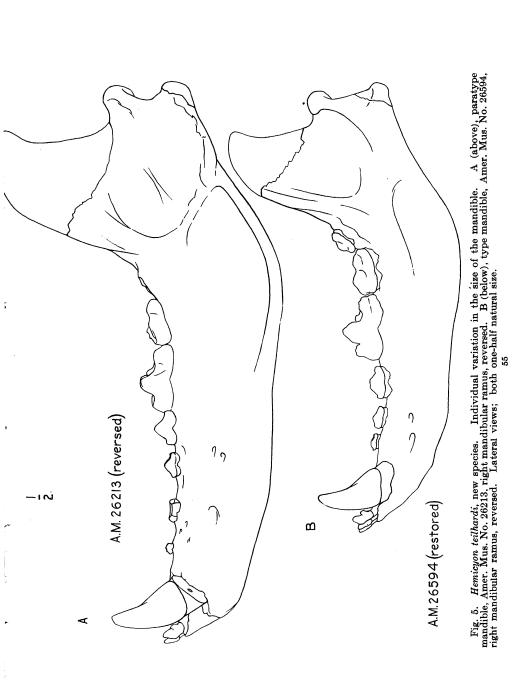
Variation in Hemicyon teilhardi

The series of specimens belonging to this new species, small though it is, affords some insight into the degree of variability that may be expected in a single species of a fossil mammal.

Of the material on which Hemicyon teil-hardi is based, three of the jaws came from one locality, a quarry. Consequently there can be no doubt about these specimens belonging to a single species. The large fragmentary jaw was found near the quarry. The jaw which was not associated with the rest of the material (No. 26213) came from the same escarpment in which the quarry was located, but at a locality some fifteen miles distant.

As for the upper dentition, comparisons must be made on the basis of two specimens, namely, the type skull (No. 26594) and the maxilla (No. 26595). Differences between the two are slight. The teeth of the paratype are somewhat smaller than those of the type, and M² is somewhat more "slender" in the former than it is, in the latter specimen. One other small difference is to be noted; in the paratype the internal cusp of the carnassial is relatively smaller than it is in the type.

It is in the lower jaws that the real differences between individuals become apparent. The variability in the lower premolars between three and four, mentioned above, is the most important discontinuous variate in the species. Of the continuous



variates, those of size are most noteworthy, and will be considered in the following remarks.

The large mandible (No. 26213) is so much larger than any of the specimens from the quarry that the question of its specific identity with these specimens at once

as is shown in figure 5. Yet in spite of the much greater size of the mandible in one individual over another, a comparison of the teeth shows a close correspondence between them. Consequently the differences in the jaws of the two specimens must be attributed to variation within the species.

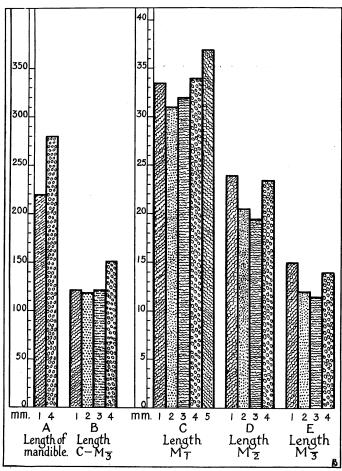


Fig. 6. Graph to show the individual variation in the lengths of (a) the mandible, (b) C-M₃, (c) M_1 , (d) M_2 , (e) M_3 , in *Hemicyon teilhardi*, new species. 1. No. 26594; 2. No. 26595; 3. No. 26596; 4. No. 26213; 5. No. 26544.

comes to mind. A glance at the graphs and measurements will show that this specimen is, for instance, about one-fifth or twenty per cent longer than the type mandible. And this difference in linear dimensions becomes much more apparent in the relative massiveness of the two specimens,

The above remarks apply also to the large fragmentary jaw, No. 26544.

Whether this variation is individual or sexual is a question that cannot be answered on the basis of the five jaws now known. It is an interesting fact that the three mandibles from the quarry are about equal to each other in size, and are all smaller than the large, isolated jaw. If the differences cited above were due to sexual development, it would mean that the large jaw was that of a male, while the three jaws found together were those of females. Of course, it is quite possible that this is so, but the chances against it are about eight to one.¹ The differences obviously are not

due to age, since all of the jaws are of mature animals.

A great deal of variation is to be seen in the actual and relative sizes of the last two molars. This is particularly noticeable in the second molar, which is very large in the type jaw (No. 26594), somewhat smaller in the large jaw (No. 26213) and very much smaller in the other two specimens (Nos. 26595, 26596). The size differences are shown graphically in the accompanying comparative figures and charts.

MEASUREMENTS

	H. te	ilhardi	$H.\ ursinus$
	A. M. 26213	A. M. 26594 (type)	F:A. M. 21101 (neotype)
Skull		~	
Greatest length, over all		316 mm.	357 mm.^{1}
Basal length (Inc. alvfor. mag.)		267e	311^{1}
${f I}$ -alveolus- ${f M}^2$		152	146^{1}
Height, above M ¹	*	77e	82
Height, basioccipital-sagittal crest		90	122
Breadth, post-orbital processes		68	76
Breadth, zygomatic arches		160e	201^{1}
Breadth, mastoids		95e	120^{1}
Breadth, palate at M ¹		40	53
Breadth, muzzle at canines		59	73^{1}
Length of bulla		32.5	26
Width of bulla		19.5	17
Length of basicranium; for. ovale-for. mag.	•	43e	67
Mandible			
Length—condinc. alveolus	276 mm.	219	256
Depth — M_2	67	47	62

¹ From Frick, 1926.

COMPARATIVE MEASUREMENTS OF THE UPPER TEETH IN Hemicyon teilhardi and Related Species

	H. teilhardi A. M. 26594 A. M. 2659 (type) (paratype		H. ursinus F:A. M. 21101 (neotype) ¹	H. barstow- ensis (type) ¹	H. californ- icus (paratypes)
Upper Dentition		((=====)	(03 PC)	(paraty pes)
C. alv. $-M^2$	105 mm.	99 mm.	103 mm.		
P^4-M^2	68 60e mm.	62	62	54.5 mm.	
$I^1 L \times W$	9×6.5				
I^2	9.5×7				
\mathbf{I}_3	15×9.5				
· · · C	19×13		$[23 \times 16]$		
\mathbf{P}^{1}	7.5×5		9 × [5]		
\mathbf{P}^2	12.5×7.5	9.2	$11.7 \times [6]$		
\mathbf{P}^3	13×8	16.7			
P4	25.5×17 24.5×15	25×16.3	$8\ 26.2 \times 17.2$	22.5×13.3	26.8×16
$\mathbf{M}^{_1}$	$23 \times 25 21 \times 23$		$5\ 23.5 \times 25.4$		23×22.5
\mathbf{M}^{2}	$19 \times 25 18 \times 22$		16.5×24.5		15.5×20

¹ Frick, 1926.

¹ This proportion was given to me by Dr. G. G. Simpson, who recently has been making detailed statistical studies on fossil mammals.

	H. cali- fornicus (type)											15.5	33×15	20×13.5		
ATED SPECIES	H. barstow- ensis (type) ¹												29.2×12.7	17.7×12	10.5×8.5	
ardi and Rel	H. sansan- H. ursinus 44 iensis (neotype) ¹ 1 (type) ¹		1961	[70.5]					-		$10 \times [8]$	$16.5 \times [9]$	35.4×15	23×15	(alv.)	
on teilh	. sansan- iensis (type) ¹												30.6	18.8	14.5	
IN Hemicy	A. M. 26544 (referred	specimen) (roots only)							5.5							
ower Teeth	H. sansan-A. M. 26213 A. M. 26544 tensis (paratype) (referred (type) ¹			151 70				22×15.5	5.5×3.5		12.5×6.5	17×8.5	34×14	23.5×16	(alv.)	
TIVE MEASUREMENTS (IN MM.) OF LOWER TEETH IN Hemicyon teithardi and Related Species	H. teilhardiA. M. 26596(paratype)		9	122 62			7 × 7.5	14 × 11				15×7.5	32×13.5	19.5×13.5	11.5×9	
SASUREMENTS	A. M. 26595 (paratype)		,	49 49											12×9.5	
COMPARATIVE MI	A. M. 26594 (tŷpe)		•	70Z	7 × 4.5	8 × 5.5	8.5 × 8.5	17.5×13.5	(absent)	8.5 × 5	11×7.5	16.5×9.5	33.5×15	24×15.5	15×11.5	
သိ			Lower Dentition	C. alv.–M3 M1- 3	I, L × W	I_2	I³	٥	P_1	\mathbf{P}_{2}	P3	P4	Mı	$\mathbf{M_2}$	Ms	¹ Frick.

Canidae

Amphicyon tairumensis, new species

Type.—Amer. Mus. No. 26606, a left mandibular ramus with P_{3-4} , M_1 preserved.

PARATYPES.—None.

Horizon.—Tung Gur formation; Upper Miocene.

LOCALITY.—Tung Gur escarpment, about twenty miles northeast of Gur Tung Khara Usu,

Inner Mongolia.

Diagnosis.—A small Amphicyon with a slender jaw. No premasseteric fossa. Canine of medium size, separated from second premolar by a diastema; first premolar absent. Premolars small, characterized by the posterior cusp on the median ridge behind the main cusp—a typical feature of Amphicyon. P4 with a very slight postero-internal expansion. Lower carnassial of medium size—not elongated. Meta-

the ramus in *Hemicyon*. Correlative with the lack of a premasseteric fossa is the relatively straight lower border of the horizontal ramus, as contrasted with the strikingly convex border in the Tung Gur *Hemicyon*. In all of these characters the form now under consideration shows its affinities with the true *Amphicyon*, using the word in its strict sense.

There are only three premolars in this jaw. There is, however, a diastema between the canine and the second premolar, showing that the low premolar count characteristic of this species is due simply to the loss of a tooth, and is not accompanied by any shortening of the jaw. The last pre-

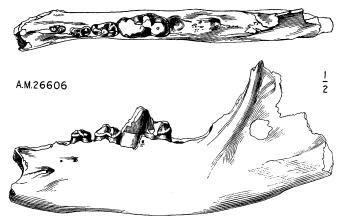


Fig. 7. Amphicyon tairumensis, new species. Type, Amer. Mus. No. 26606, left mandibular ramus with P_3 - M_1 . Crown view above, lateral view below; one-half natural size.

conid seemingly small; talonid probably trenchant. Third molar present, but seemingly single-rooted.

No very definite conclusions are to be drawn concerning this specimen, because of the imperfect state of its preservation. Of the anterior teeth, only the last premolar is adequately preserved; of the molars, only the carnassial is present, and it is very much worn and broken.

The ramus is rather slender, though heavier in its anterior portion than the ramus of *Hemicyon teilhardi*. Since there is no premasseteric fossa, the back portion of the horizontal ramus is considerably shallower, but thicker than the same part of

molar, the only tooth of the series well preserved, is quite small as compared with the lower carnassial, but the difference between the teeth is probably no greater than in the case of *Hemicyon teilhardi*. The one character that stamps this last premolar as undoubtedly of *Amphicyon* affinities is the large posterior cusp, swelling the ridge that runs back from the main cusp to the heel of the tooth. This is a characteristic *Amphicyon* feature and is in decided contrast to the premolars of *Hemicyon*, which lack this cusp.

The carnassial is relatively shorter and heavier than the same tooth in *Hemicyon*

teilhardi, and likewise than the same tooth in the generic type, Amphicyon major. its general proportions (but not size) it would seem to resemble to some extent the carnassial of the American form. Amphicyon frendens. The paraconid is broken away, but it would appear that this lobe was rather short, as is typical of Amphicyon. Likewise the metaconid is missing. but there are definite traces of its presence. The talonid is very much worn, but enough of it is preserved to show that there was a large, fairly centrally placed hypoconid, probably crested, and a broad entoconid shelf. But there seemingly was no basin in this talonid-again a character linking this form with Amphicyon rather than with Hemicyon.

Recently, in a paper descriptive of a new Upper Miocene fauna from Shantung, Dr. C. C. Young has described a large canid jaw under the name of Amphicyon confucianus. The Shantung Amphicyon is extraordinarily large, in this respect resembling the large jaw of Hemicyon teilhardi (No. 26213) figured above. That it is a true Amphicyon is shown by the characters of the lower carnassial, which is elongated and narrow as compared with the more robust Hemicyon carnassial, and in which the paraconid is set at a considerable angle to the mid-line of the tooth, the metaconid is small and the talonid is trenchant.

There would seem to be sufficient justifications for regarding Amphicyon tairumensis as specifically distinct from Amphicyon confucianus. Of course there is the great difference in size between the two, which may or may not be important. (The description of Hemicyon teilhardi, above, has shown the possibility of considerable size variations within a single species of these animals.) But discounting size differences, the differences in the carnassials of the two species would seem to be sufficiently great to separate them as validly distinct each from the other. Amphicyon confucianus the lower carnassial is very long and slender, while in Amphicyon tairumensis the same tooth is shorter, both actually and proportionally, and more robust.

MEASUREMENTS

Amer. Mus. No. 26606	
Length, posterior border of canine	
to M ₃	109e mm.
Depth of ramus beneath M_1	41.5
P ₃ length	11
width	5.5
P4 length	14
width	7.5
M_1 length	28
width	13

Gobicyon macrognathus, new genus and species

Type.—Amer. Mus. No. 26597, a lower jaw, with broken incisors and canines, right and left P₁-M₂, of which only left P₃₋₄ are perfectly preserved.

REFERRED SPECIMEN.—(This species?) Amer. Mus. No. 26601, an associated right maxilla, with I²⁻³, DC, P¹⁻³, and a right mandibular ramus, with I₃, DC, C (unerupted), P₁₋₄.

Horizon.—Tung Gur formation; Upper Miocene.

LOCALITY.—"Wolf Camp" quarry, about five miles southwest of Gur Tung Khara Usu, Inner Mongolia.

Diagnosis.—A large canid with a heavy jaw, broad mandibular symphysis and large premolars. Dental formula 3/3, 1/1, 4/4, 2(?)/3. Mandible heavy with a straight lower border. Symphysis massive and broad, and deep, with a strong "chin." Incisors large and uncrowded. Canines robust. Premolars very large, except for P 1/1, which is small and single rooted. Upper premotars with a high central cusp, a large median cusp posterior to it and a broad. somewhat swollen basal cingulum. Lower premolars elongated and very large, with a central cone, a large median cusp posterior to it and a posterior cingular shelf or heel. Lower carnassial seemingly with a basined talonid. Second lower molar large. A third lower molar was present.

The type of this new species is a large, heavy mandible with the dentition imperfectly preserved. This specimen is chosen as the type rather than the associated adolescent maxilla and mandible, because although the teeth of the latter are unworn they are considered as being less definitive than those of the type.

This is a large canid, at once characterized by the deep mandibular ramus, broad robust symphysis and enlarged premolars. The extraordinary broadness of the symphysis gives to the jaw a "hyaenid" appearance, not at all unlike that of some of the hyaenognathid canids, such as *Hyaenognathus*, *Borophagus*, *Osteoborus* and to a lesser extent *Aelurodon*. The resemblance

of this jaw to the last two named of the above genera is particularly striking in its lateral aspect, because of the straight front border of the symphysis and the straight lower border of the mandibular ramus. fact, there is an angular "chin" as seen from the side, similar to that of certain ursids, and, by analogy, to the same structure as developed in some of the hyaenids. approach to this angularity between the lower border of the horizontal ramus and the front border of the symphysis is to be seen in Aelurodon although this genus retains to a considerable extent the rounded "chin" typical of most of the canids. mental foramen is beneath the second lower premolar.

The dental formula is certainly 3-1-4-3 so far as the lower dentition is concerned. As to the upper teeth, the referred specimen shows that there were three incisors, a canine, and four premolars. It would seem probable that there were two molars.

In the type the incisors, though very much broken, appear to be of large size, and they increase in size from the median to the lateral members of the series. They are uncrowded, and because of the great width of the symphysis, form a transverse row between the canines. Here again this new form may be compared with Aelurodon, in which the incisors are similarly developed.

The canine is large and heavy, and seemingly with a round cross-section. In the type mandible the presence of a first lower premolar is indicated by the remains of a very small root, immediately in front of the anterior root of the second premolar. Evidently the first premolar was extremely small and single rooted—a tooth that was on the verge of disappearing. The other lower premolars are all large and well developed.

The second, third and fourth lower premolars are all essentially alike. Each tooth consists of an anterior central cone, very high and with a strongly convex, keeled anterior border, and the referred specimen shows that the back of this central cone is also keeled, the keel being convex, particularly in the fourth premolar. Behind this central cone is a well-developed

accessory cusp, and behind this latter cusp a third cusp which is actually a trenchant blade formed by an upgrowth from the swollen cingulum. This most posterior cusp or blade is well developed in the fourth premolar, smaller in the third premolar and hardly distinguishable from the posterior cingulum in the second premolar. Naturally, all of these teeth are elongated. The second premolar is set at an angle to the mandibular ramus, its front border being directed antero-externally.

The carnassial in the type mandible is so badly broken that there is little to be said concerning it. About the only definite information revealed by this tooth is the fact that the talonid consists of a well-developed hypoconid and entoconid, on either side of a median depression or basin. These cusps were approximately equal to each other in size, as in *Tomarctus*, and *Osteoborus*, and may be contrasted with the enlarged hypoconid characteristic of *Aelurodom*. The second lower molar is an elongated tooth of relatively large size. It shows a distinct facet posteriorly, where a third molar was in contact with it.

The referred maxilla is fragmentary, and contains only the teeth in front of the carnassial. The first incisor, although broken away, is shown to have been relatively small by a portion of its root that remains in the alveolus. The second and third incisors are large, the latter being considerably larger than the former. These teeth are long and are characterized by strong lateral keels. A broken deciduous canine is present in this maxilla—evidently the permanent canine had not yet erupted. The first upper premolar is small and single rooted, and crowded between the tooth following it and the canine alveolus. second and third upper premolars are similar to each other; each consists of a high central cusp with anterior and posterior keels, back of which is a trenchant accessory cusp, rising from the center of a swollen base. In front of the main cusp on the third premolar is a very small, low cusp, rising from the swollen base of the These teeth are characterized by their inflated basal cingula. The maxilla

would appear, from this fragment, to have been rather short and high.

The referred mandible contains the four premolars of the right side, a permanent canine in the process of eruption and two anterior teeth which have been identified as the third incisor and the deciduous canine. The incisor is a long tooth, similar in its general appearance to the upper incisors, and like them it has lateral keels.

deciduous canine. Moreover, this lower tooth is in the proper place for a milk canine, and the permanent canine, which is fully formed and in the jaw beneath it, would seem to be pushing up to replace it.

The first lower premolar is a well-developed tooth in this mandible—evidently proportionately larger than the same tooth in the type mandible. The posterior premolars are similar to the same teeth in the



Fig. 8. Gobicyon macrognathus, new genus and species. Type, Amer. Mus. No. 26597, mandible. Lateral view of left mandibular ramus, one-half natural size.

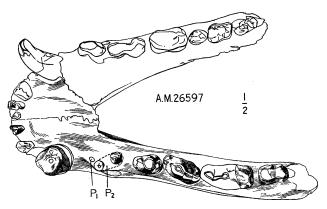


Fig. 9. Gobicyon macrognathus, new genus and species. Type, Amer. Mus. No. 26597, mandible. Crown view, one-half natural size.

The tooth tentatively identified as the deciduous canine is of rather peculiar construction, being flattened laterally, and having a long root and a short crown. At the base of the crown, posteriorly is a small "heel" which gives to this tooth an incisiform appearance. It is an interesting fact that this same construction would seem to be characteristic of the upper deciduous canine, a consideration favoring the identification of this lower tooth as the

type, and need not be described in detail here.

Gobicyon, though at first glance a seemingly aberrant canid, is in reality only a Tomarctus that has grown large and robust. It has paralleled Aelurodon, but numerous characters show that it is distinct from this latter genus. In Aelurodon the lower premolars tend to become transversely broad, whereas in Gobicyon they are elongated as in Tomarctus, and as in the more advanced

hyaenognathid, Osteoborus. In Aelurodon the hypoconid is large as compared with the entoconid, a character whereby it may be compared with Gobicyon and Tomarctus. In Gobicyon the second molar is relatively cyon and Aelurodon, the two genera are rather closely related—seemingly as descendants of a common Tomarctus ancestor.

There are certain resemblances to be seen between Gobicyon and the American

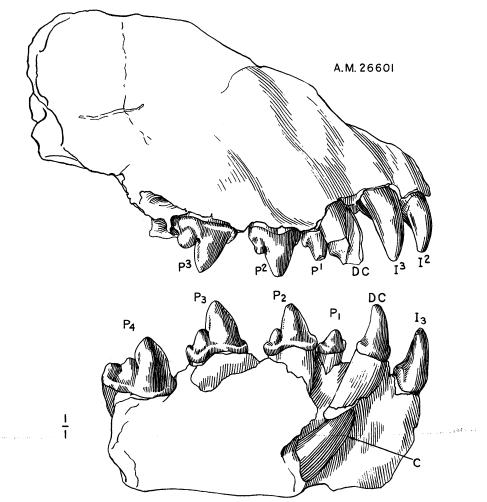


Fig. 10. Gobicyon macrognathus, new genus and species. Referred specimen, Amer. Mus. No. 26601, right maxilla (above) and right mandibular ramus (below) with deciduous and permanent teeth. Lateral views, natural size.

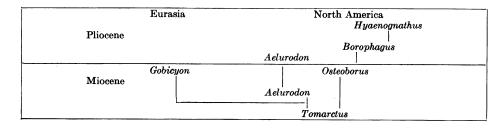
large, as in *Tomarctus*, not reduced as in *Aelurodon*. In both *Gobicyon* and *Tomarctus* the second lower premolar is set at an angle to the ramus, whereas in *Aelurodon* this tooth aligns itself with the ramus. Yet in spite of these differences between *Gobi-*

genus, Osteoborus. These are particularly in the form of the last lower premolar, the lower carnassial and the general robustness of the ramus. Osteoborus diabloensis, a new species recently described by Richey, would seem to be very similar to Gobicyon

in the structure of the last lower premolar and the carnassial. On the other hand, Osteoborus shows certain specializations, such as the reduction of the anterior premolars, leading to the later hyaenognathid canids such as Borophagus and Hyaenognathus.

All in all, Gobicyon may be considered as following a trend of development parallel to that of the American hyaenognathids, but nevertheless along a distinct line of its own. Thus, although Gobicyon shows many similarities to Aelurodon, probably the result of their common descent from a Tomarctus-like ancestor, it does not show the tendencies toward the characteristic hyaenognathid specializations typical of Simocyon, Osteoborus, Borophagus and Hyaenognathus. The Mongolian form has diverged, seemingly at a precocious rate. along a path whereby emphasis has been placed on the elongation of the lower premolars, without a corresponding transverse growth and a reduction of the anterior premolars that is so typical of the later hyaenognathid dogs. This early specialization of *Gobicyon* is marked also by a great increase in size, and in the massiveness of the ramus.

With these considerations in mind, it seems logical to suppose that the ancestry of Gobicum is to be sought in North America, rather than in Eurasia. Consequently this genus may be considered as an immigrant form in the Tung Gur fauna. This interpretation would not, however, be at all incompatible with the probabilities, for there was seemingly a considerable amount of intercontinental migration of certain mammals between North America and Eurasia during the Upper Miocene and subsequent periods. In fact, certain other elements of the Tung Gur fauna, particularly Platybelodon and Amblycastor, are also present in North America. The relationships of Gobicyon—phylogenetic, geologic and geographic—might be represented in the following manner.



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	brevirostris	wheeler-	macro-	macro-	primi	$cynoides^2$	pachyodon
	A. M. 13836	ianus A. M. 8307	gnathus A. M. 26597 (type)	$\begin{array}{c} \textit{gnathus} \\ \text{A. M. 26601} \\ \text{(referred)} \end{array}$	genius A. M. 13229		A. M. 30071
Length \times width Length \times width	٠	5.2 × 3.2 6.0 × 4.2					
Length X		(X		9.5×8.5			
Length X	9.0×6.3	_	17.5×15.5		13.0×9.5	12×9.3	15.5×13.0
Length X	:	6.5 × 5.0	C	7.5 × 6.0			
Length	× :	X)	13.5 × 8.0	×)		>	
Length X	9.5 × 5.7	13.0 × 8.5	17.5 × 10.0	16.5 × 10.0	>	8.0 × 0.2	>
Length X	< ×	< ×	22.0 × 11.0 29e × 121	<	21.5×10.5	< ×	31.5×17.0
M ₂ Length × width	X	11.0×8.5	15.5×10.5		15.0×9.3	\times	
Length X width		6.0×4.8			,		I
Depth of ramus at M ₁ Depth of symph. at C	22.5 19.5	34.0 30.0	40.0 38.0		25.0 22.0		37.0 36.0
$_{\rm radex} \frac{ m W \times 100}{ m V}$) •) ; , t))))	Ş		9	
Tuner	09	99	10	09		6/	
$\frac{\rm W \times 100}{\rm L}$	55	79	51	55	09	99	77
Ratio, $\frac{\text{L of } P_2 \times 100}{\text{L of } M_1}$. 17	17	7.4				
Ratio, $\frac{\text{L of P}_3 \times 100}{\text{L of M}_1}$. 47.	87	09			33	
Ratio, $\frac{\text{L of P}_4 \times 100}{\text{L of M}_1}$	59	19	78		72	99	óż.
Ratio, $\frac{\text{L of M}_2 \times 100}{\text{L of M}_1}$	50	41	53		20	77	35
Ratio, $\frac{\text{L of } M_1 \times 100}{\text{D. of ram. at } M_1}$	88	08	7.2		98		86
Ratio, D. of sym. \times 100 D. of ram. at M ₁	28	. 88	96		88		97
It Length X width				9.0×7.0			
						e he	
P^2 Length \times width P^3 Length \times width				$14.5 \times 9.0 \\ 18.5 \times 11.0$			

Mustelidae

Melodon (?) sp.

Specimen under Consideration.—Amer. Mus. No. 26607, portion of a left mandibular ramus with the carnassial.

Horizon.—Tung Gur formation; Upper Miocene.

LOCALITY.—Tung Gur escarpment, about twenty-five miles northeast of Gur Tung Khara Usu, Inner Mongolia.

The specimen now under consideration is not very well preserved, particularly due to the fact that it seems to have been subjected to a certain amount of abrasion, caused perhaps by transportation, but more probably by a weathering of the fossil. The carnassial tooth is, however, sufficiently preserved to show some of its diagnostic characters.

This jaw is representative of a large meline, comparable in size to the modern European badger. The jaw is heavy and

question more difficult to decide. As was stated above, it is comparable in size to the modern badger, Meles. In many ways. however, the fossil is more primitive than Meles, as might be expected. Thus, the trigonid of the lower carnassial retains more of its primitive sectorial character in the fossil. The metaconid is distinctly smaller than the protoconid, whereas in Meles these two cusps are approximately equal to each other in size. In the fossil specimen the talonid is primitive in the lack of supernumerary cusps along its external and internal rims, and in its relatively smaller antero-posterior dimension. In there are two cusps on the external and a similar number on the internal rim of the talonid. These extra cusps, together with the elongation of the talonid, give to the carnassial of the modern form its characteristic appearance. The lower carnassial of

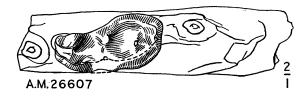


Fig. 11. Melodon (?) sp. Amer. Mus. No. 26607, left mandibular ramus with M_1 . Crown view, twice natural size.

robust. The lower carnassial, the only tooth preserved, is somewhat elongated, with a narrow trigonid and a relatively broad talonid. The cusps of the trigonid, though low, are appreciably higher than those of the talonid, and the outer cusps (paraconid and protoconid) have retained to some extent the primitive sectorial character. The metaconid is definitely smaller than the protoconid and is located postero-internally to this latter cusp. The talonid is in the form of a broad basin, on the external rim of which there is a swelling denoting the presence of the hypocone. However, the remainder of the talonid rim is smooth. There would seem to be a slight external cingulum on the talonid. second lower molar was evidently rather large.

That this jaw belongs to a member of the Melinae would seem to be a certain fact; to just what genus it should be referred is a Arctonyx is similar to that of Meles but is even more elongated, so that it is more completely separated in form from the same tooth of the fossil now under consideration than is the carnassial of Meles.

The Pikermi genus, *Promeles*, is considerably smaller than this Mongolian form. And in *Promeles* the lower carnassial is relatively more slender, with a cuspidate rim around the talonid, much as in the modern *Meles*. This genus shares with the Mongolian form the primitive character of a rather sectorial trigonid blade and a relatively small metaconid.

Perhaps the closest comparison with the new fossil is to be found in the North Chinese genus, *Melodon*, described by Zdansky in 1924. *Melodon incertum* from North China is somewhat smaller than the Mongolian form, but in many ways the two are comparable. Thus, in both there is a trigonid shear, with the metaconid smaller

than the protoconid. In both, the talonid is not greatly elongated, but is surrounded by a generally smooth rim. There is not the tendency to a polybunodont development so characteristic of the later badgers, and even of other fossil forms like *Promeles* and *Parataxidea*. There would seem to be, however, some differences between the North China *Melodon* and the Mongolian referred specimen. Thus, in the Mongolian form the talonid would seem to be rela-

tively wider than in the North China species, and it would appear that the talonid rim is smoother (that is, with fewer swellings indicative of distinct cusps) than is the case with the North China *Melodon*.

Therefore, although the resemblance between this jaw from Mongolia and *Melodon* from North China would seem to be fairly close, there are enough differences to justify only a provisional assignment of the Mongolian specimen to the genus *Melodon*.

	MEASUREMENTS Melodon (?) sp.	Melodon	$incertum^1$
	A. M. 26607	Ex. 1	Ex. 2
M_1 length	15.0 mm.	12.1 mm.	12.7 mm.
breadth (talonid)	6.9	6.3	6.3
Depth of ramus below M ₁	17.5		

¹ From Zdansky.

Viverridae

Tungurictis spocki, new genus and species

Type.—Amer. Mus. No. 26600, a virtually complete skull with the molar teeth well preserved, but lacking the incisors of the right side, the canines and some of the premolars.

PARATYPE.—Amer. Mus. No. 26610, a fragment of a left mandibular ramus containing the premolars.

Horizon.—Tung Gur formation; Upper Miocene.

Locality.—"Wolf Camp" quarry, about five miles southwest of Gur Tung Khara Usu, Inner Mongolia (for the type). Escarpment, about twenty-five miles northeast of Gur Tung Khara Usu (for the paratype).

Diagnosis.—A slender, medium-sized viverrine. Skull characterized particularly by the extreme constriction of the frontals behind the post-orbital processes, and by the relatively short, broad basicranial region. Sagittal crest distinctly developed. Posterior nasal choanae reaching as far forward as the second molars, alisphenoid canal short. Tympanic bulla large, its anterior edge being far forward, opposite the postglenoid process; basicranial foramina showing the usual viverrine arrangement. Incisors small and crowded, premolars without appreciable diastemata between them. Carnassial with a very long shearing blade, approximately parallel to the midline of the skull; protocone constricted. First molar extended transversely and compressed antero-posteriorly, with a sharp, V-shaped protocone. Second molar small. Lower premolars simple, P₄ without an appreciable heel.

The skull on which this new species is based is extraordinarily well preserved, for it lacks only the left zygomatic arch, and certain teeth as noted above. It might be noted, too, that one bulla, though present, is badly crushed and partially missing, while the other is completely destroyed, thereby adding to the difficulties of determining the characters of these structures.

The skull is relatively slender and rather delicately built. The muzzle is comparatively long, as in Viverra zibetha and not wide and abbreviated as in Civettictis civetta, or as in the fossil form, Viverra antiqua. In size, this skull is about one-fifth smaller linearly than a skull of Viverra zibetha from North China, and about the same proportion smaller than the extinct Viverra antiqua. In general appearance and its structure it resembles very much the skull of Viverra zibetha, being indeed more closely comparable in the totality of its characters to this modern species than it is to any other single genus or species.

One of the most characteristic features of this skull is the extreme constriction of

¹ In honor of Dr. L. E. Spock, geologist on the Central Asiatic Expeditions, who discovered and named the Tung Gur formation.

the frontals behind the post-orbital processes—a development more typical of the modern *Genetta* than of the genus *Viverra*, as strictly defined. This constriction would be due, of course, to a lesser development of the olfactory lobes in the fossil form as compared with those of the recent species, and it is what might be expected in a relatively early viverrid. It may be in-

The sagittal crest is developed as a single ridge, running from the post-orbital region to the lambdoidal crest. It is very low, much lower than in *Viverra antiqua* or *Civettictis* and it differs from the crest in the later species of *Viverra*, such as *Viverra zibetha*, by the absence of any anterior longitudinal division or doubling. The brain case is as much expanded, relative to the

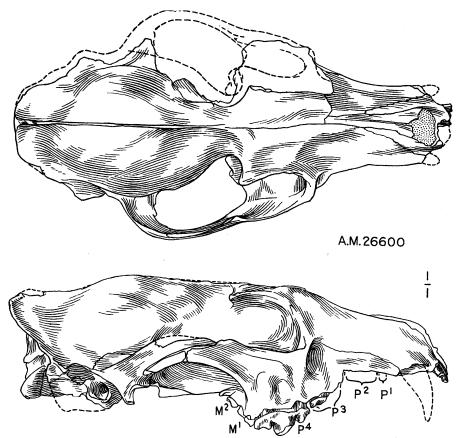


Fig. 12. Tungurictis spocki, new genus and species. Type, Amer. Mus. No. 26600, skull. Dorsal view above, lateral view of right side below; natural size.

teresting to call attention to the fact at this place that the skull of *Viverra antiqua*, from the Miocene of France, has the frontal constricted behind the post-orbitals—though not to the extent seen in *Tungurictis spocki*. All in all, this constriction in the form under consideration may be considered as a genet-like and likewise a primitive character.

size of the skull, as in the modern forms of *Viverra*.

In side view, the skull now being described is very similar to the skull of *Viverra zibetha*. In both, the muzzle is relatively slender (as mentioned above), the infraorbital foramen is above the third premolar, the front of the orbit is above the anterior edge of the carnassial, the zygo-

matic arch is slender and up-arched. The main differences are to be seen in the long, prominent post-orbital processes of the fossil skull and the less posteriorly expanded occipital region. This latter character will be discussed below.

The anterior border of the posterior nasal choanae is transversely in line with the posterior border of the second molars. In *Viverra antiqua* and *V. zibetha* the nasal choanae are somewhat behind the second molars. The pterygoid, instead of being

zibetha they extend back so that they are opposite the post-glenoid processes.

The basicranial region of *Tungurictis* is short and wide, and it is comparable in its general aspect to the basicranium of *Nandinia* and to that of *Viverravus* of the Phosphorites of Quercy. A short, broad basicranium is seemingly a primitive character among the Viverridae, retained in such persistently primitive forms as *Nandinia*, and curiously enough, retained in this new Mongolian form, the skull of

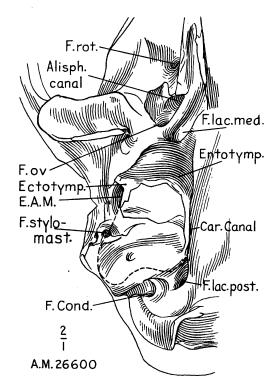


Fig. 13. Tungurictis spocki, new genus and species. Basicranium of type skull, Amer. Mus. No. 26600. Twice natural size.

virtually a single, posteriorly extended process, as in *Viverra zibetha*, is strongly doubled to form parapterygoid and mesopterygoid plates, for the origins of the external and internal pterygoids muscles, respectively. Incidentally, a close resemblance to this structure of the pterygoids is to be found in *Cryptoprocta*. The posterior extremities of these pterygoid processes are opposite the anterior border of the glenoid fossa, whereas in *Viverra*

which in its general habitus has advanced to a condition more or less comparable with the skull of *Viverra*. The shortness of the basicranium of *Tungurictis* is particularly well shown by the position of the auditory bulla, the anterior end of which is far forward so that it is even with the postglenoid process. Here again the fossil genus resembles *Nandinia*, and also, in this respect, *Paradoxurus*. In *Viverra zibetha* the anterior end of the bulls lies considerably

back of the postglenoid process. Not only is the bulla and its surrounding structures anteriorly placed in Tungurictis, but also the occipital condyles are set forward, seemingly rather close to the paroccipital processes. This condition may be contrasted with the position of the condyles in Viverra, which are more posterior in their position. In other words, there has been a backward shifting of the entire basicranium in Viverra and a majority of the later Viverridae, so that the basicranial structures are less compressed than they are in the earlier and the persistently primitive species. a correlative development to the short basicranial region in *Tungurictis* is the overhang of the supraoccipital portion of the skull posterior to the occipital condyles. In Viverra zibetha and other similarly advanced civets the condyles, due to the backward extension of the basicranium, project back of the supraoccipital and the lambdoidal crest. A development such as this often may be seen in the progression from earlier to later forms in a phylogenetic series.

The arrangement of the basicranial foramina is similar to that in *Viverra zibetha*, with the exception that the posterior outlet of the alisphenoid canal and the foramen ovale are close together, a natural result of the short basicranium. The alisphenoid canal is short, considerably shorter than in later species of *Viverra*.

Unfortunately only a portion of the right bulla is preserved, so that a detailed description and comparison cannot be set forward at the present time. It would seem. however, that the entotympanic was very large and extended forward, to virtually cover the ectotympanic. In this respect Tungurictis has advanced far from the primitive condition of the Viverridae, in which the entotympanic is cartilaginous (as in *Nandinia*), or from the more "typical" condition in which the ectotympanic and the entotympanic are sharply separated, even exteriorly (as in Viverra). Thus the bulla of Tungurictis resembles to a considerable degree the bulla of the paradoxurine civets, particularly Paradoxurus and Arctictis. The bulla was seemingly well developed, long and egg-shaped. Nothing

definite can be said as to the development of the paroccipital processes, but they were probably closely appressed to the back portion of the entotympanic.

The incisors are very small and are set closely together. They form a transverse row across the premaxillaries, in distinct contrast to the incisors of *Viverra antiqua*, *Viverra zibetha* and other species, in which the incisors form a decided arch. They increase in size from the central to the lateral member of the series, and the third incisor is much larger than the other two teeth. It has a distinct facet or surface on its postero-lateral portion for occlusion with the lower canine.

The canines are not preserved, having dropped out of the skull before it was fossilized, and the first three premolars are virtually destroyed. Enough can be seen of the third premolar to show that it was an elongated tooth, without any appreciable inner cusp.

The fourth premolar is a distinctive tooth in this specimen. It is relatively quite long—proportionately much longer than the same tooth in *Viverra* or in other closely related genera. Its shearing blade is almost parallel to the median axis of the skull, while the internal cusp is much constricted. All of these characters form a decided contrast to the same characters in the typical *Viverra*, in which the shearing blade of the carnassial is set at a high angle to the median line and the protocone is prominent.

The long fore and aft blade and the constricted protocone of the upper carnassial of *Tungurictis* are characters by which this tooth resembles the same tooth in Cryptoprocta. Of course, this might be considered as an advanced condition, whereby Tungurictis approaches the cat-like viverrids, which in turn are seemingly close to the cats. On the other hand, the evidence of fossil forms, particularly "Viverravus" and other related genera of the Phosphorites, would seem to show that the long, antero-posterior shearing carnassial is a primitive structure in the Viverridae. ancestral viverrids possessed such a tooth and in this respect they were close to the ancestral cats. The Viverridae as a group

evolved along lines that for the most part resulted in the loss of this highly developed shearing blade and the development of more transverse shears, or secondary adaptations for crushing. The Felidae, on the other hand, evolved by accentuating the shearing carnassial. Cryptoprocta, since it has descended from a viverrid ancestor that was close to the felid ancestor, has retained the shearing carnassial. Tungurictis, although developing a Viverra-like habitus in most respects, also retained the primitive shearing carnassial.

In this connection it might be said that the basined talonid of the lower carnassial is probably a specialization in the Viverridae, while the small, trenchant talonid is

primitive.

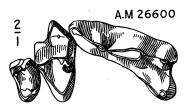


Fig. 14. Tungurictis spocki, new genus and species. Type, Amer. Mus. No. 26600, right P4-M2. Crown view, twice natural size.

The first molar is a slender tooth, similar to the same tooth in *Viverra zibetha*. It is characterized by its long transverse diameter, and its short antero-posterior diameter. The protocone is sharply acute. The second molar is similar to the tooth preceding it, but is very small. This tooth is subject to a great deal of individual variation in the viverrids, and so its diagnostic value is limited.

The fragment of a lower jaw is so incomplete that no very definite conclusions may be drawn as to its relationships. It is, however, seemingly viverrine, and because of its association in the Tung Gur formation it is here arbitrarily placed in the same species as the skull.

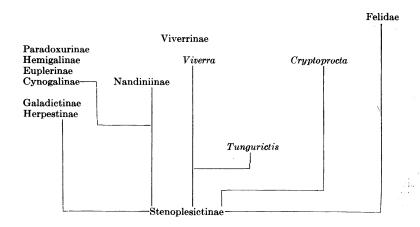
The premolars, as preserved in this mandible, would seem to be on the whole similar to the premolars of *Viverra zibetha*. They are, however, simpler in that the posterior cingular heels are less developed and the posterior portions of the last two premolars are transversely less expanded than is the case in the modern form. The first premolar would seem to be single-rooted, and crowded between the canine and the second premolar. There is a diastema between the second premolar and the tooth succeeding it.

All in all, it would seem that *Tungurictis* is a late Tertiary viverrid most closely related to the viverrine branch of the family. In many ways it closely resembles *Viverra* itself, and it is probably more or less on a line that eventually led to the modern genus. On the other hand, it shows certain characters that not only define it as a separate genus, but also place it in a somewhat isolated position away from the direct ancestry of *Viverra* and related genera.

Some of these characters are primitive holdovers from an ancestral viverrid type. Such are the short, wide basicranium, the constricted postorbital region and the strongly shearing carnassial. Other characters are specializations, and the most notable of these is the large, inflated entotympanic bulla that has grown over to largely cover and conceal the ectotympanic ring.

The probable position of *Tungurictis* is indicated in the following diagram.

Viverra



MEASUREMENTS

	spocki A. M. 26600	zibetha [A. M. 57056]
Length of skull, inccond.	114.0 mm.	139.0 mm.
Length of basicranium, postglcond.	29.5	41.0
Width of skull, across zygomata	66.0e	68.0
Width across postorbital processes	30.0e	28.0
Width, narrowest part of frontals	13.5	23.0
Width of brain case, greatest	33.0	40.0
Width of palate at M ¹	18.0	19.5
Vertical diameter of orbit	18.0	22.0
Height of skull above M ¹	36.5	40.0
Length of premolar series	40.5	39.5
Length of molar series	9.0	12.0
I^1 , length \times width	2.0×1.5	2.9×2.6
I^2	2.0×1.5	3.0×2.8
I_3	3.5×3.2	3.6×3.1
C (alveolus)	7.0×3.7	7.8×4.8
\mathbf{P}^{3}	9.7×4.5	9.0×4.0
P4 (length parallel to shear)	15.0×7.7	14.3×8.5
\mathbf{M}^1	5.5×11.5	7.5×13.0
M^2	3.7×6.0	7.5×4.5
Ratio; basicranial length/skull length	26	<i>30</i>
frontal width/brain case width	41	57
$P^4 \operatorname{length}/M^{1-2} \operatorname{length}$	167	119

Hyaenidae

Crocuta tungurensis, new species

Type.—Amer. Mus. No. 26602, a skull and mandible containing the complete dentition. The occipital and basiccipital regions of the skull are missing, as is the back portion of the right ramus.

PARATYPE.—Amer. Mus. No. 26603, right and left mandibular rami with right P₄ (erupting) and M₁, and left P₃₋₄ (erupting) and M₁; No. 26598, right and left mandibular rami with dentition complete except for right M₁.

Horizon.—Tung Gur formation; Upper Miocene.

Tungurictis

LOCALITY.—"Wolf Camp" quarry, about five miles southwest of Gur Tung Khara Usu, Inner Mongolia.

DIAGNOSIS.—A large, robust *Crocuta* with a short facial region. Premolar teeth very heavy. Carnassial blades of medium length. Inner cusp of upper carnassial reduced so that it is virtually absent. First upper molar greatly reduced. Lower carnassial lacking a metaconid, and with a reduced, trenchant talonid.

Crocuta tungurensis is a large, robust hyaena, exceeding in size the modern spotted hyaena and equaling in size some of the largest fossil species such as Hyaena gigantea, Hyaena mordax and Hyaena variabilis. So far as may be accurately determined, the facial region in this new species is short as compared with the facial length in the modern Crocuta and Hyaena. It should be mentioned, how-

is so very short that it constitutes a real difference, in this regard, between the fossil and the modern species.

Unfortunately the posterior portion of the skull of *Crocuta tungurensis* is missing, but from the cross-section of the cranium somewhat behind the preorbital region it would appear that the cranial portion of the skull (and probably the occiput as well) was narrow and high, as in the modern

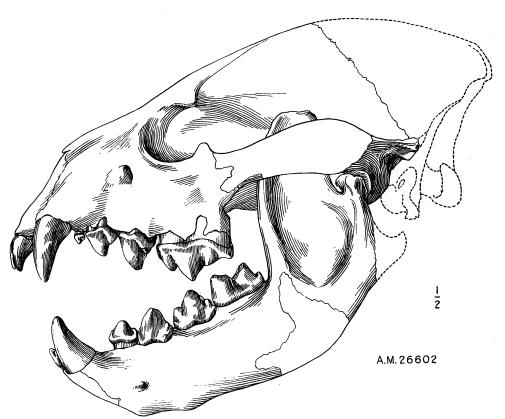


Fig. 15. Crocuta tungurensis, new species. Type, Amer. Mus. No. 26602, skull and mandible. Lateral view of left side, one-half natural size.

ever, that the skull (Amer. Mus. No. 26602) has been crushed to a certain extent, so that the preorbital portion may appear to be slightly shorter than it actually was before fossilization took place. Even taking this into account, it will be noticed from the accompanying ratios (see tables of measurements) that the preorbital portion of the skull in *Crocuta tungurensis*

Crocuta. Certainly the postorbital processes in this Mongolian fossil resemble those of Crocuta much more closely than they do those of Hyaena (sensu stricto).

The mandible is heavy, with a strong, high coronoid. In the type mandible it would appear that the symphysis is excessively long and heavy, an appearance that may be in part illusory, due to the

crushing of the specimen. In one of the paratypes (No. 26598) the symphysis is of the normal hyaenid type, comparable to the symphyses of *Crocuta* and *Hyaena*.

One of the characteristic features of this new species is the large, robust teeth, particularly the premolars. In this respect the fossil form now under consideration resembles *Crocuta* rather than *Hyaena*.

The upper incisors are of the usual hyaenid type, the lateral ones being very large, and the central and median ones much

development of the strong posterior keel and of a prominent antero-internal ridge.

The first upper premolar is a very small, single-rooted tooth, similar to the same tooth in the modern *Crocuta*, but of relatively lesser size. The second and third upper premolars are very strong, and they have been expanded laterally to such a degree that they are much rounder and less elongated than the same teeth in the modern *Crocuta* or *Hyaena*. In this respect they may be compared with the

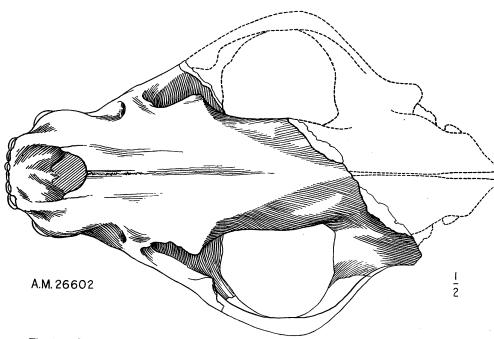


Fig. 16. Crocuta tungurensis, new species. Type, Amer. Mus. No. 26602, skull. Dorsal view, one-half natural size.

smaller and subequal in size. The posterior cingula of the central and median incisors are relatively small, so that these teeth lack the strong posterior shelves that are to be found in many hyaenid incisors. It might be mentioned that in their general shape, the cingula of these teeth are quite similar to the same structures in the modern *Crocuta*, but in the fossil they are much smaller than in the modern form.

The upper canines are somewhat flattened on their inner surfaces, due to the

same two upper premolars in *Hyaena* variabilis, but they are even more transversely developed than are the teeth of the Chinese species. Correlative with the expansion of the upper premolars is the emphasis of their central cones, so that the anterior and posterior cingula are much less prominent and shelf-like than they are in the modern *Crocuta*. Here again the Mongolian species may be compared with the Chinese *Hyaena variabilis*.

The upper carnassial is noteworthy par-

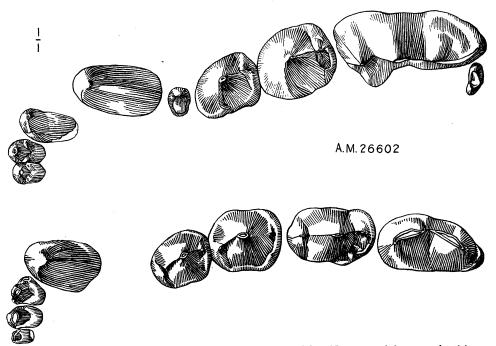


Fig. 17. Crocuta tunquensis, new species. Type, Amer. Mus. No. 26602, left upper dentition above and right lower dentition below. Crown views, natural size.

ticularly because of the extreme reduction of its internal cusp. In fact, this element is almost completely suppressed in the new Mongolian species, in which respect it is more completely specialized than any of the other fossil forms in which there is a marked reduction of the protocone. Otherwise the carnassial of this new species is typically hyaenid, but very robust. The first upper molar is present but very small in this species. Evidently it was on the point of complete disappearance.

The lower incisors are much smaller than the upper ones, and they diminish in size from the lateral to the central member of the series. The central incisor is very small and peg-like. These teeth are crowded, so that the second incisor is pushed back to a position that is posterior to the teeth on either side of it—a condition that is apparent in both the type (No. 26602) and one of the paratypes (No. 26598).

The lower canine is similar to the

upper canine in that it has a posterior and an antero-internal ridge.

The first lower premolar is absent, a character of both Crocuta and Hyaena. The other lower premolars in Crocuta tungurensis are robust, as might be expected from the construction of the upper premolars, and they are transversely broad in comparison to their length. It is an interesting fact that the third premolar is relatively smaller in this fossil species than it is in the modern form, or than in certain other fossil species of Crocuta.

The lower carnassial is very similar to the same tooth in the modern *Crocuta*, but in general structure it is more robust than this tooth in the modern species. It has a long blade, quite devoid of an internal metaconid, and the talonid is very small.

The two mandibles (Nos. 26598, 26603), listed above as paratypes of this species, show certain differences of detail from the type jaw. In the first place, they are ap-

Hyaena striata	[A. M. 54512] 163 mm	82	108 5.5 × 4	6.5 × 5.5	9.5 × 8	15×10.5	16 5 7 10	21.5×13	31×18	5.5×14.5	160	36.5	4 × × × × ×		××××××××××××××××××××××××××××××××××××××	15 × 11	13.5×9	19.5×11.5	21×12	20×10.5	101		87		86	88		80	
Crocuta Hyaena entiabilis stricts a M on occur	A. M. 20372 180 mm.	94	7.5×5.5	9 × 6.5	13.5×9.5	16×13 75×7	18.5 × 19.5	23 × 16	39 \times 16	(absent)	196	45.5)		0 × 7.5	16 × 12.5	16.5×11	20×14	23 × 14	27.5×13	601)	94		8%	. 98		84	
Crocuta cross	[A. M. 90969] 175 mm.	91	7.5 × 5	6 ×	12.5×10	16 × 11.5	15 × 11	23.5×16	35×22	(absent)	177	41	7.0 X.0 7.0 7.0 7.0	7.5 × 5.5	8.5 × 8.5	15×11.5	14.5×10	21×15	22.5×12.5	28.5×12	108		78	;	98	112		98	
3 A M 96603	A: 141. 20009																	20 ×	20.5×13	X 6.02									
Crocuta tungurensis												42 mm.	3.5 × 3	6.5 × 5	7.5 × 6	(not fully erupted)	13.5×11	17.5×13	20 × 12.5	21 × 07									
type A. M. 266021	188 mm.	88 125	8.5 × 5	10×6.5	12.5 × 9	*1 × × 9	19×14.5	22.5×18.5	39.5 × 20 4 × 9	< <	189								24 × 15		88		45	\$	8/	87	;	88	
	Skull Length, incpostgl.	Length, incorbit Length, incP4	I', length X width	1^z , length \times width 1^3 length \times 1.14.		\times	X	P_3 , length \times width P_4 length \times width	' length X		Length, inccond.	Depth, M ₁	11, length X width	I_2 , length \times width					r_4 , length \times width M_1 , length \times width	(orbit-incisor × 100	length. P ⁴ \times 100	length, P1-4	length, $P_s \times 100$		$(P_3 \text{ length} \times \text{width}) \times 100$ $P_4 \text{ length} \times \text{width}$	length M ₁ shear	length M ₁	

¹ All measurements except M1, P2 and M1 from left side.

preciably smaller than the type, and the teeth would seem to be less robust. is particularly apparent in the premolars, which more nearly approach the premolars of Crocuta crocuta than do those of the type jaw. But in both of these paratypes, as in the type, the third premolar is comparatively small—evidence of an evolutionary lag with regard to this one tooth, in decided contrast to the generally advanced habitus of Crocuta tungurensis. It might be said, also, that this tooth shows a resemblance to the same tooth in Hyaena in that the main cone does not "rake back" as is the case in Crocuta, but rather it is directed vertically. Moreover, the small anterior cusp is fairly well developed in the Tung Gur species, as it is in Hyaena; it has not undergone the reduction typical of Crocuta. All in all, therefore, the third lower premolar of Crocuta tungurensis does not show the Crocuta-like specializations that are so evident in the other teeth and in the skull of this new Mongolian form.

The hyaenas constitute a peculiar mammalian group in that the family would seem to have become established very suddenly in mid-Tertiary times and to have continued, for the most part without change since then. That is, most of the fossil hyaenas are fully as advanced in their evolutionary specializations as are the modern hyaenas, and what is more surprising is the fact that some of the most structurally advanced hyaenas are some of the earliest known members of the family, living contemporaneously with their structural ancestors. For instance, the Tung Gur hyaena now under consideration is in most respects as far advanced along the lines of hyaenid specializations as are any later members of the group, if not farther, and yet this form, occurring in the upper Miocene, is one of the earliest hyaenas that we know. It is contemporaneous with, and in many cases earlier than Ictitherium, which latter form may be considered as approximating to a very fair degree the structural ancestor of the hyaenas, descended from more primitive Viverridae.

This fact was recognized by Dr. Pilgrim,

who in several papers placed most of the fossil hyaenas in the genus Crocuta, postulating that this genus, although structurally advanced, appears much earlier than does Hyaena (sensu stricto). Pilgrim suggested that the ancestral species of Hyaena are not known as fossils because "we have not as yet explored the original centre of distribution for the hyaenas " Most of the fossil hyaenas, except the members of the more primitive genera such as Ictitherium, Lycyaena, and Hyaenictis are more closely comparable to the modern Crocuta than they are to the modern Hyaena. Yet strangely enough, these fossil forms show mixtures of characters that would seem to link them with both Crocuta and Hyaena, which may be an indication that these two genera, in spite of their differences, are not very far apart.

According to Pilgrim, "Even where our material does not yield any character of diagnostic value other than the presence of a distinct metaconid in M₁, yet this character, in my opinion, affords sufficient reason for placing the species that show it in the genus *Hyaena*, and those in which the metaconid is normally absent in the genus *Crocuta*." This would seem to be placing too much emphasis on a single character, particularly in view of the fact that in some of the fossil forms the metaconid may be seen in various stages of reduction.

The modern *Hyaena* and *Crocuta* may be separated on the basis of skull and tooth characters as follows:

Hyaena

- 1. Occiput low
- 2. Brain case restricted
 2. Bulla strongly in-
- 3. Bulla strongly inflated
- Premolars slender
 Carnassial shears
- short
 6. P⁴ protocone small
- 7. M¹ present
- M₁ with metaconid
 Talonid large, basined

Crocuta

- 1. Occiput high
- 2. Brain case expanded
- 3. Bulla less inflated
- 4. Premolars (P 3) robust
- 5. Carnassial shears long
- 6. P4 protocone large
- 7. M¹ absent
- 8. M₁ lacking metaconid
- 9. Talonid small, trenchant

¹ Pilgrim, G. E. 1931. Cat. Brit Mus., p. 115.

The Tung Gur hyaena is like Hyaena in number seven of the above listed characters. It is like Crocuta (so far as may be determined) in all of the other characters with the exception of number six. In this character it is like neither of the above genera, for the protocone is entirely absent. Some of the other fossil hyaenas, such as Hyaena variabilis, Hyaena eximia, etc., show much the same resemblances and differences as does the Tung Gur form, except that they may show distinct Hyaena characters in the skull, particularly in the form of the occiput, and the development of the bulla.

Therefore when the fossil species are taken into consideration no hard and fast lines can be drawn between *Hyaena* and *Crocuta*.

Short diastema between canine and third premolar. Premolars with a high central cone and a low anterior cusp and with a well-developed cone on the posterior edge of the main cusp, behind which there is a cingular heel. Lower carnassial with an anterior blade approximately equal in height to the last premolar, a much higher posterior blade and a reduced heel. Mental foramen beneath the anterior portion of the third lower premolar.

This new species is undoubtedly referable to the genus Metailurus because of its close resemblances to the two Chinese forms, Metailurus major and Metailurus minor, described by Zdansky in 1924. Indeed, it is structurally very close to the two Chinese species, and is intermediate between them in size. The characters of the new species have been enumerated in the diagnosis, above, and need not be repeated here, but it might be

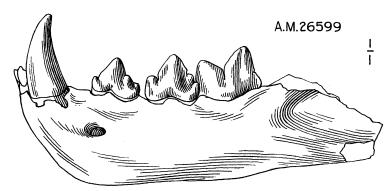


Fig. 18. Metailurus mongoliensis, new species. Type, Amer. Mus. No. 26599, left mandibular ramus. Lateral view, natural size.

Felidae

Metailurus mongoliensis, new species

Type.—Amer. Mus. No. 26599, a mandible, lacking only the ascending rami.

PARATYPE.—Amer. Mus. No. 26609, fragment of a mandibular ramus with right P4, M1. HORIZON.—Tung Gur formation; Upper Miocene.

LOCALITY.—"Wolf Camp," about five miles southwest of Gur Tung Khara Usu, Inner Mongolia (for the type). Twenty-five miles northeast of Gur Tung Khara Usu (for the paratype).

Diagnosis.—A medium-sized felid, more or less comparable in this respect to a modern Lynx. Lower border of mandibular ramus straight. Incisors small, of which the third incisor is the largest. Canine large, with a keeled posterior edge and a strong inner ridge.

well to point out a few salient features of the new species at this point.

The incisor teeth are relatively much smaller than are the same teeth in the two Chinese species; thus, in the Mongolian form, which is considerably larger than Metailurus minor, the incisor teeth are somewhat smaller than in this last-named species. The third incisor is characterized by an external lobe, as is the case in the North China forms. The posterior ridge of the canine is sharp and quite free of serrations, even when seen under a glass. As in the Chinese species, the inner ridge on the canine is strong.

Perhaps one of the most noticeable

differences between this species and the Chinese forms is the relatively short canine-premolar diastema in the Mongolian jaw.

The resemblances between the Mongolian and the North China species are very close in the cheek teeth. About the only noticeable difference is the slightly greater height (in comparison to length) of the last premolar and the carnassial of the Mongolian form.

cone normally would be developed. There are four external cusps, as in the machairodonts, namely, a small parastyle in front of the paracone, the paracone, metacone and the shearing metastyle. The vertical furrows separating the main cusp from the paracone in front and from the metastyle shear behind it are shallow, as in the sabretoothed cats, so that the external wall of the tooth is rather continuous. This may be contrasted with the external surface

	MEASUREMENTS		
	M. mongoliensis A. M. 26599	M. major	$M{\frac{2}{2}}$
I_1 length	2.0 mm.	3.3 mm.	$2.7~\mathrm{mm}$
width	2.3	2.7	${\bf 2.2}$
I ₂ length	2.7	$oldsymbol{4}$. $oldsymbol{2}$	3.0
width	3.0	3.8	2.9
I ₃ length	3.3	5.3	3.9
\mathbf{width}	3.7	5.6	4.1
C length	11.5	12.7	8.8
width	7.5	9.0	6.5
P ₃ length	12.0	15.5	9.9
width	5.7	8.4	5.3
P4 length	15.0	21.0	14.5
\mathbf{width}	6.8	9.3	6.5
M_1 length	17.3	23.2	18.1
width	7.2	10.1	7.2
C-P ₃ diastema	5.5	18.5	8.4
Depth of mandible below M_1	22.0		

^{1,2} Zdansky.

Machairodus (?) sp.

Specimen under Consideration.—Amer. Mus. No. 26608, a right upper carnassial.

Horizon.—Tung Gur formation; Upper Miocene.

LOCALITY.—Five miles southwest of "Wolf Camp," and about ten miles southwest of Gur Tung Khara Usu, Inner Mongolia. This locality is the "Platybelodon quarry," where numerous individuals of Platybelodon grangeri were discovered.

This single upper carnassial, though much worn, shows certain characters that would seem to link it with the sabretoothed cats. The shearing function of this tooth is highly developed and apparently there is no trace of an internal cusp, or protocone. This latter character can be determined with some degree of certainty, because the internal surface of the main cusp (the metacone) is preserved, just at the place where the proto-

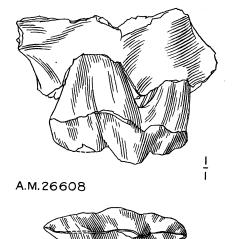


Fig. 19. Machairodus (?) sp. Amer. Mus. No. 26608, right P⁴. Lateral view above and crown view below, natural size.

of the carnassial in the hyaenas, where the several cusps are more distinctly separated each from the other, due to the less perfectly developed shearing function of the tooth. The metastyle shear is virtually straight, not concave on its external surface as is the case in the hyaenas.

Perhaps the most interesting character of this specimen is the degree of wear to which it has been subjected. The internal surface of the tooth is cut back so that the external cusps are only about half of their original width. The wearing surface, moreover, shows the effect of a very straight vertical shear, with no lateral or rotary movement. Numerous vertical striations, all parallel to each other, mark the wearing surface—again an indication that this carnassial is probably machairedont.

In size the tooth under consideration is closely comparable to the same tooth in Machairodus palanderi, described by Zdansky from the Hipparion beds of North China.

Of course there is the possibility that this might be a hyaenid tooth that has taken on a cat-like appearance due to extreme wear. But the absolute absence of a protocone, the seeming presence of four external cusps. the shape of the metastyle shear and the development of the internal wear are all characters that suggest a machairedont rather than a hyaenid relationship for the tooth.

MEASUREMENTS

Amer. Mus No. 26608, right P4. Length Breadth

37.0 mm. 10.5

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