MEGISTOTHERIUM, GIGANTIC HYAENODONT FROM MIOCENE OF GEBEL ZELTEN, LIBYA

BY

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CONTENTS

SYNOPSIS

A description is given of *Megistotherium osteothlastes*, g. et sp. nov., based largely on a complete skull from Lower Miocene sediments of Gebel Zelten, Libya. The beast is the largest known carnivore: a functional analysis is given and fragments of comparable species from Eurasia and East Africa are discussed.

I. INTRODUCTION AND ACKNOWLEDGMENTS

IN the course of preliminary geological exploration around Gebel Zelten in 1962 and 1963, prospectors found bones among which were some that appeared to belong to a gigantic carnivore. During my first expedition to Gebel Zelten in 1964 I found several more post-cranial fragments that appeared to belong to a similarly large beast. In 1966 I discovered a complete skull of a gigantic hyaenodont, the subject of this paper. An account of the geological setting and the faunal assemblage of the Gebel Zelten area is given in the first paper in the series (Savage & Hamilton 1972). Others on each of the major groups in the mammalian fauna will follow.

It is a great privilege to acknowledge my very grateful thanks to Mr George L. de Coster, of Esso Standard Libya Inc., through whose generosity the magnificent skull is now in the collection of the British Museum (Natural History). I should also like to acknowledge the co-operation and facilities offered my parties in the field by Esso Standard and Oasis Oil Company. The field work has been supported by grants from the Leverhulme Foundation and the Natural Environments Research Council. I have profited from discussions on the brain with Dr L. B. Radinsky and on the ear region with Dr G. T. MacIntyre. I am indebted to Mr R. Godwin for the photography, to Mrs Joyce Treuherz for the drawings in Figs. 1–5, to Miss Mary Rampton for all the other drawings, and to my wife Shirley Coryndon for her patience, criticism and help at all times.

II. SYSTEMATIC DESCRIPTION

Family **HYAENODONTIDAE** Leidy 1869

DIAGNOSIS. Creodonta with upper molars either three or reduced to two; two front upper molars specialized as carnassial teeth, either tuberculosectorial or

completely sectorial; last upper molar, when present, transversely extended; all the lower molars specialized as carnassial teeth; P $\frac{1}{1}$ two-rooted, except in some specialized genera; primitive forms with long and slender skulls, tail long and heavy; later forms with robust skull, claws blunt; cursorial adaptations to a varying extent (Savage 1965).

REMARKS. This is not the place to discuss the problems of higher taxonomic grouping. Within the Family Hyaenodontidae I place only the Proviverrinae and the Hyaenodontinae. I follow Gazin (1946) in separating the Limnocyoninae and the Machaeroidinae in a separate family the Limnocyontidae. The Teratodontidae (Savage 1965) seems best left as a separate family until more is known.

Subfamily HYAENODONTINAE Leidy 1869

DIAGNOSIS. Hyaenodontidae with narrow skull and long face; M $\frac{3}{3}$ or M $\frac{2}{3}$; molars sectorial, length greater than width; M³ small and transverse or absent; M¹⁺² with paracone and metacone completely or nearly connate, protocone reduced or absent; lower molars without metaconid, talonid vestigial or absent (Savage 1965).

REMARKS. Van Valen (1966) used the term 'tribe Hyaenodontini' essentially as synonymous with my use (Savage 1965) of it at subfamily rank. Van Valen (1967) abandoned the use of tribes and lumped into his 'subfamily Hyaenodontinae' all Hyaenodontinae *sensu stricto*, Proviverrinae, Hyainailourinae and Teratodontidae; this makes a very unmanageable subfamily of 19 genera. The subfamily Hyaenodontinae as defined above and as used below, differs from Savage (1965) in essentially only one aspect, namely the inclusion of the now much better known Hyainailourinae. Basically the subfamily comprises the genera *Pterodon*, *Metapterodon*, *Hyaenodon*, *Leakitherium*, *Hyainailouros* and *Megistotherium*. Three further genera are of less certain affinity; *Apterodon* [=*Dasyurodon*], which was placed in a separate tribe of the subfamily by Szalay (1967); *Propterodon*, poorly known and placed in the tribe Proviverrini by Van Valen (1966); and *Ischnognathus*, again poorly known but compared by Patterson (in Stovall 1948) to *Hemipsalodon*, which is very similar to if not synonymous with *Pterodon*. The new material described below makes clear the inclusion of *Hyainailouros* in the subfamily.

Genus MEGISTOTHERIUM gen. nov.

DIAGNOSIS. Gigantic hyaenodontine, dental formula $\frac{1\ 1\ 4\ 3}{?\ 3\ 1\ 4\ 3}$; single large upper incisor, very large upper canine, laterally placed with respect to other teeth; palate very constricted around P¹⁺²; P³⁺⁴ three-rooted, P⁴ width greater than length; M¹⁺² trenchant; M³ small transverse. Jugal arch heavy and wide, sagittal crest high.

TYPE SPECIES. *M. osteothlastes* gen. et sp. nov.

REMARKS. The completeness of the cranial material makes comparison with the poorly known *Hyainailouros* difficult, but the dentitions where comparable

show sufficient differences for the new material to warrant generic distinction. The genus is larger than any other known hyaenodontid.

Megistotherium osteothlastes sp. nov.
(Text-figs 1–17; Plates I–IV)

DIAGNOSIS.   As for genus.   The generic name is derived from the Greek μεγιστος greatest and θηρός beast.   The trivial name comes from ὀδτεος bone and θλαδτος crusher.

HOLOTYPE.   M 26173.   Collections of British Museum (Natural History).   From the southeast corner of Gebel Zelten, Libya, at 28° North, 20° 30′ East.   Early Miocene.   Site 6412.

HYPODIGM.   Holotype together with the following, all from Gebel Zelten.

Reg. No.	Site	
M 26515	6424	Cranium
M 26516	,,	Premaxillae with root of left incisor
M 26517	,,	Left maxilla fragment with root/alveoli of M^{1-3}
M 26518	,,	Right maxilla fragment with roots/alveoli of M^{1-3}
M 21902	,,	Atlas
UB 20576	6412	Distal end of right humerus
UB 20577	6405	Distal end of right humerus
UB 20578	6412	Left magnum
UB 20579	6412	Right astragalus
UB 20580	6412	Metapodial
UB 20581	6416	Metapodial
UB 20582	6416	Metapodial
UB 20583	6424	Metapodial

Four specimens in the British Museum collections (M 26515–26518) are associated fragments of a second skull.   These were collected by oil prospectors and the exact location is unrecorded.   The second skull is slightly smaller than the type and by the presence of open sutures patently that of a younger individual.   Item M 26515 comprises the braincase and the description below of the brain and sinuses is based very largely on this specimen.   Registered numbers with the prefix UB refer to the collections in the Geology Museum, University of Bristol.

DESCRIPTION.   The most striking feature of this impressive skull is its size; the overall length is 66·4 cm. and span across the jugal arches is 47·1 cm.   The skull possesses the largest sagittal crest known and enormous canines.   The whole structure of the skull is extremely massive and robust; the bones are well fused. Although the crowns of the teeth are in most cases lacking, those that survive do not suggest that the individual was very old.   There are several areas of bone disease which could have been the cause of death.
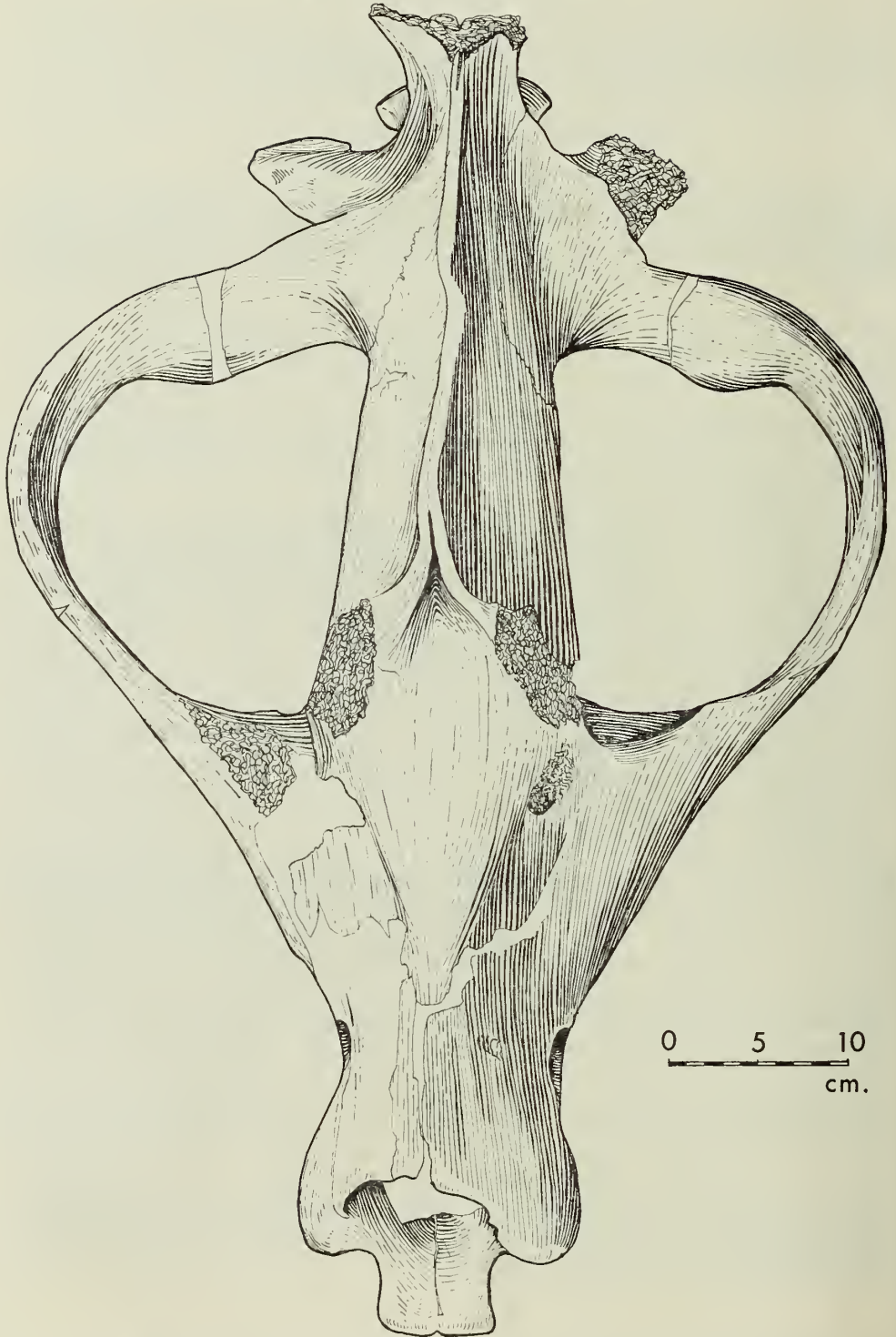
FIG. I. *Megistotherium osteothlastes* gen. et sp. nov. Holotype (M26173), Gebel Zelten.
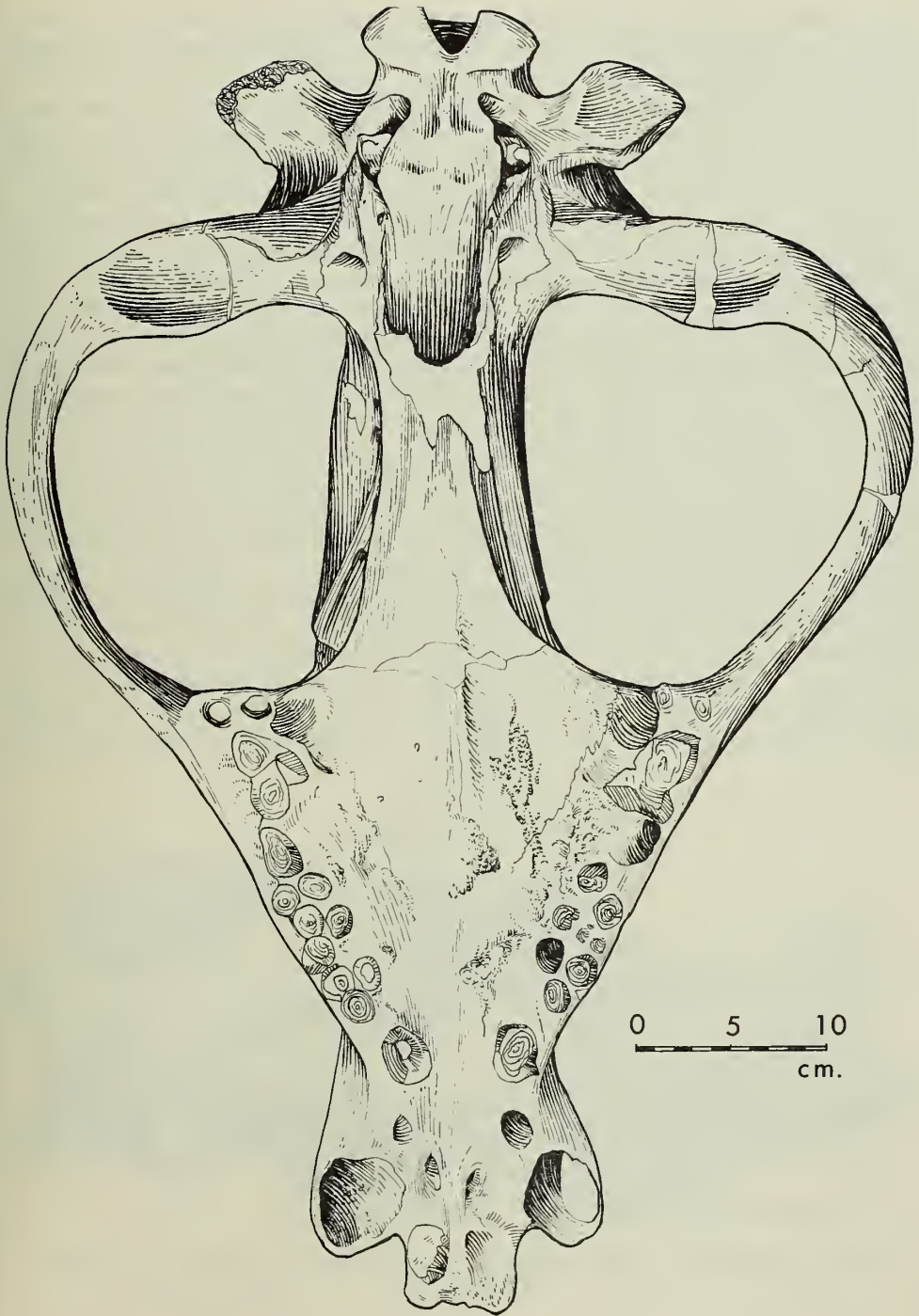Dorsal aspect.

FIG. 2. *Megistotherium osteothlastes* gen. et sp. nov. Holotype (M26173), Gebel Zelten. Ventral aspect.

No attempt is made to give an exhaustive account of every bone in the skull. The aim is rather to point to the salient features which characterize the animal and lead to a functional understanding.

Premaxilla. Although the limits of the bone cannot be defined, the major function is to carry the single large pair of incisors. The premaxillae stand well proud of the canines; between the anteriorly placed premaxilla and the laterally placed canine behind, is a deep groove for the accommodation of the lower canine.

Maxilla. The anterior margin of the maxilla is greatly expanded laterally to house the large upper canine; the canine alveolus and infra-orbital foramen are about the same size. The palate is V-shaped, extremely narrow at the level of P^1 and very wide posteriorly opposite M^3. The palatine fossae are close together between the canines and numerous nutrient foramina perforate the palate. A series of large deep and highly vascularised embrasure pits is developed on the palate between the protocones of the molars and premolars, reminiscent of the condition seen in the larger mesonychids.

Nasal. The right nasal is broken but on the left side the bone appears to extend back as far as the postorbital process of the frontal. The anterior narial opening is wide and high.

Lacrymal. Wanting on the right side, while on the left the area around the foramen is poorly preserved.

Jugal. On both sides the bone is well preserved, due in no small measure to its robust build; the bone carries a prominent infraorbital tubercle. Posteroventrally the ramus extends almost as far as the glenoid articulation of the squamosal.

Palatine. The anterior suture between the maxilla and the palatine can be partially traced; much of the very wide palate posterior to M^1 is roofed by palatine bone; this narrows dramatically behind the last molar and extends posteriorly
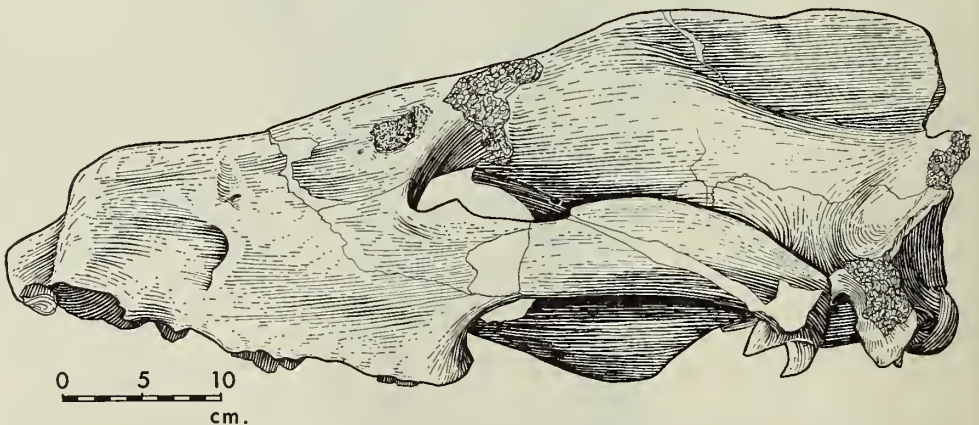

0   5   10
cm.

FIG. 3. *Megistotherium osteothlastes* gen. et sp. nov. Holotype (M26173), Gebel Zelten. Lateral aspect.

almost to the level of the glenoid articulation. The posterior margin is broken, but even allowing for this it is clear that the hard palate extends posteriorly considerably further than in other hyaenodonts. The posterior narial opening is 5 cm in diameter, similar in area to the anterior nares. There is a median longitudinal ridge along the ventral length of the palatine; the absence of the lateral walls suggests a thinning of the bone in this region.

Vomer. This bone cannot be seen in the specimen.

Frontal. In the absence of sutures the limits of the frontals cannot be drawn. In transverse section across the frontals the skull has the form of two cylinders; the lower and smaller one for the narial passage, and the upper formed of frontal bone which is extended dorsally to form the anterior part of the sagittal crest. Though broken, there appears to have been a massive postorbital frontal process. From near each postorbital process a ridge arises, increasing in height posteromedially until the two meet in the midline; they then continue posteriorly as a great plate of bone, the sagittal crest. The consequent V-shaped pit left anterior to the crest is reminiscent of some bats and bears witness to the origin of the crest by the upfolding of a pair of ridges.

Parietal. Even though the sutures are not open, it is clear that this bone contributes very largely to the formation of the sagittal crest. The crest is 30 cm long and some 15 cm deep. This depth is attained not so much by raising the crest as by the comparatively minute braincase which enables the crest to descend much lower than would be the case in a true carnivore. The crest is flared out postero-
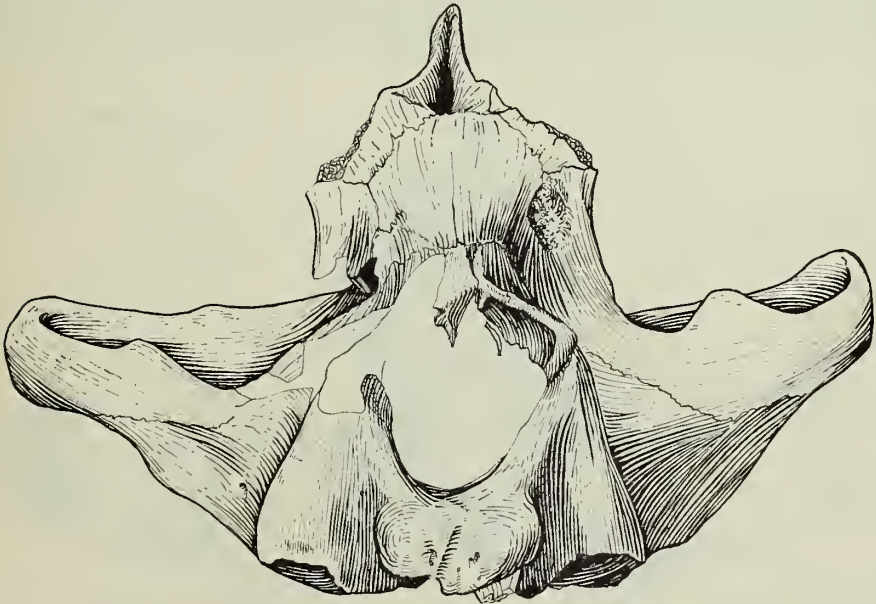

FIG. 4.   *Megistotherium osteothlastes* gen. et sp. nov.   Holotype (M26173), Gebel Zelten.
Anterior aspect.

laterally against the supraoccipital. Although the crest forms a vertical plate of bone, it is not quite flat; the distinct kinks could reflect slight differences in development of temporal muscle on left and right sides, or may be due to postmortem changes—the skull was fossilized with the dorsal surface facing downwards. The crest carries on the right side a large nutrient foramen.

Occipital. Viewed posteriorly the skull presents a trefoil pattern, formed of supraoccipital and two exoccipitals. The supraoccipital, broken dorsally, is sphenoidal, narrowing toward the foramen magnum. A pair of very large pits occupying most of the supraoccipitals witness the enormous rectus capitis musculatture. Immediately below these are two very large nutrient foramina which pass ventrally to a common opening on the roof of the foramen magnum. The exoccipital is dominated by the wide and massive paraccipital process; no separate mastoid process can be distinguished. The heavy paroccipitals must have carried heavy rectus capitis anterior and lateralis muscles for lateral head movements. The foramen magnum is roughly circular in outline and about 3·5 cm in diameter; on its inner margin it carries dorsally an opening which communicates with the two nutrient foramina on the supraoccipital. On the internolateral border can be seen the posterior lacerate foramen which passes anteriorly to open in the ear region. On the ventrolateral border is a further opening from the foramen magnum to the basioccipital, with a passage leading toward the ear region. The occipital condyles are large ovoidal facets, strongly keeled, with long axis directed ventromedially; the condyles almost meet ventrally with only a shallow notch separating them. The basioccipital is a relatively thin bridge of bone between the exoccipitals and the massive basisphenoid; the paired anterior condyloid foramen is clearly visible.
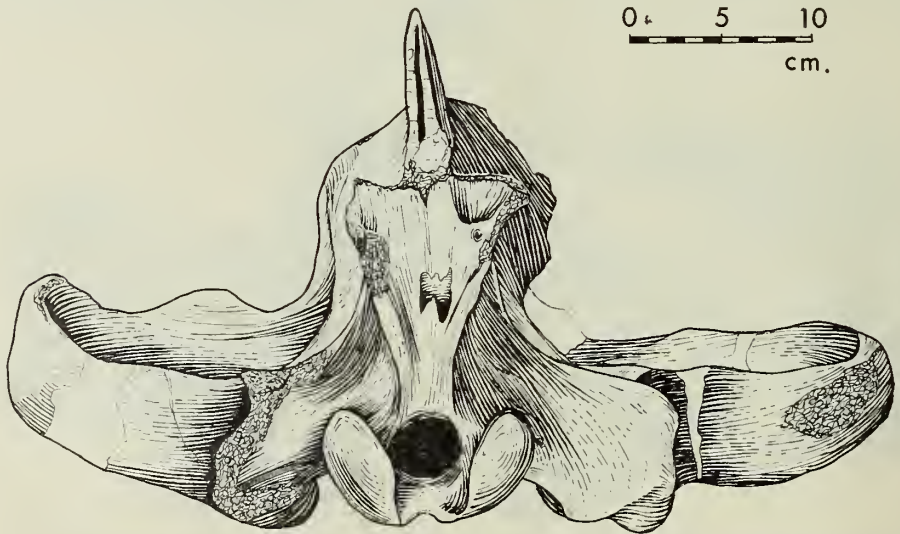

FIG. 5. *Megistotherium osteothlastes* gen. et sp. nov. Holotype (M26173), Gebel Zelten. Posterior aspect.

Ethmoid. This bone is not preserved in the fossil.

Sphenoid. The orbitosphenoid is lacking, the presphenoid is not visible and probably not preserved. The basisphenoid is massively built and literally deserves its name by forming a solid wedge between the squasomal glenoid articulations: without this the jaw joint would lack rigidity, powerful muscle action become impossible and there would be risk of crushing in the ear region and damage to the brain. The ventral surface of the basisphenoid carries a transverse ridge, which would have added strength to the bone and may have also served for the attachment of anterior strands of the rectus capitis anticus musculature: on the dorsal surface the sella turcica is shallow and poorly defined. Most of the alisphenoid is present; although the tips of the pterygoid processes are missing these appear to have been of normal proportions. The alisphenoid is pierced by a series of five openings for the cranial nerves and these have been identified as shown in Fig. 6. The separation of the foramen rotundum and the foramen lacerum anticum points to the un-crowded condition in this region, rarely seen in other creodonts. As in *Hyaenodon* there is no alisphenoid canal and the carotid artery lay in a shallow groove alongside the alar process.

Squamosal. The ·bone is dominated by the massive glenoid articulation for the mandible. The glenoid is deep, concave and with a length of 13 cm; it is buttressed by stout processes anterolaterally and posteromedially. A stout ridge extends on the dorsal surface from the glenoid area, posteromedially above the paraccipitol process, strengthening the bone to resist mandibular forces. The suture of the squamosal with the parietal remains open anteriorly. As mentioned above, no separate mastoid process is dinstinguishable and it is presumably fused with the paroccipital process. A long deep trench, extending laterally and horizontally between the
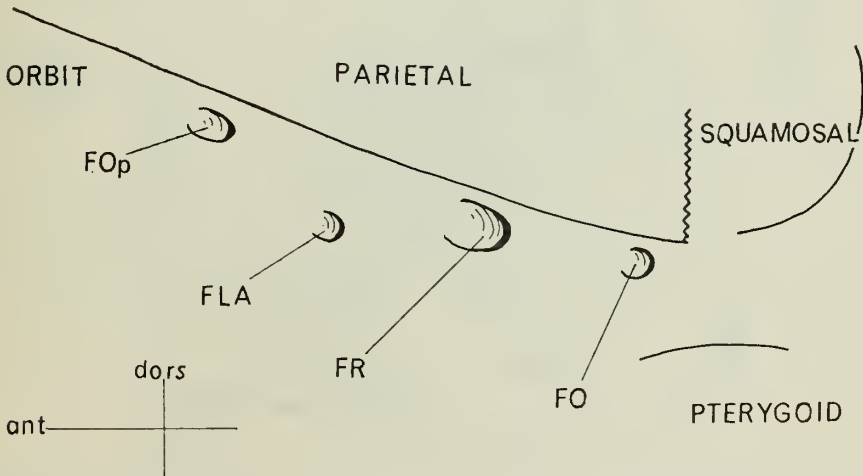

FIG. 6. *Megistotherium osteothlastes* gen. et sp. nov. Left sphenoid showing openings for cranial nerves. FLA = foramen lacerum anticus VI + V_1; FO = foramen ovale V_3; FOp = foramen opticum II; FR = foramen rotundum V_2.

paroccipital and postglenoid processes accommodated the external auditory meatus. The elongate glenoid carries the ramus of the squamosal far out laterally before it curves anteriorly to join the ramus of the jugal.   The zygomatic arch is notable for being extremely wide and stoutly built, although the height of the bone dorso-ventrally is proportionately not as great as in for example *Patriofelis*.

Ear Region.   The course of the external auditory meatus is horizontal along a passage between the postglenoid process and the paroccipital process.   As in all creodonts, there is no tympanic bulla and no indication that one was ever present. A small triangular window around the sphenoid, exoccipital and squamosal reveals the petrosum.   A small protuberance on the anterior face of the exoccipital may have
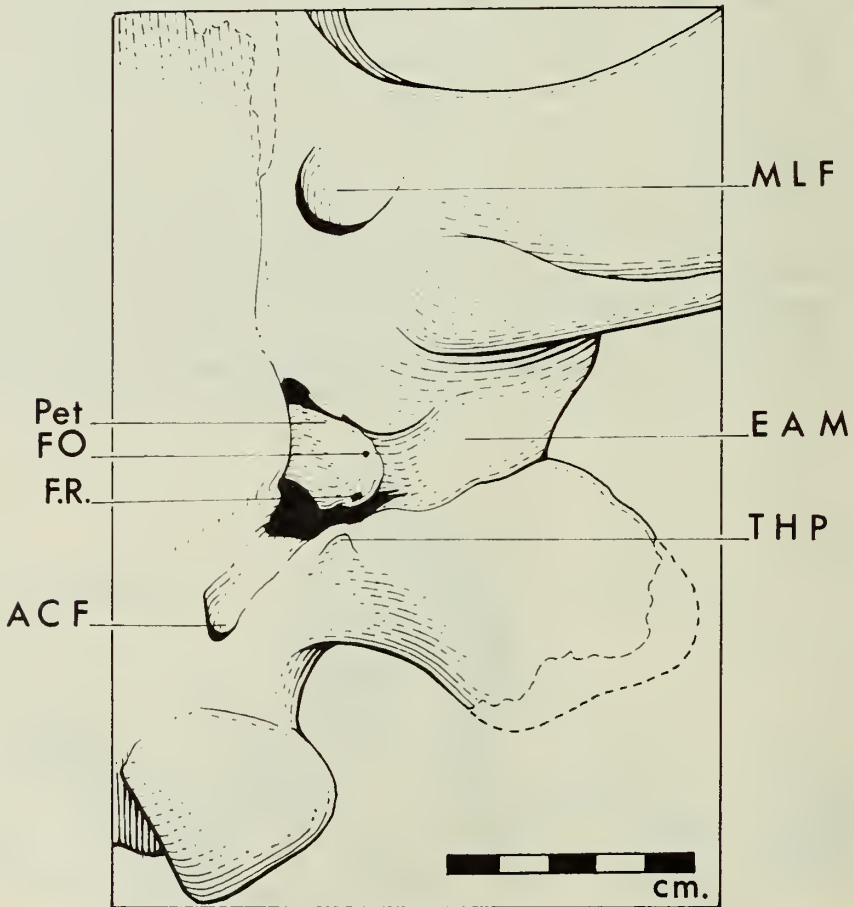

FIG. 7.   *Megistotherium osteothlastes* gen. et sp. nov.   Left ear region, ventral aspect.
ACF = anterior condylar foramen; EAM = external auditory meatus; FO = fenestra ovale;   FR = fenestra rotunde;   MLF = medial lacerate foramen;   Pet = petrosum; THP = tympanohyal process.

served for posterior attachment of a tympanic ring.   The left petrosum is complete
and the right broken to reveal the cochlea with probably three spiral turns.   The
identification of the openings is shown in Fig. 7.

 Sinuses.   Sinuses make up a large proportion of the skull volume, much more than
in any other known carnivorous mammal.   The brain is completely surrounded by
sinuses, dorsally, laterally and ventrally.   In specimen M 26515 the area of sinuses
seen in transverse section immediately anterior to the sella turcica is 2·6 times
greater than the area of the brain (16·25 cm² to 6·25 cm²).   In the domestic cat a
section in the same area shows the brain to be five times greater than the sinuses.
According to Paulli (1900) the extent of pneumaticity is dependent on skull size;
large skulls have greater pneumaticity.   The sinuses are extensive in bears, and in
the giant panda *Ailuropoda* the sinuses make up a greater volume than the brain
(Davis 1964).   The differential in *Megistotherium* is even greater due partly to the
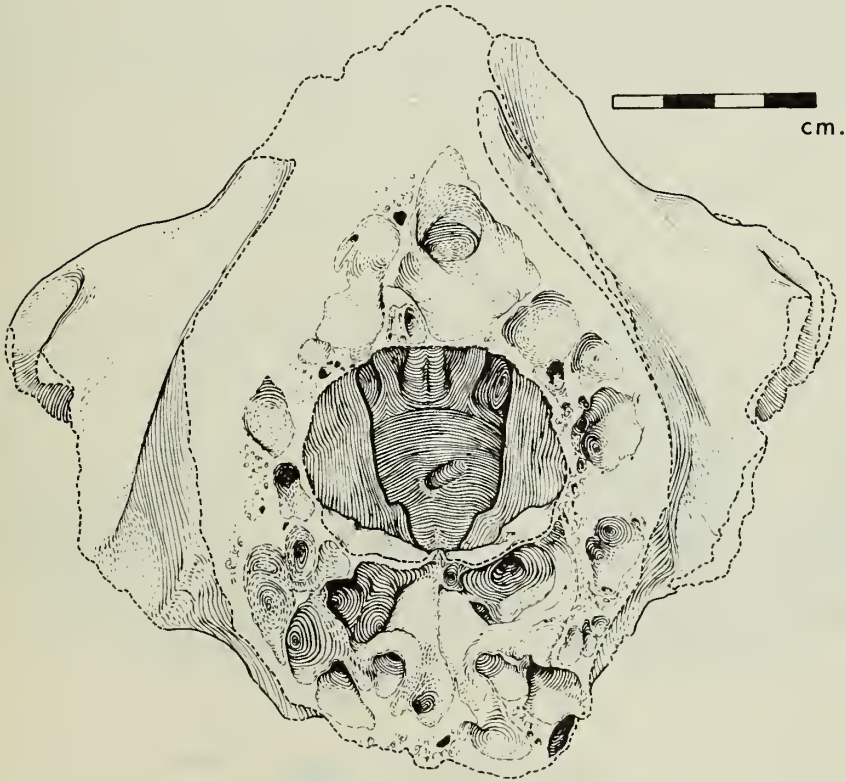large size of the fossil species and partly to the smaller creodont brain.

Fig. 8.   *Megistotherium osteothlastes* gen. et sp. nov.   Transverse section of cranium
(M26515) showing sinuses; viewed from front.

Brain. The endocast taken from specimen M26515 shows that the brain was basically similar to that of *Hyaenodon* and *Pterodon*, though larger and rather more complex. The olfactory lobes and the anterior of the cerebrum are lacking and the volume of the remaining brain is around 280 cc; thus the total brain volume cannot have been less than 300 cc but may have been over 400 cc.

The cerebrum has a well developed series of sulci, four from the median line to the pyriform lobe. The sulci are traversed by a series of blood vessels which give the whole a chequerboard appearance. Unlike *Pterodon*, the pyriform lobe is well developed. The tentorium separating the cerebrum from the cerebellum is inclined to the brain axis at 50°; this steep angle allows for a larger cerebrum and it completely masks the mid brain and no trace of the quadrigeminae are visible, a feature which is markedly different from *Hyaenodon* and *Pterodon* in which the quadrigeminal tubercles are exposed. The cerebellum is large, occupying perhaps as much as 25% of the brain volume; it is clearly divided into vermis and two lateral lobes, and their surface is corrugated. On the ventral surface the beginnings of the olfactory tracts can be seen anterior to the optic chiasma. The hypophysis has no definable lateral extent and appears to merge with the optic tracts, between which can be seen the loop made by the oculomotor nerve. Lateral to this the trigeminal and facial nerves issue. There is no distinct pons varolii and in this region the medulla oblongata is obscured only by the passage of the pyramidal tracts.

cm.

Fig. 9. *Megistotherium osteothlastes* gen. et sp. nov. Brain endocast. Dorsal aspect. From cranium (M26515), Gebel Zelten.

There are few accounts of creodont brains for comparison; the brain of *Megisto-therium* retains a number of primitive characters, but displays in the cerebrum and cerebellum more complexity than is usual in creodonts.

Dentition. The dental formula for the upper dentition is 1 1 4 3. This differs from normal hyaenodonts only in the great reduction of the incisors to one. The teeth are poorly preserved but sufficient survives to establish most of the salient features.

The single incisor is very large and probably the third; it is absent on the right and only the root remains on the left side. The transverse section of the tooth just below the base of the crown is egg-shaped, the point directed anteriorly. The incisors are closely juxtaposed and stand proud, anterior to the canines.

The canine is missing on both right and left sides, but the alveolus betokens its enormous size, massive root and near circular transverse section.

The first premolar is missing on both sides; it was a small single rooted tooth placed behind and slightly medial to the canine. The rest of the cheek dentition, P^2 to M^3, lies on a straight line; this line if continued anteriorly would pass through the incisor tooth on the opposite side. The angle between the line of the right and left cheek dentition is 50°. Almost the whole of the second premolar is preserved on the left side; the root is doubled and the crown single cusped. The crown of P^2 is longer than broad, has a posterior keel, thick enamel. and the tip of the cusp is worn flat so that overall the tooth resembles P^2 or P^3 of *Crocuta*. Small diastemae separate P^2 anteriorly and posteriorly from P^1 and P^3. P^3–M^3 form a tight series without any gaps between the teeth. Of P^3 only the roots survive and the tooth is notable in possessing three roots, each of equal size; the internal root is opposite
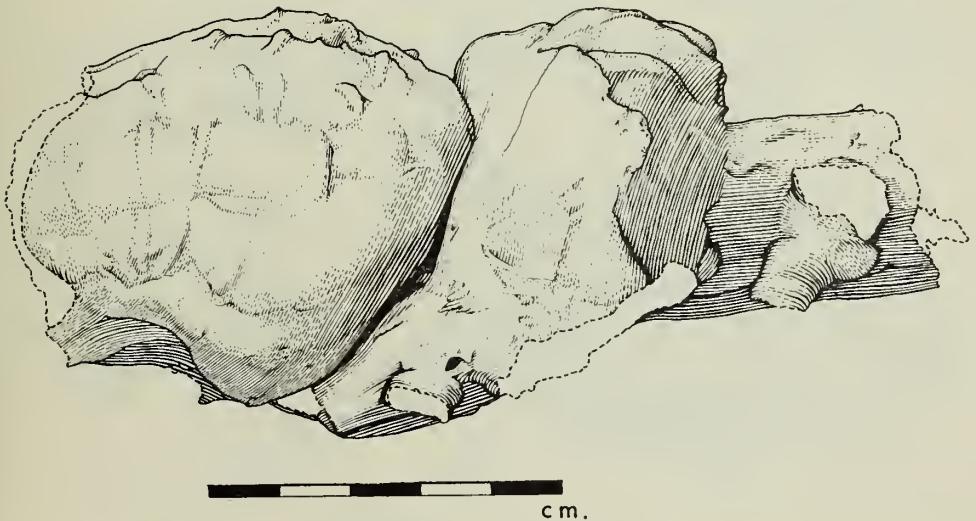

cm.

FIG. 10. *Megistotherium osteothlastes* gen. et sp. nov. Brain endocast. Lateral aspect. From cranium (M26515), Gebel Zelten.

the posteroexternal and not anteroexternal root, and the tooth length was apparently slightly greater than the width. From the three roots preserved on the left side P^4 appears to have been a larger version of P^3, although the transverse width across the root is greater than their length. On the right side the anterior root has been resorbed and the internal root is in process of being resorbed; this condition may relate to the bone pathology.

Only the roots of M^1 survive; the posterior root is the largest and the internal root is opposite the anteroexternal root. The slightly larger size of the internal root would suggest that the protocone was rather larger than the paracone. The second molar was the largest cheek tooth and is partially preserved on both sides; the tooth closely resembles in pattern the first (not second) molar of *Pterodon*. The paracone and metacone are connate but distinguishable and succeeded by a stout shearing metastyle; there is a small parastyle and well developed protocone; the tooth is considerably longer than broad. The third molar was a small two-rooted transverse tooth, again much as in *Pterodon*, although known only from root fragments.

Post-cranial Skeleton.

In the absence of associated remains, the attribution of post-cranial bones is rarely easy, often difficult and frequently impossible. The bones described below are for the most part indubitable creodont carnivore and their size distinguishes them from small species in the same beds.
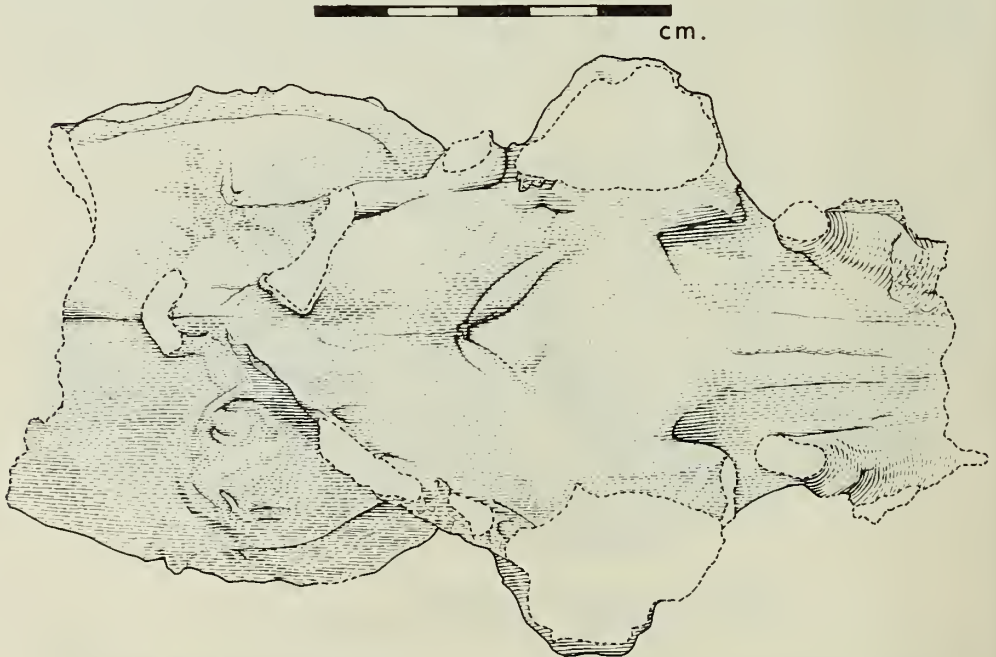

FIG. 11. *Megistotherium osteothlastes* gen. et sp. nov. Brain endocast. Ventral aspect. From cranium (M26515), Gebel Zelten.

Atlas. Specimen M21902 is the only indubitable vertebra of *Megistotherium*. It is essentially similar to that of *Hyaenodon* which differs but little from a canid atlas. The transverse process is greatly expanded in *Megistotherium*, which gives the bone a similarity to that of rhinoceros. The posterior margin of the process is greatly thickened to form a strong strut. On the ventral surface of the neural arch the longus colli tubercle is well developed while the dorsal surface of the arch is heavily scarred by the origin areas of the rectus capitis muscles. The cotyloid facets are deeply curved and firmly enclose the occipital condyles. The posterior axial facets are circular and flat (a distinguishing feature from rhinoceroses where the facets are ovoid and concave). The vertebral canal opens posteriorly close to the axial facet, and anteriorly has a large opening on the ventral surface of the wing. The oblique foramen is situated relatively close to the anterior margin of
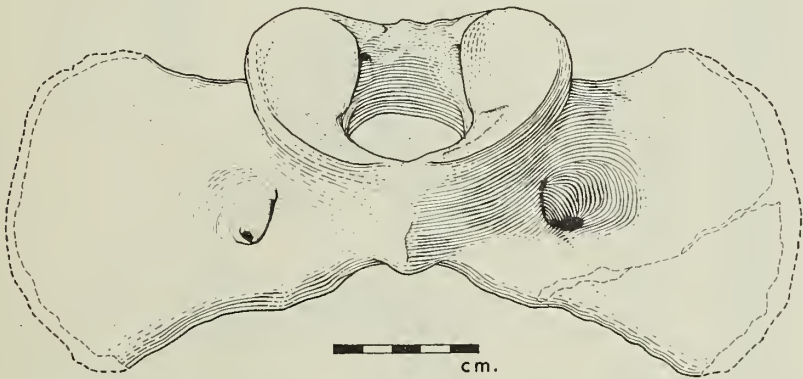
FIG. 12. *Megistotherium osteothlastes* gen. et sp. nov. Atlas. Dorsal aspect. (M21902), Gebel Zelten.
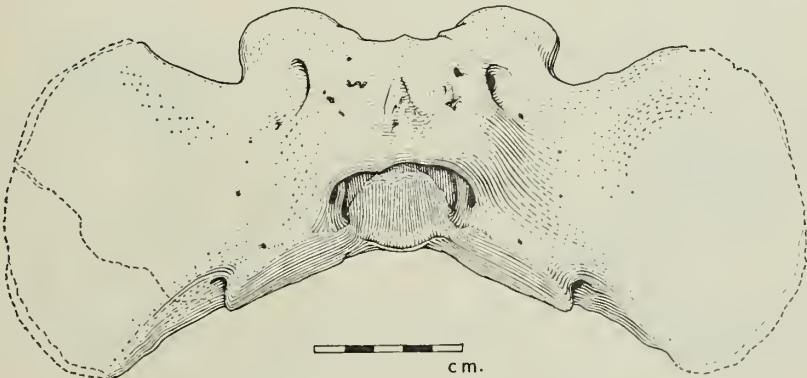
FIG. 13. *Megistotherium osteothlastes* gen. et sp. nov. Atlas. Ventral aspect. (M21902), Gebel Zelten.

B

the neural arch and a wide alar notch allows for the passage of the ventral root of the first spinal nerve.   Within the neural arch can be seen the pit for the transverse ligament and an opening for a branch of the vertebral artery.

The wide alar processes and stout posterior border signal a heavy obliquus and longissimus musculature for lateral and upward head movements.

Humerus.   The humerus is known only from two incomplete distal ends.   The entepicondyle appears to have been larger than the ectepicondyle.   The entepicondylar foramen is long and narrow; the olecranon fossa is deep and the trochlea spans about 270°.

FIG. 14.   *Megistotherium osteothlastes* gen. et sp. nov.   Right humerus, distal end. Anterior aspect.   (UB20576), Gebel Zelten.

FIG. 15.   *Megistotherium osteothlastes* gen. et sp. nov.   Right astragalus.   (UB20579), Gebel Zelten.   (a) Distal aspect.   (b) Proximal aspect.

Astragalus. The bone is typically creodont. The trochlea groove is asymetrical, the lateral border high and the fibular articulation facet prominent. The astragular foramen has a small opening on the trochlea surface, but a large distal opening between the calcar facets at the head of a deep groove for the interosseous ligament. The head, carried obliquely on a short neck, has a large convex navicular facet. Specimen UB20578 is a left magnum, and from its size probably referable to *Megistotherium.*

Metapodials. Four metapodials, two of them poorly preserved, are referable to *Megistotherium;* all are probably metatarsals and two are likely to be the third.

Fig. 16. *Megistotherium osteothlastes* gen. et sp. nov. Left magnum. (UB20578), Gebel Zelten. (a) Proximal aspect. (b) Lateral aspect. (c) Distal aspect.
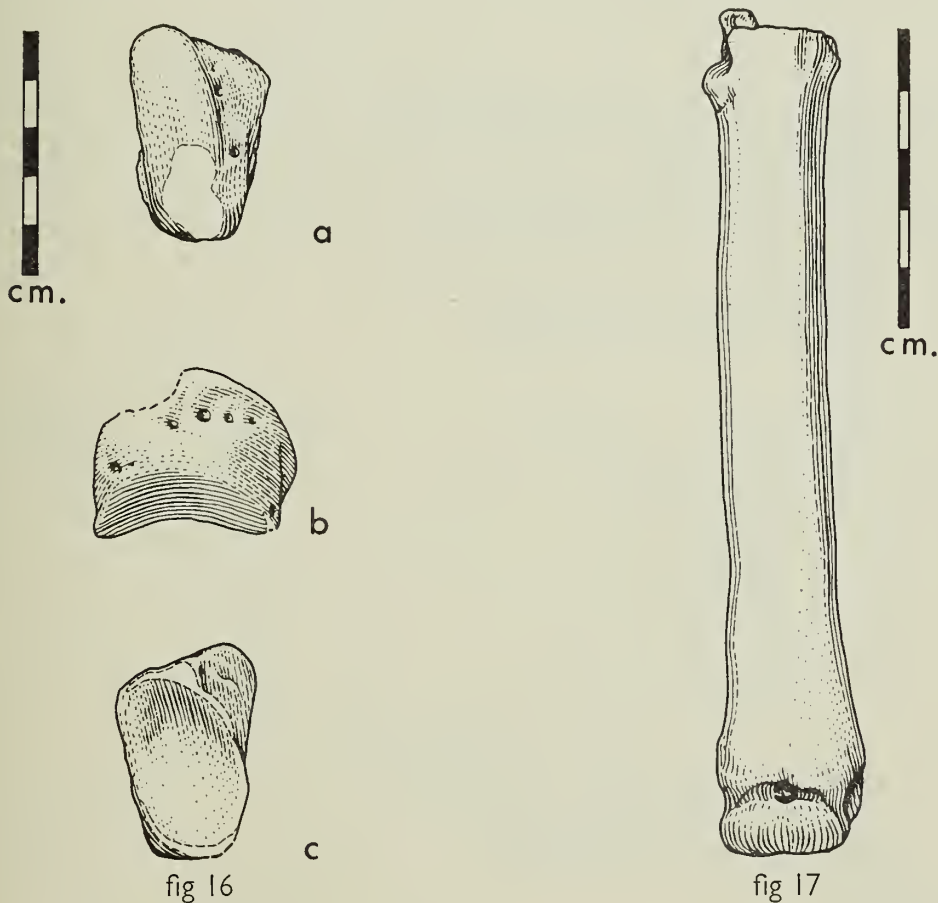
Fig. 17. *Megistotherium osteothlastes* gen. et sp. nov. Metapodial. (UB20580), Anterior aspect.

B*

TABLE I

Measurements.

Megistotherium osteothlastes gen. et sp. nov.

Type specimen M26173

	cm
Occlusal aspect	
Maximum transverse width across occipital condyles	9·3
,, ,, ,, ,, paroccipitals	ca 22·9
,, ,, ,, ,, zygoma	47·1
Maximum length, premaxilla—occipital condyles	66·4
Maximum width at level of M^3	24·1
,, ,, ,, ,, ,, P^2	8·5
,, ,, ,, ,, ,, C	15·1
,, ,, ,, ,, ,, I	5·9
Dorsal aspect	
Maximum width between external auditory meati	17·6
,, ,, ,, infraorbital foramina	11·1
Length of sagittal crest	ca 31·0
Lateral aspect	
Dorsoventral height of infraorbital foramen	3·0
,, ,, from palate at P^1 to nasal	12·1
Posterior aspect	
Height from roof of foramen magnum to sagittal crest	19·4
Dorsoventral height of foramen magnum	3·4
Transverse width of foramen magnum	4·1

Dentition	anteroposterior	transverse
	cm	
Incisor (alveolar)	3·2	2·0
Canine (,,)	6·0	3·8
,, depth of root 8·7		
P^1 (alveolar)	1·8	1·4
P^2 (crown)	2·8	1·7
,, crown height 1·6		
P^3 (alveolar)	3·4	3·2
P^4 (,,)	3·3	4·0
M^1 (,,)	4·1	3·4
M^2 (crown)	4·6	3·9
M^3 (alveolar)	1·3	3·0

Second Skull M26515–26518

Maximum transverse width across occipital condyles		9·1
Maximum width transverse across paroccipitals		20·0+
Dorsoventral height of foramen magnum		3·2
Transverse width of foramen magnum		3·5
Dentition	anteroposterior	transverse
Incisor	—	1·9
M^2 (alveolar)	4·0	3·9
Post-cranial		
Atlas: maximum width across alar processes		26·5
Humerus: maximum distal width	est.	12·3
Astragalus: trochlea width		5·6
Magnum: long axis length		4·0
Metapodial UB20580 maximum length		14·0
,, ,, width distal condyle		2·3

III. DISCUSSION

Weight. The skull of *Megistotherium* directs comparison among living carnivores with hyaenas, bears and the larger cats; the fossil has no single analogy among the present day stock and hence an attempt to reconstruct the whole animal from so few postcranial remains would be futile. Estimates can however be made of weight. Jerison (1961) made a revised statement of Dubois's formula for the ratio of brain/body weight, incorporating in it a constant which varied through the Tertiary. Jerison expressed the formula as $E = kP^{2/3}$, where E is the brain weight, P the body weight and the value of k varies from 0·03 for Eocene to 0·12 for Recent. On the evidence of the endocranial cast it is known that the cranial capacity of *Megistotherium* cannot have been less than 300 cc. Substituting 300 g for E in the equation gives a body weight P of 1,000 Kg.

A second estimate is based on the use of the humerus. The distal width of the humerus in *Megistotherium* (12·3 cm) is equal to that in a large brown bear, though the largest bears have humeri in excess of this (12·6 cm recorded on a British Museum specimen). Individuals of *Ursus arctos* are known to reach 780 Kg; although it has not been possible to correlate directly individual weights and humeral widths; it seems reasonable to suggest that a bear with a humeral width of 12·3 cm could
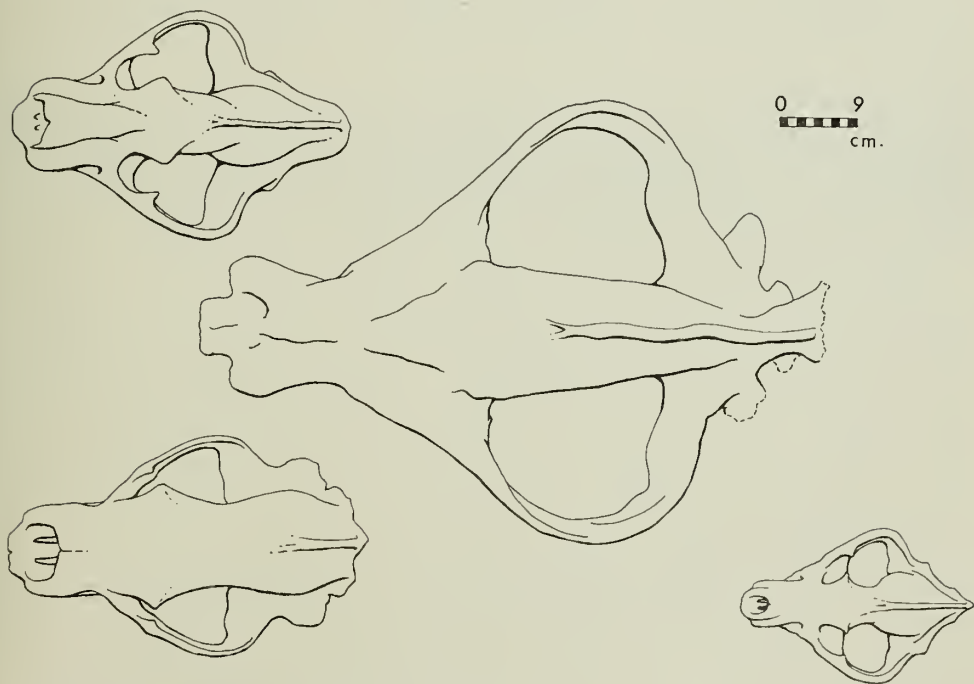

FIG. 18. *Megistotherium osteothlastes* gen. et sp. nov. Holotype skull compared with lion, bear and hyaena skulls.

weigh around 760 Kg; this estimate assumes body proportions not dissimilar to bear.   It is unlikely that a carnivore as large as *Megistotherium* could gallop like lion or hyaena and the bear analogy seems reasonable.

The hyaenodonts have unusually large heads in proportion to their bodies; this would make the first estimate too high and the second too low.   Taking this factor into account the most likely figure is around 880 Kg. for *Megistotherium*.

From the above estimates the brain/body weight ratio in *Megistotherium* is 1/3,000.   Since body weights are highly variable in a species, the ratio is subject to considerable fluctuations.   Few sources give the necessary data to measure this variation, but among them must be singled out the superb recent work of Brauer & Schober (1969).   The pertinent examples are:—

TABLE II

Species	Body weight grams	Brain weight grams	Ratio	Source
Thalarctos maritimus	450,000	509	1 : 880	B & S 1969
Ursus arctos	200,000	296	1 : 675	,,
Panthera tigris	180,000	315	1 : 570	,,
,, *leo*	155,000	241	1 : 640	,,
,, ,,	119,500	291	1 : 545	Weber 1927
Crocuta crocuta	75,000	165	1 : 450	R.J.G.S.

The *Ursus* example was only half the weight of the *Thalarctos;* brown bears are known to exceed polar bears in weight and the heaviest polar bear is nearly double the example.   The two examples of lion show a wide difference in ratio.   The hyaena is based on a cranial capacity measurement of a large individual and a weight based on figures in Walker (1968).   However even allowing for all these variables, the ratio in *Megistotherium* is lower by a factor of two or three.

Functional analysis of the jaw and dentition.   The whole architecture of the skull of *Megistotherium* is moulded for maximum efficiency in feeding.   The most striking feature is the enormous temporal musculature, witnessed by the very wide zygoma together with the high and long sagittal crest.   The weight of each temporal muscle was probably around 10 Kg.   The zygomatic arch while wide is not excessively heavy as in for example *Patriofelis* (see Denison 1938, fig. 19).   This implies that the masseter was not developed to the same extent and the temporal was, as in most carnivores, the major muscle used in jaw closing.   Turning now to the dentition let us examine how this musculature could have been used to best effect.

In *Megistotherium* M^3 is vestigial and M^{1+2} are carnassial.   These latter teeth could be compared with the powerful and efficient carnassial P^4 in *Crocuta* and *Panthera*.   Crusafont & Truyols (1956) have given a quantitative measure of the degree of carnassality in the different families of fissipeds.   This measure is based on the angle formed on P^4 between protocone-metacone and paracone-metacone. The more carnivorous species have small protocones and longitudinal shears and hence low angles.   In tiger the angle is 13°, in hyaena 15°.   In the Oligocene

hyaenodont *Hyaenodon mustelinus* the angle is also 15° on the carnassial. In both *Pterodon* and *Megistotherium* the angle rises to 35° indicating a considerable loss of shearing efficiency. Further the size of the carnassials in *Megistotherium* is proportionately small. None of this suggests that the temporal musculature was developed primarily to operate on the carnassial dentition.

Megistotherium has like *Crocuta* heavy blunt premolars. In *Crocuta* P3 is used in bone crushing and can exert a pressure of 1 ton per cm^2; as the tooth crown has an area around 0·5 cm^2, this means an effective pressure of about half a ton, which is approximately 2·5 times greater than the pressure man can exert on his back molars. It is not possible to make a precise calculation for *Megistotherium*, but is likely that the P3+4 were not less efficient than in *Crocuta*.

The canine of *Megistotherium* is unfortunately missing, but the alveolus indicates that it was large, stout and ovoid. The canines from Kenya are exactly the shape and size one would expect for *Megistotherium*. The efficiency of the canine is dependent on its size and proximity to the fulcrum (glenoid). Hence the facial shortening in hyaena and giant panda improve considerably the efficiency of the canine. (See Table III.) A remarkable feature of *Megistotherium* is the long face; even with this apparent disadvantage, the ratio of canine area to canine-glenoid length is greater than in any living fissiped. This suggests that the canine is the most important factor in food capture.

Smith & Savage (1959) gave an equation for the mechanical efficiency of musculature, $T = P \times \frac{a}{l}$ where T is the force exerted, P is the pull or tension in the muscle, and $\frac{a}{l}$ corresponds to the mechanical advantage of a lever, i.e. the ratio of the distance of the applied force from the fulcrum to the distance of the load from the fulcrum (see Fig. 19). In this case a is the moment arm of the temporal muscle, l the distance from the glenoid to the canine, and for P we can take the area of the temporal
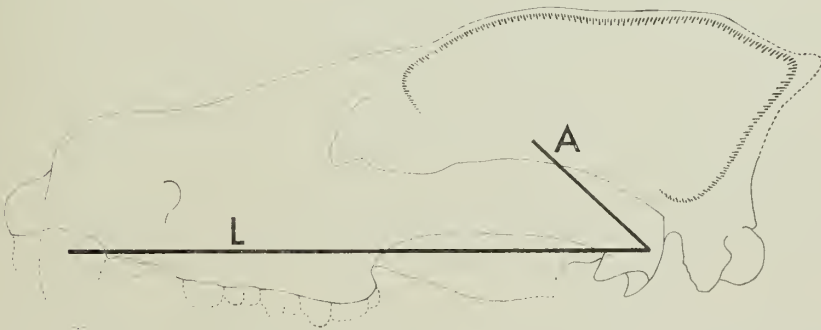

FIG. 19. Mechanics of the skull of *Megistotherium*. gen. nov. A = moment arm of the temporal muscle; L = distance from glenoid to canine.

muscle enclosed by the zygomatic arch. In Table III the last column gives the results of the substitution. It will be seen how very much more powerful is the canine of *Megistotherium* than that of any other species; five times greater than bear or tiger, and ten times greater than hyaena. However when a similar calculation is done for *Crocuta* on the P³ it is seen to be much more powerful than the canine, and similarly when the P⁴ in tiger is measured.

Finally there is the question why did *Megistotherium* maintain such a long jaw when it could have achieved similar power with much less effort had the jaw been shortened. Two arguments are possible; it is a genetical trait of the Hyaenodontidae to have long faces while their close relatives the Oxyaenidae had short faces. Secondly can be considered the likely prey; the large ungulates in the fauna are anthracotheres, pigs, rhinoceroses, mastodonts and deinotheres. The remains of proboscideans are much more abundant than any of the other taxa (see Savage 1968). *Mastodon angustidens* and *Prodeinotherium hobleyi* were about the size of living elephants, and also present was a smaller and much rarer species *Mastodon pygmaeus*. Without a skeleton it is impossible to determine how *Megistatherium* would have brought down its prey; it is likely to have had a good sense of smell and so long as it could move quicker than its prey no great turn of speed would be necessary. The wide and stout exoccipital processes and the large alar wings on the atlas point to the massive development of lateral musculature for turning the head sideways—or for resisting a struggling prey. In lion and tiger the mandible has a gape of around 50°, measuring the angle between the upper and lower dentitions Although the mandible of *Megistotherium* is unknown and assuming no exceptional specialisations, it is reasonable to except the gape to be similar. A gape of 50° in *Megistotherium* would give a clearance of 40 cm at the alveolar margin of the canines, or a clearance of 30 cm between the tips of the canines. Living elephants have a leg diameter of around 30 cm. Had *Megistotherium* a shorter jaw it would have been unable to bite into a proboscidean limb.

The incisors remain to be considered. Only one pair is present in the premaxilla, and these are large; if the Bugti specimen is correctly assigned, then the mandible possessed two functional pairs and possibly a vestigial third. Comparison is closest with *Sarkastodon*, the Mongolian oxyaenid second only to *Megistotherium* in size, (omitting *Andrewsarchus*, the mesonychid which was non-carnivorous and now classified among the condylarths). *Sarkastodon* was short jawed, had efficient shearing teeth and the incisor formula was $\frac{2}{1}$; in the premaxilla I² was vestigial and a large I³ the only functional incisor. As in *Megistotherium* there is a diastema between the canine and incisor to allow for the accommodation of the lower canine. Denison (1938) in his excellent review of the group concluded the reduction of the lower incisors in *Sarkastodon* pointed to diminution of function; this may be true if the lower incisor was as small as indicated in his reconstruction, but can hardly apply to the upper. If *Megistotherium* used its canine as suggested above, then small incisors would be in danger of being broken by struggling prey or by occluding accidentally on bone. Reduction in number and increase in size is the best defence against this and also supplements the canine.

TABLE III

		Canine area (C) cm²	$\dfrac{10 \times C}{l}$	Carnassial angle	$\dfrac{a}{l}$	P cm²	$P \times \dfrac{a}{l}$
Ailuropoda		2·2	1·16		0·43	40	17·2
Thalarctos		6·1	2·65		0·28	58	16·2
Ursus		5·7	2·45		0·37	65	24·1
Megistotherium		22·8	4·47	35°	0·35	314	109·9
Hyaenodon mustelinus		0·45	0·41	15°	0·24	8·7	2·1
Crocuta	C	2·2	1·33	15°	0·36	28·3	10·2
	p³				0·52		14·7
Panthera tigris	C	5·5	2·68	13°	0·34	59	20·1
	P⁴				0·54		31·9
Panthera leo		5·3	2·65		0·37	61	22·6

IV. OTHER MATERIAL REFERABLE TO AND COMPARABLE WITH *MEGISTOTHERIUM*

Specimens which could be referred to the genus *Megistotherium* or the closely allied genus *Hyainailouros* are known from Africa, Asia and Europe.

Considering first the African specimens, material from Egypt and Kenya will be discussed. Fourtau (1920) described from Moghara, Egypt an upper third premolar which he named *Hyaena* sp. indet. (loc. cit. pp 91–92; fig. 62). Von Koenigswald (1947) re-examined the tooth and concluded it was an upper third premolar which he assigned to the genus *Hyaenaelurus* and gave a new specific name, *H. fourtaui*. The tooth has parameters which are very close to those of *Hyainailouros sulzeri* (see Table IV). In *Megistotherium*, only P³ and P⁴ are three-rooted, and both teeth are much larger than the Moghara specimen. Further, *Megistotherium* is clearly distinguished from *Hyainailouros* in having a P⁴ whose width much exceeds the length. The author concurs with Von Koenigswald in placing the Moghara tooth in the genus *Hyainailouros*. While the Moghara fauna is apparently of similar age to that of Gebel Zelten (Savage & Hamilton 1972), with several species in common, the Moghara carnivore is unknown in the larger Gebel Zelten fauna.

Three very large canines are known from Kenya (Fig. 20a, b & c). It is not clear whether they are uppers or lowers and they are considered Hyaenodontidae indet. The specimen from Rusinga (R2–4, 232'49) comes from strata which yield a fauna which can be correlated with that of Gebel Zelten (Savage & Hamilton 1972). The other two teeth however come from Fort Ternan whose fauna is much younger and placed by Bishop et al. (1969) in the late Miocene, with radiometric age of around 14–15 million years. If correctly assigned, then these teeth represent another example of a late survival of hyaenodonts in Africa; this would not be unexpected as from Kenya and Pakistan we know of the survival of hyaenodontids in the Pontian (Savage 1965).

Andrews (1914) described and illustrated (loc. cit. p. 179, Plate II fig. 2) a left astragalus from Kachuku, Karungu, Lake Victoria. The specimen (M10635) is about the size of a lion astragalus and has an astragalar foramen. Andrews

thought it might be creodont and compared it to *Apterodon*.   The astragalus is very different in size and proportions from that of *Megistotherium*, and I would agree with him that it could belong to a creodont of about the size of *Apterodon*.

Savage (1965) described some material of *Pterodon africanus* from Kenya, and he referred three additional teeth to a new species, *P. nyanzae*.   The teeth are very similar to those of *Hyainailourus sulzeri*, but slightly smaller and comparable with what would be expected of *H. fourtaui*.   My present view is that they should be transferred to the genus *Hyainailourus* and the specific name retained until further evidence is available.

Five specimens from the Bugti Beds of Pakistan arrest our attention.   Forster Cooper (1924) described and figured a mandible (M12049) as *Anthracotherium ingens*.   The specimen is patently not an anthracothere but could belong to *Megistotherium*, of a species rather larger than *M. osteothlastes*.   The specimen has a large canine which recalls the Rusinga specimen mentioned above.   The evidence of the alveoli suggests three incisors were present.   The I_1 alveolus is preserved on both sides and that of $I_{2\&3}$ on the left side only.   The alveoli decrease in size toward the canine, and the third incisor has a small alveolus almost tucked under the canine. Immediately behind the canine is a deep alveolus suggesting the presence of a single
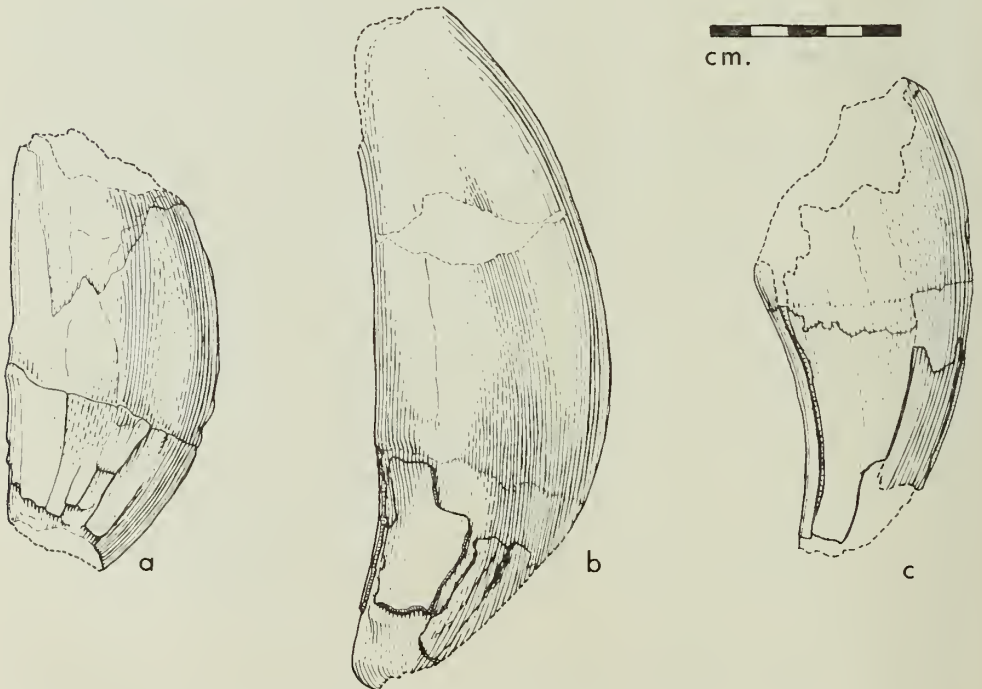

FIG. 20.   Hyaenodontid canines.   (a) R 2–4, 232 '49.   (b) FT 2 '59.   (c) FT 11 '59.

rooted P_1. $P_{2\&3}$ are well preserved double rooted teeth with well developed cingula anteriorly and posteriorly, the third premolar being a larger version of P_2.   Without further evidence the author would hesitate to give a specific determination, and will assign it to *Megistotherium* sp. indet.

Pilgrim (1912 and 1932) described four creodont specimens from the Bugti Beds. In his 1912 paper all were assigned to *Pterodon*, but in 1932 he re-allocated two specimens to the genus *Hyainailouros*, a third *Amphicyon* and the fourth he regarded as indeterminate.   Specimen D 107, is the type of *Hyainailouros bugtiensis* and I regard the two teeth in the mandibular fragment as $M_{2\&3}$; the species has a resembl-ance to the European *H. sulzeri*, but I would accept Pilgrim's opinion that it be retained as a separate species.   I would also assign to *H. bugtiensis* specimen D 109 which I regard as a P_4 and which Pilgrim (1932) left as indeterminate.   Specimen D112 is a toothless mandibular symphysis and I concur with Pilgrim in assigning it to *H. bugtiensis*.   Specimen D108 was named by Pilgrim in 1912 as *Pterodon* sp., but in 1932 he assigned it to *Amphicyon shabazi* and with this transfer to the fissipeds I also concur.   Pilgrim (1932) described a new species of *Hyainailouros* from the Kamlial Stage of the Attock District, Salt Range: *H. lahiri* comprises a mandibular ramus with the last two teeth preserved.   Pilgrim regarded these as P_4 and M_1 and hence concluded it was a very large species.   If however the teeth are interpreted as M_2 and M_3, which seems more plausible, then the specimen conforms closely to the type of *H. bugtiensis* and I see no reason why it should not be synonymised with the Bugti species.

In summing up, we can now point to the radiation of three genera of large mid Tertiary hyaenodonts.   *Pterodon* is the smallest of the three and its species and their distribution were recorded by Savage (1965).   The genus occurs in North America, Eurasia and Africa and ranges in time from Mid Eocene to Early Miocene; species are all strikingly similar and vary mainly in size.   *P. grandis* from the Oligocene White River Beds of Saskatchewan is the largest and may be more correctly placed in the genus *Hyainailouros*.   *Hyainailouros* has until the present been regarded as the largest form; the genus is not well known and until Van Valen (1966) reclassified the Hyaenodontidae it was usually considered as an appendix to the Felidae.   The type species is *H. sulzeri* Biedermann from the Vindobonian of Veltheim in Switzerland; specimens are known from Burdigalian, Vindobonian and even Pontian deposits in France, Germany and Switzerland.   Although all may not with certainty be assigned to the type species, no other good species have been established.   Beaumont (1970) has reviewed the type material of *Hyainailouros sulzeri* from Switzerland, and given a reinterpretation of the work of Helbing (1925) on the species.   From the early Miocene of Egypt comes *H. fourtaui* and from a similar level in Kenya comes *H. nyanzae;* these species are of doubtful validity. All the Asiatic specimens can be referred to *H. bugtiensis*, probably a distinct species from *H. sulzeri* and more primitive than its European counterpart.

The new genus *Megistotherium* is a gigantic form with distinctive dental differences from *Hyainailouros*.   Apart from the type area in Libya, a mandible from Pakistan is confidently assigned to the genus, but not determined specifically.   *Megistotherium* is thus limited as far as is known to the Early Miocene of Africa and Asia.

TABLE IV

Upper Dentitions (*mm*)

		C	P¹	P²	P³	P⁴	M¹	M²	M³
Megistotherium osteothlastes									
HOLOTYPE Libya	a.p.	60	18	28	34	33	41	46	13
	trs.	38	14	17	32	40	34	39	30
Hyainailouros fourtaui									
HOLOTYPE Egypt	a.p.				26				
	trs.				20				
Hyainailouros nyanzae									
M19091 HOLOTYPE Kenya	a.p.					30			
	trs.					24			
M19092 ,,	a.p.					29			
	trs.					24			
M19093 ,,	a.p.						—		
	trs.						28		
Hyainailouros sulzeri									
HOLOTYPE Veltheim	a.p.			27		34	38		
	trs.			23		26	29		
Hyaenodont indet									
R 2–4 232'49 Kenya	a.p.	51							
	trs.	32							
F.T. 2 ,,	a.p.	51							
	trs.	37							
F.T. 11 ,,	a.p.	51							
	trs.	37							

Lower Dentitions (*mm*)

		C	P¹	P²	P³	P⁴	M¹	M²	M³
Megistotherium sp.									
M12049 Bugti	a.p.	7·0		36	38				
	trs.	4·9		21	23				
Hyainailouros bugtiensis									
HOLOTYPE D 107 Bugti	a.p.							42	55
	trs.							23	28
H. bugtiensis D109 Bugti	a.p.					27			
	trs.					15			
H. bugtiensis D236 Attock	a.p.							36	50
	trs.							25	32
H. sulzeri HOLOTYPE									
Veltheim	a.p.					24	41	51	
	trs.					21	22	28	

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PLATE 2