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GEOLOGY AND PALAEOBIOLOGY OF THE CENTRAL AND SOUTHERN NAMIB

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PALAEONTOLOGY OF THE ORANGE RIVER VALLEY, NAMIBIA

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New Proboscidea from the Miocene strata in the lower Orange River Valley, Namibia

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Five genera of Proboscidea have been discovered in Early Miocene and basal Middle Miocene sediments of the lower Orange River Valley. *Deinotherium*, *Eozygodon*, *Progomphotherium* (nov. gen.) and *Gomphotherium*, occur at Auchas in the proto-Orange terrace aged about 19-20 Ma, while *Deinotherium* and *Afromastodon* (nov. gen.) occur at Arrisdrift in proto-Orange deposits aged about 17.5 Ma.

Version française abrégée

Le site d'Auchas (ca 19 Ma) en Namibie, a livré quatre espèces de Proboscidiens. Le petit deinothère *Deinotherium hobleyi* est représenté par plusieurs mâchoires et des dents isolées, dont une molaire lactéale. L'éozygodonte *Eozygodon morotoensis* est connu par des crânes et quelques fragments de mandibules. Les crânes montrent que cette espèce avait un basicrâne fortement redressé, et si fortement, qu'en vue latérale le crâne a un contour presque carré prolongé à l'avant par un prémaxillaire prominent. P4/ à M3/ sont simultanément en occlusion. Un mastodonte primitif est représenté à Auchas par un crâne et des fragments de mandibules. Il s'agit de *Progomphotherium maraisi* nov. gen. nov. sp., dont les caractères primitifs sont représentés par des dents jugales très bunodontes avec un faible développement des conules et mesocones, et la conservation de l'occlusion simultanée de la série dentaire P3/ à M3/. Le crâne est allongé, le basicrâne n'est pas du tout redressé et de ce fait rapelle un peu la morphologie des proboscidiens de l'Oligocène tels *Phiomia* et *Palaeomastodon*. Les défenses inférieures avaient une section elliptique au long diamètre vertical, totalement différente de l'orientation des défenses inférieures de *Gomphotherium* et *Archaeobelodon*. Enfin, on trouvé à Auchas dans un dépôt légèrement plus récent un plus grand gomphothére appartenant peut être au genre *Gomphotherium*.

Arrisdrift (17 à 17.5 Ma) a foumi de nombreux restes de proboscidiens mais l'on n'y connaî pas de crâne où de mandibules complets. *Deinotherium hobleyi* est attesté par un fragment mandibulaire, plusieurs dents isolées, et quelques os. Le proboscidien le plus fréquent de ce gisement est le gomphothère *Afromastodon coppensi* nov. gen. nov. sp. qui est le plus grand des proboscidiens du Miocène moyen. Cette espèce est connue par de nombreuses dents jugales et plusieurs fragments de défenses supérieures et inférieures. Les défenses sont munies d'une large bande d'émail comme celles des autresgomphothères, etles défenses inférieures montrent une section ovale à arrondie sans aucune tendance à l'aplatissement où au creusement qui caractérise les défenses inférieures d'*Archaeobelodon* et *Gomphotherium*. Les molaires d'*Afromastodon coppensi* sont relativement archaïques au sein des gomphothères, formées de quatre lophes (3 lophes plus un cingulum distal plus étroit) à la M3/, et 4.5 lophides à la m/3. Une des m/1 présente du cément dans les vallées entre les lophides mais la plupart des dents en sont dépourvues. Les molaires lactéales possédént un émail crénelé (ptychodontie).

La comparaison des nouveaux genres de Namibie avec les fossiles d'autres régions d'Afrique montre que *Progomphotherium* est present dans plusieurs localités du Miocène inférieur du Kenya et d'oùganda, tandis qu *Afromastodon* se trouvé dans les sites du Miocène moyen du Kenya et de l'Afrique du Nord (Libye, Egypte) où de nombreux restes découverts autrefois ont été interprétés comme des formes voisines des gomphothères européens.

Le genre *Eozygodon* est, lui aussi, présent dans le Miocène inférieur du Kenya, de l'Ouganda et de l'Egypte, tandis que les deinothères sont largement répandus en Afrique et l'Eurasie.

Introduction

Proboscideans have been recorded from the lower Orange River Valley on several previous occasions, but the only specimens to have undergone detailed scrutiny were the deinotheres from Arrisdrift (Harris, 1977). Corvinus & Hendey (1976) recorded the presence of *Gomphotherium* at Arrisdrift, and Pickford *et al.*, (1995) reported the occurrence of *Deinotherium*, *Eozygodon* and a gomphothere at Auchas.

During the past seven years many new specimens have been found at both Auchas and Arrisdrift, some of them being complete skulls. The purpose of this paper is to provide detailed descriptions of the material and to discuss its systematic, phylogenetic and biochronologic implications.

Geological setting and Age

Auchas and Arrisdrift are two sites where fluviatile sediments assigned to the Arrisdrift Gravel Formation (SACS, 1980) crop out in abandoned loops of the Proto-Orange River some 32-41 metres above modern sea-level between 35 and 50 km upstream from the mouth of the river (Pickford & Senut, 2000). Both sites are diamondiferous, Auchas being an active mine which has yielded abundant fossils during exploitation. Arrisdrift is an exploration pit which first yielded fossils in 1976 (Anon, 1976) during diamond prospecting activities. The Namibia Palaeontology Expedition has excavated Arrisdrift systematically since 1993, but at Auchas, which is an active mine, the recovery of fossils has generally been done on an *ad hoc* basis by mining personnel and by the examination of mine dumps by the members of the Namibia Palaeontology Ex-pedition. Mr Daan Marais, Pit Superintendent at Auchas, has made a great contribution to the palaeontology of the mine by collecting two of the proboscidean skulls and several of the teeth described herein.

Faunal remains from Auchas indicate an Early Miocene age, perhaps 19-20 Ma (Pickford *et al.*, 1995) whereas those from Arrisdrift are early Middle Miocene (ca 17-17.5 Ma) (Pickford, 1995). Furthermore, the Auchas deposits appear to span an appreciable span of geological time, with Pits AM 02, AM II and AM 59 being older than Pit AM SE.

Systematic Descriptions

Order Proboscidea Illiger, 1811
Family Deinotheriidae Bonaparte, 1845
Genus *Deinotherium* Kaup, 1829
Species *Deinotherium hobleyi* Andrews, 1911

Material: *Auchas* - AM 3’93 right dM4/; AM02 left m/3; AM 111’97 left m/3; Unnumbered specimens in the Sperrgebiet Museum, Oranjemund, mandible with p/4-m/3 in a block of conglomerate; right mandible with m/1 to front half of m/3; AM 4’99, fragment of left mandible with damaged m/3. *Arrisdrift* - PQ AD 299 left M3/; AD 200’97 right p/3; PQ AD 1661 right P4/; PQ AD 650 right p/4; AD 95’00, left mandible fragment with m/2-m/3.

Descriptions: AM 3’93 is a right dM4/ (Pl. 2, Fig. 1). It has three lophs which are heavily worn on the pretrite half of the crown. The anterior loph is the narrowest and the central one is the broadest. The buccal ends of the lophs are tall and are curved anteriorly. The transverse valleys are deep. There is a distally projecting knob of enamel on the distobuccal corner of the crown and the enamel is thin.

AM 4’99 is a fragment of left mandible with a broken third molar. There is a broad, obliquely oriented retromolar space between the distal end of the molar and the root of the ascending ramus, and there appears to be a coronoid foramen entering the ramus 50 mm behind the m/3. Coronoid foramina are unusual features among mammals, the main group exhibiting such a structure being the Hyracoidea (Pickford, 1994). 120 mm behind the m/3 there is a large mandibular foramen on the lingual side of the body of the mandible. The body of the mandible is ca 110 mm broad and is 110 mm deep at m/3.

AD 200’97 is a lower left third premolar (Pl. 1, Fig. 1). It is triangular in occlusal outline with rounded corners. It has a prominent main cusp with a lesser lingual cusp confluent with it. There is a distal crest which descends towards cervix in the midline of the tooth. Distolingually there is a small cusplet which broadens out the rear of the crown. The roots are long, robust and partly fused.

PQ AD 650 (Pl. 1, Fig. 4) is a heavily worn, right p/4 (Harris, 1977). It is bilophodont. The anterior and posterior dentine lakes are joined by a narrow isthmus in the transverse valley. There are weak anterior and posterior cingula.

In the Sperrgebiet Museum, Oranjemund, there is a right mandible from Auchas with complete first and second molars and the anterior loph of the third (Pl. 1, Fig. 7). The first molar is heavily worn and is slightly damaged. The crown is trilophodont, the distal loph being the narrowest, the other two lophs being nearly the same breadth. The pretrite portion of each loph is antero-posteriorly longer than the posttrite part with the result that with wear the pretrite portions produce larger dentine lakes than the posttrite half.

The second lower molar is bilophodont with a centrally positioned talonid cusp. Wear facets on the two lophs are steeply angled along the rear of each loph, producing a sharp cutting edge as wide as the crown. Each loph is virtually straight distally but anteriorly their lingual and buccal ends have crests descending towards the cervix. The buccal crests lead centrally and end in the midline of the crown, whereas the lingual crests descend more directly towards the base of the crown.

AM 11 1’97 (Pl. 1, Fig. 5) and Auchas AM 02 (Pl. 1, Fig. 3) are lower left third molars. Both are in light wear. The crowns are bilophodont with a labially positioned talonid cusp. Apart from the off-centred talonid these teeth are similar to second molars.

PQ AD 1661 is a right P4/ (Pl. 1, Fig. 6). It is moderately worn with three main areas of dentine exposure, two lingually and one labially. The labial cusp has an indentation on its lingual border suggesting that it is incipiently doubled. The anterolingual cusp is slightly smaller than the posterolingual one.

PQ AD 299 (Pl. 1, Fig. 2) is a poorly preserved upper third molar, the enamel surface having been etched by gypsum attack (Harris, 1977, refers to this tooth as AD 229, an M2/). It consists of two lophs with a small talon positioned slightly to the buccal side of the midline.

AD 95’00, a left mandible, contains the second and third molars in light wear. The m/2 is bilophodont with a prominent distal cingulum forming an antero-posteriorly narrow shelf which is slightly less wide than the main cusps. The two pretrite cusps

Table 1: Measurements (in mm) of the teeth of *Deinotherium hobleyi* from Auchas and Arrisdrift, Namibia.

Specimen	Length	Breadth
AM 3'93 dM4/	42.4	30.4
AM02 left m/3	66.3	51.9
AM 11 1'97 left m/3	69.0	51.8
Mandible with p/4 to m/3		
p/4	38.7	--
m/1	52.2	--
m/2	60.0	--
m/3	--	--
Right mandible with m/1 to front half of m/3		
m/1	53.3	37.1
m/2	58.5	47.3
m/3	--	51.5
AM 4'99 left m/3	ca 70	--
PQ AD 299 left M3/	58	60
AD 200'97 right p/3	39.0	34.6
PQ AD 1661 P4/	45.3	48.0
PQ AD 650 p/4	47.5	43.2
AD 95'00 left mandible with m/2-m/3		
m/2	57.4	52.9
m/3	68.0	53.3

have crests running from their tips obliquely towards the midline of the crown. The third molar is bilophodont with a well developed but low distal cusplet positioned in line with the pretrite cusps and extending as a cingulum towards the lingual part of the crown.

Discussion: The deinothere specimens from Auchas and Arrisdrift are typical of the small species *Deinotherium hobleyi* (Andrews 1911, 1914) known from deposits in eastern and northern Africa (Harris, 1973) which is itself similar to small *Deinotherium* species from middle Miocene deposits in Europe such as *D. cuvieri* and *D. bavaricum* (Ginsburg & Chevrier, 2001). Some authors prefer to classify small deinotheres such as *D. hobleyi* in the genus *Prodeinotherium* Ehik, 1930, but, as shown by Ginsburg & Chevier (2001), the features which are supposed to distinguish the two genera from each other are variable and occur in some individuals of both groups. They are thus examples of individual variation and have no value for determining the generic status of the populations in which they occur.

Mammutidae Cabrera, 1929

Genus *Eozygodon* Tassy & Pickford, 1983

Species *Eozygodon morotoensis* (Pickford & Tassy, 1980)

Material: AM 02, skull with right tusk, M1/-M3/ and left P4/, M2/ to M3/ (Pl. 2, Fig. 2-3; Pl. 3-4). AM 02, edentulous skull with section of tusk (Pl. 5). AM 02 1994, worn lower third molar.

Description: Skull. The two skulls are similar in their preserved parts and can be described together.

Palatal view (Pl. 3, Fig. 3; Pl. 5, Fig 4). The front of the snout is damaged but it appears to have been relatively short especially when compared to that of *Progomphotherium*. The tusks are oriented forwards, downwards and slightly outwards, with the enamel band on the external side and slightly ventrally. Behind the tusk there are long diastemata edged by sharp crests (the inter alveolar crests of the maxilla) which curve sagittally before swinging outwards to the front of P4/. P4/ to M3/ form a closed series and all the cheek teeth are in wear at the same time. The palate is widest at the M2/, the tooth rows converging anteriorly and posteriorly producing curved occlusal surfaces in palatal view. The palate is deep, especially between the two first molars. The posterior choanae are immediately behind the rear of the third molars. The anterior root of the zygomatic process of the maxilla departs from the face on a level with the front of the first molar and it swings slightly forwards as it rises towards the orbits. The infraorbital foramen is tucked into a niche just anterior to the root of the zygomatic. The rear edge of the zygomatic process of the maxilla leaves the face on a level with the middle of the second molar.

The basicranial portion of the skull is located well above the plane of the palate, much as in *Anancus* (Tassy, 1986, fig. 35). This position effectively greatly shortens the rear part of the skull compared with *Progomphotherium* with the result that the occipital condyles are high and close behind the palate. The angle between the midline of the palate and the basicranium is 35° in the edentulous palate and 45° in the complete skull. *Lateral view* (Pl. 3, Fig. 2; Pl. 5, Fig. 2). In lateral view the skull is high and almost square in proportions with a projecting snout. The orbit is located above the first and second molars and the infra-orbital foramen is positioned above the fourth premolar. The premaxilla is directed forwards and ventrally with the upper tusk curving in the same sense. The maxilla-premaxilla suture zigzags on the lateral surface of the skull from the anterior of the snout to the superior antorbital foramen. The occipital condyles project distally well beyond the occiput which slopes anteriorly from the condyles to the dorsal surface of the skull. This is in marked contrast to many gomphotheres in which the occiput overhangs the condyles. The external auditory meatus and the occipital condyles are in line with each other, whereas in most gomphotheres the meatus is located in a position well anterior to the occipital condyles.

Dorsal view (Pl. 3, Fig. 1; Pl. 5, Fig. 1). In dorsal view the temporal lines curve towards each other distally from above the postorbital bar and their closest approach is at the posterior end of the skull. This contrasts with gomphotheres where the temporal lines approach each other distally and then diverge as they approach the occipital area. The widest part of the skull is the distal end of the zygomatic arch which projects well beyond the lateral flanges of the occipital. Even though the nasals are incomplete in both of the Auchas skulls, the impression is that they were weakly developed and did not greatly overhang the nasal *fossa*. The rostral trough in the complete skull is relatively shallow, whereas in the other one it is deep. The rostral region broadens slightly towards the anterior of the snout, the tusks diverging from each other at a small angle.

Posterior view (Pl. 4, Fig. 1; Pl. 5, Fig. 5). In posterior view the occipital bones slope forwards from the occipital condyles to the dorsal surface. There is a large nuchal *fossa* which reaches almost to the top of the occiput.

Basicranial flexure, Both skulls of *Eozygodon* from Auchas have markedly reflexed basicrania, with the occipital condyles well above the level of the palate.

Dentition. (Pl. 2, Fig. 2-3, Pl. 3, Fig. 3). The cheek teeth are similar in size and morphology to those of the holotype from Moroto, Uganda and referred material from Meswa Bridge, Kenya (Pickford & Tassy, 1980; Tassy & Pickford, 1983). The P4/ is quadricuspidate, forming a bilophodont crown. There is a deep sulcus between the two anterior cusps, but wear of the distal loph has proceeded to the stage where the sulcus has been eradicated. The main cusps are antero-posteriorly compressed, as are the lophs in the molars.

The upper first molar is deeply worn with the pretrite cusps completely worn away. The labial edges of the posttrite cusps reveal that the crown was trilophodont, but the fine details of the cusps have been destroyed.

The second molars are also trilophodont with narrow anterior, lingual and posterior cingula. There are also cingular remnants in the buccal ends of the transverse valleys. Wear has eradicated much of the cusp morphology, but it is possible to see that the lophs were antero-posteriorly compressed and that the median sulcus is deep and separates the pretrite half from the posttrite half even when the crowns are deeply worn. The pretrite cusps produce a weakly trefoil-shaped dentine lake in advanced wear whereas the posttrite cusps produce a compressed oval dentine exposure.

The third molars differ from the second ones by their greater dimensions and the possession of a better developed distal cingulum. At the distobuccal corner of the tooth there is a prominent cusplet defining the end of the distal cingulum. The third molars are not heavily worn and the antero-posterior compression of the cusps is clearly expressed. It is possible to see that the four main cusps (protocone, paracone, metacone, hypocone) are accompanied by mesocones (conelets of Tobien, 1975, 1978) located between the main cusps and the median sulcus. These mesocones are in line with the main cusps and with each other, forming a straight loph-like structure interrupted only by the median sulcus. Anterior and posterior conules are reduced to such an extent that the transverse valleys are unobstructed from buccal to lingual sides. Zygodont crests are well developed on the buccal ends of the posttrite main cusps.

A lower left third molar from Auchas is deeply worn and reveals nothing about the morphology of the two anterior lophs. The talonid is short and simply constructed, the third loph being composed of antero-posteriorly compressed cusps, the lingual ones being somewhat twisted with respect to the labial ones, and the distal cingulum being offset to the buccal side of the crown.

In the edentulous skull from Auchas, the cheek tooth roots are preserved (Pl. 5, Fig. 4). These reveal that in the P4/ and the three molars, there are two compressed transversely oriented roots on the buccal two thirds of the crown and one elongated, compressed lingual root. The upper tusk is oval in section with a flat lateral part covered in enamel.

Discussion and comparisons: The Auchas specimens of *Eozygodon morotoensis* are important because they represent the first skull material ever found of the genus. A major surprise is how greatly flexed the basicranium is, in this respect being more like a late Miocene proboscidean *Anancus* (Tassy, 1986) than one from the early Miocene. The skull is high, and contrasts strongly with the much flatter skull of *Progomphotherium* from the same deposits. The temporal fossae are further apart in *Eozygodon* than they are in *Archaeobelodon* and *Gomphotherium*, the closest that the temporal lines approach each other is near their posterior ends where they are 140 and 150 mm apart in the two specimens, in contrast with 130 mm in *Archaeobelodon* aff. *filholi* from Mwiti, Kenya (Tassy, 1986). The anterior course of the temporal lines is displaced forwards compared to the situation in *Progomphotherium maraisi*. In effect the lines are directed vertically upwards from just behind the orbits, before turning rearwards, whereas in *P. maraisi*, the lines angle steeply upwards and rearwards from their origin behind the orbit. Furthermore, the point of nearest approach of the temporal lines in *Eozygodon* is at their junction with the occipitals, whereas in other gomphotheres, the temporal lines diverge distally from their point of nearest approach which is well forwards of the occipitals. Even though the material is incomplete, it appears that the nasals of *Eozygodon* do not project as far anteriorly as they do in *P. maraisi* but the external choanae are similarly wide from side to side and narrow dorsoventrally. The zygomatic arches leave the face appreciably further forwards in *Eozygodon* than in *P. maraisi*. In *Eozygodon*, the anterior and posterior edges of the zygomatic root lie opposite the front of the first molar and the middle of the second molar respectively, in contrast to *P. maraisi* where they lie opposite the front of the second molar and the middle of the third molar respectively.

The layout of the tooth rows in *Eozygodon* and *Progomphotherium maraisi* is quite different, those of *Eozygodon* being widest at the second molar and converging both anteriorly and posteriorly, whereas those of *P. maraisi* diverge from the fourth premolar back to the third molar. In adults of both genera the posterior choanae lie between the distal ends of the third molars.

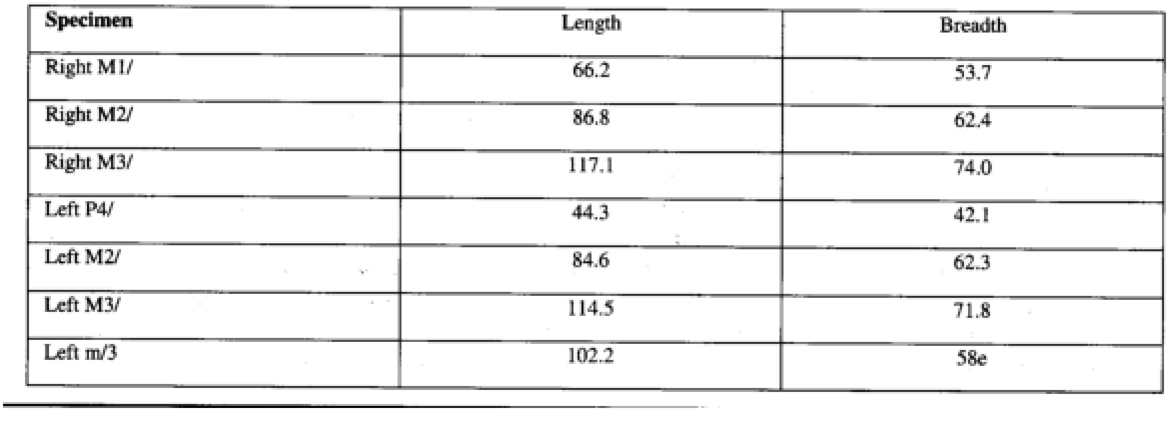
A less complete skull from Auchas (AM 02) provides additional evidence of the size and proportions in *Eozygodon morotoensis*, and yields precious information about variability in this species.

The major differences in skull structure between *Eozygodon* and *Progomphotherium* are as marked as the differences in the dentition, and it is probable that the lineages diverged a considerable time prior to the early Miocene, providing some support for the phylogenetic hypothesis of Tobien (1978) in which the zygodont and bunodont proboscideans of the Miocene evolved from *Phiomia* and *Palaeomastodon* respectively.

Family Gomphotheriidae Hay, 1922
Genus *Progomphotherium* nov.

Diagnosis: Small gomphothere with short but massive mandibular symphysis with deep dorsal gutter, lower tusks with ovoid section oriented with greatest diameter of section vertical and with no grooves, m/3 with 3.5 lophids, marked angle between dorsal profiles of splanchnocranium and neurocranium, basicranium almost in same plane as palate, squamosals and occipitals not widely flaring laterally, zygomatic process

Table 2: Measurements (in mm) of the teeth od *Eozygodon morotoensis* from Auchas, Namibia



Specimen	Length	Breadth
Right M1/	66.2	53.7
Right M2/	86.8	62.4
Right M3/	117.1	74.0
Left P4/	44.3	42.1
Left M2/	84.6	62.3
Left M3/	114.5	71.8
Left m/3	102.2	58e

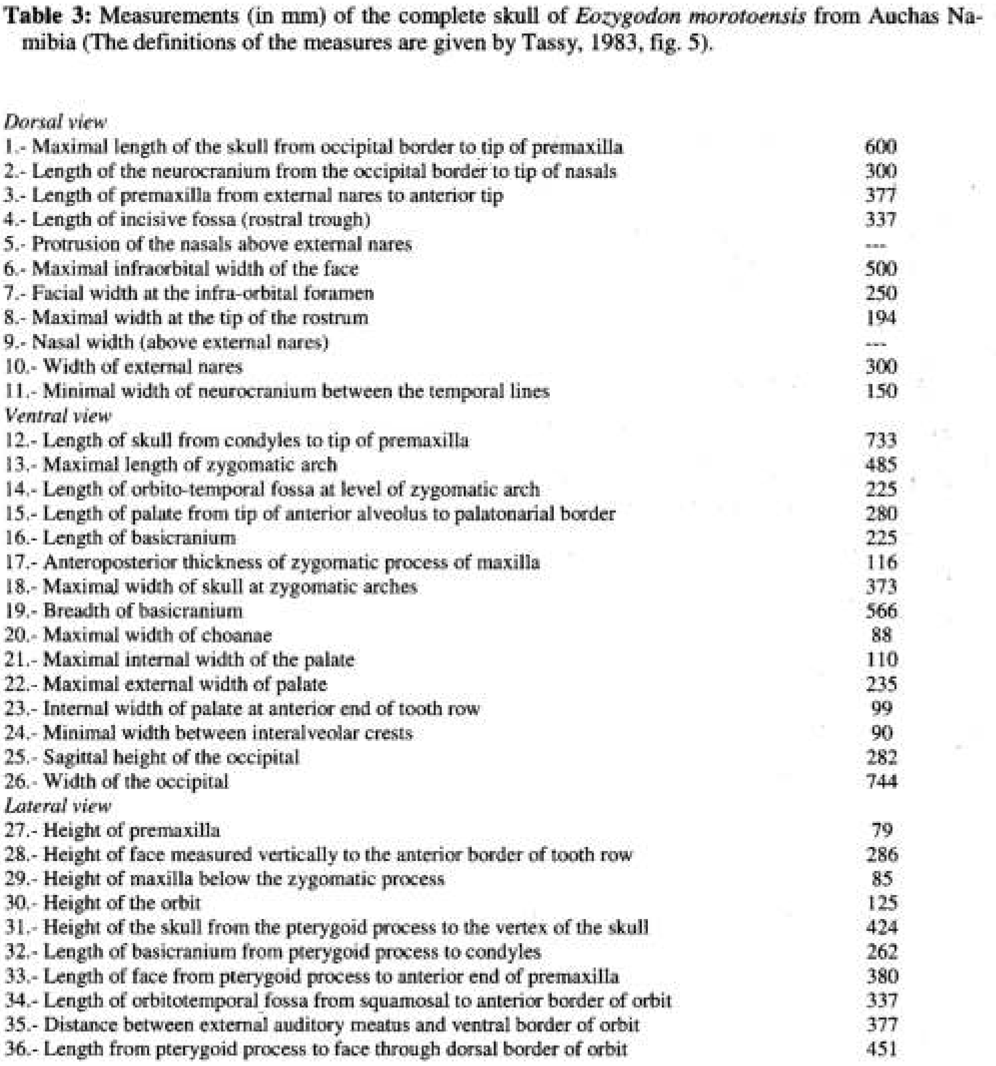


Table 3: Measurements (in mm) of the complete skull of *Eozygodon morotoensis* from Auchas Namibia (The definitions of the measures are given by Tassy, 1983, fig. 5).

Dorsal view	
1.- Maximal length of the skull from occipital border to tip of premaxilla	600
2.- Length of the neurocranium from the occipital border to tip of nasals	300
3.- Length of premaxilla from external nares to anterior tip	377
4.- Length of incisive fossa (rostral trough)	337
5.- Protrusion of the nasals above external nares	---
6.- Maximal infraorbital width of the face	500
7.- Facial width at the infra-orbital foramen	250
8.- Maximal width at the tip of the rostrum	194
9.- Nasal width (above external nares)	---
10.- Width of external nares	300
11.- Minimal width of neurocranium between the temporal lines	150
Ventral view	
12.- Length of skull from condyles to tip of premaxilla	733
13.- Maximal length of zygomatic arch	485
14.- Length of orbito-temporal fossa at level of zygomatic arch	225
15.- Length of palate from tip of anterior alveolus to palatonarial border	280
16.- Length of basicranium	225
17.- Anteroposterior thickness of zygomatic process of maxilla	116
18.- Maximal width of skull at zygomatic arches	373
19.- Breadth of basicranium	566
20.- Maximal width of choanae	88
21.- Maximal internal width of the palate	110
22.- Maximal external width of palate	235
23.- Internal width of palate at anterior end of tooth row	99
24.- Minimal width between interalveolar crests	90
25.- Sagittal height of the occipital	282
26.- Width of the occipital	744
Lateral view	
27.- Height of premaxilla	79
28.- Height of face measured vertically to the anterior border of tooth row	286
29.- Height of maxilla below the zygomatic process	85
30.- Height of the orbit	125
31.- Height of the skull from the pterygoid process to the vertex of the skull	424
32.- Length of basicranium from pterygoid process to condyles	262
33.- Length of face from pterygoid process to anterior end of premaxilla	380
34.- Length of orbitotemporal fossa from squamosal to anterior border of orbit	337
35.- Distance between external auditory meatus and ventral border of orbit	377
36.- Length from pterygoid process to face through dorsal border of orbit	451

of maxilla departs from face at a right angle, two infraorbital foramina located along anterior margin of zygomatic process of maxilla, M3/ with 3.5 lophs, massive, inflated, main cusps, poorly differentiated mesocones, and small, low posterior pretrite conules. P3/ to M3/ in wear at the same time. Low angle of eruption of M3/ (ca 30°), upper tusks oval with greatest diameter almost vertically oriented, enamel band on ventro-lateral aspect. Rostrum not flaring greatly anteriorly.

Species *Progomphotherium maraisi* nov.

Diagnosis: As for genus.

Holotype: AM 1'95 (Pl. 6, Fig. 1-3), skull with part of right dentition and alveolar portions of both tusks.

Type locality: Auchas, Pit AM 02, Orange River Valley, southern Namibia.

Age: Early Miocene (ca 19-20 Ma).

Etymology: The generic name combines the prefix 'pro', with the sense 'prior to', and the well known generic name *Gomphotherium*. The species name is for Oom Daan Marais, who collected several proboscidean skulls from the Auchas diamond mine, Namibia.

Referred material: AM 7'93, palate with damaged right and left M1/ to M3/ (Pl. 8, Fig. 1-3). AM 4'95, mandible fragment with right m/3 lacking the first two lophs (Pl. 9, Fig. 3). AM 5'99, mandibular symphysis with alveoli for two tusks (Pl. 6, Fig. 4). AM 2'95, maxilla fragment with left M3/ lacking two anterior lophs (Pl. 9, Fig. 4). Auchas, unnumbered deeply worn left M1/ in the Geological Survey Museum, Windhoek. Auchas, 89/214, left M3/ (preserved in the Sperrgebiet Museum, Oranjemund) (Pl. 7, Fig. 2-3).

Description: Skull. The holotype skull of *Progomphotherium maraisi* was collected in five main pieces which could be fitted together by aligning the broken edges together. Thus even though there are substantial pieces of surface bone missing, good contacts could be found be-tween each piece. The reconstruction is thus reliable and reveals that the specimen was not seriously distorted in the sediment, which is often the case with proboscidean skulls on account of the pneumatised bone which tends to deform relatively easily. The broken surface of the skull reveals that the neurocranium was heavily pneumatised.

The teeth were recovered by screening the dumps in which

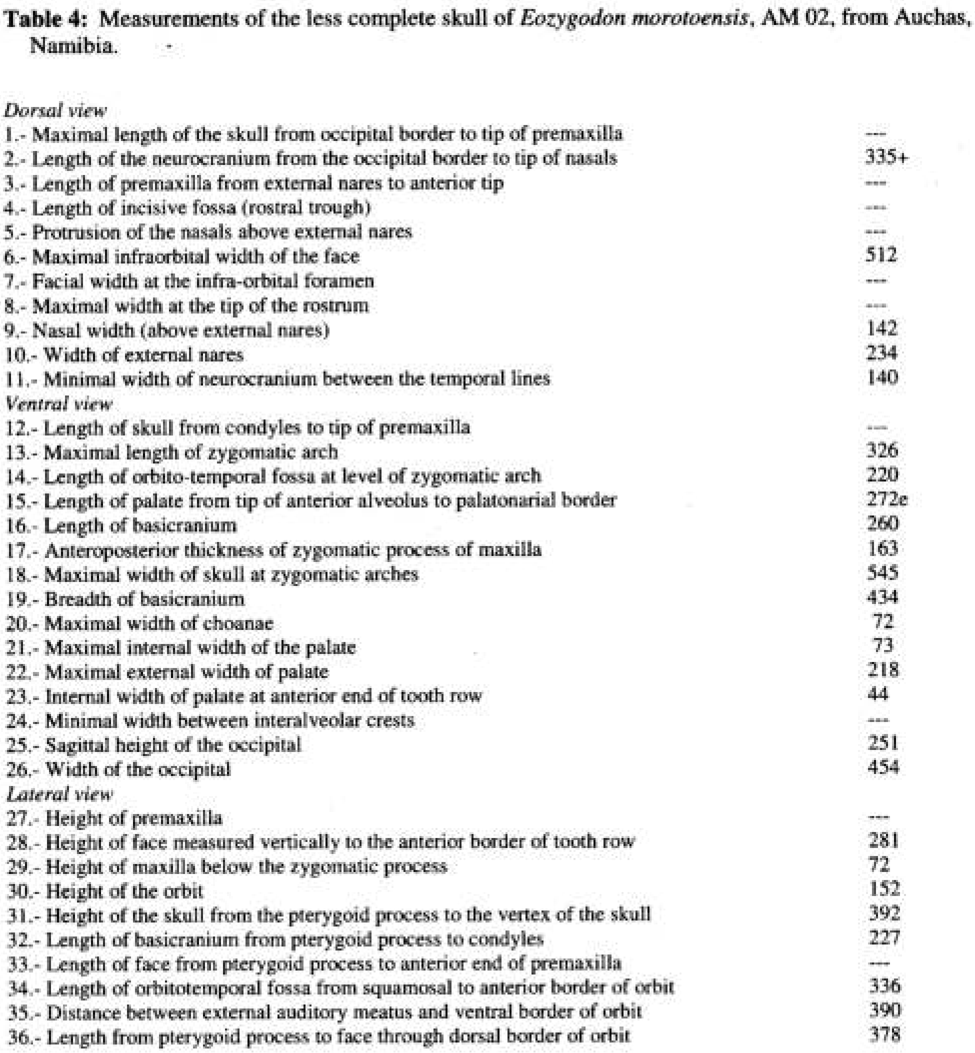


Table 4: Measurements of the less complete skull of *Eozygodon morotoensis*, AM 02, from Auchas, Namibia.

Dorsal view	
1.- Maximal length of the skull from occipital border to tip of premaxilla	---
2.- Length of the neurocranium from the occipital border to tip of nasals	335+
3.- Length of premaxilla from external nares to anterior tip	---
4.- Length of incisive fossa (rostral trough)	---
5.- Protrusion of the nasals above external nares	---
6.- Maximal infraorbital width of the face	512
7.- Facial width at the infra-orbital foramen	---
8.- Maximal width at the tip of the rostrum	---
9.- Nasal width (above external nares)	142
10.- Width of external nares	234
11.- Minimal width of neurocranium between the temporal lines	140
Ventral view	
12.- Length of skull from condyles to tip of premaxilla	---
13.- Maximal length of zygomatic arch	326
14.- Length of orbito-temporal fossa at level of zygomatic arch	220
15.- Length of palate from tip of anterior alveolus to palatonarial border	272e
16.- Length of basicranium	260
17.- Anteroposterior thickness of zygomatic process of maxilla	163
18.- Maximal width of skull at zygomatic arches	545
19.- Breadth of basicranium	434
20.- Maximal width of choanae	72
21.- Maximal internal width of the palate	73
22.- Maximal external width of palate	218
23.- Internal width of palate at anterior end of tooth row	44
24.- Minimal width between interalveolar crests	---
25.- Sagittal height of the occipital	251
26.- Width of the occipital	454
Lateral view	
27.- Height of premaxilla	---
28.- Height of face measured vertically to the anterior border of tooth row	281
29.- Height of maxilla below the zygomatic process	72
30.- Height of the orbit	152
31.- Height of the skull from the pterygoid process to the vertex of the skull	392
32.- Length of basicranium from pterygoid process to condyles	227
33.- Length of face from pterygoid process to anterior end of premaxilla	---
34.- Length of orbitotemporal fossa from squamosal to anterior border of orbit	336
35.- Distance between external auditory meatus and ventral border of orbit	390
36.- Length from pterygoid process to face through dorsal border of orbit	378

the skull fragments were found, but the M1/ and M2/ were shattered into many pieces. The P3/ was not found and it had evidently fallen from its socket prior to fossilisation. The alveolus for P3/ is preserved on both side of the palate, and there can be little doubt that at the time of death this individual possessed P3/ to M2/ in wear and the anterior loph of M3/ coming into wear (Pl. 7, Fig. 1).

Ventral view (Pl. 6, Fig. 3). In the holotype skull (AM 1‘95) the tooth rows diverge from P3/ to M2/, but converge at M3/ because this tooth was still erupting at the time of death. The posterior choanae are damaged but open up about half way along the third molar. The anterior edge of the zygomatic process of the maxilla lies above the front of M2/ and its posterior edge overlies the anterior loph of the third molar. P3/ to M3/ are in use at the same time. The part of the snout anterior to the P3/ is relatively short (110 mm) although the rostrum as a whole is elongated. Part of the basisphenoid is preserved and retains portions of both carotid canals, and lateral to these are two large foramina on each side, the foramen ovale + foramen lacerum medium and the posterior opening of the alisphenoid canal.

In the adult snout AM 7’93, the molars lie in a straight line and the two tooth rows diverge to the rear. The posterior choanae open up between the talons of the upper third molars. The anterior edge of the root of the zygomatic process of the maxilla departs from the face at a right angle on a level with the rear of the first molar, whilst its rear edge lies over the third loph of the third molar. It departs from the maxilla at a right angle and in this respect is markedly different from the root of the zygomatic process in *Gomphotherium angustidens* and *Archaeobelodon filholi* which leave the face at a gentle angle.

Dorsal view (Pl. 6, Fig. 1). In AM 7’93 (Pl. 8, Fig. 2), the rostral trough is broad and extends as far back as the front loph of the third molar. In the type specimen, the trough is roughly parallel sided, its lateral walls not diverging anteriorly. Indeed, even though the tips of the premaxillae are broken, it is possible to observe that the lateral wall of the rostral trough on the right side swings medially as it approaches the anterior tip of the snout. The centre line of the trough is slightly raised to form a median rostral crest or ridge. Because of the shape of the rostral trough, the upper tusks would hardly have diverged, the preserved parts of the tusks *in situ* in the snout being virtually parallel to each other.

The external nares are slightly narrower overall than the rostrum, whereas in the Mwiti skull assigned to *Gomphotherium* sp. (Tassy, 1986) they are appreciably wider. In AM 1’95, the nasals overhang the external nares, but their tips are broken away. The suture between the nasals and the frontals is well marked in this skull, forming a clearly visible, uncomplicated line. The temporal lines are relatively close together, the minimal distance between them being 70 mm. The squamosals flare laterally to a small extent, the width of the brain case at the squamosals being less than its width at the orbital processes of the frontal bone. In the Mwiti skull assigned to *Archaeobelodon* aff. *filholi* by Tassy (1986) the squamosals flare laterally to a much greater extent, and the width of the brain case measured at the margins of the squamosals is appreciably greater than it is taken at the postorbital processes of the frontals.

Lateral view (Pl. 6, Fig. 2). The skull of *Progomphotherium maraisi* is low and elongated. The basicranium is not redressed and it consequently lies in almost the same plane as the palate. The angle between the occlusal plane and the occlusal surface of the third molar which is in the process of erupting is about 27° (Figure 4). In proboscideans with strongly reflexed basicrania, such as *Loxodonta africana*, the angle of eruption of the upper third molars is considerably steeper (87° according to Beden, 1979). Low angles of eruption occur in European *Gomphotherium* and *Archaeobelodon* and a steeper angle (ca 40°) in *Paratetralophodon hasnotensis* from the Siwaliks of Pakistan (Tassy, 1983). An even steeper angle of eruption (73°) occurs in African *Tetralophodon* from Samburu Hills (Nakaya *et al.*, 1987, give a figure of 117° which is 180°-73°). In this respect, *Progomphotherium* is primitive, being barely more derived than *Phiomia*. The neurocranium and the splanchnocranium of *Progomphotherium* are almost equal in length - the orbit is virtually in the midline of the skull.

The lower infraorbital foramen is large and is located immediately in front of the anterior root of the zygomatic process of the maxilla, and the upper infraorbital foramen is directly above it. The position of these foramina differs from the situation in *Gomphotherium angustidens* and *Archaeobelodon filholi*, where the lower foramen is below the root of the zygomatic process and the upper foramen is above it. In AM 7'93 the lower foramen is located above the anterior loph of the M2/ whereas in the holotype, a young adult with M3/ still erupting, it is positioned marginally more anteriorly between the M1/ and M2/.

The lachrymal bone is entirely within the orbit. It is broadly triangular in outline with a prominent lachyrmal canal, and the base of a lachrymal spine is present though the apophysis itself has broken away. Below and behind the lachrymal there is a large foramen which leads anteriorly to emerge as the infraorbital foramina. The suture between the maxilla and the frontal passes from the inner extremity of the lachrymal bone obliquely downwards towards the foramen rotundum and the anterior opening of the alisphenoid canal, both of which are hidden behind a thin flange of frontal bone. The postorbital process of the frontal sends a crest of bone (the orbito-temporal crest) obliquely downwards and slightly distally towards the anterior opening of the alisphenoid canal, thus separating the orbital from the temporal *fossa*.

In lateral view the dorsal profile of the skull rises from the tip of the premaxillae to the nasals, and then bends downwards towards the occiput, making an angle of about 120° between the dorsal profiles of the splanchnocranium and the neurocranium. This contrasts with the Mwiti skull (Tassy, 1986) and *Gomphotherium angustidens* in which the dorsal surface of the parietals is more nearly in line with the dorsal profile of the premaxillae. A result of this morphology is that the external nares are proportionally higher and narrower than they are in other gomphotheres.

The suture between the premaxilla and maxilla is well developed on the right side and runs in a slightly zigzag but almost straight line from the front of the snout towards the upper infraorbital foramen.

Anterior view. The upper tusks are oval (Fig. 1), with the greater diameter almost vertical, the long axes leaning slightly inwards dorsally. There is a band of enamel on the ventro-lateral surface of the right tusk. The snout section is 8-shaped, with deep palatal and rostral troughs (Fig. 1).

Posterior view. In posterior view, the occipital surface is relatively flat in the supraoccipital part with swollen lateral portions. The nuchal line is distinguishable as a raised feature at the contact of the supraoccipital and the parietal. The *fossa* for the nuchal ligament is well developed and deep and the sagittal crest within the *fossa* is narrow but strong. The lower parts of the supraoccipital and the exoccipitals have broken away.

Mandible. The only gomphothere mandible fragments from Auchas are a symphysis with matrix-filled alveoli of the lower

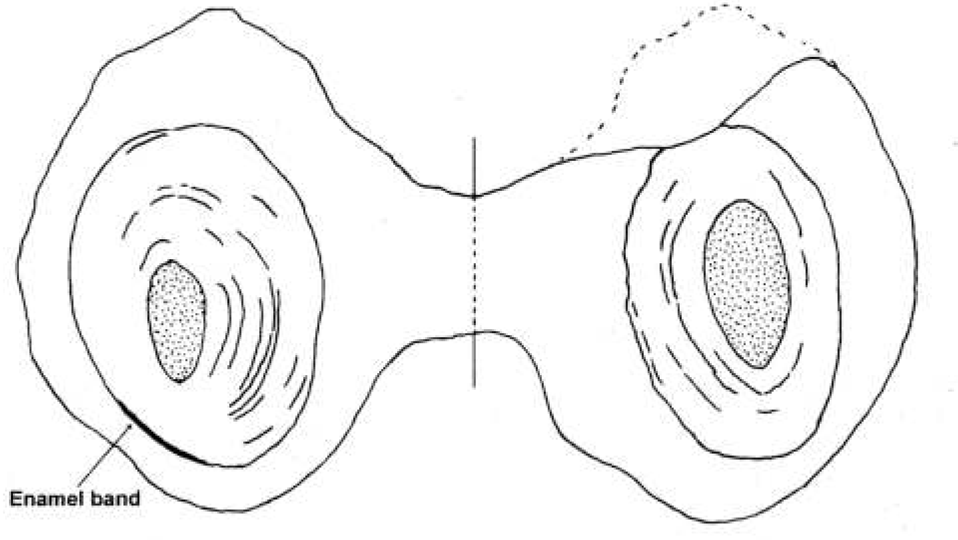


Figure 1: Section through the anterior part of the snout of *Progomphotherium maraisi* showing the orientation of the upper tusks and the position of the enamel band on the ventrolateral side.

Table 5: Measurements (in mm) of the skull of *Progomphotherium maraisi* (The definitions of the measures are provided by Tassy, 1983, fig. 5).

Dorsal view	
1.- Maximal length of the skull from occipital border to tip of premaxilla	706
2.- Length of the neurocranium from the occipital border to tip of nasals	ca 270
3.- Length of premaxilla from external nares to anterior tip	ca 450
4.- Length of incisive fossa (rostral trough)	350
5.- Protrusion of the nasals above external nares	ca 40-50
6.- Maximal infraorbital width of the face	320 (160 x2)
7.- Facial width at the infra-orbital foramen	240
8.- Maximal width at the tip of the rostrum	200
9.- Nasal width (above external nares)	ca 90
10.- Width of external nares	115
11.- Minimal width of neurocranium between the temporal lines	70
Ventral view	
12.- Length of skull from condyles to tip of premaxilla	---
13.- Maximal length of zygomatic arch	---
14.- Length of orbito-temporal fossa at level of zygomatic arch	187
15.- Length of palate from tip of anterior alveolus to palatonarial border	ca 300
16.- Length of basicranium	---
17.- Anteroposterior thickness of zygomatic process of maxilla	106
18.- Maximal width of skull at zygomatic arches	---
19.- Breadth of basicranium	---
20.- Maximal width of choanae	---
21.- Maximal internal width of the palate	90
22.- Maximal external width of palate	188 (94 x 2)
23.- Internal width of palate at anterior end of tooth row	88
24.- Minimal width between interalveolar crests	ca 107
25.- Sagittal height of the occipital	---
26.- Width of the occipital	290 (145 x2)
Lateral view	
27.- Height of premaxilla	122
28.- Height of face measured vertically to the anterior border of tooth row	132
29.- Height of maxilla below the zygomatic process	48
30.- Height of the orbit	101
31.- Height of the skull from the pterygoid process to the vertex of the skull	ca 310
32.- Length of basicranium from pterygoid process to condyles	---
33.- Length of face from pterygoid process to anterior end of premaxilla	ca 390
34.- Length of orbitotemporal fossa from squamosal to anterior border of orbit	230
35.- Distance between external auditory meatus and ventral border of orbit	---
36.- Length from pterygoid process to face through dorsal border of orbit	ca 260

tusks and a portion of right ramus with part of the third molar preserved. The right side of the symphyseal portion is partly broken but the left side is complete from the anterior end to the posterior margin of the symphysis (Fig. 2). The symphysis is not greatly elongated, and in a gomphotherian context would be described as brevirostral. It is certainly much shorter than the symphyses of *Gomphotherium angustidens* from Europe, *Archaeobelodon* species and *Afromastodon libycus*.

Dorsally there is a deep gutter between the left and right diastemal ridges. In section the symphysis is widest at about half its height. In lateral view there are two mental foramina below the diastema, the lower one being larger and more anteriorly positioned than the upper one. The alveoli for the tusks are taller than they are broad, the outline being a compressed oval with the median side relatively flat. The alveoli are separated from each other by a thin plate of bone.

The symphysis is short in comparison with those of other longirostral gomphotheres such as *Archaeobelodon* and European species of *Gomphotherium*, its total length being ca 200 mm compared with its dorsoventral depth of 125 mm and its breadth of ca 200 mm. In *Archaeobelodon* and *Gomphotherium* the mandibular symphyses are considerably longer. In *Archaeobelodon*, the lower tusk is twisted longitudinally to such an extent that the greatest diameter is horizontal where it emerges from the tip of the symphysis, but is more nearly vertical where the root terminates inside the mandible (Tassy, 1986, text-fig. 15). In *Progomphotherium* in contrast, the long diameter of the tusk section is almost vertical where it emerges from its alveolus.

Upper Dentition. The alveolar portions of the upper tusks are preserved in AM 1‘95. They are slightly compressed oval in section with an enamel covering on the ventro-lateral surface. The tusks extend well back into the skull at least as far as the first molar if not further. They appear to diverge very slightly as they emerge from their alveoli and are oriented with the long axis of the section almost vertically.

In the skull, AM 1‘95, there is a well preserved alveolus for the upper third premolar on both sides, immediately behind which there is the P4/ in its socket. The P4/ in AM 1‘95 is a quadricuspidate tooth, but it is too worn to reveal much about its morphology. The first and second molars in AM 1‘95 are so broken that virtually nothing can be said about their morphology even though it is possible to estimate their lengths and breadths. The first two lophs and the pretrite half of the third loph of the upper right third molar are complete and unworn, the tooth having been in the process of erupting when the individual died. The pretrite half of the first loph has an extremely poorly developed mesocone which is barely distinguishable from the main cusp, being demarcated from it by two shallow grooves. It is positioned slightly posteromedially from the

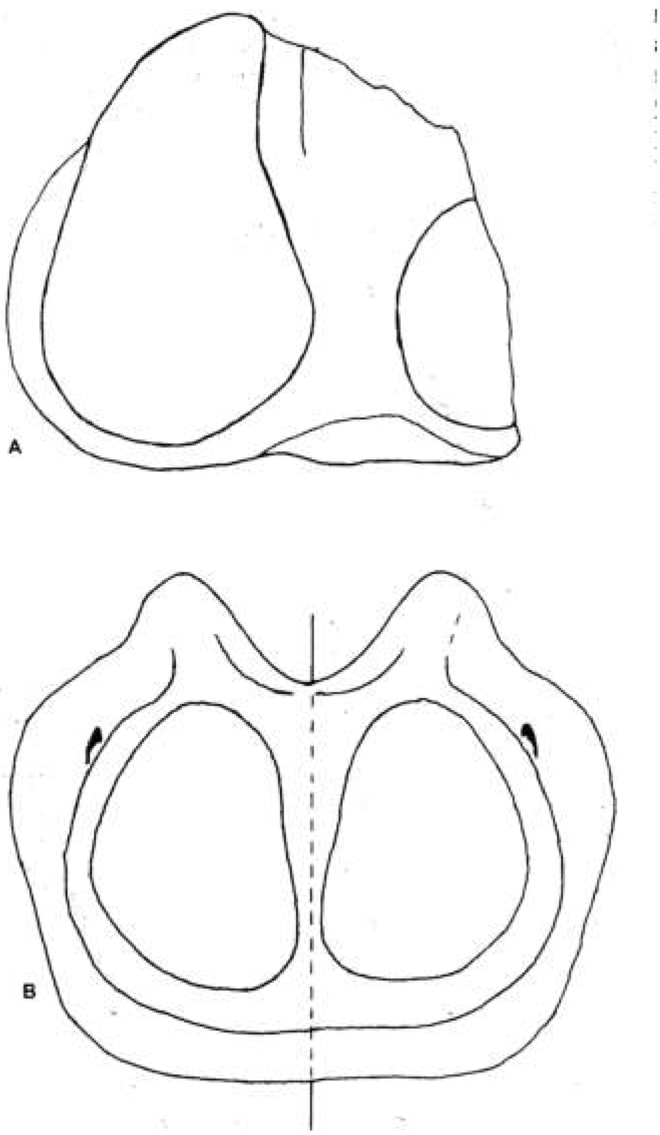


Figure 2: Transverse sections of the symphysis of *Progomphotherium*. A = Mfwangano specimen, B = Auchas specimen (reconstructed) by mirror imaging. Note that the lower tusks (or their alveoli) are taller than broad.

main cusp. There is a large anterior conule which merges into the anterior cingulum by way of a smaller conule. The posterior conule of the first pretrite is appreciably smaller and lower than the anterior one, but it interrupts the transverse valley to some extent.

The second pretrite has a well developed mesocone in the same transverse line as the entire loph. The anterior conule is smaller but helps to block the transverse valley. The posterior conule is low, being only about half the height of the crown. The third pretrite is simple, with a large mesocone poorly demarcated from the main cusp and there are no anterior and posterior conules.

The first posttrite is simple with the faintest of mesocone development and has no sign of an anterior conule and a tiny posterior one. The second posttrite is similar in morphology to the first but the mesocone and posterior conule are somewhat better developed. There are low cusps in the transverse valleys between the posttrite halves of the lophs, but these do not appear to be homologous to posterior conules. The labial cingulum extends across the buccal ends of the transverse valleys.

In the palate AM 7'93 (Pl. 8, Fig. 1), the intermediate molars are trilophodont and the third upper molar has three and a half lophs. The mesocones are small and close to the main cusps. The anterior conules of the first and second pretrites are large and block the transverse valleys. The posterior conules are low and small, but in heavy wear contribute to the development of a trefoil dentine outline. The mesocones of the posttrites are close to the main cusps and there are no conules, so that the dentine lakes produced by wear are oval in outline. The talon and talonid cusps of the upper and lower third molars are simple, with mesocones closely applied to the main cusps. The anterior conules, if present, are small, and there are no posterior conules. In the third molars the talonid is slightly better differentiated than the talon, as is usual in bunodont proboscideans (Tobien, 1975, 1978).

Eruption angle of the upper third molar

The M3/ in the holotype of *Progomphotherium maraisi* is in the process of erupting, with the anterior loph already at the occlusal level. In lateral view the crown is angled at about 27° to the occlusal surface, whilst in palatal view it is oriented with its posterior end closer to the sagittal plane than its anterior end. In the fully adult specimen, AM 7'93, the M3/ is in line with and at the same level with the rest of the cheek teeth, indicating that as it erupts the rear of the third molar migrates laterally and rotates occlusally about an axis near the anterior loph. However, these motions are relatively modest in comparison with the situation in 'tetralophodonts' and Elephantidae (Fig. 4).

Lower dentition. A fragment of mandibular symphysis found near AM 1'95 (Pl. 6, Fig. 4), contains the alveoli of the lower tusks. In section the alveolus is a flat sided oval, with the greater diameter of the cross section almost vertical and there is no sign of a sulcus or groove in the outline of the section. The alveolus is 65 mm high by 46 mm broad. The alveolus passes backwards beyond the rear margin of the symphysis, but it is not known how far it would have extended into the body of the mandible.

A mandible fragment with the rear half of a right m/3 (AM 4'95) (Pl. 9, Fig. 3) represents a young individual with the third molar in the final stages of eruption. The M3/ in the skull AM 1'95 is at a similar stage of eruption and it may well belong to the same individual. The first two lophs of the m/3 of AM 4'95 are broken off. The third loph consists of massive, bunodont main cusps in line with one another, the pretrite half possessing a small mesocone and a reduced anterior conule. The posttrite consists of a single cusp without mesocone or conules. The fourth loph is even simpler, with no sign of a mesocone on the pretrite side.

Discussion: The Auchas gomphothère is appreciably smaller than *Archaeobelodon* aff. *filholi* and *Gomphotherium* sp. from East Africa (Tassy, 1986) (Fig. 3), and differs from them in a number of morphological details - the Auchas mandibular symphysis is shorter and is not spatulate, the section of the lower tusk is an upright ovoid, without any grooves and its mesial side is relatively flat, quite unlike the flattened, helicoidally twisted tusks of *Archaeobelodon* or the pyriform lower tusks with two grooves that occur in European *Gomphotherium* species (Fig. 4). In addition the symphysis is massively constructed, much more so than in either *Gomphotherium* and *Archaeobelodon*. The upper third molar has 3.5 lophs and the mesocones of the upper third molars are in line with the anterior conules. In most of these dental characters (apart from the mesocones being poorly differentiated from the main cusps and the posterior pretrite conules being low and small) the Auchas fossils are closer to species of *Gomphotherium* than to any other genus but in cranial and mandibular features the Auchas material diverges significantly from *Gomphotherium*. For instance, the mandibular symphysis from Auchas is shorter than it is in *Gomphotherium angustidens*, the zygomatic process of the maxilla departs from the face at a right angle in sharp contrast to the gentle angle at which it is oriented in *Gomphotherium angustidens* and *Archaeobelodon filholi*, there is marked angulation between the dorsal profiles of the neurocranium and the splanchnocranium, and the margins of the occiput do not overhang the supraoccipital.

In its dentition, the Auchas material is closer to *Gomphotherium* sp. from Mwiti, Kenya (Tassy, 1986) and other taxa belonging to the *Gomphotherium annectens* group (Tassy, 1996a) than it is to *Archaeobelodon* aff. *filholi* from Buluk and Mwiti or *Gomphotherium angustidens* from Europe. The upper third molars have three lophs with a well developed but low distal complex forming the beginning of a fourth loph (counted here as 3.5 lophs). The anterior and posterior pretrite conules are weakly developed. The anteroposterior fissure is deep and separates the pretrite and posttrite halves even when ‘the teeth are moderately worn, and a clear trefoil pattern is not developed with wear. The first and second pretrites have a posterior swelling but not a clear posterior conule. The lophs consist of massive tubercles, two on the pretrite side and three on the posttrite side but these are only weakly subdivided near their tips. Lingually the cingulum of the upper third molar is well developed at the end of the transverse valley. Low, rounded crests are developed on the posterior edges of the buccal cusps.

The section of the lower tusks from Auchas, based on the alveolar shape in the symphysis, is ovoid with a slightly flattened medial surface (Fig. 2) and without any signs of longitudinal grooves or guttering. In section and size (height 65 x breadth 46) the Auchas alveoli are similar to the lower tusks from Mfwangano Island, Kenya, first identified by MacInnes (1942) as those of *Deinotherium hobleyi* but subsequently recognised as belonging to a gomphothere by Tassy (1986) (height 64.3 x breadth 41.8). I agree with Tassy (1986, p. 81) that the greatest diameter of the tusk section is upright, and I presume that the illustration provided by Tassy (1986, fig. 11, I, and Tassy, 1996a, fig. 10-2 b) in which the long axis of the section is oriented horizontally is a lapsus, as is the position of the specimen on the bivariate plot (Tassy, 1986, fig. 4). When plotted correctly (Fig. 5), the Mfwangano and Auchas specimens fall outside the range of variation of *Gomphotherium*, once again highlighting the distinctiveness of the African material.

In the shortness of the symphysis and the oval lower tusks oriented with the long axis of the section more or less vertical, the Auchas specimen recalls “*Gomphotherium” browni* and an indeterminate trilophodont gomphothere illustrated by Tassy (1983, Fig. 25) from the Chinji levels of Pakistan.

Examination of proboscidean lower tusks of various genera reveals that the dorsal surface is consistently more worn than the ventral surface. The Mfwangano tusks are more worn on one aspect than on the other, and if this side is dorsal, then their orientation would be closely similar to those in the Auchas symphysis. The tusks would thus have been somewhat procumbent relative to the occlusal surface of the cheek teeth

Table 6: Measurements (in mm) of the dentition of *Progomphotherium maraisi* from Auchas, Namibia.

Specimen	Length	Breadth
Upper Cheek Teeth		
AM 1'95 right P4/	35.5	34
AM 1'95 right M1/	52	45
Auchas left M1/	64e	40e
AM 1'95 right M2/	92	51e
AM 7'93 right M2/	81.2	50.3
AM 7'93 left M2/	80e	50e
AM 2'95 left M3/	118e	66.2 (measured at second loph)
AM 7'93 right M3/	108e	57e
AM 7'93 right M3/	--	--
OMD 89/214 left M3/	119e	70.5e
AM 1'95 right M3/	121	63
Lower Cheek Teeth		
AM 4'95 right m/3	114e	48e (measured at third loph)
Tusk	Breadth	Height
AM 4'99 left lower tusk	46	65

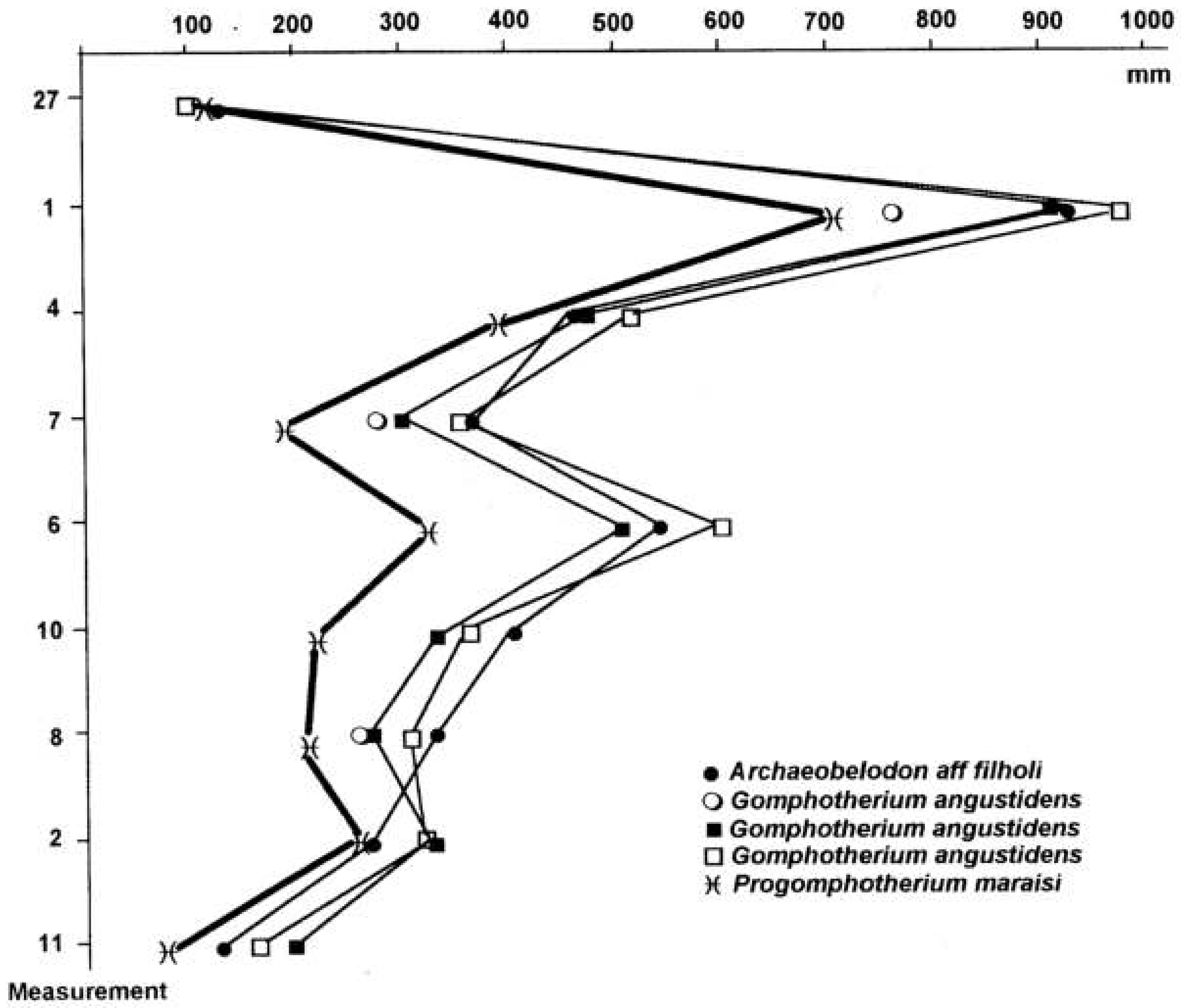


Figure 3: Comparison of measurements of the skull of *Progomphotherium maraisi* with those of *Archaeobelodon* aff. *filholi* from Kenya, and three specimens of *Gomphotherium angustidens* from France (Data for *Archaeobelodon* and *Gomphotherium* are from Tassy, 1986, fig. 17). The diminutive size of *Progomphotherium maraisi* shows clearly in the diagram, as do differences in proportions of the skulls. (Measurement 27 = height of the premaxillaries, 1 = maximum length of the skull measured from the occipital margin to the front of the premaxillae; 4 = length of the incisive fossa taken from the posterior margin of the premaxilla to the front of the snout; 7 = breadth of the face at the level of the lower antorbital foramina; 6 = maximum supraorbital breadth of the face; 10 = width of the nasal fossae; 8 = maximum breadth of the front of the snout; 2 = length of the neurocranium taken from the occipital margin to the point of the nasal bones; 11 = minimum breadth of the neurocranium taken between the temporal lines).

(oriented obliquely downwards). Thus, even though the Auchas symphysis is difficult to orient, lacking, as it does, any part of the body below the cheek teeth, it is possible that it was oriented obliquely downwards, not dissimilar to the Wadi Moghara mandible assigned to *Mastodon spenceri* by Fourtau (1918) (Osborn, 1936) but here considered to represent *Afromastodon libycus*.

The skull from Auchas differs in a number of important respects from those of *Gomphotherium angustidens* from Europe (Tassy *et al.*, 1977). In lateral view *Progomphotherium* has a marked angulation (120°) between the dorsal profiles of the splanchnocranium and neurocranium, whereas in *G. angustidens* the two parts are almost in line with one another (Tassy *et al.*, 1977; Tassy, 1996a). The lateral flare of the squamosals and occipitals is much less in the Auchas specimen than in *G. angustidens*, presumably because, being a much smaller creature, it did not require as massive nuchal muscles to hold the head up than was required by *G. angustidens*. Anteriorly, the rostrum of the Auchas specimen does not flare outwards as much as it does in *Archaeobelodon* and *Gomphotherium angustidens* with the result that the tusks would not have diverged as greatly as in the latter taxa.

The shortness of the Auchas mandibular symphysis is a significant difference from both *Archaeobelodon filholi* and *Gomphotherium angustidens*. Dentally, the Auchas species is extremely primitive within a gomphothere context, but is clearly derived relative to *Palaeomastodon* and *Phiomia*. The poorly developed posterior conules of the pretrites, the weakly differentiated mesocones and massive main cusps indicate that this species is in some features intermediate between the Fayum proboscidean taxa and middle Miocene gomphotheres, but lies closer to gomphotheres than to palaeomastodonts. Furthermore, the specimen has a clear alveolus for P3/ which was apparently lost *post mortem*, and retains the P4/, M1/ and M2/ in wear and the M3/ in eruption, the anterior loph being almost at the occlusal level. In *Gomphotherium angustidens* from Simorre-Tournan, a slightly younger individual shows no sign of P3/ but retains the P4/ and the first and second molars with the third molar erupting (Tassy, 1977). Tassy (1977) remarked that the major innovation acquired by the gomphotheres compared to palaeomastodonts is the "linear progression of the teeth (i.e. : M3 in function after the loss of P4 and M1)". The Auchas species, which retained the third and fourth premolars at least until the third molar was almost erupted, seems to occupy a position intermediate between palaeomastodonts and classic gomphotheres.

The upper, tusks of *Progomphotherium* are oval in section (Fig. 1) with a band of enamel on the lateral side and the greatest diameter oriented almost vertically. The lower tusks are ovoid, with no sign of grooving, not even as weak as the grooves in the lower tusks of *Gomphotherium angustidens*.

Species *Gomphotherium* sp. indet.

Material: AMSE 1'95, worn left M2/ and M3/ germ in a maxilla fragment (Pl. 8, Fig. 1). AMSE 45, lower tusk (Pl. 8, Fig. 2).

Description: A maxilla from Auchas AMSE (Pl. 9, Fig. 1) has a worn M2/ and an unerupted M3/ which falls close to the range of metric variation of *Archaeobelodon* aff. *filholi* from East Africa (Tassy, 1986) but morphologically the molars are closer to those of *Progomphotherium maraisi*. The M2/ is deeply worn and reveals little of its morphology despite the fact that the third molar is still deep in its crypt. The M3/ lies at a marked angle to the occlusal surface of the M2/ (55°) in this respect the eruption angle being different from that in *Progomphotherium maraisi*, in which the M3/ erupts at a much more moderate angle. The two anterior lophs of the third molar in AMSE 1'95 are well preserved except for some damage to the tip of the second posttrite. The mesocones are small and closely applied to the main cusps. The anterior conules are large and block the transverse valleys. The first posttrite possesses a low posterior conule which partly obstructs the transverse valley. The remains of the third loph are similar to the second loph, put the rest of the talon is missing.

A lower tusk from AMSE (Pl. 9, Fig. 2) is relatively straight with a slight curve towards its apex. It is oval in section without any sign of grooves and it has no enamel.

Genus *Afromastodon* nov.

Generic diagnosis: Trilophodont bunodont gomphothere, lower tusks oval in section with no enamel cover, straight up-

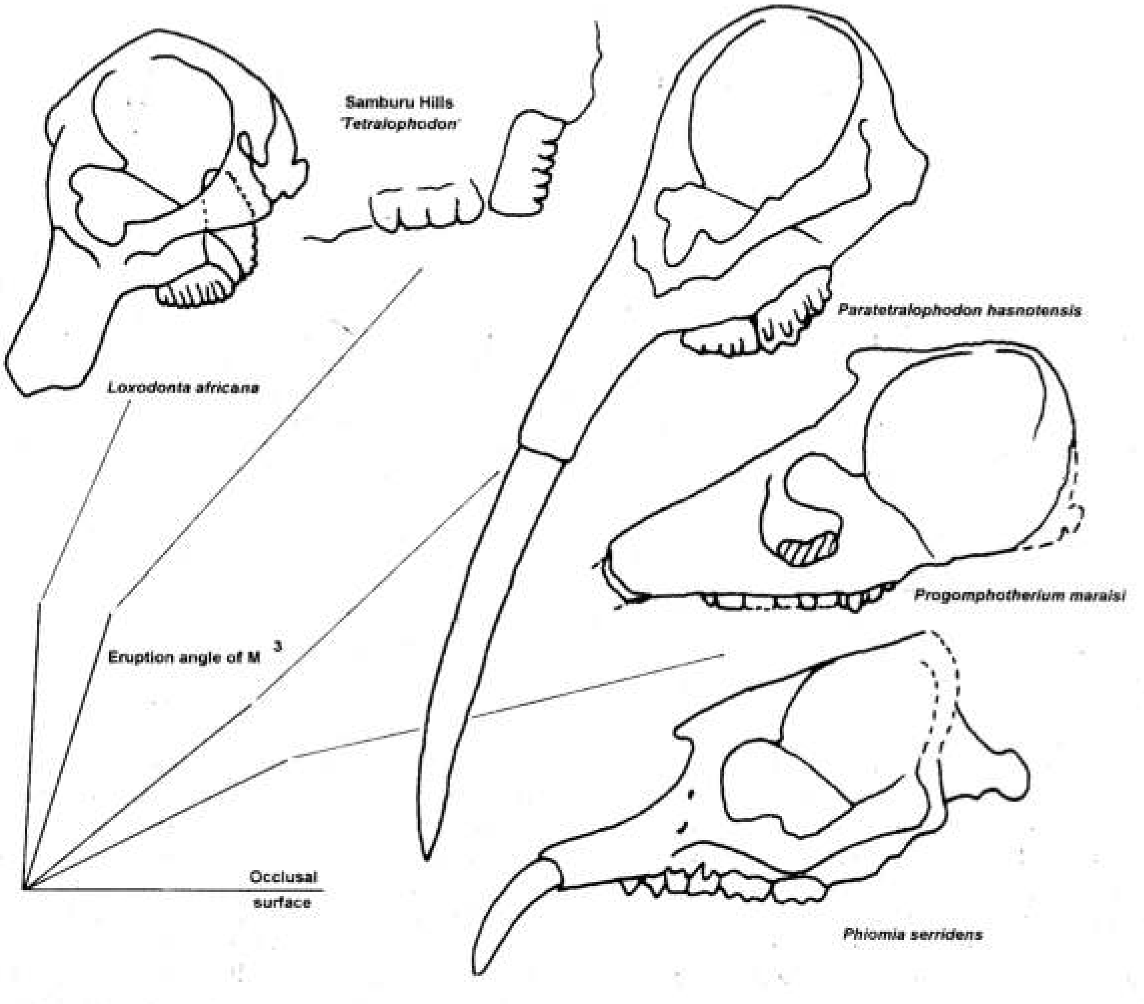


Figure 4: Eruption angles of the upper third molar of various proboscideans showing general tendency for the angle to increase in more derived species with retroflexed basicrania. (*Paratetralophodon* from Tassy (1983); Samburu Hills from Nakaya *et al.*, (1987); *Loxodonta* from Beden (1979)). *Progomphotherium* is intermediate between *Phiomia* on the one hand and *Paratetralophodon* on the other.

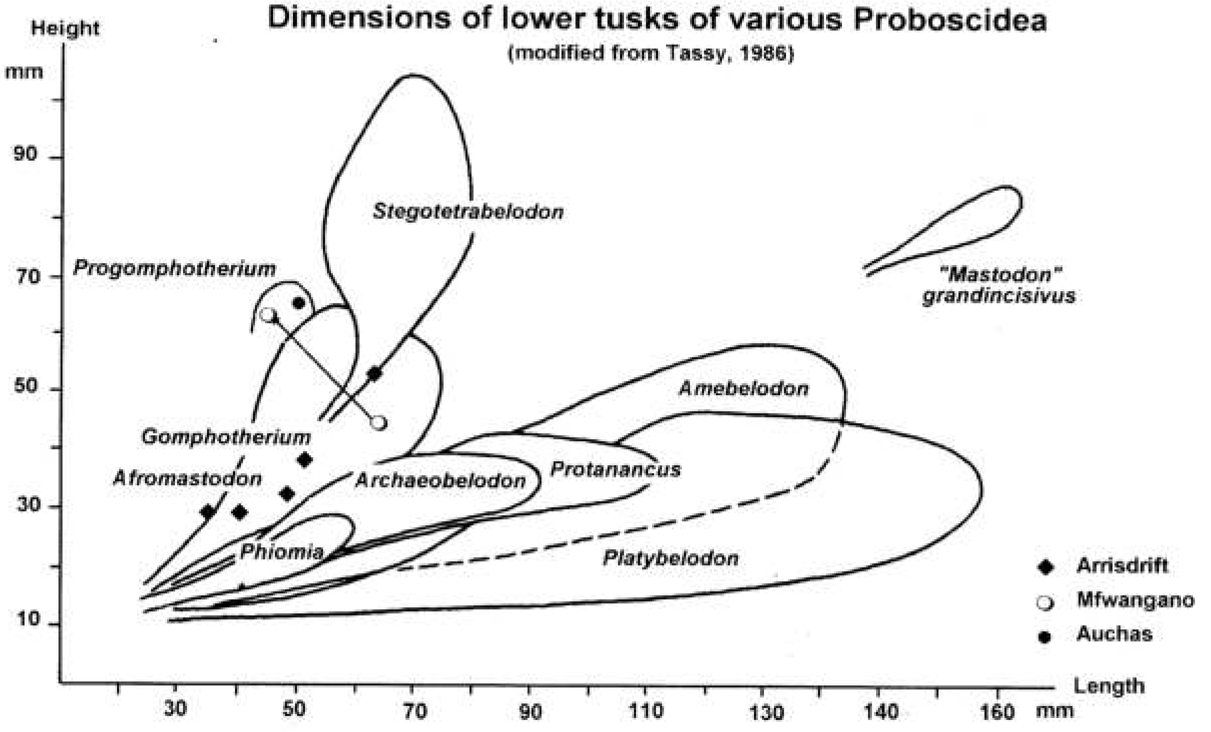


Figure 5: Length - Height plot of lower tusks of various mastodonts. Note that the lower tusks of *Progomphotherium* are higher than wide, differentiating them from *Gomphotherium*. *Afromastodon* lower tusks are oval in outline, which differentiates them from those of *Gomphotherium* which are pyriform in section. No flattened lower tusks have been found in the Orange River deposits. (Figure based on Tassy, 1986, figure 14). Note that the lower tusks from Mfwangano assigned by Tassy (1986) to *Gomphotherium* sp., plot out in the field of *Progomphotherium* when correctly oriented (open circles joined by arrow show alternative plots for the Mfwangano tusks).

per and lower third molars with only minor helicoidal longitudinal twist, well developed median sulcus in molars separating pretrite and posttrite complexes, third pretrite cusps in upper molars rotated so that the mesocone faces into the second transverse valley and the posterior conule lies between the main pretrite cusp and the posttrite cusp, occupying a position analogous to the mesocones of pretrites 1 and 2. One mesocone on pretrite cusps, two mesocones on posttrite cusps. Posttrite cusps without anterior and posterior conules. Zygodont crests on first posttrite cusps moderately developed, poorly developed on second and third posttrites. Sexually bimodal cheek teeth.

Etymology: The generic name combines *Afro* for the African continent with the word *mastodon*, which itself is a combination of the Greek words for breast (mastos) and tooth (odous).

Species *Afromastodon coppensi* nov.

Diagnosis: Large species of *Afromastodon* (known range of length of upper third molars 160-192 mm and lower third molars 166-196 mm).

Holotype: AD 600'00, right maxilla with M2/ to M3/ (Pl. 10, Fig. 1-2).

Type locality: Arrisdrift, Orange River Valley, southern Namibia.

Age: Early Middle Miocene (ca 17-17.5 Ma).

Etymology: The species name honours Prof. Yves Coppens, who has made significant contributions to the study of fossil proboscideans of Africa.

Referred material: Lower teeth. PQ AD 257 left m/3 (Pl. 14, Fig. 1, Pl. 15, Fig. 6); PQ AD 252, right m/3 (Pl. 14, Fig. 2, Pl. 15, Fig. 2); PQ AD 1888, left m/3 (Pl. 13, Fig. 3); PQ AD 3237, left m/3 (Pl. 13, Fig. 1); PQ AD 1663, right m/3 (Pl. 13, Fig. 2, Pl. 15, Fig. 1); AD 585'98, left m/3 (Pl. 15, Fig. 3); PQ AD 294, left m/3 (Pl. 15, Fig. 4); AD 206'95, right m/2 (Pl. 12, Fig. 1); AD 400'99 left m/2 (Pl. 16, Fig. 1); AD 527'99 worn right m/2 (Pl. 17, Fig. 1¬2); AD 546'97, worn right m/2; AD 778'97, right m/1 (Pl. 16, Fig. 3); PQ AD 65, worn m/1; AD 237'95, fragment of m/1; AD 495'00, right p/3; AD 582'98, right dm/3 (Pl. 16, Fig. 5); AD 336'95, lower tusk fragment; AD 539'97, lower tusk; AD 325'95, lower tusk; AD 365'99, lower tusk; AD 122'96, lower tusk fragment; PQ AD 3139, lower tusk fragment; AD 496'00, fragment of lower tusk.

Upper teeth. AD 476'94, right M3/ (Pl. 11, Fig. 3); AD 978'97, left M3/ (Pl. 11, Fig. 2); AD 583'98, right M3/; AD 831'97, right dM3/ (Pl. 16, Fig. 4); PQ AD 1065, right M2/ (Pl. 16, Fig. 2); AD 51'94, worn M2/; AD 399'99, anterior two lophs of M2/ (Pl. 11, Fig. 4-5); PQ AD 2784, unworn loph of a posterior molar; PQ AD 2128, worn M1/; PQ AD 2812, worn M1/; PQ AD 1659, upper tusk (Pl. 11, Fig. 1).

Remarks: Corvinus & Hendey (1976) and Hendey (1978) described a few of the above specimens, but adopted a cautious approach to determining their systematic position, suggesting

Table 7: Summary comparison of the skulls of *Progomphotherium* and *Gomphotherium*.

Character	*Progomphotherium*	*Gomphotherium*
1. Overhang of occipital margin over the supraoccipital	None or very slight	Extensive
2. Upper P3/	Alveolus still open when M3/ is nearly erupted	Lost before M3/ is erupted, no sign of alveolus
3. Premaxilla/maxilla suture	Entirely on lateral surface of snout	Runs obliquely from ventral anteriorly to dorsal distally
4. Zygomatic process of maxilla	Leaves maxilla at a right angle	Leaves maxilla at a gentle angle
5. Squamosal flange	Not wide	Flaring greatly
6. Infraorbital foramina	Anterior to zygomatic process of maxilla	Above and below zygomatic process of maxilla
7. Lachrymal bone	Entirely within orbit	Extends to outer margin of orbit
8. Mandibular symphysis	Not greatly elongated	Greatly elongated
9. Mandibular symphysis	Not spatulate anteriorly	Spatulate anteriorly
10. Mental foramina	Two large ones on lateral surface of symphysis	One on symphysis, one on body of mandible
11. Alveoli of lower tusks	Long axis of section vertical	Long axis of section horizontal
12. Dorsal profile of skull	120° angle	Not markedly angled

that the material belonged to the genus *Gomphotherium*. These authors noted that the lower tusks from Arrisdrift differed from the flattened tusks from Maboko assigned to *Protanancus*, and presumably for this reason opted for an uncontroversial identification of the Arrisdrift gomphothere.

Description: Upper dentition. The upper tusk (Pl. 11, Fig. 1) is truncated oval in section (D-shaped) with a straight and flat enamel band running the preserved length of the tooth (Fig. 6).

The intermediate molars are trilophodont, with a strong distal cingulum. The second molar in the holotype has deeply worn pretrite cusps and lightly worn posttrite cusps. The first pretrite is so worn that no significant morphological details can be made out. The second pretrite cusp has a trefoil shaped outline, with weak indentations marking the trefoil. The third pretrite has a prominent anterior conule, a mesocone that faces somewhat anteriorly and a weak posterior conule that is in line with the posttrite cusp, which gives a somewhat anancoid appearance to the third loph. The wear outlines of the posttrite cusps are elongated oval and there are no anterior or posterior conules. The anteroposterior sulcus between the pretrite and posttrite cusps is clear but not wide. The anterior cingulum is low and has suffered substantial interstitial abrasion against the upper first molar. The beaded posterior cingulum is well developed and descends from the tip of the posterior lingual corner of the pretrite cusp to the base of the postero-labial side of the posttrite by way of a low cusplet located just to the posttrite side of the anteroposterior sulcus. The buccal and lingual ends of the anterior transverse valley are blocked by cingular cusps. There are thin traces of cementum in the buccal ends of the transverse valleys.

A right upper second molar, PQ AD 1065 (Pl. 12, Fig. 2), is unworn and provides better evidence about the morphology of this tooth than does the second molar in the holotype. It consists of 3 lophs and well developed anterior and posterior cingula. The main cusps are barely offset from one another, the pretrite ones being slightly anterior to the posttrite ones, but not to the extent of being anancoid. The mesocones of the pretrite cusps are slightly behind the main cusps while those of the posttrite cusps are slightly in front of the main cusps, a disposition which imparts a slightly oblique aspect to the lophs. The anterior and posterior pretrite conules are well developed, being larger than the mesocones, the anterior conules blocking the transverse valley. The pretrite mesocone is clear on the 2nd and 3rd loph, but is absent from the 1st one. Lophs 1 and 2 have prominent anterior and posterior conules on the pretrite side, that of the 1st loph leading into the beaded anterior cingulum. The third pretrite has no conules. The posttrite mesocones are slightly advanced on the main cusps, producing a weak chevron pattern. Posttrite anterior and posterior conules are absent, save for some low cuspules behind the 2nd posttrite mesocone. The first pretrite has a particularly strongly developed anterior conule in line with the anterior cingulum, which is heavily beaded (broken up into several small conules) and which reaches the labial edge of the crown, ending rather low down (as in *Protanancus MacInnesi*) (cf. Tassy, 1986, fig. 23). The anterior most transverse valley is obstructed by the anterior conule of the second pretrite, but the other transverse valleys are open. Behind the third loph there is a swollen distal cingulum, with a large pretrite cusp

Table 8: Dental measurements (in mm) of *Gomphotherium* sp. indet. from Auchas, Namibia. (e = estimated)

Specimen	Length	Breadth
AMSE 1'95 left M2/	102e	54e
AMSE 1'95 left M3/	115e	73 (only three lophs preserved)

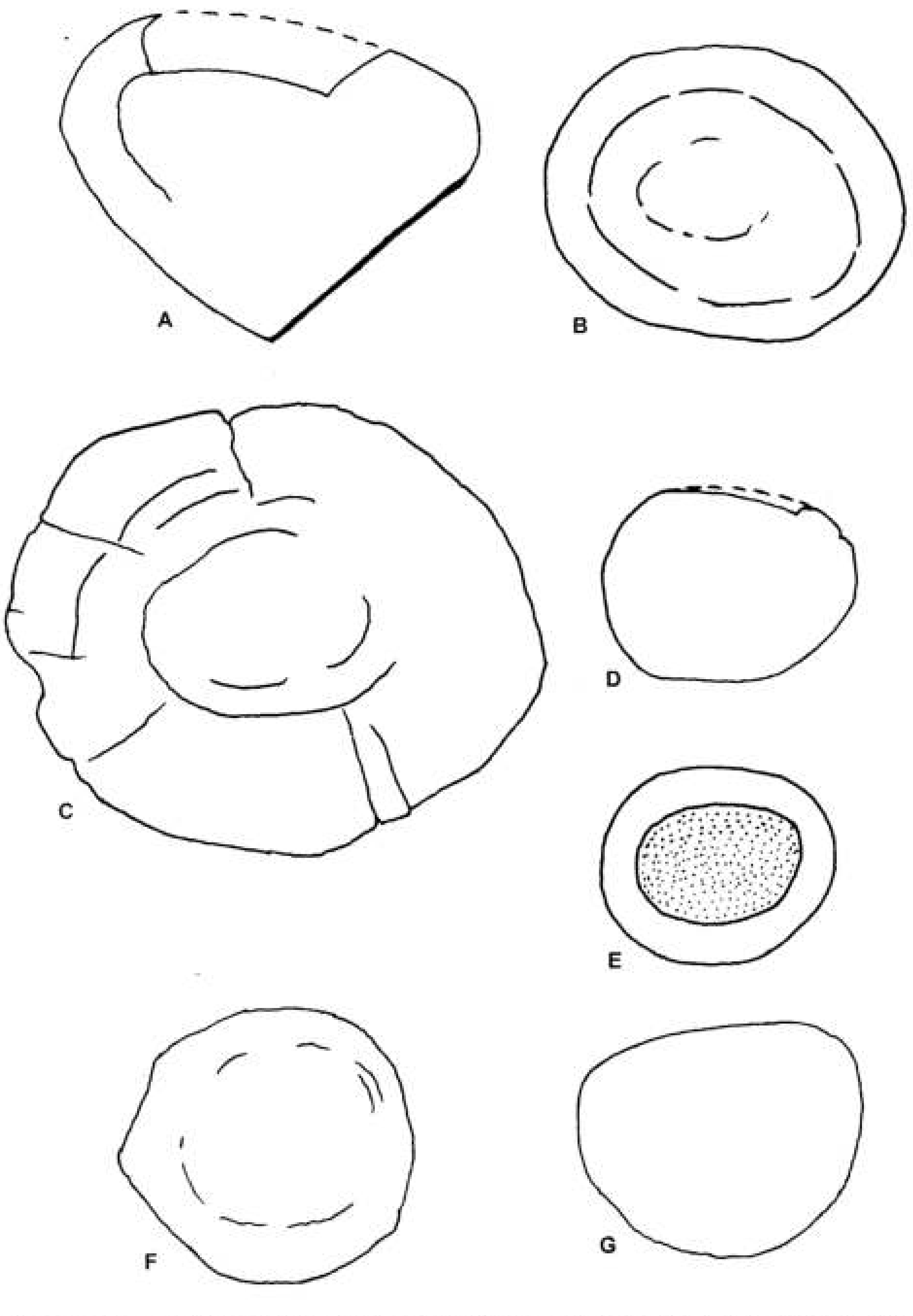


Figure 6: Sections of upper and lower tusks of *Afromastodon coppensi*. A = upper tusk, D-shaped section with long enamel band, B-G = lower tusks of generally oval section without enamel bands.

in the disto-buccal corner of the crown.

The upper second molars (Pl. 10, Fig. 1-2; Pl. 16, Fig. 2) can be differentiated from lower molars, not only on the basis of the disposition and number of roots, but also by the fact that the crowns do not widen markedly to the rear, as the measurements of M2/ in table 9 show.

The upper third molars (Pl. 10; Pl. 11, Fig. 2-3) have four lophs, the distal one being narrower than the anterior ones. The upper third molar in the holotype is still in the process of eruption, with only the tip of the first pretrite cusp in slight wear producing a small dentine lake at its tip. The crown consists of four lophs and prominent anterior and posterior cingula. The anteroposterior sulcus is well developed and runs virtually straight from the first to the fourth loph. The first pretrite possesses a small mesocone in line with the bucco-lingual axis of the loph. The anterior and posterior conules descend from the tip of the main cusp towards the anterior cingulum and the first transverse valley respectively. There are three anterior conules and two posterior ones, but they are not well separated from each other. The anterior cingulum forms a prominent ledge on the anterior aspect of the pretrite cusp. The second pretrite cusp has a mesocone that is slightly oblique to the axis of the second loph, being slightly in advance of it. There are prominent anterior and posterior conules, one on each side of the main cusp. The bases of the pretrite conules touch each other to block off the transverse valleys. The third pretrite has similar elements to the second pretrite, but their disposition is such that the cusp appears to have been rotated clockwise in the right M3/, anticlockwise in the left one. Thus the mesocone leads obliquely forwards into the second transverse valley, and the posterior conule occupies the position which in the first and second pretrites is occupied by the mesocone. Correlating with this, the anterior conule of the third pretrite is more lingually situated than its counterparts in the first and second pretrites. The fourth pretrite is lower crowned than the first three and consists of four conules arranged in an arc. Posteriorly, the cingulum is fused with the main cusp and swings round the distal end of the tooth towards the fourth posttrite cusp. The first posttrite cusp consists of the main cusp and two mesocones in line with the axis of the loph. There is a low ridge descending from the tip of the main cusp into the first transverse valley, but it does not obstruct the valley in any way. The second posttrite is also composed of a main cusp accompanied by two mesocones in line with the loph, but there is no posterior ridge on the main cusp. The third posttrite is like the second, but the fourth one consists of a single low conule bordered distally by the posterior cingulum.

The angle of eruption of the third upper molar is about 35° relative to the occlusal plane of the second molar.

Three other upper third molars in the collection are all rather worn or have been damaged by gypsum attack which makes their interpretation somewhat conjectural. The heavily worn pretrite portions of the two anterior lophs produce a trefoil dentine lake. The third loph is chevron shaped and the fourth is variable but with some chevroning. The mesocones in the third lophs are anteriorly positioned with respect to the main cusps, and the anterior conules are strongly developed, being larger than the mesocones. The distal conelet on the pretrite side is also well developed in the second and third lophs, and it was probably also well developed in the first loph, judging from the outline of the trefoil. The lingual cingulum is variably developed and there is a prominent cusplet on the antero-lingual corner of the crown.

Lower dentition. There are several lower tusk fragments in the Arrisdrift collection. None of the specimens is as flat as any of the material from Maboko Island described by Tassy (1986), the section being more or less oval and none of them is grooved or guttered (Fig. 6). If the long axis of the section was horizontal then the available specimens plot out within the metric variation field of *Gomphotherium* rather than *Archaeobelodon* and *Protanancus*.

A right p/3, AD 495'00 (Pl. 15, Fig. 5) is slightly worn and has suffered some gypsum attack on the posterolingual corner, but is otherwise in excellent condition. The protoconid is set well forward over the anterior root and is accompanied on its lingual side by a prominent inner cusp. The protoconid and the two cusps behind it are disposed in a straight line descending in height from front to back, the middle cusp being the smallest in diameter but intermediate in height. Lingually to the posterior cusp there was a lingual cusp which has been partly destroyed by gypsum attack. The crown has a swollen cingulum surrounding its anterior, buccal and distal surface, but fading our lingually. The anterior cingulum is beaded and the enamel behind the anterolingual cusp is wrinkled. There are two roots. There is a posterior interstitial facet for the fourth lower premolar. The crown is 49.3 mm long by 35 mm wide and 26 mm high. In its unworn state this tooth would have been about 30 mm high.

There are a few broken and worn fragments of first molars in the sample, plus an unworn germ from the right side. The m/1 germ, AD 778'97 (Pl. 16, Fig. 3), consists of three lophs and a distal cingulum. The first pretrite loph has a well developed mesoconid plus strong anterior and posterior conulids (equivalent to the buttresses of MacInnes, 1942) the distal one of which helps to block the transverse valley. The anterior conulid reaches towards the anterior cingulum which it joins in the vicinity of the median sulcus. The first posttrite loph has a small mesoconid but the accessory conulids are absent save for a swelling in the posterior outline of the main cusp. The mesoconid of the second pretrite is doubled and there are strong anterior and posterior conulids which obstruct the transverse valleys. The posttrite half has a well developed mesoconid but there is no sign of anterior and posterior conulids. The first two lophs are straight across, but the third loph is chevronned slightly and there are no accessory conulids. The distal cingulum possesses a large centrally placed cusplet. There is cementum in the bottoms of the transverse valleys.

Two well preserved, lightly worn m/2s in the sample (Pl. 12, Fig. 1; Pl. 16, fig. 1) show the basic structure of the intermediate molars very well. The pretrite cusps are not offset from each other to any marked degree. The pretrite mesoconids are in line with the main cusps and are generally larger than the anterior pretrite conulids. The posterior pretrite conulid of the first loph is enlarged and obstructs the transverse valley in side view, but the one on the second loph is broken into three conelets which are smaller and only partly obstruct the transverse valley. The posttrite lophs have no anterior conulids but there are low posterior ones. The anterior cingular shelf is narrow, but the posterior one is broader and is comprised of two large conulids and several smaller ones. The crown broadens appreciably backwards, the third loph being the widest. In the available second lower molars the lengths and breadths of the first, second and third lophs are given in table 10.

The lower third molars (Pl. 13, Fig. 1-3; Pl.]4, Fig.]¬2; Pl.] 5, Fig. 1-4) are in general much better preserved than the uppers, so that their detailed morphology can be discerned without ambiguity. They consist of four lophs and a distal cingulum, being slightly more elongated and possessing more elements than the uppers. The lower third molars are not curved buccally and there is only slight helicoidal twisting of the crown.

Table 9: Measurements (in mm) of the upper second molars of *Afromastodon coppensi* from Arrisdrift, Namibia.

Specimen	Length	Breadth 1st loph	Breadth 2nd loph	Breadth 3rd loph
PQ AD 1065 M2/	118.4	66.1	69.0	66.2
AD 51'94 M2/	113e	76e	72.3	76.5
AD 600'00 M2/	117	72.3	69.0	73.0

Table 10: Measurements (in mm) of the lower second molars of *Afromastodon coppensi* from Arrisdrift, Namibia.

Specimen	Length	Breadth 1st loph	Breadth 2nd loph	Breadth 3rd loph
AD 206'95 m/2	118.2	56.7	63.8	70.4
AD 546'97 m/2	113e	59.0	65.5	70.7
AD 400'99 m/2	117	56.8	64.0	68.2
AD 527'99 m/2	127	61.0	67.9	74.3

As with the upper molars, the main cusps of the first two lophs are slightly offset from one another, the pretrite cusps being further back than the posttrite ones. The mesoconids of the pretrite cusps are slightly in advance of the main cusps, and they are smaller than the anterior conulids which block the transverse valleys. The distal conulids are weaker, sometimes doubled. The posttrite mesoconids are only slightly in advance of their main cusps or are in line with them. There is usually no anterior posttrite conulid, but several specimens have a small posterior posttrite conulid which does not block the transverse valleys. With wear, the pretrite cusps produce a trefoil shaped dentine lake, whereas the posttrite cusps produce an oval lake.

There is no sign of cementum in most of the Arrisdrift molars, but a first molar, AD 778'97, does possess a thin coating of cementum in the valley bottoms as does an M3/ (AD 583'98), suggesting that the absence of cementum in other specimens could be related to post-depositional loss rather than to its absence during life.

Deciduous dentition. The right dM3/ (AD 831'97) (Pl. 16, Fig. 4) possesses two lophs separated by a wide transverse valley. Each of the lophs is composed of pretrite and posttrite cusps separated by a median sulcus. The anterior pretrite cusp has a mesocone in line with the loph and a blunt distal crest descending towards the midline of the transverse valley. The posttrite cusp has a distinct mesocone and a posterior accessory conule. The posterior loph is virtually a repetition of the anterior one. There is a well developed antero-posteriorly wide anterior cingular complex comprised of wrinkled enamel and distinct cusplets. This passes distally into a strong lingual cingulum that reaches the distal end of the crown where it merges with a moderately developed distal cusplet. The enamel is somewhat ptychodont. The crown is wider anteriorly than distally and is waisted at the median valley. The posterior termination of the crown is pointed.

The right dm/3 (AD 582'98) (Pl. 16, Fig. 5) is a bilophodont tooth with an elongated anterior platform bearing several small cusps. It also has a beaded distal cingulum bearing a centrally positioned posterior cusplet. The distal loph is wider than the anterior one and the transverse valley is wide and partly obstructed by a centrally positioned conulid. The pretrite halves of the lophs each have a prominent main cusp with small mesoconids in line with the lophs, as well as small, low, anterior and posterior conulids. The mesoconids on the posttrite halves are small. The anterior posttrite has two low anterior conulids but there are no posterior ones. The second posttrite has no conulids. There is a distinct wasting in the occlusal outline of the crown at the transverse valley. There is no labial or lingual cingulum.

Discussion: It is clear from the publications of Tobien (1975, 1978) and Tassy (1986) that the identification of isolated bunodont trilophodont proboscidean teeth can be a difficult undertaking, not only at the specific, but also at the generic level. This is because gomphothere (s.l.) cheek teeth are highly variable in morphology and the various lineages developed certain characters in parallel. Thus weak anancoid tendencies have been reported to occur in *Protanancus* as well as in primitive species of *Choerolophodon* (Tassy, 1986) recently assigned to the new genus *Afrochoerodon* (type species *A. kisumuensis*) (Pickford, 2001). Likewise chevroning can occur in both these lineages. To illustrate this difficulty it should be noted that Tassy (1986) listed two molars from Maboko, Kenya (M 15535 and M 32434) in the hypodigms of both *Protanancus MacInnesi* and *Choerolophodon kisumuensis*. The latter specimen belongs to the same individual as M 15292, *A. kisumuensis*, while the former is heavily worn and 'is practically unidentifiable. A third lower molar (M 15539) which Tassy identified as *C. kisumuensis*, is in my opinion more likely to represent *P. MacInnesi*, being curved buccally and not having the base of the pretrite anterior conulid positioned buccally. It is thus quite different from the other specimen assigned to the species (M 15542) which is straight buccally and which has the base of the pretrite anterior conulid almost on the buccal margin of the crown. Metrically it is closer to the latter than to the former species. Many of the isolated teeth (13 specimens) from Maboko were left unidentified by Tassy (1986), partly because they are worn or broken, but mainly because of the inherent difficulty of identifying isolated gomphothere teeth. In my opinion, 31 of the Maboko specimens are practically unidentifiable.

There are several points which plead in favour of a close, but not identical, relationship between the Arrisdrift gomphothere and the genus *Protanancus* and which distance it from *Afrochoerodon*, *Choerolophodon*, *Archaeobelodon* and *Gomphotherium*. These are 1) the depth of the anterior cingulum in the upper molars which was a feature employed by Tassy (1986, fig. 23) to sort out isolated teeth from Maboko, Kenya, 2) the position of the mesocones relative to the main cusps, 3) the slight offset of the main cusps but not reaching anancoid status, 4) the tendency to produce strongly trefoil shaped dentine lakes in the pretrite half of the crown, 5) the relatively narrow molars (wider in *Afrochoerodon*), 6) the separation of the pretrite and posttrite cusps by a deep median sulcus. Against a close relationship to *Protanancus* is the oval section of all the lower tusks from Arrisdrift which contrast with those of *Protanancus MacInnesi*, which according to Tassy (1986) are flattened, widened and possess a prominent dorsal sulcus. It should be noted however, that there is no direct association between the flattened tusks from Maboko and the cheek teeth assigned to *Protanancus*.

The Arrisdrift gomphothere has lower tusks which are oval, quite unlike the wide, flat tusks with a dorsal sulcus assigned to *Protanancus MacInnesi*. Furthermore, the seven lower molars from Arrisdrift show a considerably narrower range of morphological variation than the Maboko sample which consists of 10 specimens. Among the more obvious features that occur in some of the Maboko teeth but not in the Arrisdrift sample are the buccal curvature of the crowns, the marked helicoidal twisting of the occlusal surface and the markedly angled posterior root of the m/3. The evidence indicates that the Maboko *Protanancus* sample probably contains two taxa. The differences suggest that there are two genera in the Maboko sample of cheek teeth hitherto identified as *Protanancus MacInnesi* a suggestion borne out by the presence of two kinds of lower tusks at the site.

Morphologically, the molars of the Arrisdrift species are more primitive than those of *Protanancus MacInnesi* from Maboko (ca 15 Ma), the third molars possessing one loph fewer than those of *P. MacInnesi*. However, the most surprising aspect of the Arrisdrift proboscidean is its large size. Other evidence from the site indicates that Arrisdrift is basal Middle Miocene in age, some would say even Early Miocene (ca 17.5 Ma) and thus about 2 to 2.5 million years older than Maboko. When the third molars are plotted onto bivariate graphs (Fig. 7-8) they fall well above the range of variation of all known African Early and Middle Miocene bunodont proboscideans including *Protanancus MacInnesi* and *Afrochoerodon kisumuensis*. Instead they plot out within the variation fields of Late Miocene taxa such as *Choerolophodon corrugatus* and *C. pentelici*.

Family incertae sedis
Genus incertae sedis
Species indet.

Material: An isolated loph of a molar from Arrisdrift, PQ AD 2748 (Pl. 17, Fig. 3-5).

Description: PQ AD 2748 (Pl. 17, Fig. 3-5) differs from all other proboscidean teeth from Arrisdrift by being heavily ptychodont (possessing markedly wrinkled enamel) and choerodont (covered in tubercles). In size and layout of the cusps, however, it is similar to other fossils from Arrisdrift assigned to *Afromastodon*.

Discussion: According to Tobien (1973a, b) ptychodonty is usually associated with choerolophodonts and *Stegomastodon*, but its expression is variable in the Proboscidea, in some species such as *Anancus arvernensis* it is often well developed in the deciduous teeth and the first permanent molars, but is lacking in third molars. I am inclined to interpret the Arrisdrift specimen as a variant of *Afromastodon coppensi*, but until more complete specimens come to light it is perhaps more judicious to omit it from the hypodigm.

Comparison of Maboko and Arrisdrift gomphotheres

Lower third molar morphology of Maboko and Arrisdrift gom-

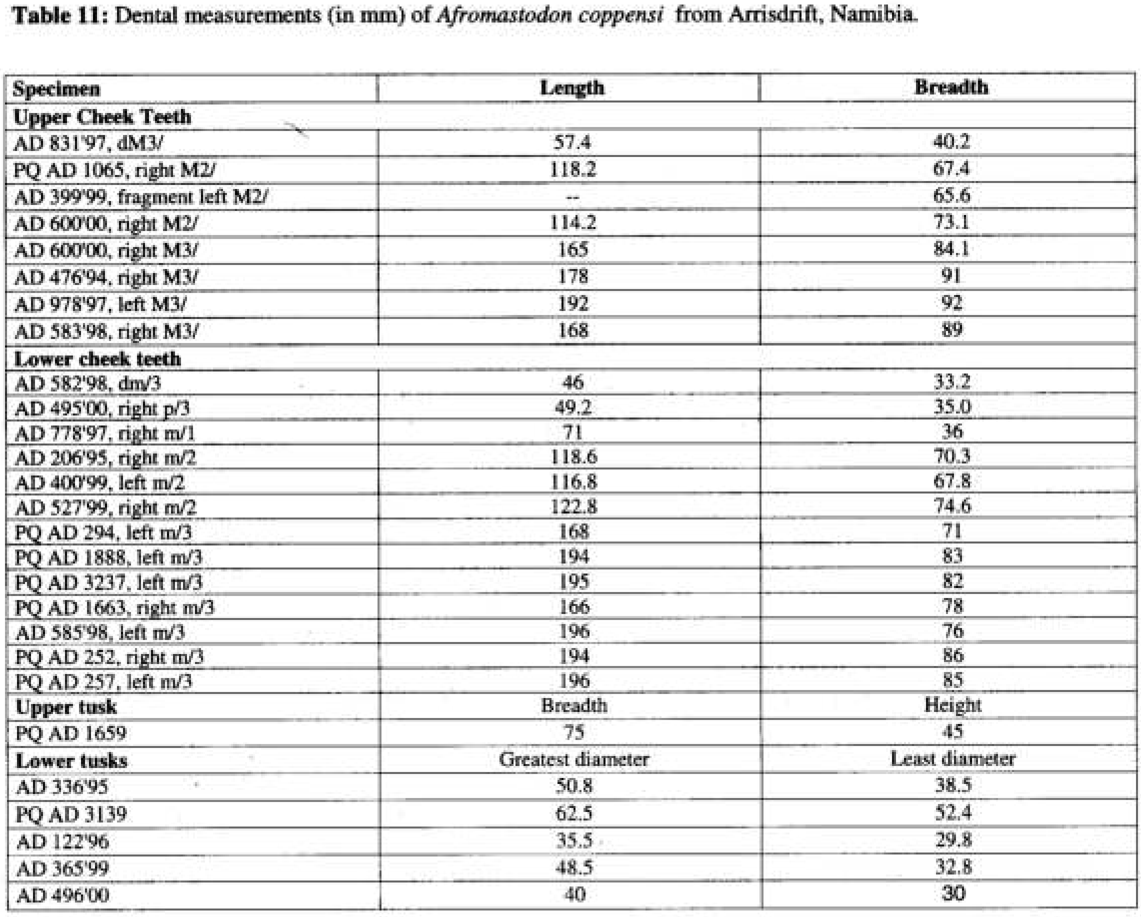


Table 11: Dental measurements (in mm) of *Afromastodon coppensi* from Arrisdrift, Namibia.

Specimen	Length	Breadth
Upper Cheek Teeth		
AD 831'97, dM3/	57.4	40.2
PQ AD 1065, right M2/	118.2	67.4
AD 399'99, fragment left M2/	--	65.6
AD 600'00, right M2/	114.2	73.1
AD 600'00, right M3/	165	84.1
AD 476'94, right M3/	178	91
AD 978'97, left M3/	192	92
AD 583'98, right M3/	168	89
Lower cheek teeth		
AD 582'98, dm/3	46	33.2
AD 495'00, right p/3	49.2	35.0
AD 778'97, right m/1	71	36
AD 206'95, right m/2	118.6	70.3
AD 400'99, left m/2	116.8	67.8
AD 527'99, right m/2	122.8	74.6
PQ AD 294, left m/3	168	71
PQ AD 1888, left m/3	194	83
PQ AD 3237, left m/3	195	82
PQ AD 1663, right m/3	166	78
AD 585'98, left m/3	196	76
PQ AD 252, right m/3	194	86
PQ AD 257, left m/3	196	85
Upper tusk	Breadth	Height
PQ AD 1659	75	45
Lower tusks	Greatest diameter	Least diameter
AD 336'95	50.8	38.5
PQ AD 3139	62.5	52.4
AD 122'96	35.5	29.8
AD 365'99	48.5	32.8
AD 496'00	40	30

photheres. All the lower third molars from Arrisdrift are anteroposteriorly straight (the median line between the three anterior lophids continues straight distally almost in the centre line of the crown) and they possess only slightly helicoidal occlusal surfaces. In the Maboko sample hitherto assigned to *Protanancus MacInnesi* there are some specimens similar to the Arrisdrift material, but in addition there are others with marked labial curvature (when the median line between the first three lophids is extended distally it passes out of the lingual side of the crown) and the occlusal surfaces are markedly helicoidal from front to rear. The differences are probably related to the form of the mandible and the position of the ascending ramus, the straight molars probably indicating a retired ramus, while the curved teeth suggest that the mandible was shorter with the ascending ramus located in a relatively anterior position. It is unlikely that these differences would be related to sexual dimorphism. Comparison of the cheek teeth from Maboko with the Arrisdrift specimens reveals that Tassy's Maboko hypodigm of *Protananacus MacInnesi* may well contain two taxa, one of which is morphologically similar to but smaller than *A. coppensi*. Thus, part of the Maboko material hitherto assigned to *P. MacInnesi* possibly belongs to *Afromastodon* while the rest of the hypodigm, including the type specimens, belong to *P. MacInnesi*. The only significant difference between the Arrisdrift and Maboko specimens of *Afromastodon* is their size, the cheek teeth from Arrisdrift being considerably larger than those from Maboko.

Upper third molar morphology of Arrisdrift and Maboko Gomphotheres. The four upper third molars from Arrisdrift are basically similar to each other. They possess four lophs and a distal complex of cusplets. They have a prominent cingular cusp let on the anterolingual corner of the crown. The cingulum is relatively wide and extends along the lingual side of the crown as far as the second loph. Lophs 3 and 4 are disposed in a chevron with the posttrite having two or more mesocones. One specimen from Maboko (M 15531) is similar to this morphology but is appreciably smaller.

The Bulk of the Maboko sample differs from the Arrisdrift material in having a small anterolingual cusp let, the cingulum is not well developed and the posttrites of lophs 3 and 4 tend to have a single mesocone.

Upper and lower tusks of Maboko and Arrisdrift Gomphotheres

Lower tusks. At Maboko there is no direct association between cheek teeth and tusks. Tassy (1986) assigned several wide, flat tusks with a dorsal sulcus or gutter to *Protanancus MacInnesi*. No lower tusks were assigned to *Choerolophodon kisumuensis*. However, two small tusks with rounded sections are present in the Maboko collection at the Natural History Museum, London. Do these small tusks belong to *Afrochoerodon kisumuensis*, also known from the site, or to some other taxon?

All the lower tusks from Arrisdrift are rounded to oval in section, similar to the two undescribed specimens from Maboko. The fact that both Arrisdrift and Maboko contain similar lower tusks indicates that they may share the same proboscidean taxon.

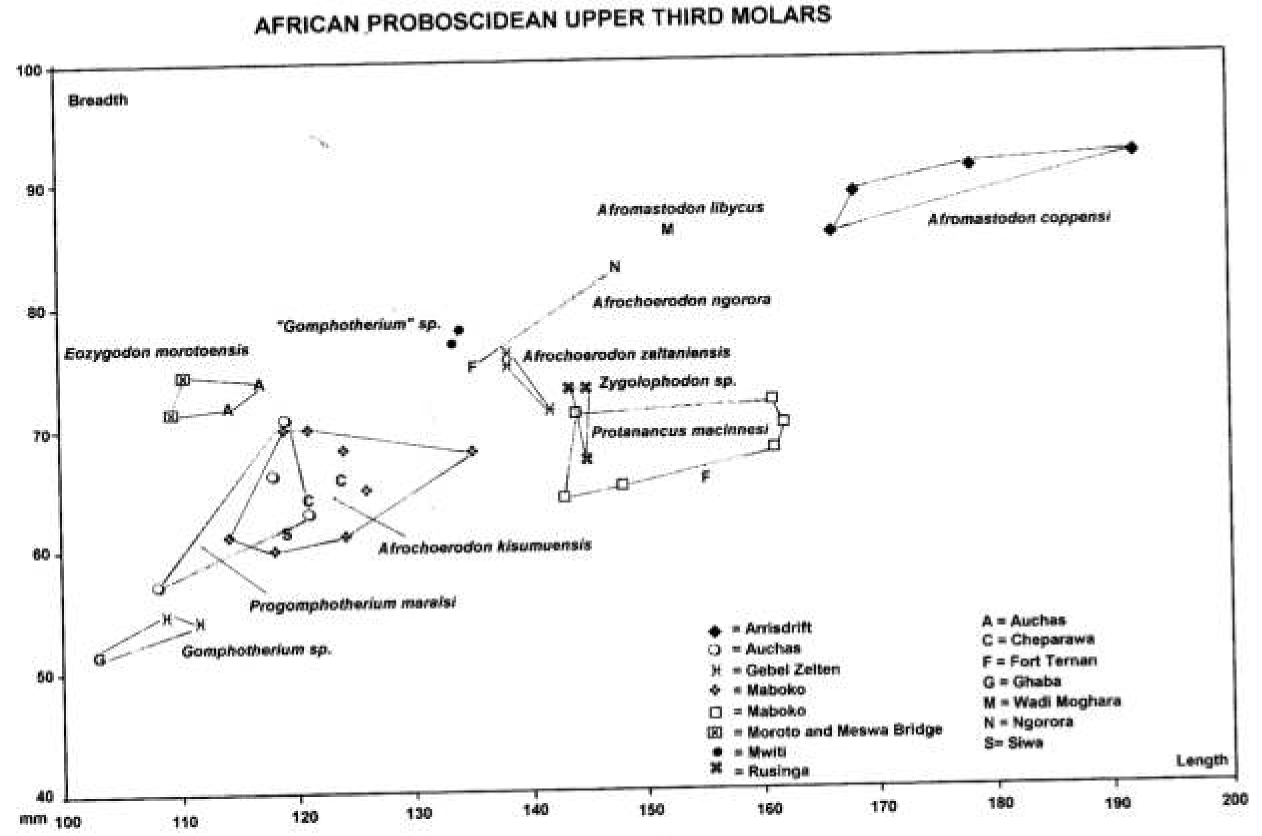


Figure 7: Bivariate plot of African proboscidean upper third molars. *Progomphotherium maraisi* is one of the smallest Neogene gomphotheres known, while *Afromastodon coppensi* is the largest Early to Middle Miocene gomphothere. *Afromastodon libycus* is smaller than *A. coppensi*, but is larger than most of the other known Early and Middle Miocene mastodonts of Africa.

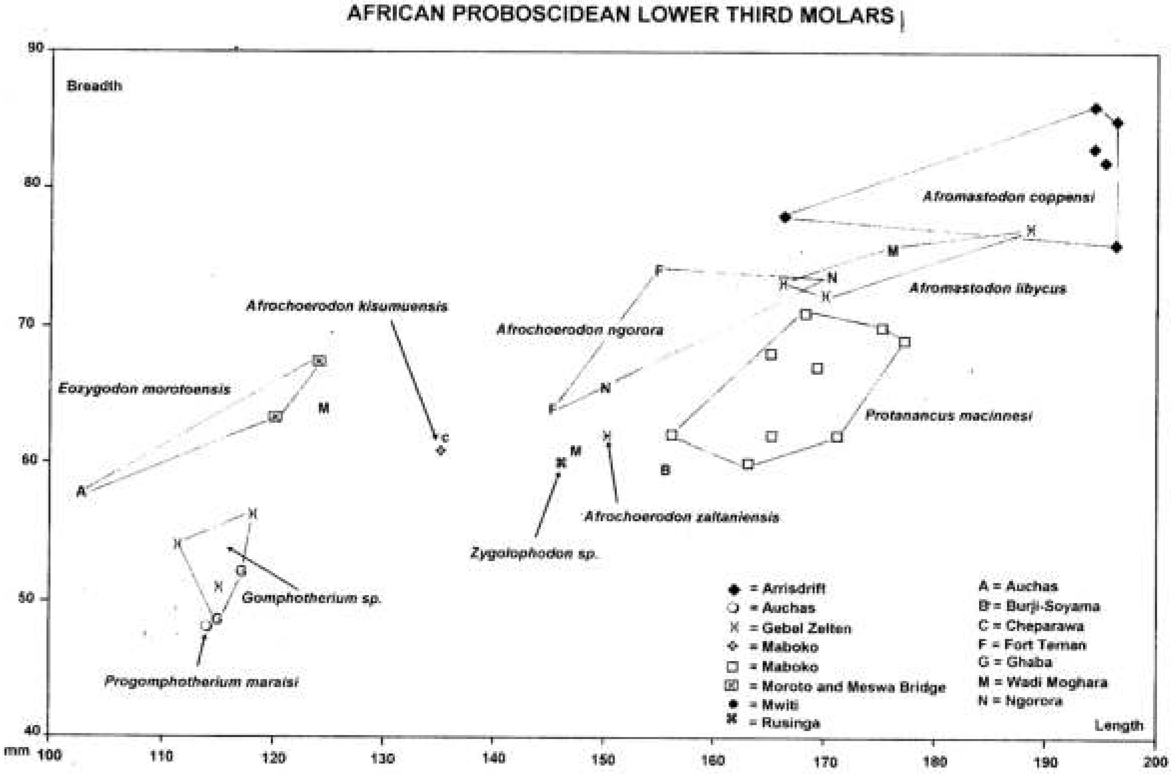


Figure 8: Bivariate plot of African proboscidean lower third molars. *Progomphotherium maraisi* is one of the smallest Neogene gomphotheres known, while *Afromastodon coppensi* is the largest Early to Middle Miocene gomphothere. *Afromastodon libycus* is smaller than *A. coppensi*, but is larger than most of the other known Early and Middle Miocene mastodonts of Africa.

In summary, therefore, it would appear likely that there are three genera of bunodont gomphotheres at Maboko; *Afrochoerodon kisumuensis* which may have lacked lower tusks, *Protanancus MacInnesi* which may have possessed flattened tusks with a dorsal sulcus, and a small species of *Afromastodon* with lower tusks which were probably rounded to oval in section. It is stressed however, that none of these tusks have been found *in situ* in mandibles, and it is not beyond the realms of possibility that the present attributions may be incorrect.

Upper tusks. Tassy (1986) assigned two upper tusks from Maboko to the species *Protanancus MacInnesi*. However, as was made clear by MacInnes (1942) the two specimens do not have the same cross section, nor is their extent of enamel covering comparable. M 32728 (KBA 005) has a flattened lateral surface (so-called D shape of Guan Jian, 1997) which is covered by an extensive, wide enamel band (MacInnes, 1942, fig. 3 left) which is similar in many ways to a specimen from Arrisdrift (PQ AD 1659). KBA 110, in contrast, is almost circular in section with a narrow band of enamel which is remarkably short (MacInnes, 1942, fig. 3 right) and which would soon disappear with further wear. The extent of enamel on the latter specimen is similar to that on a tusk from Fort Ternan, Kenya, assigned by Tassy (1986, plate VI, fig. 3) to *Choerolophodon ngorora* (recently attributed to the genus *Afrochoerodon* by Pickford, 2001)) and I consider that KBA 110 should be referred to the genus *Afrochoerodon*. This suggestion is supported by the fact that the partial alveolus in the holotype skull from Maboko is large and the preserved part (the lateral third, i.e. where the flat enamel band would occur in species with D-shaped upper tusks) forms the arc of a circle. In addition, a skull of *A. kisumuensis* from Cheparawa, Kenya, has large tusks which are circular in section (Pickford, 2001). The upper tusk of *Afromastodon* in contrast, is almost trapezoidal in section with an extensive, flat, enamel band laterally, and it is virtually straight in its preserved parts, and thus differs from the openly helicoidal and curved upper tusks of *Protanancus* and *Afrochoerodon* from Maboko (MacInnes, 1942).

Changing views of gomphotherian diversity at Maboko

MacInnes (1942) considered that all the gomphotheres from the Early and Middle Miocene of East Africa belonged to a single subspecies of *Trilophodon angustidens*. Arambourg (1945)

Table 12: Morphological distinctions between lower third molars of *Afromastodon* and *Protanancus*.

Afromastodon lower third molar morph - Arrisdrift and Maboko type 2	*Protanancus macinnesi* lower third molar morph - Maboko type 1
1. Crowns not curved buccolingually	1. Crowns markedly curved buccolingually
2. Slightly helicoidal occlusal surface	2. Markedly helicoidal occlusal surface
3. Distal root only slightly angled laterally	3. Distal root markedly angled laterally
4. Anterior valleys mesiodistally wide	4. Anterior valleys mesiodistally narrow
5. Crown relatively narrow	5. Crown relatively wide
6. 4.5 lophids	6. 5.5 lophids

Table 13: Morphological distinctions between upper third molars of *Afromastodon* and *Protanancus*.

Afromastodon upper third molar morph - Arrisdrift and Maboko type 1	*Protanancus macinnesi* upper third molar morph - Maboko type 2
1. Crown slightly twisted distally 2. Two mesocones on posttrites 3 and 4 3. Prominent lingual cingulum 4. Distal loph composed of 5 cusplets 5. Transverse valleys relatively narrow 6. Choerodonty developed near crown base	1. Crown straight 2. Single mesocone on posttrites 3 and 4 3. Cingulum on pretrite corner small 4. Distal loph composed of one cusplet 5. Transverse valleys relatively wide 6. Enamel relatively smooth

realised that the sample was taxonomically heterogeneous and removed some of the material from *Trilophodon angustidens kisumuensis* and placed it into a new genus and species *Protanancus MacInnesi*. Tassy (1977, 1979, 1986) made a further significant advance in realising that MacInnes had seriously underestimated the amount of diversity in the East African Miocene mastodonts. He recognised the presence of five genera in the region - *Archaeobelodon*, *Protanancus*, *Platybelodon*, *Choerolophodon* and *Gomphotherium*, of which two are present in MacInnes' Maboko hypodigm and a third at Rusinga. It should be pointed out that the other taxa are from sites including Loperot, Buluk and Mwiti unknown to MacInnes.

Restudy of the Maboko material assigned by Tassy (1986) to *Protanancus MacInnesi* suggests to me that there are two morphological groups in the sample. One of the groups corresponds to *Afromastodon* (straight, non-helicoidal lower third molars) while the other corresponds to *Protanancus* (buccally curved, helicoidal lower third molars). This means that there are three gomphotherian taxa at Maboko. Such diversity may at first glance appear to be excessive, but it should be borne in mind that late Miocene and Pliocene sites in East Africa often contain four or more proboscidean genera (*Anancus*, *Stegotetrabelodon*, *Primelephas*, *Stegodon*, *Mammuthus*) as well as *Deinotherium*.

Bimodal variation in gomphothere molars and lower tusks

At Arrisdrift and Maboko, bivariate plots of third molars (Fig. 7-8) reveal a common pattern of bimodal variation. Upper molars of *Afrochoerodon kisumuensis* form two clusters. The same applies to upper and lower molars of *Protanancus MacInnesi* from Maboko. The Arrisdrift sample has a comparable pattern with upper and lower third molars forming two discrete clusters of points in bivariate plots of length and breadth.

This kind of metric variation can mean several things. Firstly it may be indicating that there was sexual dimorphism in the species, with males probably being larger than females. Secondly, it may mean that there are two species or even genera in the sample. Usually, the metric data on their own would not permit one to decide on the question of multiple taxa, unless the variation was extreme, which in the case of Maboko and Arrisdrift is not so, but if the separate clusters differ morphologically, then one would be more likely to be in the presence of two species or genera.

Tassy (1996b) analysed a large sample of *Gomphotherium angustidens* from En Péjouan, France, and noticed the same tendency for the measurements of the third molars to form two discrete clusters when plotted on bivariate (length-breadth) diagrams. He concluded that the variation observed could be explained by sexual dimorphism, with the longer third molars belonging to males. A simple taxonomic consequence of this demonstration is that in many cases, small gomphothere teeth found in Miocene deposits belong to females rather than to small species.

The lower tusks of gomphotheres in which both sexes possess these teeth are not greatly sexually dimorphic (Osborn, 1936; Guan Jian, 1997; Tassy, 1996b). It seems unlikely that males would possess wide, flat tusks with a dorsal sulcus, while females would have oval tusks without any hint of a groove. For this reason, it is considered that the Arrisdrift gomphothere is not likely to represent the female of a species of *Protanancus*. Consequently the new genus *Afromastodon* is erected for it.

Other African Early and Middle Miocene bunodont mastodonts

Mastodonts have been found at many African Miocene sites but few of the specimens can be identified with confidence, mainly because the samples are small and the specimens are worn or broken.

Elisabethfeld (ca 21 Ma), Namibia. The Early Miocene locality of Elisabethfeld, Namibia, yielded a worn upper right first molar of *Eozygodon morotoensis* (specimen EF 26'93 in the Geological Survey of Namibia, Windhoek). It is 67 mm long by 44 mm wide at the distalloph. There are three roots - transversely oriented anterior and posterior roots, and an elongated antero-posteriorly oriented lingual root. The crown is deeply worn, but parts of the third posttrite and posterior cingulum are preserved which reveal a morphology, including thin enamel and a posterior ledge-like cingulum, close to that in the first molar in the Auchas skull of *Eozygodon morotoensis*. The site also yielded an isolated right p/4 (EF 25'93) which is lacking the enamel and is somewhat wind eroded. The anterior cusp pair is widely separated from the posterior pair by a well developed median transverse valley. The anterior pretrite half has a main cusp from which crests lead anteromedially and posteromedially, but the posterior crest does not block the transverse valley. The crown is 37.8 mm long x 25.8 mm wide. It is tentatively assigned to *Eozygodon*.

Bosluis Pan (ca 16 Ma), South Africa. An isolated trilophodont molar was found at Bosluis Pan, Namaqualand, South Africa (Senut, *et al.*, 1996).

Hondeklip Bay (ca 12 Ma), South Africa. A tetralophodont intermediate molar from Hondeklip Bay, Namaqualand, was described by Pickford & Senut (1997).

Rusinga island, (17.8 Ma), Kenya. The fossils from Rusinga Island (MacInnes, 1942) were identified as cf. *Archaeobelodon* by Tassy (1986). My own assessment of the specimens is that they are closer morphologically to *Zygolophodon pyrenaieus* than to any other genus or species, a conclusion also reached by other authors (Van Couvering & Van Couvering, 1976). The molars have relatively anteroposteriorly compressed lophs, the pretrite conules are low and poorly developed and do not obstruct the transverse valleys and zygodont crests are developed. The degree of loph compression and conule reduction has not reached the stage observed in *Eozygodon*, but the Rusinga specimens are morphologically closer to *Eozygodon*, in my opinion, than they are to *Arehaeobelodon*.

Mfwangano, (17.8 Ma), Kenya. The early Miocene site of Mfwangano (ca 17.8 Ma) has yielded fragmentary remains of gomphotheres assigned by Tassy (1986) to *Gomphotherium* sp. The lower tusks are similar in size and cross sectional shape (Tassy, 1986, text fig. 11-1) to those from Auchas assigned to *Progomphotherium maraisi* and I consider them to be conspecific. Note that the Mfwangano tusks are higher than they are wide, the opposite of the situation in *Arehaeobelodon* and *Gomphotherium*. These tusks were assigned, with some doubt, to *Deinotherium hobleyi* by MacInnes (1942). The upper molar fragment from Mfwangano (Tassy, 1986, Pl. 1, fig. 1) is poorly preserved and mayor may not represent another taxon.

Karungu, (17.8 Ma), Kenya. Karungu yielded teratogenic molars of a bunodont gomphothere (Tassy, 1986) which are unidentifiable. However, the same site has yielded an undescribed anterior loph of a third molar which is now housed in the Natural History Museum, London (M 32880, Nira, 15-3-35) which is so similar to the Auchas fossils assigned to *Progomphotherium maraisi* that they are likely to be conspecific. Thus Karungu would join Mfwangano in yielding specimens of *Progomphotherium maraisi*.

Lothidok, (Early Miocene), Kenya. Madden (1980) assigned a fragmentary upper fourth premolar to *Zygolophodon*. The specimen is broken obliquely across so that only the anterior loph is almost complete. In its preserved parts the tooth is close to *Eozygodon* from Auchas, and, like Tobien (1996) I have little hesitation in identifying the specimen as *E. morotoensis*. The antero-posteriorly compressed lophs, the wide interloph valley without obstruction from pretrite or posttrite conules, and the deep median sulcus are all features which ally the Lothidok fossil to the same species as that from Auchas.

Meswa Bridge, (22.3 Ma), Kenya. The site of Meswa Bridge yielded several teeth and postcranial bones from an individual of *Eozygodon morotoensis*. Originally described as *Zygolophoden morotoensis* on the basis of a set of teeth from Moroto I, Uganda, (Pickford & Tassy, 1980) the Meswa Bridge specimen revealed that the lower tusks were flattened and had a dorsal groove, thereby providing sufficient basis for generic separation from *Zygolophodon* (Tassy & Pickford, 1983).

Songhor, (19-20 Ma), Kenya. The only known proboscidean remains from the Early Miocene site of Songhor consist of a single milk molar of a "gomphothere" (Tassy, 1986) and a distal femur. Within the gomphothere grade, such specimens are virtually unidentifiable.

Moruorot (ca 17.2 Ma), Kenya. Madden (1980) reported the presence of a zygolophodont at Moruorot, which has been confirmed by Tassy (1986) and Tobien (1996). The material is most likely to represent *Eozygodon morotoensis*. Other fossils from the site are indeterminate fragments of cheek teeth and postcranial bones (Arambourg, 1933; Madden, 1972).

Buluk (ca 17.2 Ma), Kenya. Buluk is an important site in northern Kenya that yielded several proboscideans and has the potential to yield many more specimens. Tassy (1986) recognised the presence of *Arehaeobelodon* aff. *filholi* on the basis of some isolated cheek teeth and flattened lower tusks. He also reported indeterminate Elephantoidea at the site.

Mwiti (ca 17 Ma), Kenya. Mwiti yielded two gomphotheres, one represented by a skull and associated lower jaw with flattened tusks identified by Tassy, (1986) as *Arehaeobelodon* aff. *filholi*, the other a palate which he assigned to *Gomphotherium* sp.

Ombo, (ca 15 Ma), Kenya. Ombo yielded some premolars and molar fragments of a bunodont gomphothere (MacInnes, 1942; Tassy, 1986) which may represent the species *Protananeus maeinnesi*.

Alengerr, (ca 14 Ma), Kenya. Alengerr yielded a fragment of lower tusk and some cheek tooth fragments of a bunodont gomphothère which Tassy (1986) assigned to *Protananeus maeinnesi*.

Fort Ternan, (ca 13 Ma), Kenya. Fort Ternan has yielded two gomphotheres, *Afroehoerodon ngorora* and *Protananeus maeinnesi* (Tassy, 1986), the latter species being représentéd by a partial skull.

Nyakach, (ca 15 Ma), Kenya. Tassy (1986) described an isolated upper right second molar and a flattened lower tusk from the Nyakach Formation as *Protananeus maeinnesi*. Other material from the formation is fragmentary and unidentifiable.

Nachola, (15.5 Ma), Kenya. Pickford *et al.*, (1987) briefly mentioned the presence of a trilophodont gomphothere with flattened lower tusks in the Nachola and Aka Aiteputh Formations. The material was tentatively assigned to *Arehaeobelodon* aff *filholi*, because it resembles the fossils from Mwiti described by Tassy (1986). Until more informative material is collected and studied, we are unable to be more precise than this.

Kipsaraman (15.5 Ma), Kenya. Hill (1996) listed the presence of *Protananeus maeinnesi* and *Choerolophodon kisumuensis* in the Muruyur Formation at Kipsaraman, Tugen Hills. The fossils remain undescribed, but I can confirm that the Muruyur Formation contains *Afrochoerodon kisumuensis* in its type area at Cheparawa, where a lower third molar close in morphology to Maboko and Ngorora specimens has been found (Pickford, 2001). In addition a cranium from Cheparawa has cheek teeth that fall within the range of morphological and metric variation of *Afrochoerodon kisumuensis* from Maboko. In the Cheparawa skull the zygomatic arches are not retired as in Eurasian *Choerolophodon* specimens and the neurocranium is not elongated or widened. The upper tusks of the Chaparawa specimen are large and circular in section. At Kipsaraman, long, narrow molars typical of *Protananeus maeinnesi* have been recovered.

Loperot, (ca 17 Ma), Kenya. Maglio (1969) described a platybelodont tusk in which tubular dentine is preserved, thus far a unique discovery in tropical Africa. No further remains have been reported from the site (Tassy, 1986).

Ngorora, (12.5 - 10.5 Ma), Kenya. Three taxa of gomphotheres have been described from the Ngorora Formation. The most common is *Afroehoerodon ngorora*, originally assigned to the genus *Gomphotherium* by Maglio (1974), and later to the genus *Choerolophodon* by Tassy (1986), which is found in the four lower members of the formation (13-11 Ma) (Pickford, 2001). Secondly, there is an early *Choerolophodon* based on fossils from Member E (ca 10.5 Ma). The third is an unnamed tetralophodont elephantid (Tassy, 1986) based on a juvenile skull and mandible from Member D of the formation. New collections contain an isolated third molar from Member A, that differs markedly from *Afrochoerodon* and it is believed to belong to the same species as the juvenile tetralophodont skull from Site 2110, Member D of the formation. If so then this elephantid lineage dates from as early as 12.5 Ma. The interest in this taxon is that it not only indicates that the family Elephantidae probably arose in Africa, but it also throws light on the ancestral group from which the family arose and approximately when it arose. Similar material has been found in the Namurungule Formation, Kenya, and Kakara, Uganda (Nakaya *et al.*, 1987; Tassy, 1994b).

Nakali, (9.5 Ma), Kenya. A few fossil gomphothere teeth from Nakali have been ascribed to *Choerolophodon ngorora* (Tassy, 1986) but they are more likely to represent a true *Choerolophodon allied* to *C. pentelici* rather than the more primitive *Afrochoerodon ngorora*. In addition there is an indeterminate bunodont proboscidean. Some of this material was listed as *Anancus* sp. (Aguirre & Leakey, 1974) but this determination seems insecure.

Samburu Hills, (9.5 Ma), Kenya. A tetralophodont skull and some isolated teeth from the Namurungule Formation have been described in a preliminary paper (Nakaya *et al.*, 1987). The authors point out that the specimens are potentially important as a link between “gomphotheres” and elephantids. Tassy (1994b) is of a similar opinion, and lists the specimen along with one from Kakara, Uganda, as “Elephantidae, primitive form, gen. et sp. *incertae sedis*”.

Napak, (19 Ma), Uganda. A few teeth from Napak, Uganda, belong to bunodont, trilophodont gomphotheres (Bishop, 1958 fig. 2; 1962, 1963). MacInnes (1962) provided succinct descriptions and measurements of several tusk fragments as well as an M2/, M3/, p/3 and m/1 which he assigned to *Trilophodon angustidens kisumuensis*. Most of these fossils (except the p/3) seem to have been lost, although there is a cast of the lower tusk in the Uganda Museum, Kampala. The latter specimen was thought to be an upper tusk by MacInnes. MacInnes (1962) provided identifications and measurements (in mm) of the cheek teeth (Table 14).

A flattened lower tusk in the collection (Bishop, 1958, fig. 2) (height 26.2 mm; width 36 mm; length from apex to root ca 180 rum) with a dorsal sulcus and longitudinal twist suggests that some of the material belongs to a species of *Archaeobelodon* but there are also small lower tusks from Napak with oval to subcircular sections, suggesting the presence of a second taxon at the site, possibly *Progomphotherium*. My preliminary assessment of the Napak specimens is that the site contains both *Progomphotherium* and *Archaeobelodon*.

Moroto, (late Early Miocene), Uganda. Moroto I is the type locality of *Eozygodon morotoensis*, based on a set of upper cheek teeth. From Moroto II there are some undescribed teeth which have some resemblences to *Progomphotherium maraisi*, being small and extremely bunodont with reduced anterior and posterior conelets. Recently, some upper molars of *Eozygodon morotoensis* were also found at Moroto II.

Kakara (ca 9 Ma) Uganda. The Late Miocene Kakara Formation has yielded two primitive elephantids, an unnamed form with some tetralophodont features, and *Stegotetrabelodon* (Tassy, 1994b). The unnamed form, represented by an upper third molar, is close to a specimen from the Namurungule Formation, Kenya (Nakaya *et al.*, 1987) and may represent the same species as a juvenile skull and mandible from Member D of the Ngorora Formation assigned to gen. et sp. indet. (Tetralophodont form) by Tassy (1986). The *Stegotetrabelodon* from Kakara is one of the earliest known specimens of the genus.

Burji-Soyama, (15-17 Ma), Ethiopia. Suwa *et al.*, (1991) attributed a partial skeleton from Burji-Soyama, Ethiopia, to *Choerolophodon kisumuensis*. The particular value of the Burji-Soyama specimen is that it is represented by a single individual with upper and lower tusks as well as upper and lower third molars, thus clearing up the question of association between elements. The authors concluded that the specimen could not represent *Protanancus* because its lower tusks were oval in section and not greatly flattened as in the tusks assigned to this genus by Tassy (1986). If Suwa and colleagues are right, then this would mean that *C. kisumuensis* possessed oval lower tusks and upper tusks with a wide enamel band. The upper tusks of other species of the genus *Choerolophodon* are devoid of enamel, or at best have a tiny strip of enamel near the tip, which wears away with use (Tassy, 1986, plate VI, fig. 3). The Cheparawa skull of *Afrochoerodon kisumuensis* has tusks which are circular in section without enamel, sug-gesting that the Burji specimen, which has an upper tusk which possesses a wide and elongated band of enamel, does not belong to this species. In addition, the anterior cingulum of the M3/ in the Burji sample terminates low and it thus differs from *Afrochoerodon* and *Choerolophodon*. The third molars plot close to *Protanancus MacInnesi*, and this is where it may belong (Pickford, 2001) the main argument against this suggestion being the circular lower tusks attributed to it.

Ch’orora (ca 10 Ma), Ethiopia. A longirostrine “mastodon” was reported from Ch’orora by Coppens & Tassy (in Tiercelin *et al.*, (1979)) in deposits aged about 10 Ma (Sickenberg & Schönfeld, 1975). The specimens were thought to represent a tetralophodont mastodont close to Elephantidae and more particularly the *Stegotetrabelodontinae*.

Karugamania, (Miocene) Democratic Republic of Congo. The proboscidean material from Karugamania (Hopwood & Lepersonne, 1953; Hooijer 1963, 1970) was traditionally used to assign an Early Miocene age to the strata. However, Pickford *et al.*, (1993) are of the opinion that the specimens are indeterminate.

Nyamavi, (Miocene or Pliocene) Democratic Republic of Congo. Hopwood & Lepersonne (1953) first described proboscideans from the Nyamavi area, reporting the presence of mastodon teeth and *Stegodon*. Nyamavi is the type locality of the species *Stegolophodon lepersonnei* Hooijer (1963). The basis for this determination is a partial upper molar, and because of this there has been some debate about its identification. Maglio & Hendey (1970) did not accept the presence of the genus *Stegolophodon* in Africa, which prompted Van Couvering & Van Couvering (1976) to transfer the specimen to *Primelephas*, but as Tassy (1986) pointed out the tubercles are massive and thick-set, unlike those of *Primelephas* and that Hooijer’s determination was not absurd. Pickford *et al.*, (1993) thought that the material could represent *Mammuthus*

Table 14: Measurements (in mm) of gomphothere teeth from Napak, Uganda (from MacInnes, 1962).

Specimen	Length (mm)	Breadth (mm)
Nap I 26, upper M2/	ca 100	55
Nap I 24a-b, upper M3/	–	53 (second valley)
Nap I 21, lower p/3	31.5	18
Nap I 25, lower m/1	77.5	42 (posterior ridge)

subplanifrons because Ugandan fossils assigned to this species possess similarly thick enamel and a cementum cover in the transverse valleys.

Sinda-Mohari, (Miocene or Pliocene) Democratic Republic of Congo. Hooijer (1963) described several specimens from the Sinda region as *Trilophodon angustidens* cf. *kisumuensis*. One of the specimens is a flattened lower tusk from locality 531A similar in many respects to those assigned to *Protanancus MacInnesi* by Tassy (1986). Another specimen from the left bank of the Sinda River at the foot of ridge 1, thought to be a left lower third molar by Hooijer on account of the presence of four lophids, was considered by Madden (1977) to be a lower first molar of *Tetralophodon*. Still further specimens illustrated by Hooijer (1963) are extremely fragmentary and may even represent remains of *Anancus* and *Mammuthus subplanifrons* (Pickford *et al.*, 1993).

Malembe, (Early Oligocene), Cabinda, Angola. Some fragments of proboscidean premolars from Malembe were assigned to *Trilophodon angustidens* cf. *kisumuensis* by Hooijer (1963) who thought that the sediments from which they came were early Miocene. The specimens are of early Oligocene age and were redescribed as *Phiomia* or *Hemimastodon* sp. by Tassy (in Pickford, 1986).

Siwa, (Early Miocene), Egypt. An isolated and slightly damaged, heavily worn, right upper third molar from Siwa was described by Hamilton (1973) as a lower third molar of *Gomphotherium angustidens*. The presence of two anterior roots reveals that the tooth is in fact an upper molar. It consists of four lophs and a small distal talon, there is no sign of chevroning, the enamel is smooth and the trefoil wear pattern is not well developed. The crown is 119.3 mm long and its estimated original breadth is ca 61.3 mm. This tooth is quite small, plotting out within the range of variation of *Afrochoerodon kisumuensis* (Fig. 7). The position of the conules and the poorly expressed median sulcus supports this identification, at least at the generic level, but the specimen is too worn to identify with certainty.

Wadi Moghara, (late Early Miocene to basal Middle Miocene), Egypt. Fourtau (1918) described a maxilla fragment with the second and third molars (CGM 30932), a right mandible with m/2-m/3 (CGM 30930), a left mandible with the permanent teeth in their crypts (CGM 2366R) and various isolated teeth as *Mastodon* (*Gomphotherium*) *angustidens* var. *libyca*. Fourtau (1918) provided measurements of the M3/ (length 143 mm and greatest breadth at the first loph 86 mm) which suggest that the tooth was exceptionally wide. Tassy (1977) calculated an index of 59 and remarked on the great width as did Fourtau himself and Tobien (1973b). However, measurements of the photograph published by Fourtau indicate that he made an error in measuring the length, which is closer to 153 mm than to 143 mm (the figure given by Fourtau, 1918) and I presume that he misread his calipers. Recent examination of the original fossil by the author confirms the error in measurement, the length being 152.5 mm and the greatest breadth 86.2 mm. As such then, the tooth is not remarkable for its great width. The recalculated length/width proportions of the upper molar, the loph number of M3/ (4), the position of the conules and the presence of a continuous and straight median sulcus suggest that this specimen probably belongs to *Afromastodon*.

The third molar in the right mandible (CGM 30930) assigned to the same species by Fourtau is only slightly helicoidally twisted, the conules are not centrally positioned, and the median sulcus is straight suggesting that the specimen belongs to the same genus.

Two isolated symphyses from Wadi Moghara were described by Fourtau (1918, p. 88) who identified them as *M. angustidens* var. *libyca*. One of these retained a fragment of the right lower tusk which is “légèrement comprimee sur les côtes et dont le plus grand diametre est 33 millimetres”. This suggested that the lower tusk was oval in section, but not flattened, a view accepted by Tobien (1973b) who concluded that the specimen might indicate the peg type of lower tusk. Unfortunately, both symphyses (specimens CGM 32984 and CGM 32985) assigned to this species belong to the large anthracothere *Brachyodus Depéreti*. A juvenile mandible described by Fourtau was originally considered to have the m/1 in its crypt, but recent re-examination of the specimen reveals that the tooth thought by Fourtau to be the first permanent molar is in fact the fourth permanent premolar, and the root behind it belongs to the erupted m/1, the crown of which has broken off.

Fourtau (1918) also erected a new species *Mastodon* (*Gomphotherium*) *spenceri* which was later identified as *Rhynchotherium spenceri* by Osborn (1936) on account of the oblique, downwardly slanting symphysis. The second lower molar has well developed chevrons, centrally located conules and a relatively large posterior cingulum. The anterior end of the symphysis is broken, but the interior ends of the alveoli for lower tusks are preserved, but unfortunately the sectional shape of the tusks cannot be determined from the little that remains. This specimen is extremely similar to material from Gebel Zelten (pers. obs.) and Cherichera (Gaudry, 1891), and there can be little doubt that the same species of mastodont occurs at all three sites.

A left mandible with broken second and third molars (CGM 1498) is interesting in that the teeth fall close to the range of variation of *Eozygodon morotoensis* as shown in table 16.

Hamilton (1973) gave measurements of a heavily worn isolated right lower molar from Moghara (M 14075) which he as-

Table 15: Measurements (in mm) of specimens assigned to *Afromastodon libycus* housed in the Egyptian Geological Museum, Cairo.

Specimen	Length	Breadth	Identification
CGM 30932 upper M2/	106.3	68.7	*Afromastodon libycus*
CGM 30932 upper M3/	152.5	86.2	*Afromastodon libycus*
97-675 upper M1/	74.6	49	*Afromastodon libycus*
CGM 30892a upper M2/	114	61	*Afromastodon libycus*
CGM 30892b upper M2/	95	61.3	*Afromastodon libycus*
97-711 upper dM3/	40.2	26.5	*Afromastodon libycus*
88-M124 upper dM2/	27.2	17.8	*Afromastodon libycus*
88-M124 upper dM3/	40.8	30	*Afromastodon libycus*
2366R lower p/4	41	32	*Afromastodon libycus*
2366R lower m/1 root	62	32.5	*Afromastodon libycus*
CGM 82987 lower m/2	113	61	*Afromastodon libycus*
CGM 30930 lower m/3	176.5	75.6	*Afromastodon libycus*
CGM 30931 lower m/2	119	67.8	*Afromastodon libycus*
97-665 lower m/2	116.4	61.7	*Afromastodon libycus*

signed to *Gomphotherium angustidens*. The crown is 146 mm long by 60.4 mm wide, consists of 4.5 lophids and has well developed trefoil wear outlines. The tooth is not recurved buccally and the median sulcus is relatively clear despite the heavy wear. The third and fourth lophids display a chevron pattern. Taken together, the morphological characters suggest affinities with the genus *Afromastodon*, but in view of the heavy wear, there must remain some doubt about the affinities of the specimen. In terms of size this specimen plots out close to a specimen (NHM X 7) from Gebel Zelten assigned to *Afrochoerodon zaltaniensis* (Fig. 8).

In summary, it seems that most of the Moghara masto¬dont remains belong to *Afromastodon*, but that they represent a species that was smaller than *A. coppensi*. The name *Afromastodon libycus* has page priority for the Wadi Moghara species. One specimen (CGM 1498) indicates the presence of a second elephantoid at Wadi Moghara, the size and proportions of the teeth suggesting affinities with *Eozygodon*. Another specimen (M 14075) indicates the presence of a third species of gomphothere at the site, pos-sibly *Afrochoerodon zaltaniensis*.

Wadi Natrun, (Early Pliocene), Egypt. In the Egyptian Geological Museum, Cairo, there is much of an upper third molar of *Anancus osiris* from Wadi Natrun. It has a great deal of cementum in the valleys and covering parts of the walls of the main cusps, suggesting that it belongs to a derived species of the genus.

Mena, (Early Pliocene), Egypt. Arambourg (1945, 1947) described a complete upper third molar of *Anancus* from 2 km north of Mena House Hotel, Egypt as the new species *A. osiris*. The morphology of the specimen suggests that it is a derived species within the genus.

Gebel Zelten, (Early and Middle Miocene), Libya. Arambourg (1961) provided measurements of small gomphothere teeth from Gebel Zelten and Hormann (1963) described a mandible fragment with p/4 and m/1 of a larger gomphothere. Other material was mentioned by Harris (1969, unpublished PhD Thesis) as *Trilophodon pygmaeus* Gaziry (1987) described some worn molars as *Choerolophodon zaltaniensis* which are morphologically similar to those of *A. kisumuensis* but are larger than them. The Zelten specimens are larger than those of *A. kisumuensis* from Maboko but are closer in size to the Kenyan *Afrochoerodon ngorora*. The upper third molars have 4.5 lophs. Gaziry (1987) also assigned some poorly preserved molars to *Gomphotherium angustidens pasalarensis*, one specimen of which (Z 13, Gaziry, 1987, Fig. 6) resembles fossils from Ad Dabtiyah (Saudi Arabia) identified as *Gomphotherium cooperi* by Gentry (1987) and from Ghaba (Roger *et al.*, 1994). The other specimen described and figured by Gaziry (1987, fig. 7a, b - specimens Z 11 and Z 12) appears to be a lower second molar and may belong to a different taxon, possibly *Protanancus* but I hesitate to pronounce about these fragmentary specimens. The measurements of these specimens given by Gaziry (1987) appear to be erroneous.

In the Natural History Museum, London, there is a large sample of gomphotheres collected by R.J.G. Savage, that until 1999 were housed at the University of Bristol. There are at least three proboscidean taxa in the Savage collection and there is a fourth collected by the Oasis Oil Company in

Table 16: Measurements (in mm) of teeth of *Eozygodon morotoensis* from Egypt and East Africa.

Specimen	Length	Breadth	Identification
Meswa lower m/2	82.6	60.5	*Eozygodon morotoensis*
Meswa lower m/2	82.9	56.9	*Eozygodon morotoensis*
CGM 1498 lower m/2	88.4	45.6 (root)	?*Eozygodon* sp.
Meswa lower m/3	123.9	67.4	*Eozygodon morotoensis*
CGM 1498 lower m/3	124	64.2 (root)	?*Eozygodon* sp.

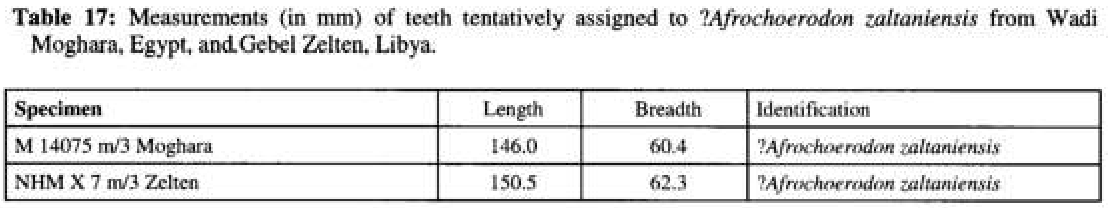


Table 17: Measurements (in mm) of teeth tentatively assigned to *?Afrochoerodon zaltaniensis* from Wadi Moghara, Egypt, and Gebel Zelten, Libya.

Specimen	Length	Breadth	Identification
M 14075 m/3 Moghara	146.0	60.4	*?Afrochoerodon zaltaniensis*
NHM X 7 m/3 Zelten	150.5	62.3	*?Afrochoerodon zaltaniensis*

1962.

1.- An undescribed left M3/ (M 21866), which is exceedingly small, being about the same size as large *Palaeomastodon* species (eg *P. parvus*, specimen NHM M 9122) differs from *Palaeomastodon* principally by the development of mesocones, a feature which brings it to the grade of mastodonts (*sensu lato*). This fossil probably represents a new genus and species of extremely primitive gomphothere.

2.- A small gomphothere is represented at Gebel Zelten by a right mandible with eroded and broken second and third molars, the incomplete symphysis and part of the left body (specimen L32). The symphysis is broken anteriorly at the level of the incisive alveoli, the internal ends of which can be seen in anterior view. The symphysis is not down turned and in this respect it recalls the situation in *Phiomia* as well as *Archaeobelodon* and *Gomphotherium angustidens*. The right body has an empty alveolus for m/1, which is positioned directly behind the sharp edged diastema. There is no sign of a cheek tooth alveolus anterior to this tooth, which means that unlike *Phiomia* (and *Palaeomastodon*) this species had only three cheekteeth in occlusion when the m/3 was erupted but unworn. It is appreciably smaller than *Gomphotherium angustidens pasalarensis* Gaziry (1976) and is likely to belong to a different species or subspecies, as does the material described by Gaziry (1987). The material mentioned by Arambourg (1961) probably belongs to this species.

3.- A maxilla in the Savage collection (specimen B2) is similar in size to the holotype of *Choerolophodon zaltaniensis* (Gaziry, 1987), but the root of the zygomatic arch is located above the second molar, and in this respect it differs from *Afrochoerodon kisumuensis* in which the zygomatic root departs from the maxilla well behind M3/. The molars in the B2 maxilla have medium sized anterior and posterior pretrite conules which are centrally positioned but they lack other choerolophodont features such as marked chevroning and cementum. In some ways this specimen resembles the holotype of Fourtau's species *Mastodon angustidens* var. *libyca*, in possessing an upper third molar with 4 lophs and moderately developed anterior and posterior pretrite conules. It has some similarities with *Afromastodon coppensi*, but is smaller and the morphology of its third pretrite loph is different. Right and left mandibles (NHM X 7), with the third molar in its crypt has 3.5 lophs. There are anterior and posterior pretrite conules on all lophs. There are no posttrite conules. The mesocones are smaller than the mains cusps and there is slight chevronning in the third loph. This specimen accords in size with maxilla B 2 and probably represents the same species.

4.- The most common proboscidean at Gebel Zelten is a large gomphothere represented by several partial mandibles which possess long symphyses which are markedly down turned as in material from Wadi Moghara assigned to *Mastodon spenceri* by Fourtau (1918). In this respect they differ markedly from *Archaeobelodon filholi* and *Gomphotherium angustidens* from France. None of the Zelten mandibles contains the lower incisor, and none of them possess alveoli for them, but it should be pointed out that all the symphyses are broken towards their anterior extremities, leaving open the possibility that they did possess lower tusks (Hormann, 1963). In the Savage collection housed in the NHM, London, there are two isolated lower tusks which are oval in section. In all of the specimens in which the symphysis is preserved there is a large mental foramen on the lateral surface of the symphysis similar to one in the holotype of *Mastodon spenceri* from Wadi Moghara. A second equally large mental foramen occurs below the anterior cheek tooth. A juvenile mandible from Wadi Moghara assigned to *Mastodon angustidens* var. *libyca* by Fourtau is similar in several respects to a specimen from Gebel Zelten (specimen L113) but is of a slightly older individual. All this material from Gebel Zelten should probably be assigned to the same species as Fourtau's material. Of the two available names for the species *libycus* has page priority over spenceri. The largest gomphothere specimens from Gebel Zelten are represented in the Savage collection by a lower jaw with a heavily worn second molar and the third molar in medium wear (specimen H2). The third molar is almost as large as material from Arrisdrift which it resembles morphologically, and the specimen is assigned to *Afromastodon libycus*. A second specimen (L76), a left mandible with heavily worn m/2 and m/3 has a straight, untwisted third molar and the root of the ascending ramus is well behind the distal end of the m/3 probably belongs to the same species. A partial upper third molar (NHM no number) of a large mastodont from Gebel Zelten not dissimilar in size and morphology to material from Arrisdrift assigned to *Afromastodon coppensi* is here assigned to *A. libycus*.

In conclusion, therefore, there are four gomphotheres at Gebel Zelten; 1) a primitive form of exceptionally small size 2) a small gomphothere in which the mandibular symphysis is not down turned and which contained lower tusks, here considered to be an unnamed species of *Gomphotherium akin* to *G. angustidens* but appreciably smaller 3) a choerolophodont, *A. zaltaniensis* (Gaziry, 1987) close in size and morphology to *A. ngorora* (Maglio, 1974) and 4) a large mastodont with down turned symphysis, possibly without tusks, or with oval to circular lower tusks, representing *Afromastodon libycus* (Fourtau, 1918).

This array of gomphotheres suggests that the Zelten sites span a considerable period of geological time. The small, primitive species is most likely basal Early Miocene or even Late Oligocene in age, while the other material is probably Middle Miocene. The bulk of the specimens appears to be about 16-15 Ma but some of it, in particular the choerolophodont described by Gaziry (1987), could be as young as about 13-12 Ma.

Cherichera, (Early Miocene), Tunisia. Gaudry, 1891, described and figured a right mandible with m/2 and m/3 from Cherichera, near Kairouan, Tunisia, as *Mastodon angustidens*.

In the lower molars the median sulcus separating the pretrite and posttrite halves is well developed, the pretrite conules do not interrupt the median sulcus, the posttrite cusps are devoid of anterior and posterior conules and the mesocones are in line with the lophids, so the specimen is unlikely to represent the genus *Choerolophodon*. The anterior and posterior pretrite conules are large and block the transverse valley, and with wear have produced a clear trefoil pattern. The third molar has 4.5 lophids, shows minor helicoidal twisting of the crown and is straight buccally. The third lop hid shows a slight chevron pattern. The symphysis is oriented obliquely forwards and downwards not dissimilar to a specimen of *Afrochoerodon ngorora* from Fort Ternan (Tassy, 1986, Pl. 5, fig. 1). There are two mental foramina, one on the body of the mandible below the anterior tooth, the other located on the symphysis, and in this respect it differs markedly from the symphyses of *Gomphotherium angustidens* and *Archaeobelodon filholi*. The symphysis is broken obliquely across some distance anteriorly of its distal margin, but there is no evidence of an alveolus for a lower tusk in the remaining portion. Bergounioux & Crouzel (1956) assigned this specimen to *Rhynchotherium* aff. *spenceri* because of its similarities to the fossils from Wadi Moghara. It probably belongs to *Afromastodon libycus*. Measurements (in mm) of the teeth of the Cherichera specimen are given in table 19.

Bergounioux & Crouzel (1956) described a partial left third molar from the Cherichera Massif as *Tetralophodon longirostris*. The specimen consists of the pretrite half of a crown lacking the anterior loph. Originally it would have possessed 5.5 loph(id)s. The authors identified it as a lower molar in the text figure, but as an upper molar in the plate. The specimen could belong to *Anancus*.

Thomas & Petter (1986) mention their discovery in the old collections at the Laboratoire de Paleontologie, Paris, of a zygodont upper molar from Cherichera. The specimen is considered by the authors to have come from a Vindobonian level.

Khenchella, (Oligocene or even Eocene), Tunisia. An isolated tooth from Khenchella, Tunisia, identified by Gaudry (1891) as a milk tooth of *Mastodon turicensis*, is more likely to be a permanent molar of *Moeritherium* (Pickford & Tassy, 1980; Tassy, 1981).

Djebel Krechem El Artsouma (Late Miocene), Tunisia. Geraads (1989) described and illustrated some isolated teeth of *Tetralophodon* from Djebel Krechem El Artsouma, a locality that also yielded *Hipparion* and isolated teeth of *Nyanzachoerus devauxi*. In the sample there was also a molar fragment with cementum that Geraads considered to represent *Choerolophodon*.

Djebel Sémène (Late Miocene), Tunisia. Bergounioux & Crouzel (1956) reported the presence of *Tetralophodon longirostris* at Djebel Sémène on the basis of what they thought was a portion of skull with the premaxillae containing the upper tusks. In fact the specimen is part of the symphysis of a mandible with the lower tusks (Tobien, 1978). The tusks are taller than broad, as in *Progomphotherium*, but unlike this genus there is a dorso-medial groove.

Kabylie, (Early or Middle Miocene), Algeria. The partial molar from Kabylie, Algeria (Depéret, 1897) was originally described as a mutation (*pygmaeus*) of *Mastodon angustidens*. The specimen, a third lower molar, lacks the first loph and, according to Arambourg (1961) it would have been about 121.5 mm when complete (the preserved part measures 88.5 x 42.5 mm). Osborn (1936) considered that it belonged to an advanced species of *Phiomia*, but this seems unlikely, not only from the morphology of the cusps but also from the thick layer of cementum that covers the crown, as well as the fact that the first loph is missing and the crown would have been considerably longer than thought by Osborn. The specimen also has wide interloph valleys, and is thus markedly different from the small, primitive gomphothere from Gebel Zelten. Ennouchi (1948) referred to a specimen from Kabylie, presumably the specimen described by Depéret, as *Phyomia Depereti* (sic) but without description or diagnosis. The specimen was mentioned by Bergounioux & Crouzel (1959) and Tobien (1973b) considered that the tooth belonged to *Choerolophodon* on account of the great thickness of cementum which practically obscures the crown. If this is so, then it is by far the smallest choerolophodont tooth ever found, being appreciably smaller than *A. kisumuensis*. (See note at end of paper)

Smendou (Late Miocene) Algeria. Gervais (1849) illustrated a broken third molar of a mastodont which he considered was closest in overall morphology and size to *Mastodon*

Table 18: Measurements of proboscidean third molars (in mm) from Gebel Zelten, Libya.

Specimen upper/lower	Length	Breadth	Identification
P 102 lower m/3	118	55.6	*Gomphotherium* sp. nov.
L 32 lower m/3	111	54	*Gomphotherium* sp. nov.
Z 13 lower m/3	115	51	*Gomphotherium* sp. nov.
X 7 lower m/3	150.5	62.3	*Afrochoerodon zaltaniensis*
H 2 lower m/3	188	77.5	*Afromastodon libycus*
X 3 lower m/3	180	--	*Afromastodon libycus*
L 76 lower m/3	166	73.3	*Afromastodon libycus*
P 131 lower m/3	170	72.5	*Afromastodon libycus*
1961-5 upper M3/	109	55	*Gomphotherium* sp. nov.
1961-5 upper M3/	112.8	54.8	*Gomphotherium* sp. nov.
B 2 upper M3/	141.5	73.5	*Afrochoerodon zaltaniensis*
Zelten upper M3/	138	75	*Afrochoerodon zaltaniensis*
Zelten upper M3/	138	76	*Afrochoerodon zaltaniensis*
M 21866 upper M3/	93.5	56	Nov. gen. nov. sp.

Table 19: Measurements (in mm) of lower molars of *Afromastodon libycus* from Cherichera, Tunisia.

1885.30	Length	Breadth 1st loph	Breadth 2nd loph	Breadth 3rd loph	Breadth 4th loph
Rt m/2	94.3	48.0	56.6	59.8	--
Rt m/3	151.0	65.5	72.0	70.2	57.0

borsoni or *Mastodon ohioticum*. Relationship with *Anancus arvernensis* is also possible, but less likely on account of the "tapiroid" morphology of the cusps.

Ad Dabtiyah, (Middle Miocene), Saudi Arabia. Several specimens from Saudi Arabia were assigned to *Gomphotherium cooperi* by Gentry (1987). The lower tusk, which has a flat section and is longitudinally twisted, is not like that of *Gomphotherium angustidens* but is similar to those of *Archaeobelodon filholi*, and on this basis I am inclined to identify the Saudi specimens as this genus. The molars, in isolation, do indeed closely resemble material from Bugti, Pakistan, the type site of *G. cooperi*, the lower tusks of which are unknown. One specimen (M 42946) from 60 km south of Ad Dabtiyah, looks more like *Choerolophodon* than *Gomphotherium*.

Ghaba, (Early Miocene), Oman. Roger *et al.*, (1994) mentioned some isolated gomphothere molars from Ghaba which were notable because of their diminutive size. The lengths of the lower third molars range from 114.6 to 116.4 mm and the upper third molar was only 102.6 mm long. Morphologically and metrically these small teeth from Ghaba are like those of the diminutive proboscidean from Gebel Zelten attributed to *Gomphotherium angustidens pasalarensis* by Gaziry (1987)

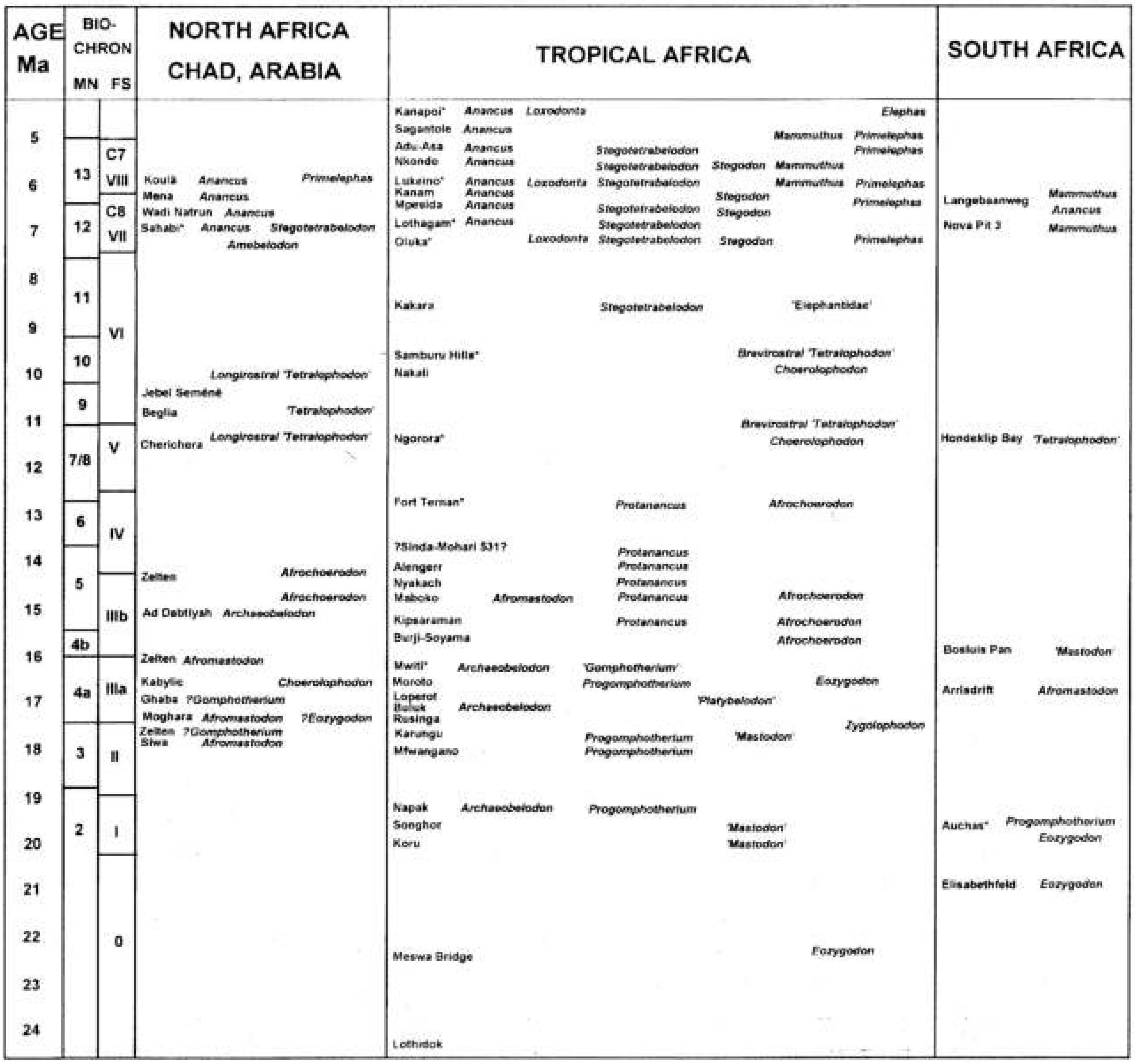


Figure 9: Geochronology of African proboscidean localities and correlations to European Faunal Zones and African Faunal Sets. Representation of mastodonts in the Miocene of North Africa, Chad, Arabia, Tropical Africa and South Africa. Sites with an asterisk (*) have yielded skulls.

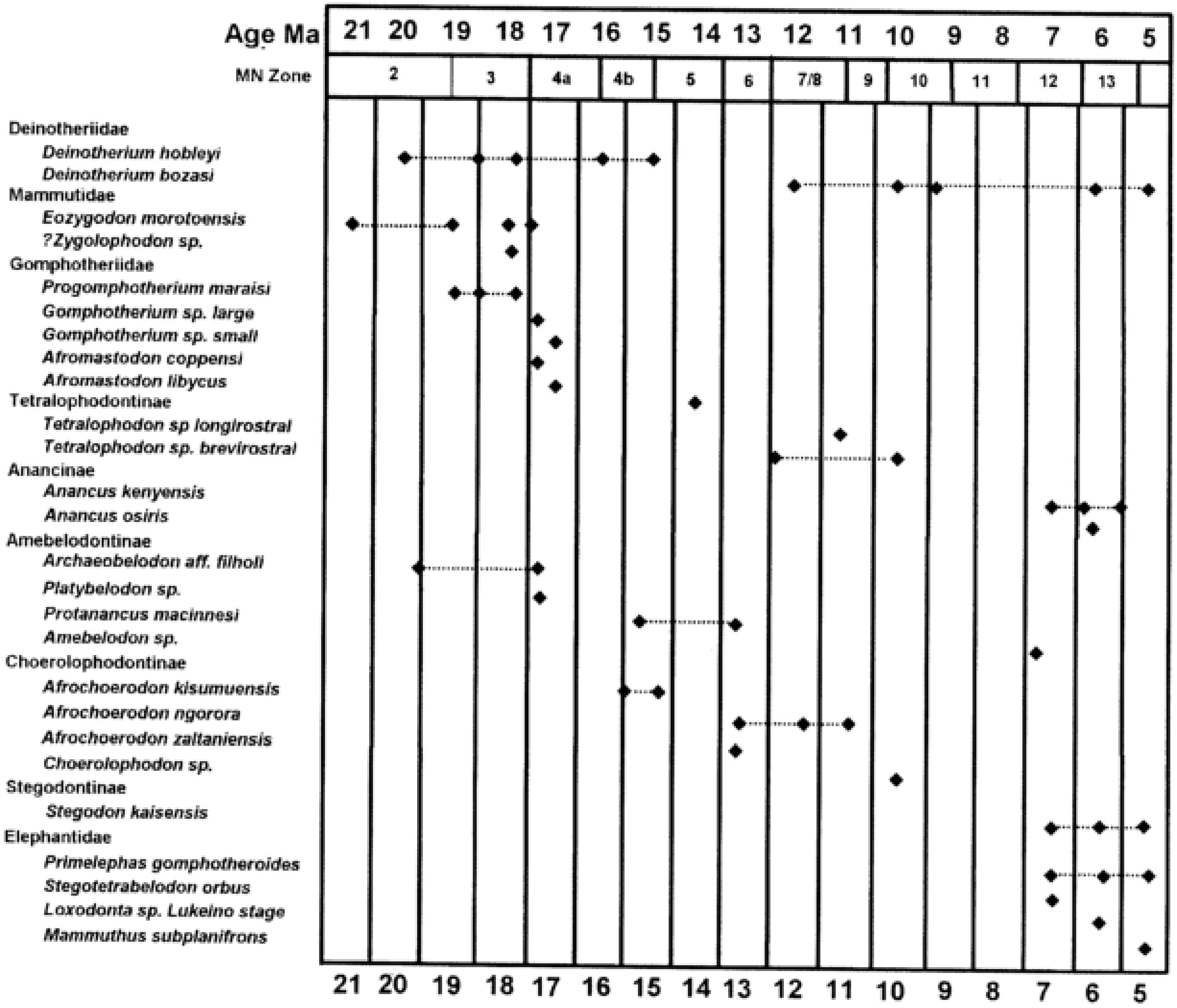


Figure 10: Range chart of African Neogene Proboscidea

but which is here considered to represent an undescribed species of gomphothere because they differ morphologically and metrically from the Pasalar fossils. Morphologically the Ghaba specimens are fully derived gomphotheres, a fact already noted by Roger *et al.*, 1994.

Biostratigraphic implications of the Orange River proboscideans

The Auchas AM 02 assemblage of proboscideans is close to that of East African Early Miocene faunas. The combination of a small species of *Deinotherium*, a primitive small gomphothere and an eozygodont is found at a number of sites in Kenya and Uganda (Moruorot, Rusinga/Mfwangano, Moroto) which range in age from about 20 to 17 Ma (Fig. 9).

The bunodont proboscidean specimen from Auchas AMSE assigned to *Gomphotherium* sp. indet. is somewhat larger than the material from Auchas AM 02 and is close in size to East African specimens aged between 18 and 17 Ma. This could mean that it is contemporary with them.

The Arrisdrift proboscidean fauna indicates an age appreciably younger than the Auchas fauna. The *Deinotherium* is the same, but the bundont proboscidean is considerably more advanced morphologically and is much larger than anything from Auchas. There can be little doubt that it is a basal Middle Miocene form somewhat older than the assemblage from Maboko (Kenya) aged 15 - 15.5 Ma. I estimate on the basis of the fossil suids found associated with it (Pickford, 1997) that *Afromastodon coppensi* is about 17 - 17.5 Ma (Fig. 9).

Figure 10 is a range chart of African Neogene Proboscidea which shows the position of the new genera *Progomphotherium* and *Afromastodon* relative to the other known genera. Figure 11 is a proboscidean range chart for Europe which can be compared with that for Africa. It appears that there were several dispersions of proboscideans from Africa towards the high latitudes. Deinotheres colonised Europe about the same time as mammutids, several million years after it was colonised by gomphotheres and amebelodonts. The appearance of tetralophodonts in Europe (ca 12 Ma) occurred almost the same time as their appearance in Africa suggesting relatively free access between the neighbouring land masses. Anancines have a slightly earlier first record in Europe than Africa but the African record between 10 and 7 Ma is rather poor. Choerolophodonts evolved in Africa during the Middle Miocene (*Afrochoerodon*) and soon colonised Europe (Chios, MN5). *Choerolophodon* may have arisen in Africa and then colonised Eurasia during the Late Miocene. Elephantids evolved in Africa and did not cross to Europe until the late Pliocene, whilst *Stegodon* ap-

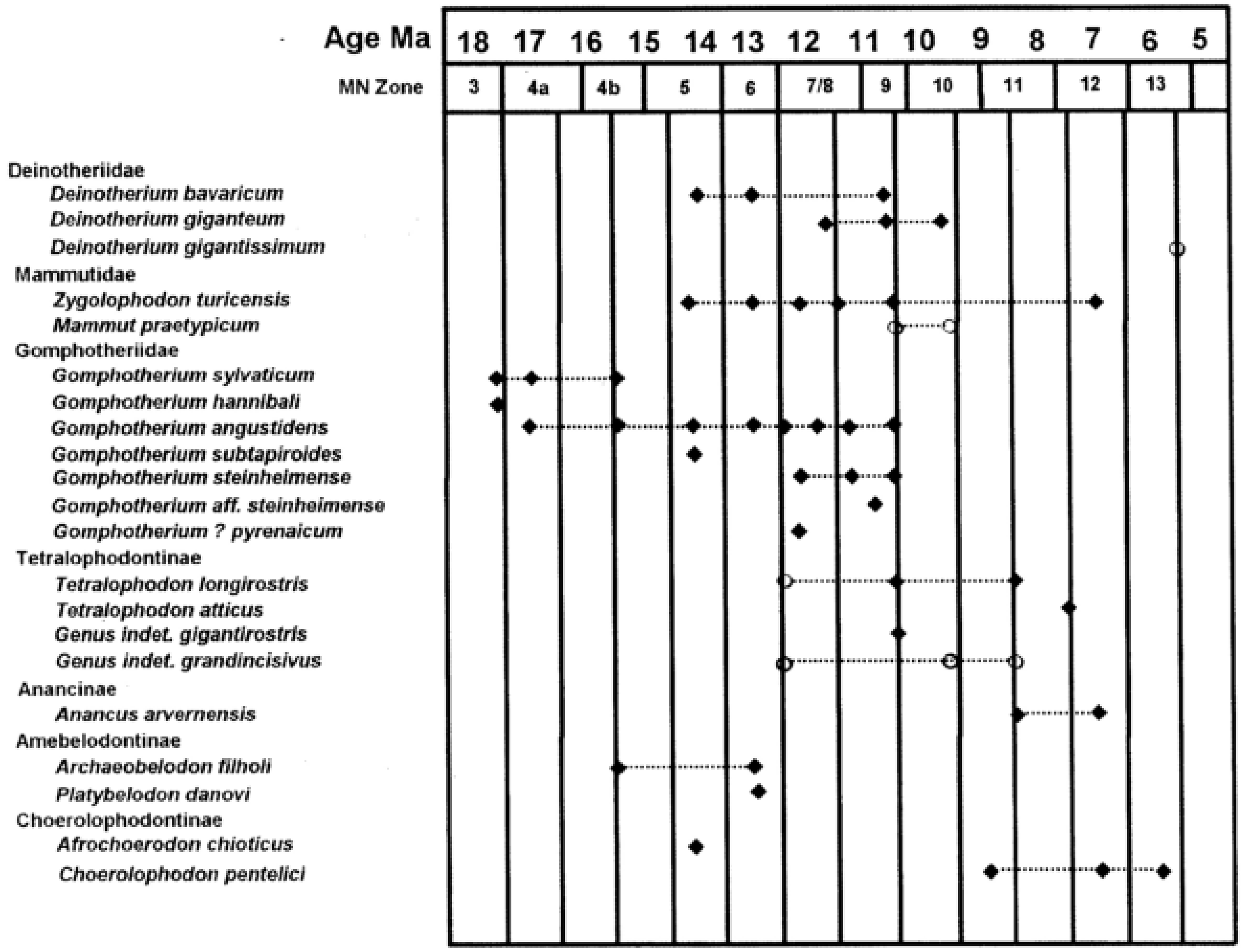


Figure 11: Range chart of European Proboscidea for comparison with Fig. 10.

pears suddenly in Africa at the end of the Miocene but has not been found in Europe although it occurs in the Far East.

The overall picture that emerges is that most of the evolutionary novelties among the proboscideans arose in Africa, after which successive waves represented by different genera and families colonised Europe and Asia well after their establishment in Africa. This seems to be so for the mammutids, gomphotheres, amebelodonts, choerolophodonts and anancines, as well as the deinotheres and elephantids. The main exceptions are the tetralophodonts which appeared almost simultaneously in Africa and Europe, and the stegodonts, which might represent a colonisation of Africa by proboscideans which had already evolved in the Far East.

Conclusions

The Miocene terrace deposits of the lower reaches of the Orange River Valley at Auchas and Arrisdrift have yielded abundant and relatively complete remains of proboscideans. Early Miocene levels at Auchas have yielded *Deinotherium hobleyi*, *Eozygodon morotoensis* and *Progomphotherium maraisi* (gen. et sp. nov.) Comparison of the fossils with material from East Africa indicates an age of ca 19-20 Ma for Pits AM 02 and AM 11. Slightly younger deposits are indicated at Pit AMSE which yielded a larger, slightly more derived gomphothere, with some similarities to *Progomphotherium* which is older and some to *Afromastodon* which is younger. Thus at Auchas the proboscideans suggest that there are at least two sets of terrace deposits with different ages, the earlier ca 19-20 Ma, the younger aged about 18 Ma.

At Arrisdrift, the sediments, which are ca 17-17.5 Ma, have yielded *Deinotherium hobleyi* and *Afromastodon coppensi* (gen. et sp. nov.). The latter species is larger than *Afromastodon libycus* (Fourtau) from Wadi Moghara (Egypt) and Gebel Zelten (Libya).

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***Note added at proof stage**

A recent discovery in the Ngorora Formation, Kenya (ca 13 Ma) (Bickford, in press) is a partial skeleton and dentition of *Choerolophodon pygmaeus*. The holotype of *Mastodon pygmaeus* from Kalylie, Algeria is exceedingly similar to the Ngorora fossils.

Reference

Pickford, M., in press. Partial dentition and skeleton of *Choerolophodon pygmaeus* (Depéret) from Ngenyin, 13 Ma, Tugen Hills, Kenya: resolution of a century old enigma.

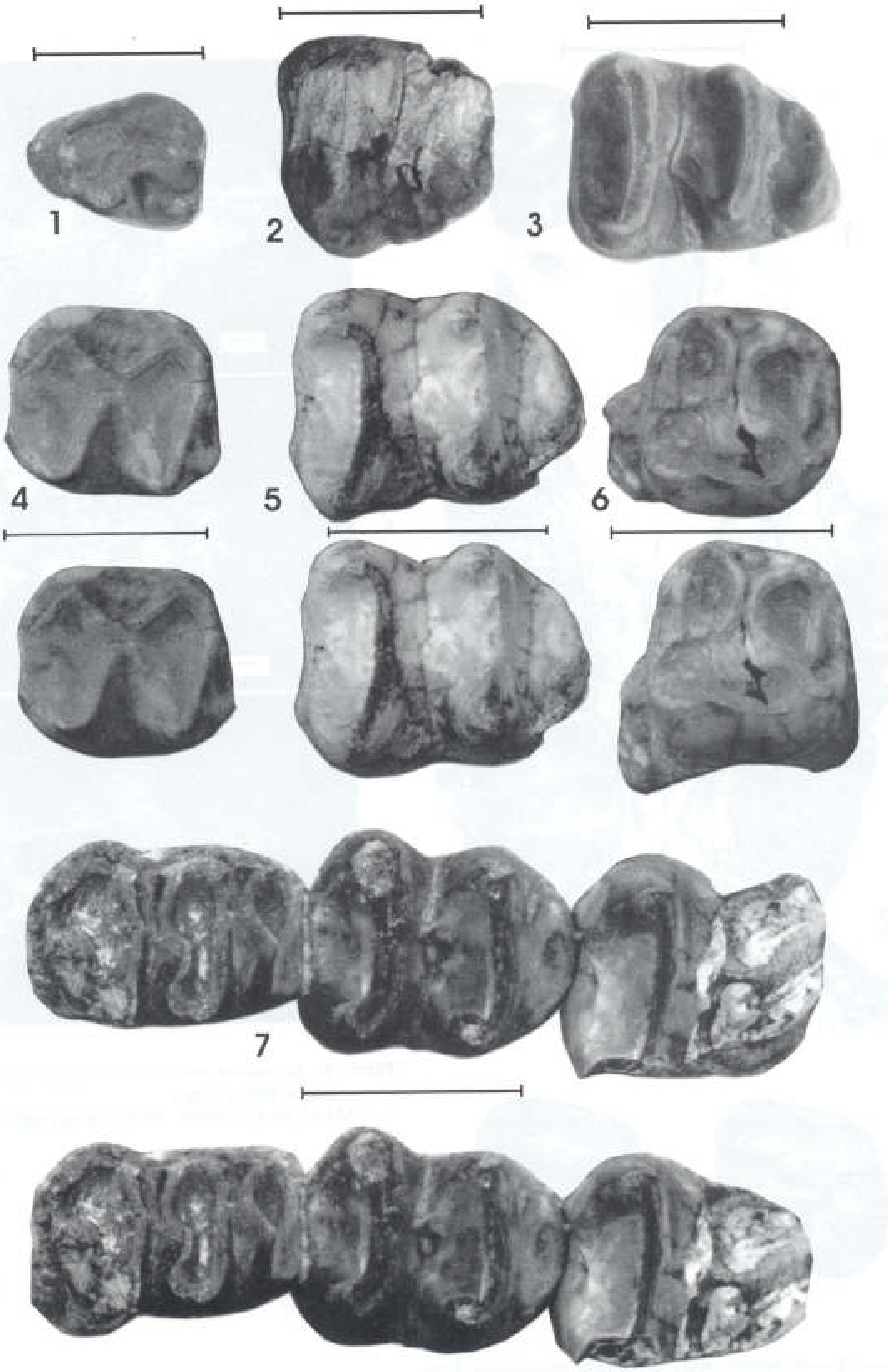


Plate 1: *Deinotherium hobleyi* from Auchas and Arrisdrift, Namibia. (Scale bars = 5 cm).
1. AD 200'97, right p/3, occlusal view.
2. PQAD 299, left M3/, occlusal view.
3. AM 02, left m/3, occlusal view.
4. PQAD 650, right p/4, stereo occlusal view.
5. AM 11 1'97, left m/3, stereo occlusal view.
6. PQAD 1661, right P4/, stereo occlusal view.
7. AM 02, Sperrgebiet Museum, right m/1-m/3, stereo occlusal view.

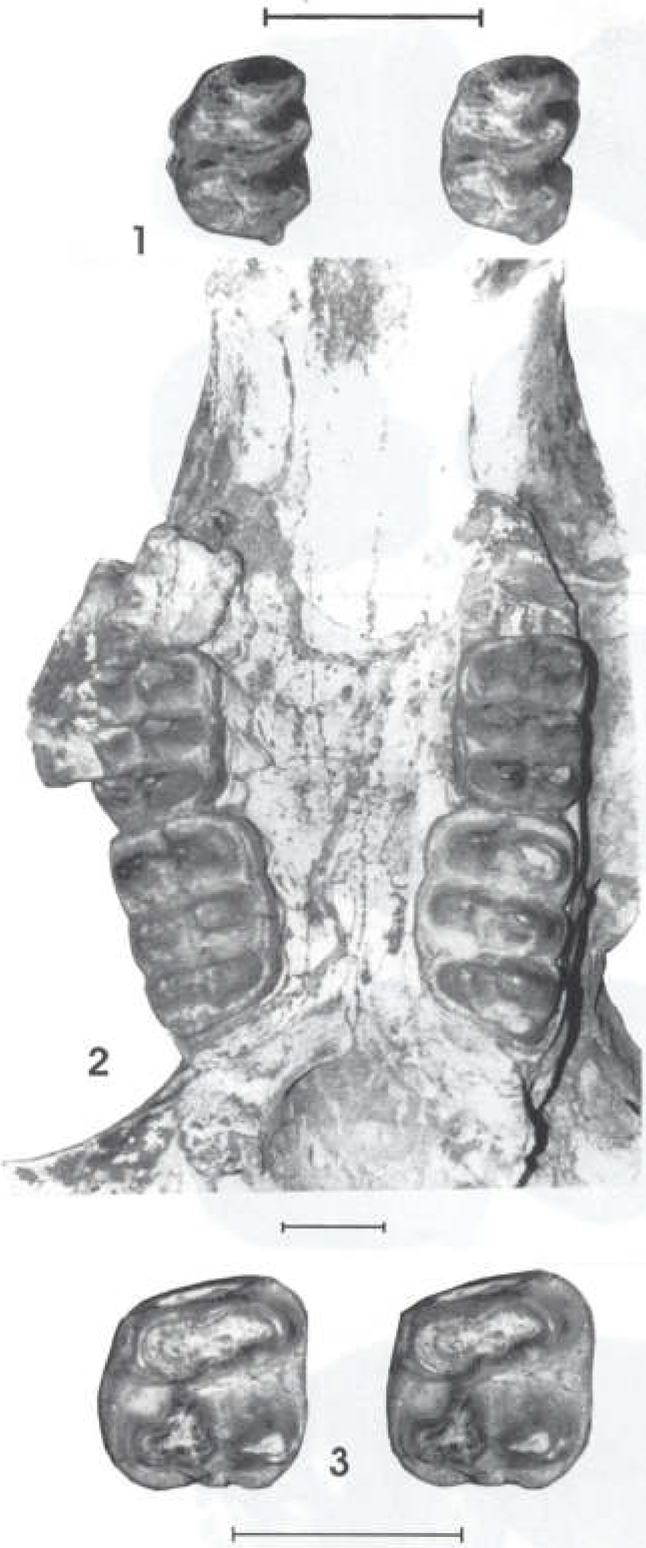


Plate 2: *Deinotherium hobleyi* and *Eozygodon morotoensis* from Auchas, Namibia. (Scale bars = 5 cm)

1. AM 3'93, deciduous right upper fourth molar, *Deinotherium hobleyi*, stereo occlusal view.
2. AM 02, skull, *Eozygodon morotoensis*, occlusal view of cheek dentition.
3. AM 02, skull, *Eozygodon morotoensis*, stereo occlusal view of left P4/.

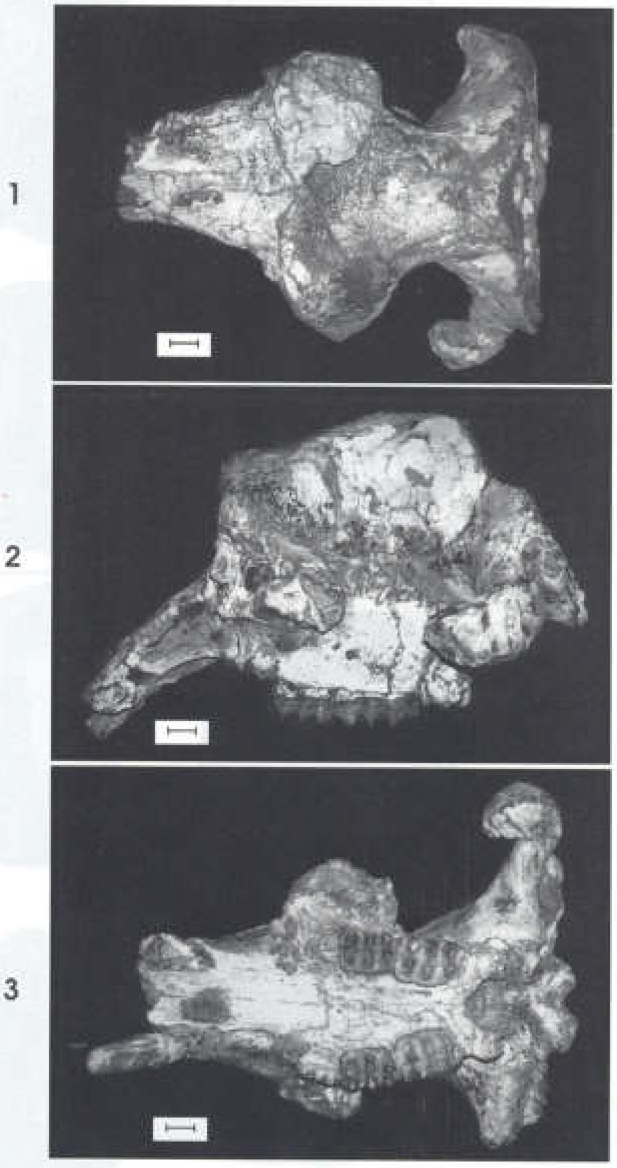


Plate 3: *Eozygodon morotoensis* from Auchas, Namibia. (Scale bars = 5 cm)

1-3. AM 02, skull in dorsal, left lateral and palatal views.

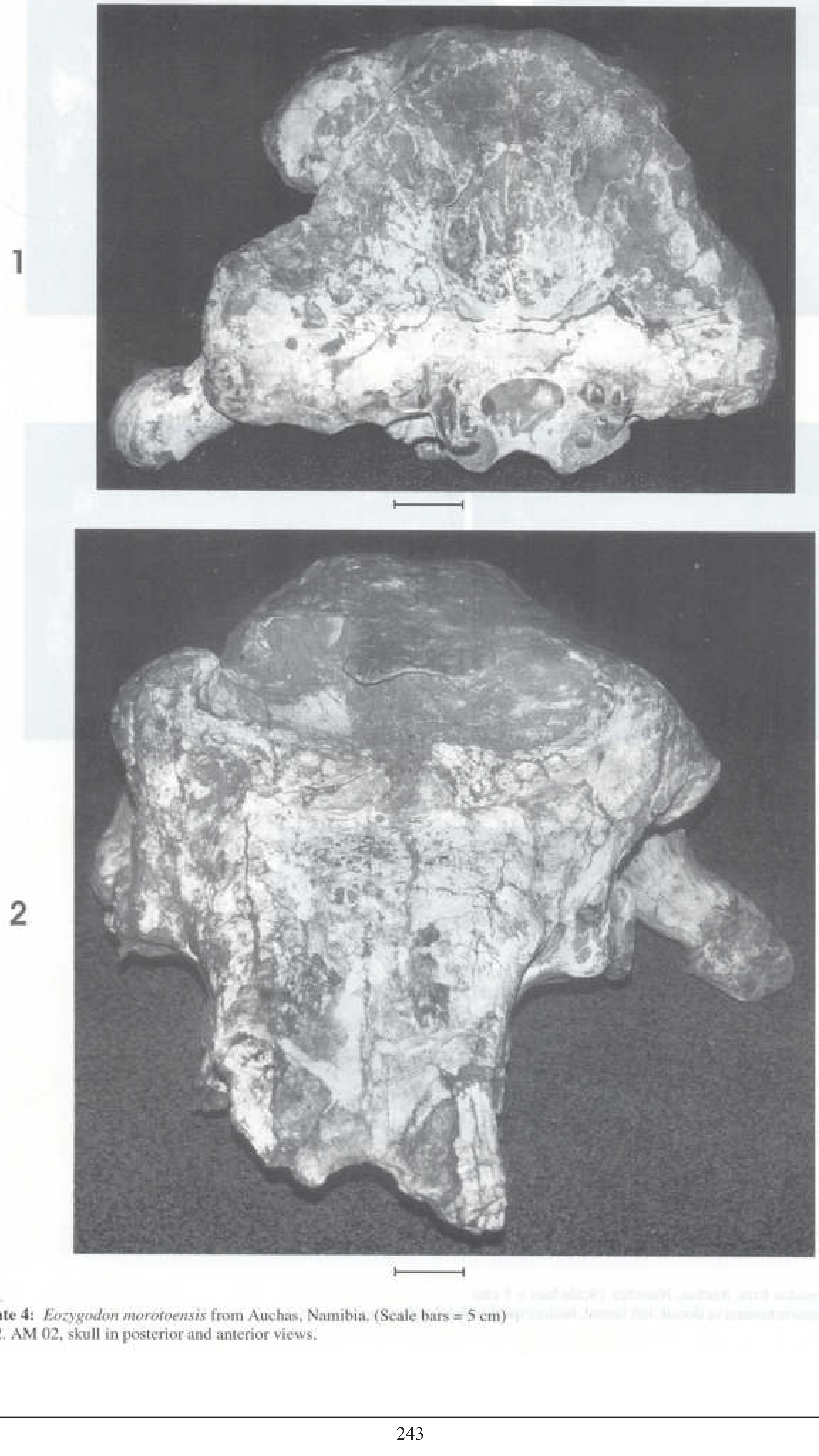
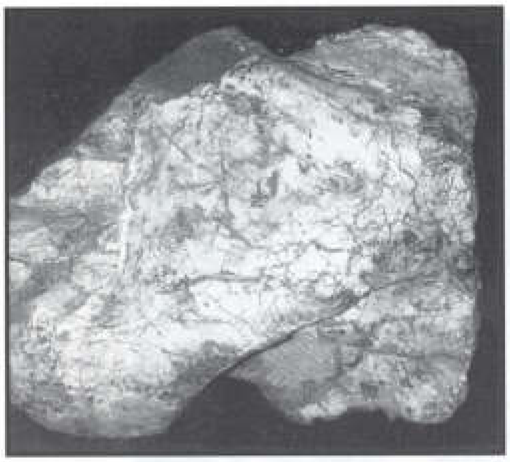


Plate 4: *Eozygodon morotoensis* from Auchas, Namibia. (Scale bars = 5 cm)
1-2. AM 02, skull in posterior and anterior views.



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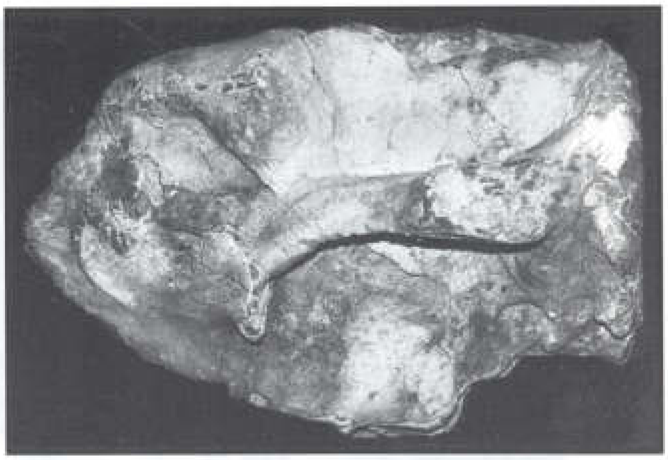

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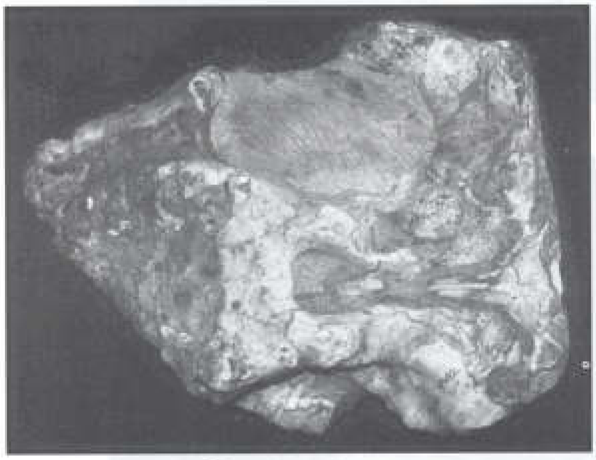

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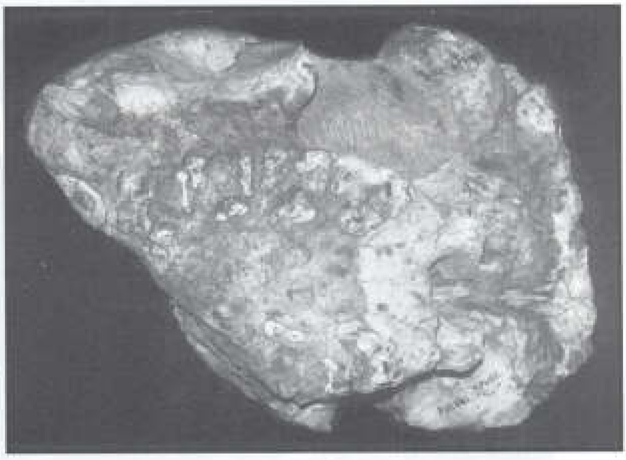

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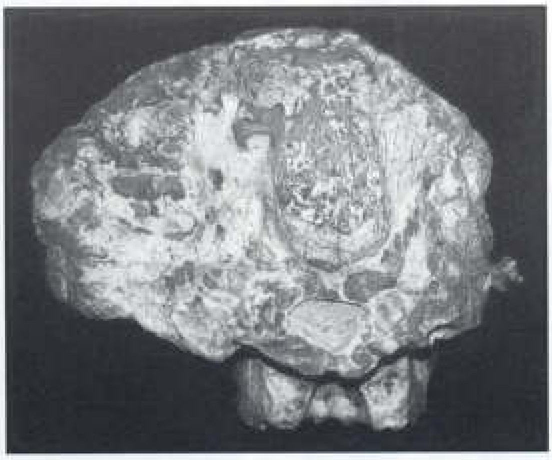

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Plate 5: *Eozygodon* from Auchas, Namibia. (Scale bars = 5 cm)
1-5. AM 02, neurocranium in dorsal, left lateral, basioccipital, palatal and posterior views.

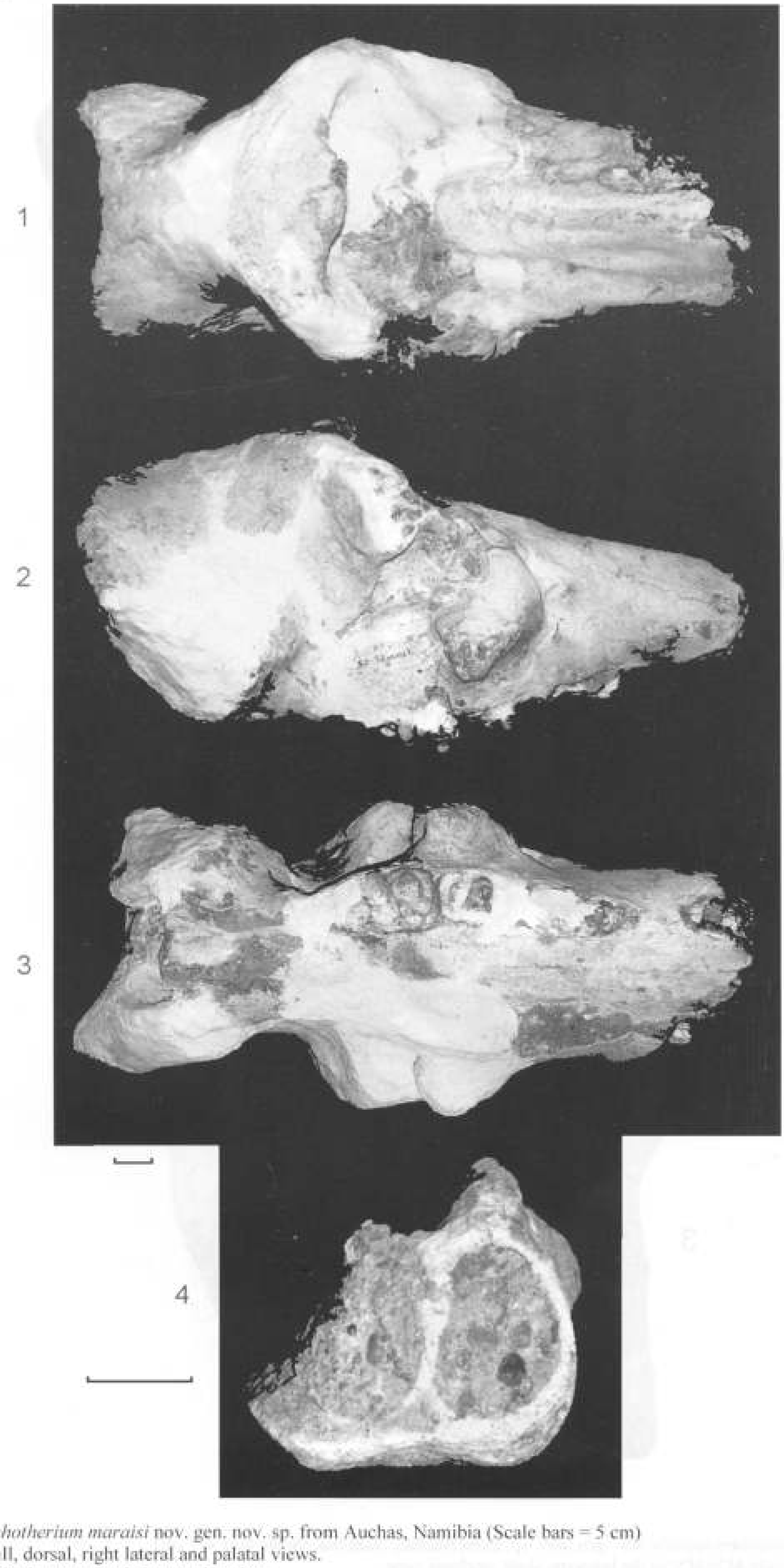


Plate 6: *Progomphotherium maraisi* nov. gen. nov. sp. from Auchas, Namibia (Scale bars = 5 cm)
1-3. AM 1'95, skull, dorsal, right lateral and palatal views.
4. AM 5'99, mandibular symphysis in anterior view.

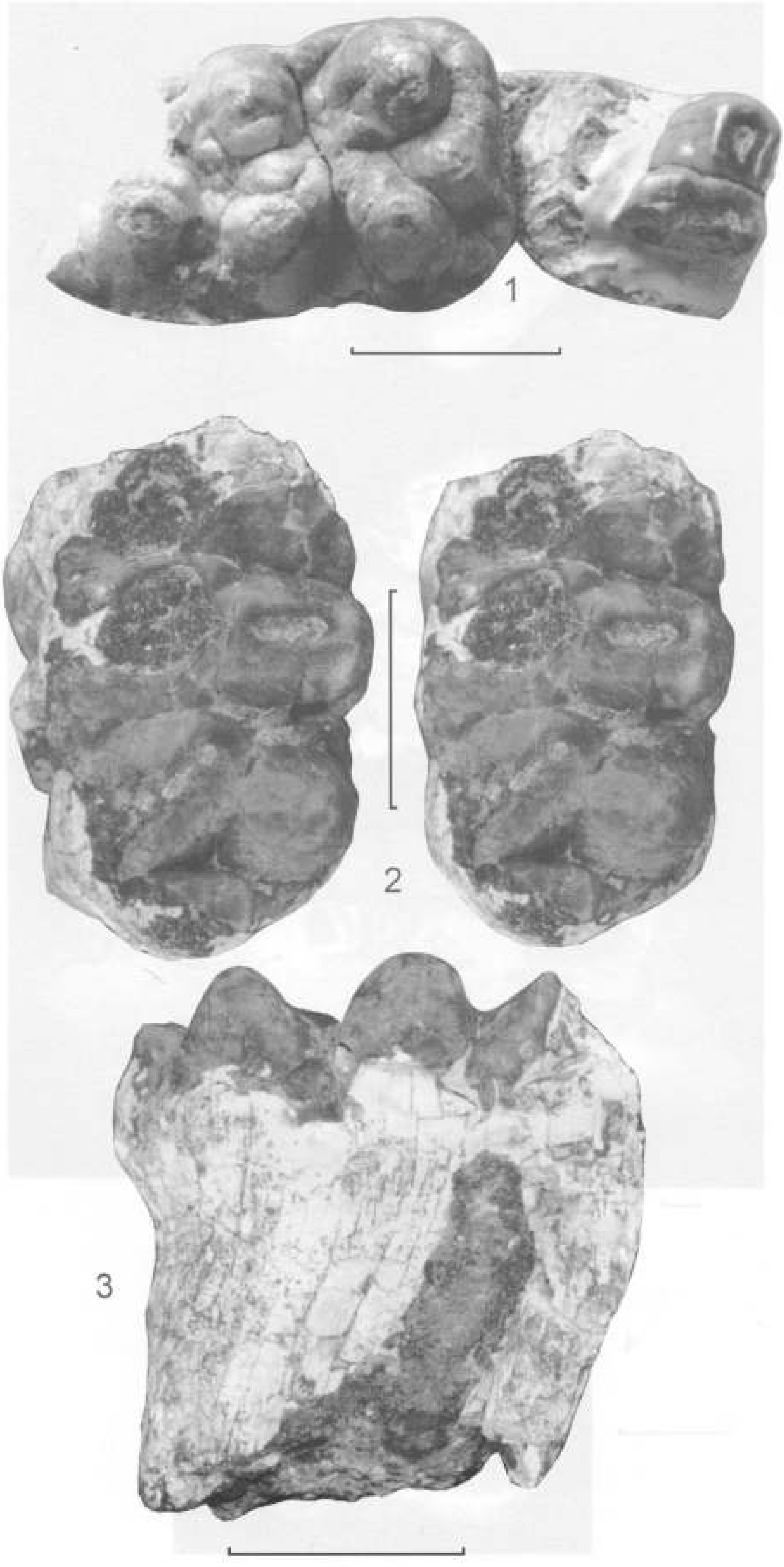


Plate 7: *Progomphotherium maraisi* nov. gen. nov. sp. from Auchas, Namibia. (Scale bars = 5 cm)
1. AM 1'95, broken right M2/-M3/ in the holotype skull, occlusal view.
2-3. 89/214 (Oranjemund Museum) left M3/, stereo occlusal and lingual views.

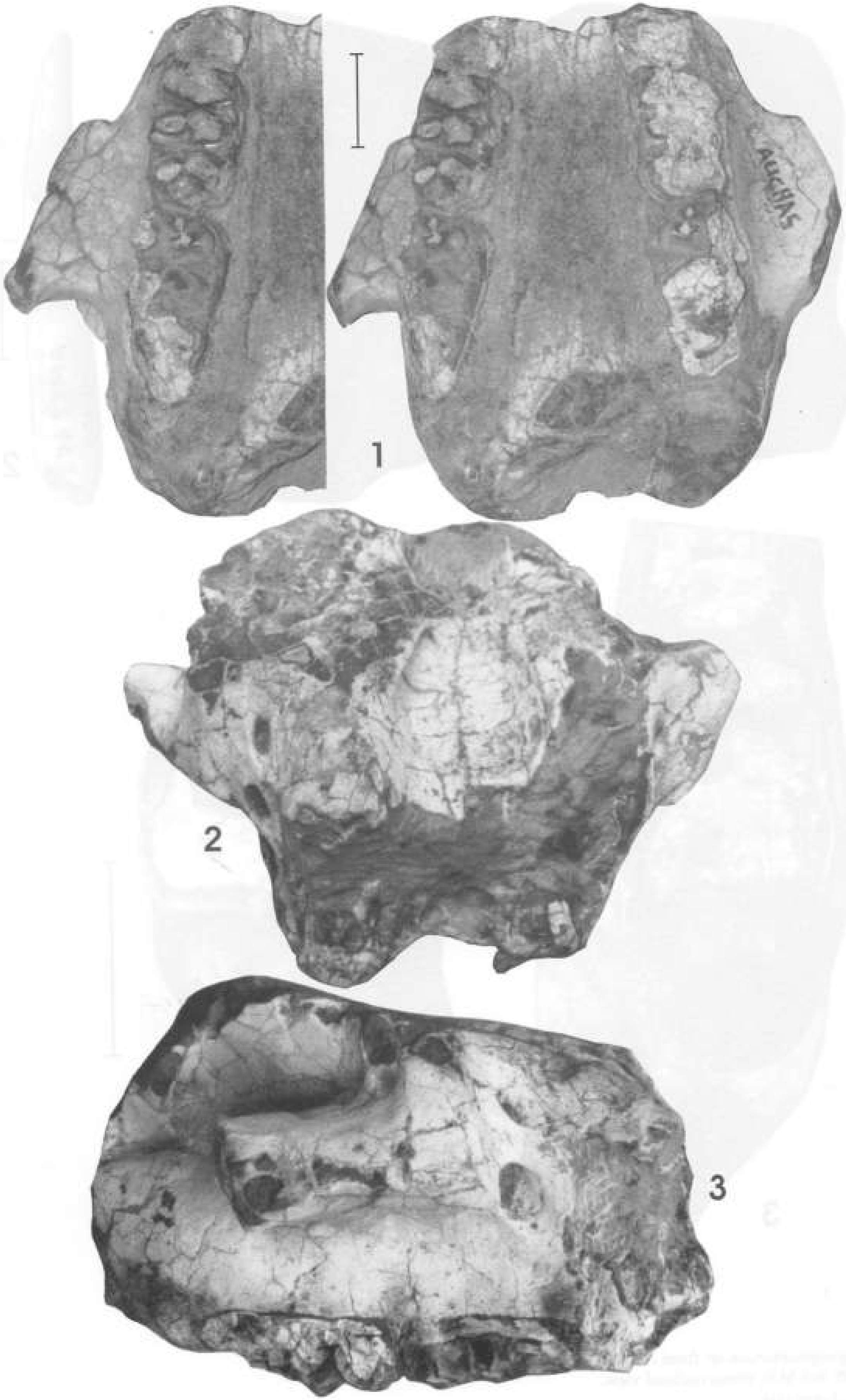
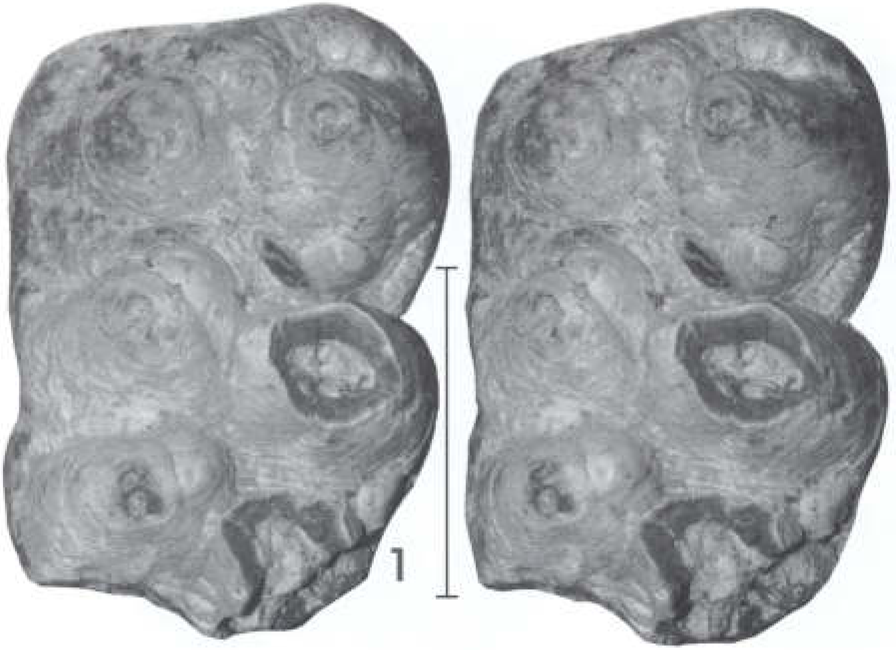


Plate 8: *Progomphotherium maraisi* nov. gen. nov. sp. from Auchas, Namibia. (Scale bars = 5 cm)
1-4. AM 7'93, palate in stereo occlusal, anterior and right lateral views.



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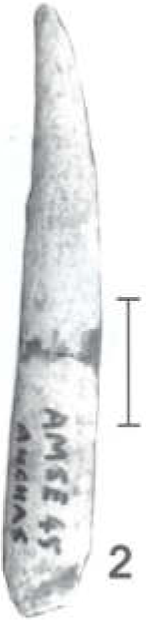

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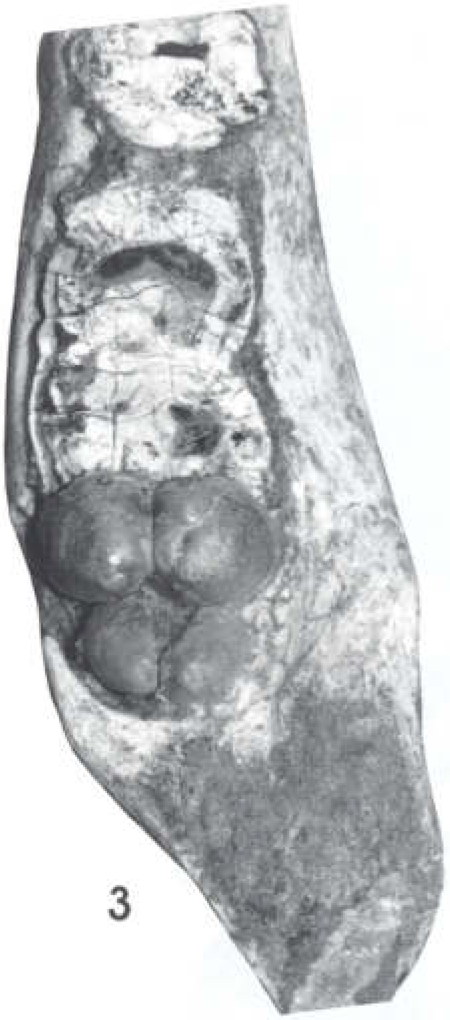

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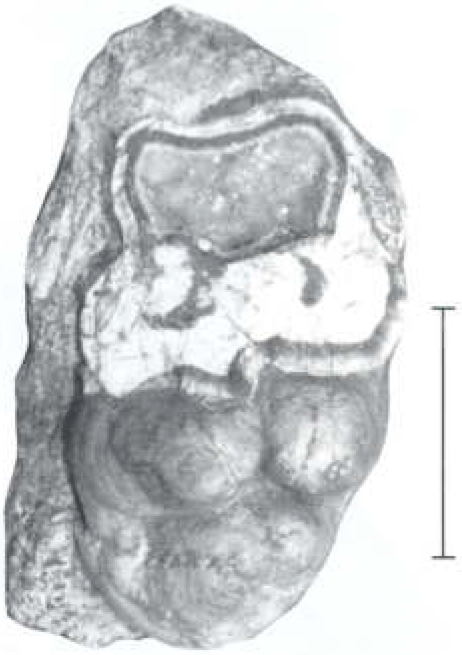

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Plate 9: *Progomphotherium* sp. from Auchas, Namibia. (Scale bars = 5 cm)
1. AMSE 1'95, left M3/, stereo occlusal view.
2. AMSE 45, lower tusk.
3. AM 4'95, *Progomphotherium maraisi* nov. gen. nov. sp., right mandible with fragment of M_3, occlusal view.
4. AM 2'95, *Progomphotherium maraisi* nov. gen. nov. sp., left M3/, occlusal view.

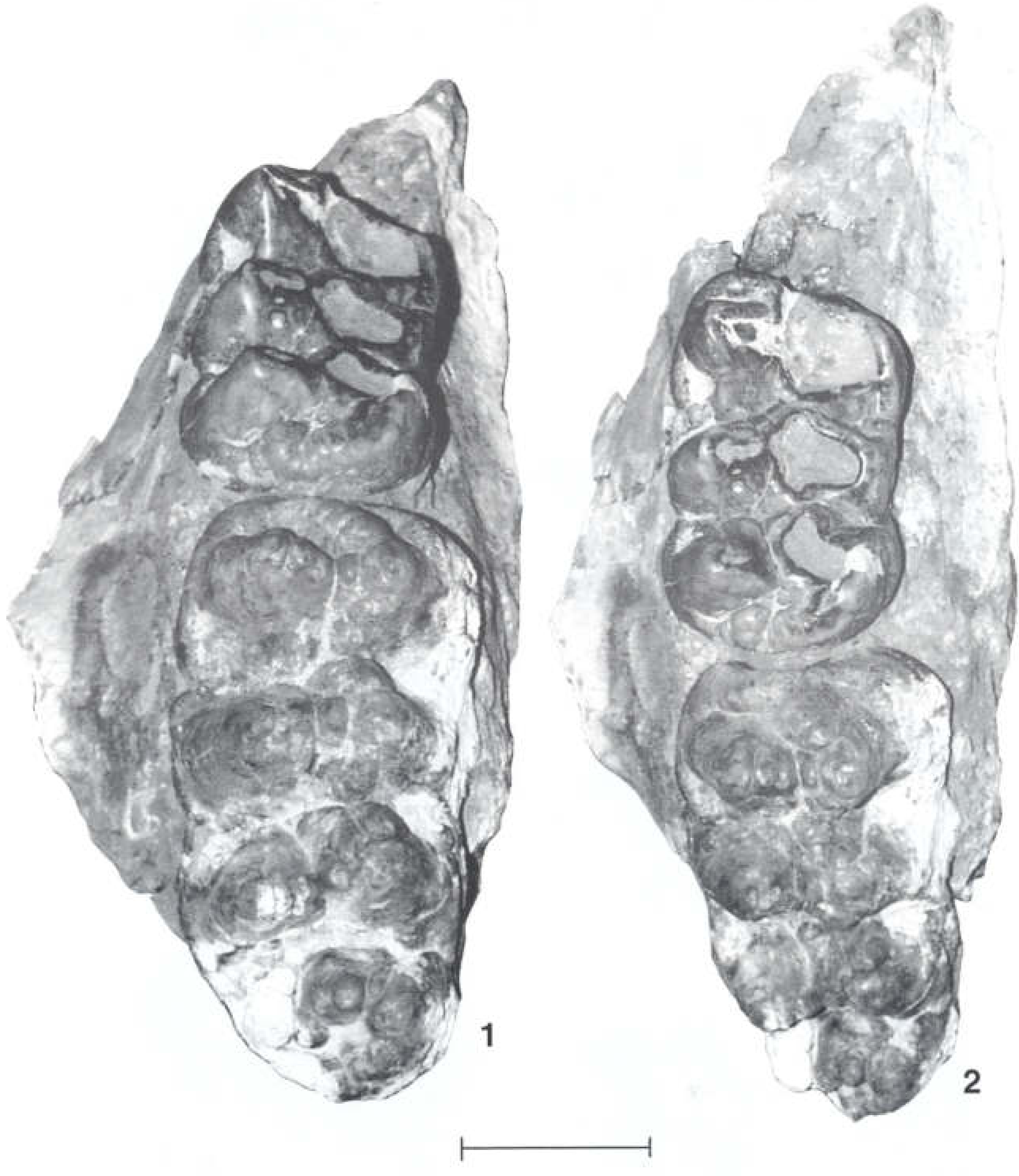
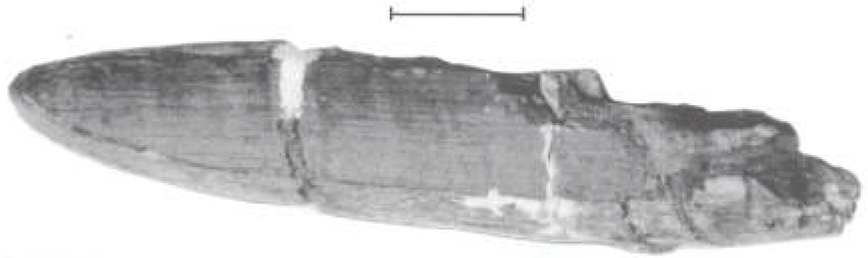


Plate 10: *Afromastodon coppensi* nov. gen. nov. sp. from Arrisdrift, Namibia. (Scale bar = 5 cm)
1-2. AD 600'00, occlusal views of right M2/-M3/.



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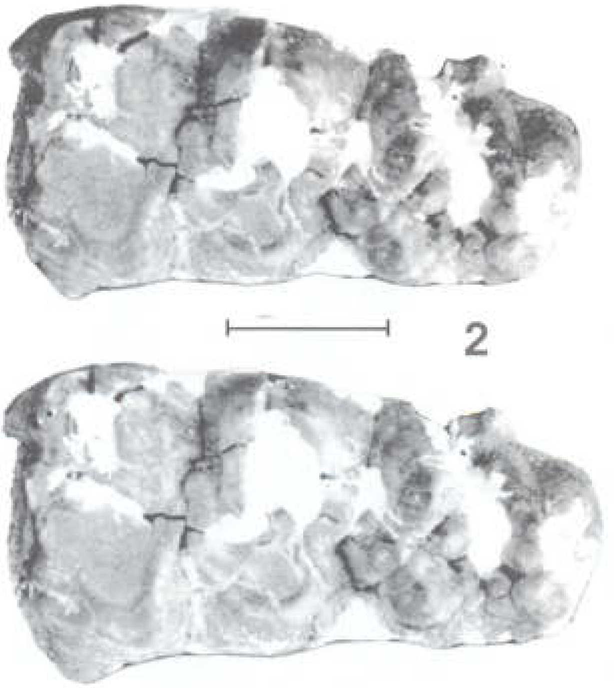

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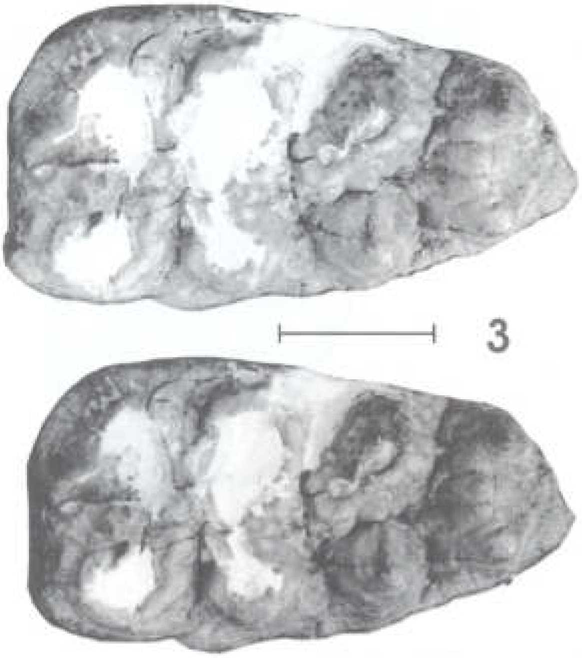

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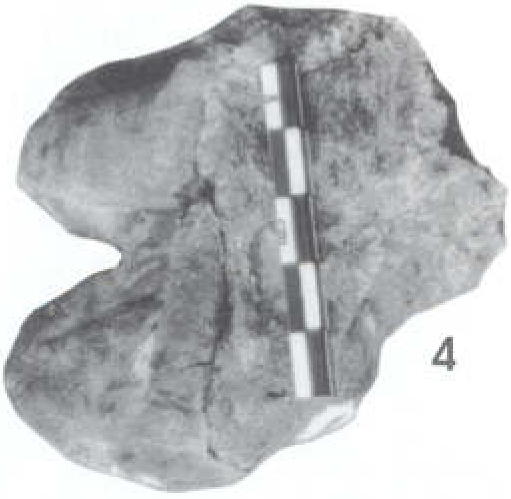

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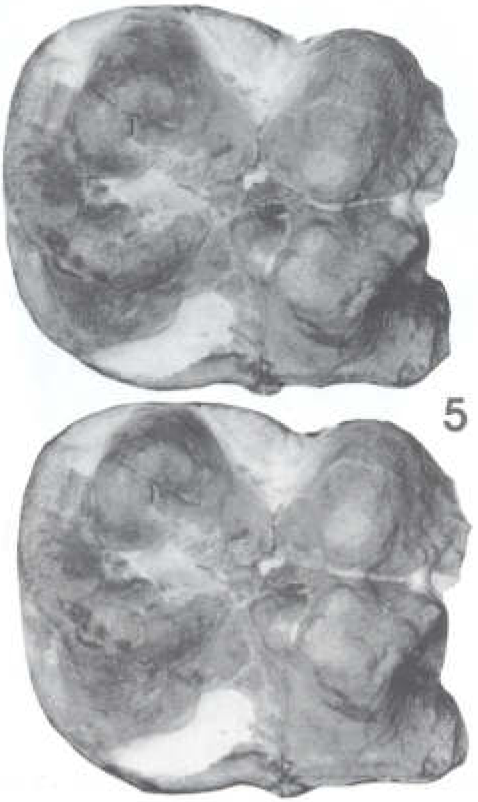

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Plate 11: *Afromastodon coppensi* nov. gen. nov. sp. from Arrisdrift, Namibia. (Scale bars = 5 cm).
1. PQAD 1659, upper tusk, lateral view.
2. AD 978'97, left M3/, stereo occlusal view.
3. AD 476'94, right M3/, stereo occlusal view.
4-5. AD 399'99, anterior two lophs of left M2/, lingual and stereo occlusal view.

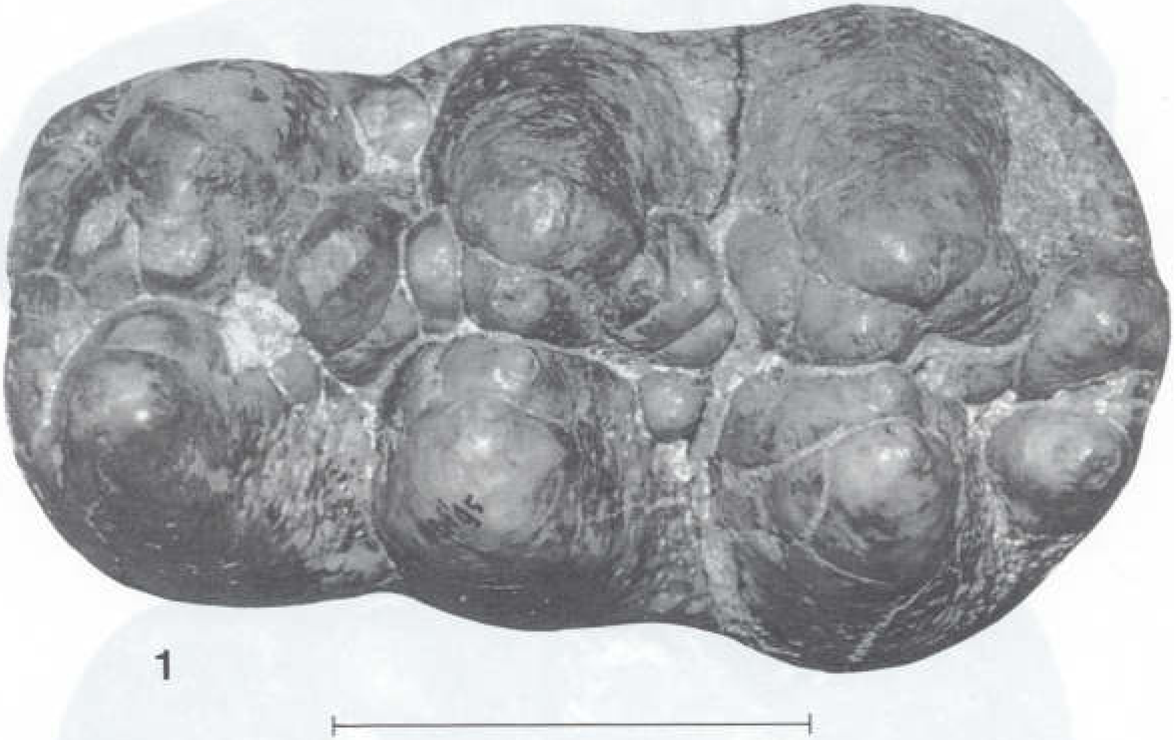

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Plate 12: *Afromastodon coppensi* nov. gen. nov. sp. from Arrisdrift, Namibia. (Scale bars = 5 cm)
1. AD 206'95, right m/2, occlusal view.
2. PQAD 1065, right M2/, occlusal view.

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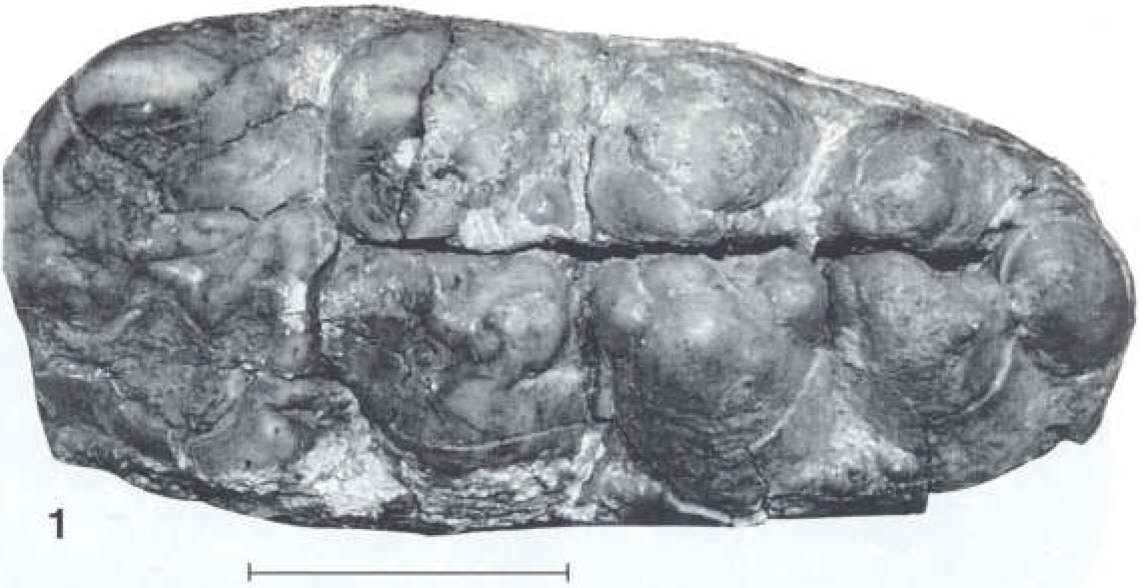

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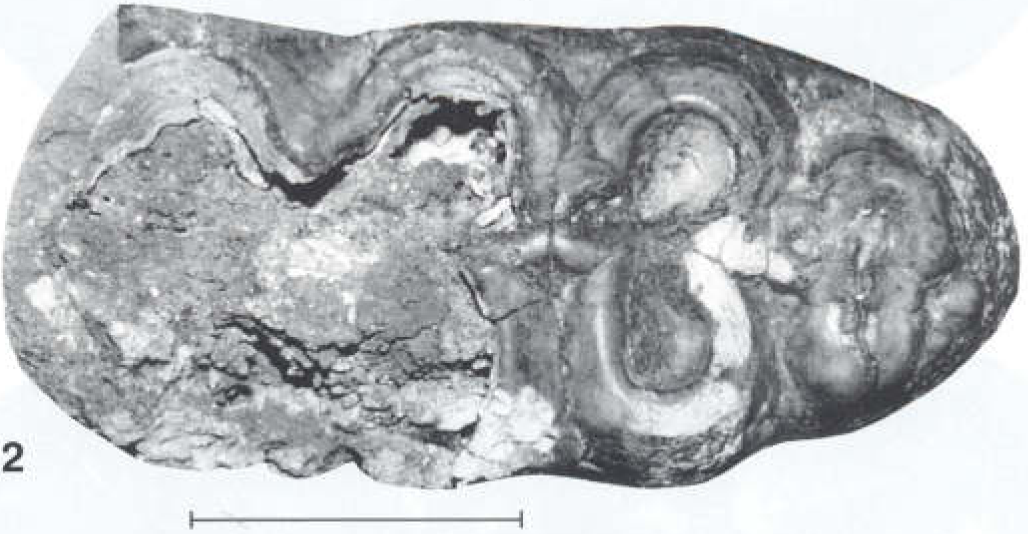

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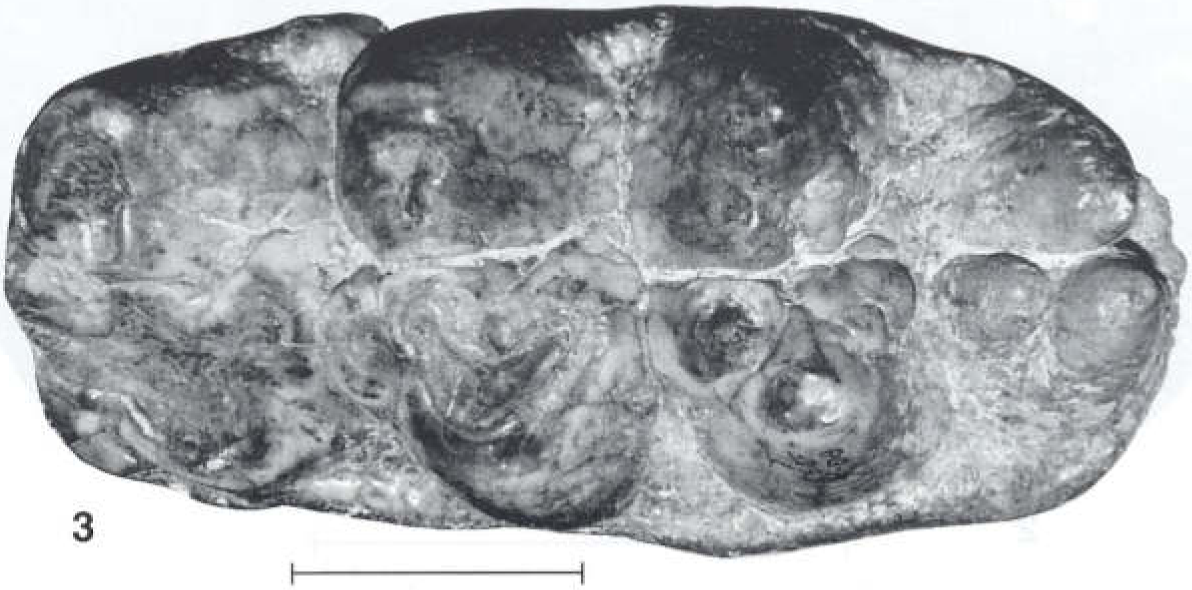
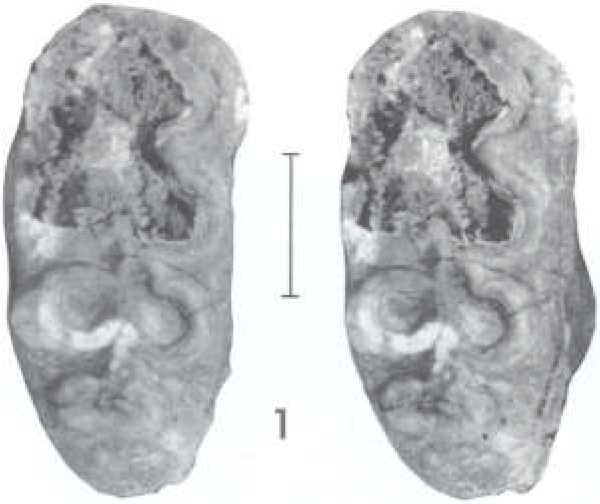


Plate 13: *Afromastodon coppensi* nov. gen. nov. sp. from Arrisdrift, Namibia. (Scale bars = 5 cm)
1. PQAD 3237, left m/3, occlusal view.
2. PQAD 1663, right m/3, occlusal view.
3. PQAD 1888, left m/3, occlusal view.

Plate 14: *Afromastodon coppensi* nov. gen. nov. sp. from Arrisdrift, Namibia. (Scale bars = 5 cm)
1. PQAD 257, left m/3, occlusal view.
2. PQAD 252, right m/3, occlusal view.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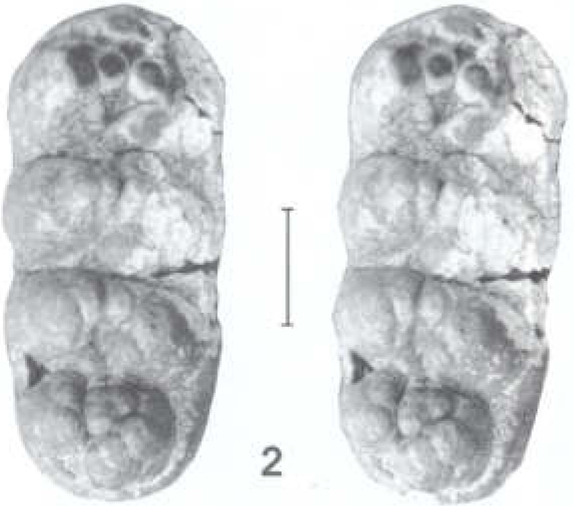
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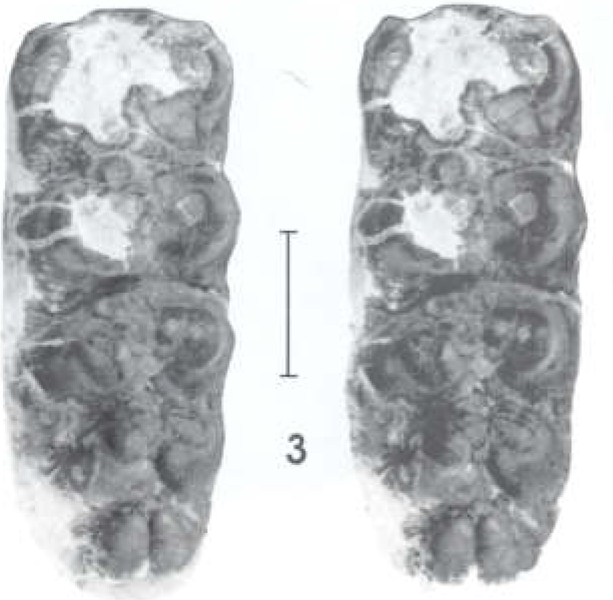
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Plate 15: *Afromastodon coppensi* nov. gen. nov. sp. from Arrisdrift, Namibia. (Scale bars = 5 cm)
1. PQAD 1663, right m/3, stereo occlusal view.
2. PQAD 252, right m/3, stereo occlusal view.
3. AD 585'98, left m/3, stereo occlusal view.
4. PQAD 294, left m/3, occlusal view.
5. AD 495'00, right p/3, occlusal view.
6. PQAD 257, left m/3, anterior view.

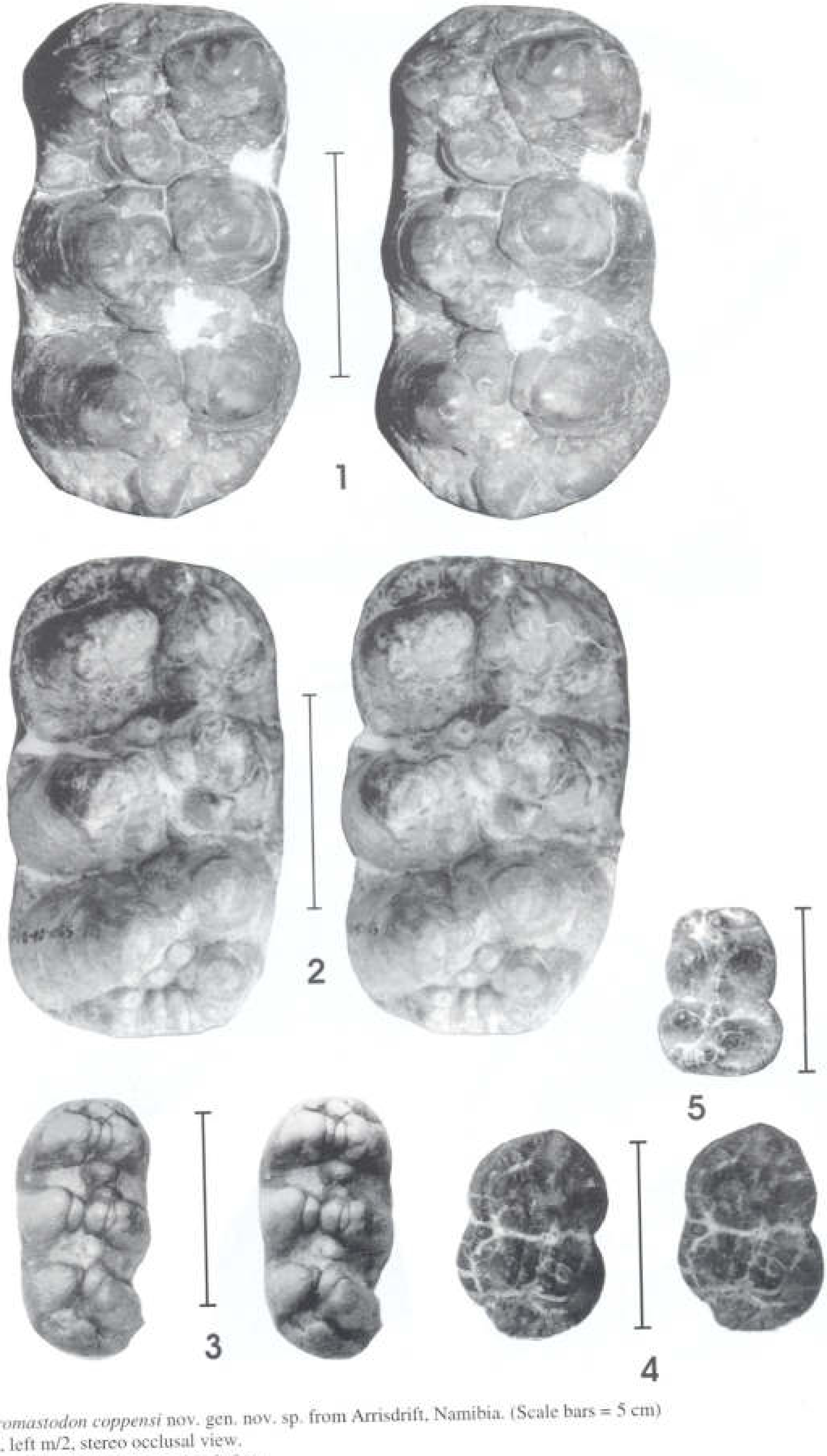

Plate 16: *Afromastodon coppensi* nov. gen. nov. sp. from Arrisdrift, Namibia. (Scale bars = 5 cm)
1. AD 400'99, left m/2, stereo occlusal view.
2. PQAD 1065, right M2/, stereo occlusal view.
3. AD 778'97, right m/1, stereo occlusal view.
4. AD 831'97, right dM3/, stereo occlusal view.
5. AD 582'98, right dm/3, occlusal view.

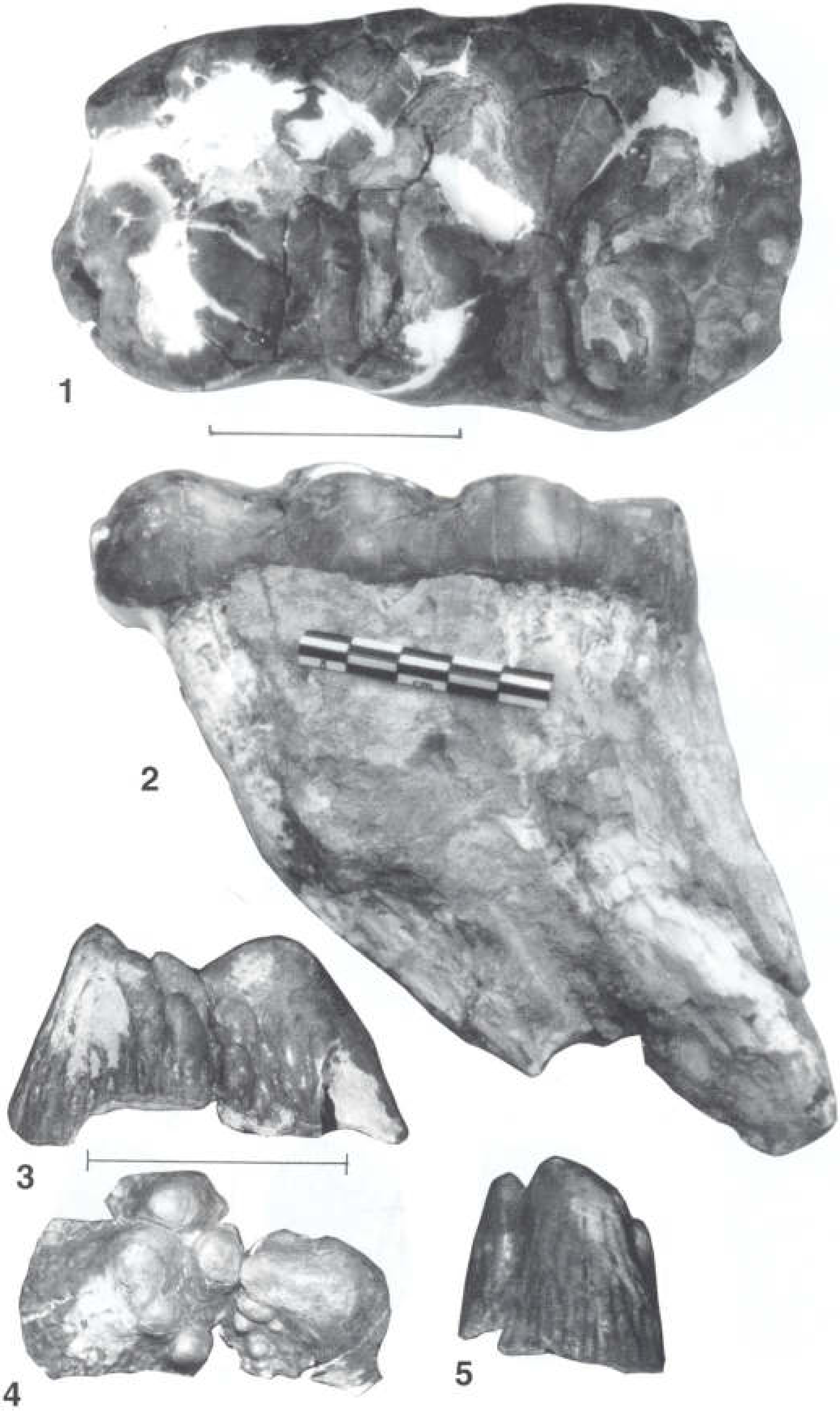

Plate 17: Mastodonts from Arrisdrift, Namibia. (Scale bars = 5 cm)
1-2. AD 527'99, *Afromastodon coppensi* nov. gen. nov. sp., right m/2, occlusal and lingual views.
3-5. PQAD 2748, gomphothere molar fragment, posterior, occlusal and lingual views.