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The Macroscelididae from the Miocene of the Orange River, Namibia

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The Macroscelididae of the Early and Middle Miocene of the Orange River (Namibia) are known from two localities, Auchas Mine and Arrisdrift. They are well represented at Arrisdrift by more than 400 dental and postcranial specimens. Among them, the hypsodont macroscelidid, *Myohyrax oswaldi* is particularly abundant. The Miorhynchocyoninae are rare and are represented by a few bracryodont specimens for which a new species is erected, *Miorhynchocyon gariepensis*. A fairly complete skull and some isolated upper incisors are tentatively allocated to this new taxon. The great hypsodonty of the myohyracids suggest that these animals were adapted to herbivory; they probably ate hard grass or seeds. This is compatible with the environmental reconstructions based on other mammals and plants. The miorhynchocyonines possibly ate soft bodied insects and possibly worms.

Version abrégée française

Les dépôts diamantifères de la rivière Oranje en Namibie ont livré une riche faune d'âge Miocene inférieur et moyen. Les rats-trompe y sont bien représentés, en particulier sur le site d'Arrisdrift, par plus de 400 spécimens dentaires, crâniens, mandibulaires et postcrâniens rapportés à au moins deux taxons: un Myohyracinae, *Myohyrax oswaldi*, très commun (représenté par plus de 400 spécimens) et un Rhynchocyoninae, *Miorhynchocyon gariepensis* sp. nov., assez rare (3 spécimens). Un crâne et quelques incisives isolées pourraient être rapportés à ce deuxième taxon.

Dans les publications antérieures, trois espèces de *Myohyrax* ont été signalées dans la Sperrgebiet de Namibie (Stromer, 1926; Hopwood, 1939): *Myohyrax oswaldi*, *Myohyrax doederleini* et *Myohyrax osborni*, ainsi qu'une autre forme hypsodonte *Protypotheroides beetzi*. En 1954, Whitworth mettait en synonyrnie *M. osborni* avec *M. beetzi* et *M. doederleini* avec *M oswaldi*. Cette position fut acceptée par Patterson (1965), puis par Butler (1984) et c'est également celle qui est adoptée ici. Jusqu'à l'étude de Patterson de 1965, *Myohyrax* était considéré comme un Hyracoïde, et les fossiles ont été interprétés dans ce contexte. Patterson (1965) réalisa que le genre était en fait un Macroscelididae et il modifia la diagnose en conséquence. Il ajouta les caractères suivants : présence de cément dans les fossettes des dents jugales, présence d'une seule racine à la M3/ et fossettes éphémères aux dents jugales inférieures (p/3-m/2). Toutefois, il apparaît que la présence où l'absence de cément est variable et peut être liée au degré d'usure et aux processes taphonomiques. Aucun des specimens d'Arrisdrift ne possédé de M^3; et le caractère observable sur cette dent pourrait aussi être variable.

La diagnose est émendée comme suit apres l'étude du matériel d'Arrisdrift : les plus grandes dents sont les P4/ et non pas les M1/ (et pas la M3/ comme signalé par Whitworth en 1954). Il y a deux foramens mentonniers à la mandibule, un à l'arrière de la p/l à l'interface p/l-p/2 et un à l'arrière de la p/3 a l'interface p/3-p/4. Les incisives supérieures sont très courbes et présentent quatre digitations. Au dents jugales supérieures, le parastyle est toujours plus bas que le paracone. La fossette linguale postérieure est généralement absente à la M2/, et il n'y a pas de fossettide aux dents jugales inférieures. Morphologiquement et métriquement, le matériel d'Arrisdrift est très similaire à celui décrit dans plusieurs sites kenyans (Karungu, Rusinga) et ougandais (Napak). *M. doederleini* tombe également dans la même variation, ce qui suggère qu'il s'agit probablement d'un synonyrne de *M. oswaldi*. L'hypsodontie de la dentition indiqué que *Myohyrax* se nourrissait de nourritures coriaces comme de l'herbe où des graines.

Le Rhynchocyoninae, *Miorhynchocyon gariepensis* sp. nov., se rapproche des autres espèces du genre (*Miorhynchocyon clarki*, *M. rusingae*, *M. meswae*), mais il en diffère par la présence d'un talonide aux p/4-m/2 beaucoup plus étroit que le trigonide et par l'absence d'une profonde gouttière séparant le paraconide du protoconide. De plus, le trigonide et le talonide sont aussi larges labio-lingualement à la p/4. L'espèce est légèrement plus petite que *M. rusingae*, mais de taille comparable a *M. clarki*. Un crâne auquel il manque le palais, mais qui possédé une incisive centrale supérieure droite (spatulée avec six digitations) pourrait être rattaché à cette espèce. Deux incisives centrales supérieures pourraient, elles aussi y appartenir. Les incisives présentent les digitations classiques des Macroscelididae, mais chez les Myohyracinae, ces dents sont plus petites et ne présentent que quatre digitations, où lobules. Aucune incisive supérieure n'a été décrite chez *Protypotheroides beetzi* du Miocene inférieur de la Sperrgebiet ; toutefois, la dentition de ce dernier étant typiquement myohyracinée, il semble logique de penser que ses incisives l'étaient également.

Les os postcrâniens de Macroscelididae d'Arrisdrift consistent en des humérus, des tibio-fibula, un astragale, plusieurs calcanéum, des métatarsiens et une phalange. Les plus petits appartiennent probablement à *Myohyrax*, alors que les pièces de plus grande taille sont rapportées à *Miorhynchocyon*.

Les Macroscelididae d'Arrisdrift nous foumissent donc une information complementaire sur le statut de *Myohyrax oswaldi* et montrent qu'il n'existe qu'une seule espèce en Namibie et en Afrique orientale et non trois comme proposé précédemment. Le Rhynchocyoninae est mal représenté mais diffère suffisamment des taxons connus pour qu'une nouvelle espèce soit créée, portant à quatre le nombre d'espèces connues du genre. Enfin, un crâne et quelques dents isolées pourraient appartenir soit à *Miorhynchocyon*, soit à un nouveau taxon.

Introduction

The diamond deposits of the Orange River in Namibia have yielded a very rich and diverse mammal fauna, among which the Macroscelididae are well represented. The site of Arrisdrift discovered in 1976 (Corvinus & Hendey, 1976) has yielded abundant macroscelidian or elephant shrew material which are, in contrast, poorly represented at Auchas mine. In

his 1978 publication on Arrisdrift, Hendey listed the East African genus *Myohyrax*, which is well known from sites such as Rusinga, Karungu, Napak and Songhor (Andrews, 1914; Hopwood, 1929; Whitworth, 1954; Patterson, 1965; Butler, 1984). Hendey (1978) interpreted the first specimens as *Myohyrax* cf. *oswaldi*, a very hypsodont species described for the first time in Kenya by Andrews (1914). During new field trips by the Namibia Palaeontology Expedition (Pickford *et al.*, 1996) abundant macroscelidid material was collected confirming the presence of *Myohyrax oswaldi* at Arrisdrift, but which also led us to the recognition of another type of elephant shrew at the site which is considerably more brachyodont, close morphologically to *Miorhynchocyon*.

The history of elephant shrews in the Sperrgebiet is not simple. Exploitation of diamonds in the region led to pro-grammes of prospecting during which the geologist F. Beetz collected several fossils, which he sent to Germany where they were studied by E. Stromer who described several new species from Lüderitzbucht in the Sperrgebiet: in 1922 the large *Protypotheroides beetzi*, then in 1924 the small species *Myohyrax doederleini*. In the same paper he highlighted the presence in the region of *Myohyrax oswaldi*, the species described by Andrews in 1914 on the basis of a mandible from Karungu, Kenya. In his monograph of 1926, Stromer provided detailed descriptions of the anatomy of the three recognised species from the Early Miocene of the Sperrgebiet: *M. oswaldi*, *M. doederleini* and *P. beetzi*. The first two differed mainly by their size and by the presence of a weaker fold in the anterior pillar of the lower molars. In 1929, Hopwood created another species *M. osborni* on the basis of a maxilla fragment from Langental; it was later said to be a synonym of *Protypotheroides beetzi* by Whitworth in 1954. The latter author also synonymised the two smaller specie", *M. oswaldi* and *M. doederleini*, a position reiterated by Patterson in 1965, then by Butler (1984); we are also of this opinion, because it is cotierent with the new view based on the new material collected by the Namibia Palaeontology Expedition which consists of hundreds of specimens, including complete skeletons which will be described in detail later.

Material

The material is very abundant and the list is given in the annex. It comprises specimens found during the pioneer excavations carried out in 1976 to which is added the material collected by the Namibia Palaeontology Expedition between 1993 and 2000. The specimens are often contained in blocks of indurated conglomerate deposited by the proto-Orange River (Plate II : fig. 1).

Systematic description

Ordre Macroscelidea Butler 1956
Family Macroscelididae Bonaparte 1838
Sub-family Myohyracinae Andrews 1914

Type species: *Myohyrax oswaldi* Andrews 1914

Species *Myohyrax oswaldi* Andrews 1914
(Pl. 1, II, III ; Fig. 2)

Holotype : M 10610, mandible containing p/2-m/1 from Karungu (Kachuku) in Kenya. In the 1914 article, Andrews identified the dental series as p/3-m/2, but he himself raised a doubt because he published the measurements with question marks.

Distribution: Early and Middle Miocene of Kenya (Chamtwara, Songhor, Mfwangano, Karungu and Fort Ternan) and basal Middle Miocene in southern Africa : Bosluis Pan in Namaqualand (Senut *et al.*, 1995) and Arrisdrift, Auchas Mine and Bohrloch des Betriebes 4 in the Sperrgebiet, Namibia.

Original description of the genus: The jaw itself is slightly convex from above downwards externally, and nearly flat internally.

p/3 (in fact the p/2) : composed of two elongated U-shaped lobes, separated externally by a short deep groove, which does not extend to the base of the crown. On the inner face, the lobes are not so clearly separated; the face being nearly flat in consequence of wear. The anterior lobe is the bigger, and is borne on a large root. The enamel is quite smooth and is thickest on the outer face of the tooth; there is no trace of a cingulum.

p/4 (in fact p/3) is also composed of two elongated lobes, somewhat V-shaped on the outer surface, the anterior arm of the V being much the longer. Externally, the lobes are separated by a deep vertical groove extending nearly to the base of the crown, which is here becoming very high and prismatic in form; the tooth, as a whole, is slightly curved, with the convexity directed forward. On the inner face, the columns are likewise separated by a vertical groove; the anterior column is the longer from before backwards; its postero-internal edge forms a prominent ridge (metaconid) on the inner side of the tooth, constituting the anterior lip of the vertical groove already mentioned.

m/1 (in fact the p/4): this tooth is still more hypsodont and the columns are stouter and broader, their crescentic form being less distinctly shown. The same is also true of the next tooth (m/2 - in fact m/1), in which the hypsodonty reaches its highest pitch, so that there is considerable resemblance to some Rodent molars. Despite the hypsodonty, the roots of the molars are well formed and clearly separated from the crown; they are closed at the ends, except for the entrance of the nerve. There are two in number, each extending transversely across the tooth. The crown of the tooth is entirely covered by enamel, which in the anterior premolar is smooth, but in the hypsodont teeth is raised into faint irregular ridges at right angles to the long axis of the tooth. On the crown, the dentine is worn into deep hollows surrounded by enamel, highest at the outer side and at the angle formed by the metaconid

Upper molar: this tooth is very hypsodont prismatic molar, which shows a wear pattern that might be easily derived from a Hyracoid molar. The ectoloph consists of a well developed parastyle, of an antero-external cusp (paracone) and a postero-external cusp (metacone), all of which form prominent vertical ridges on the outer face; there does not appear to be any mesostyle. The inner part of the tooth is composed of two transverse crests (protoloph and metaloph), the inner end of the protoloph being somewhat imperfect. Each crest seems to be made up of a smaller middle tubercle (protoconule and metaconule respectively) and a larger inner tubercule (protocone and hypocone respectively); these are separated on the

inner face of the tooth by a deep vertical cleft. In wear, two islands of cement surrounded by enamel are formed in each crest, the larger outer islands being crescentic and situated immediately internal to the paracone and metacone respectively. The smaller islands are situated just external to the protocone and hypocone; in wear, the latter tubercle becomes continuous with the posterior wall of the tooth. The anterior and posterior faces of the tooth are flat with a band of cement near the outer edge; the inner face is slightly concave from above downwards, the outer correspondingly convex. There is a slight increase in size in the tooth towards the roots, of which there seem to have been four.

Whitworth's (1954) diagnosis: A moderately long-snouted, pygmy hyracoid. Skull fairly low and somewhat narrow, zygoma commences above M1/ and rises sharply towards the rear, so that the glenoid *fossa* lies high above the palate. False palate extends at least as far back as M3/. Mandibular ramus comparatively shallow, deepening gradually behind, with high, slender, pillar-like, articular process and elongate articular condyle. Posterior angle of ramus with prominent hook-like process. Symphysis long and shallow. Dental formula:

$$\frac{3143}{3143}$$

P4 or M3 largest tooth in either jaw. Cheek teeth high-crowned, prismatic, rooted. Enamel sometimes shows irregular annular wrinkling. Curved transverse ridges of enamel developed in wear on occlusal surface, paralleling condition in microtine rodents. Upper series closed, except for very short diastema between P1/ and C. Upper cheek teeth lophoselenodont, approximately quadrangular, sloping back from base to apex. C and P1/peg-like; P2/ sub-molariform; P3/-P4/ molariform; M3/ much reduced. Three large, pro-odont upper incisors, somewhat flattened labiolingually, and slightly reduced in size from front to rear. In 11/-12/ enamel confined to labial surface. 11/ of male probably not different from that of female. Lower series not so tightly closed as upper, but evenly spaced throughout. Forward sloping lower cheek teeth of two sub-circular pillars. Anterior pillar generally narrower than posterior pillar in premolars, sub equal or wider in molars. p/2-p/3 submolariform, p/1 simpler, p/4 molariform; m/3 much reduced. Anterior incisors large, flattened, procumbent; enamel confined to labial surface, ill chisel-shaped, and slightly larger than the spatulate i/2, i/3 and c/1 styliform. Milk molars brachyodont; less specialised than permanent cheek teeth.

Diagnosis emended by Patterson (1965) : Myohyracines with cement in fossettes of cheek teeth; M3/ single rooted; fossettids on p/3-m/2 ephemeral.

Emended diagnosis: The presence of cement is not constant in the upper cheek teeth. It seems to correlate with hypsodonty and degree of wear of the teeth; but does not appear to be a diagnostic feature. It is the P4/ and M1/ which are the largest teeth (and not the P4/ and M3/ as suggested by Whitworth). The presence of two mental foramina in the mandible is constant: one located distal to the p/1, at the interface p/1-p/2 and the other at the rear of the p/3, at the interface p/3-p/4. The mandibular symphysis ends at the level of the p/2. The upper incisors are very curved and possess four digitations. In the upper cheek teeth, the parastyle is always lower than the paracone, and particularly at P3/ and P4/. The lingual posterior fossette is generally absent in M2/. The M3/ is not constant. No fossettids in the lower cheek teeth.

Descriptions:

Maxilla (Pl. 1). Several maxillae are known: PQ AD 1050 (fragment of right maxilla with P2/-P3/), PQ AD 1685 (fragment of left maxilla with P4/ and M1/-M2/), PQ AD 2455 (fragment of left maxilla with base of the zygomatic arch, P4/ and M1/-M2/), PQ AD 2528 (fragment of right maxilla with base of the zygomatic arch and M1/-M2/), PQ AD 3030, (fragment of right maxilla with base of zygomatic arch, P2/-P4/ and M1/-M2/), PQ AD 3384 (fragment of right maxilla of which the bone is eroded and bearing P3/-P4/ and M2/-M2/), AD 251'94 (fragment of right maxilla with P1/-P2/), AD 138'95 (fragment of right maxilla with P2/-P3/), AD 426'96 (fragment of left maxilla with P3/-P4/, M1/), AD 100'97 (fragment of skull with I1/-I3/, C, P1/-P4/), AD 369'97 (fragment of right maxilla with P4/, M1/-M2/), AD 870'97 (fragment of the most complete skull with skull roof crushed proximodistally and laterally, broken at the level of the P1/, with right P2/-P4/, M1/-M2/, and left P2/), AD 265'98 (fragment of right maxilla with base of zygomatic arch and P1/-P4/, M1/-M2/), AD 677'99 (fragment of right maxilla with zygomatic arch and P3/-P4/, M1/-M2/), AD 696'99 (fragment of left maxilla with P4/, M1/-M2/), AD 712'99 (fragment of right maxilla with base of zygomatic arch, M1/-M2/), AD 657'00 (fragment of damaged maxilla with P3/-P4/, M1/-M2/), AD 665'00 (fragment of maxilla in two pieces with the base of the zygomatic arch, P2/-P4/, M2/-M2/).

No specimen is well enough preserved to reveal the form of the sutures, nor the height of the skull roof.

In overall form the muzzle is quite elongate and narrow. The premaxillary teeth are inclined forwards whereas the cheek teeth are inclined backwards as seen in AD 100'97. There is a short diastema between the canine and the first premolar.

The zygomatic arch, which is thick at its root, becomes flat rapidly; it starts above the M1/ and curves strongly towards the rear parallel to the tooth row. However, it is not very salient laterally (PQ AD 2578, PQ AD 3030, AD 265'98, AD 677'99, AD 712'99) as in extant Macroscelididae.

In AD 870'97, the most complete specimen, the bony palate is preserved and extends just behind the M2/. It seems to be deep, but this is possibly due to crushing. Between the M2/and M1/, there are the margins of a fenestra, but as the skull is crushed we cannot determine its development. In lateral view, the left orbit is preserved, but be-cause of the poor state of preservation of the fossil, we can't say much about its morphology. On the right lateral side there is an infra-orbital foramen just above the P4/; the hole is rounded and relatively large (about 1.8 mm) compared to the overall size of the skull (length of skull preserved: 36.2 mm).

In superior view, there is a weak sagittal crest towards the posterior part of the fragment. Its size is equivalent to that in the skull of *Myohyrax oswaldi* (Whitworth, 1954) estimated using the dental tooth row (Length P2/-M2/ : 14,3 mm in AD 870'97, 14,0 mm in PQ AD 3030; length P1/-P2/ : 15,2 mm in AD 265'98; estimated length of P2/-M2/ on the drawing

published by Whitworth (1954, fig. 9b) is 15 mm.

Mandible (Pl. 11, Pl. 1II, Fig. 5). The horizontal body of the mandible thickens progressively from front to back, in liaison with the increasing hypsodonty of the teeth. Its maximum thickness is located at the level of m/2 or m/3 depending on the age of the individual. The ascending ramus of the mandible is almost vertical, differing in this respect from extant Macroscelididae. The dental row is slightly concave from postero-labial to antero-lingual. The premolars are inclined backwards from root to apex, while the molars are inclined towards the front. The only specimen which has the distal part of the mandible (AD 672'99) shows a clear crest in the internal gonial region suggesting the presence of well developed pterygoid muscles.

Teratological case (Pl. 1II, Fig. 5): on the mandible AD 170'96, there is a dental anomaly at the base of the crown of m/2. Another tooth is growing under the m/2 and is joined to it. It is a low tooth with two clear pillars subequal in width which are joined to the root above. The overall morphology recalls that of m/2. It is not an m/3 which does not have the pillars so clearly expressed. Perhaps it is a supernumerary germ.

Dentition.

Dental eruption. The cheek teeth are extremely hypsodont in the maxilla as in the mandible. The right mandible of a young individual, AD 331'99, reveals the order of dental eruption: premolars, p/2 to p/4, are in the process of eruption. It is possible to estimate the sequence of eruption on the basis of wear of the teeth: m/1, m/2, p/4, p/3, p/2.

Lower teeth (Pl. 11):

Anterior teeth:

Isolated i/1 : PQ AD 1043 (left), AD 180'96 (left), AD 110'97 (left), i/1 in mandibles: AD 247'94 (left), AD 248'94 (left), AD 568'94 (left), AD 569'94 (left), AD 420'96 (right), AD 421'96 (right), AD 585'97 (left), AD 750'97 (left), AD 949'97 (right), AD 648'98 (right), AD 327'99 (left), AD 328'99 (left), AD 329'99 (right), isolated i/2 : AD 674'00 (right); i/2 in mandible: AD 247'94 (left), AD 248'94 (left), AD 566'94 (left), AD 569'94 (left) AD 421'96 (right), AD 372'97 (right), AD 750'97 (left), AD 647'98 (right), AD 648'98 (right), AD 327'99 (left), AD 329'99 (right).

The i/1 and i/2 have been observed in mandibles. They are slightly curved and have quite sharp cutting edges. They are very procumbent, elongated, flat and spatulate, without enamel on the lingual surface. The ill is slightly helicoidally twisted inwards towards the mandible, its anterior surface is weakly recurved towards the mesio-distal axis of the mandible. The i/2 is more strongly spatulate than the ill. Wear in the two incisors is oblique towards the distal part, more oval in the ill and flattened triangular in the i/2, due to the mesio-distal extension of the apex of the crown. The i/2 is very weakly twisted and its apical surface curved towards the ill, where it touches it. In the i/2, AD 647'98, we note in labial view a very small notch at the apex of the tooth, in the mesial region. This could corre-spond to the remnant of a very worn digitation. Apart from this weak notch in i/2, the lower incisors do not appear to possess digitations as is often the case in extant Macroscelididae.

An i/3 is present in only one specimen, AD 421'96, in which all three incisors are preserved. The i/3 is smaller and less spatulate than the i/2. It is by far the smallest and shortest of the three incisors (mesio-distal length 1,17 mm for ill, 1,25 mm for i/2 and 0,7 mm for i/3). However, be-ing poorly preserved it is not possible to provide more information.

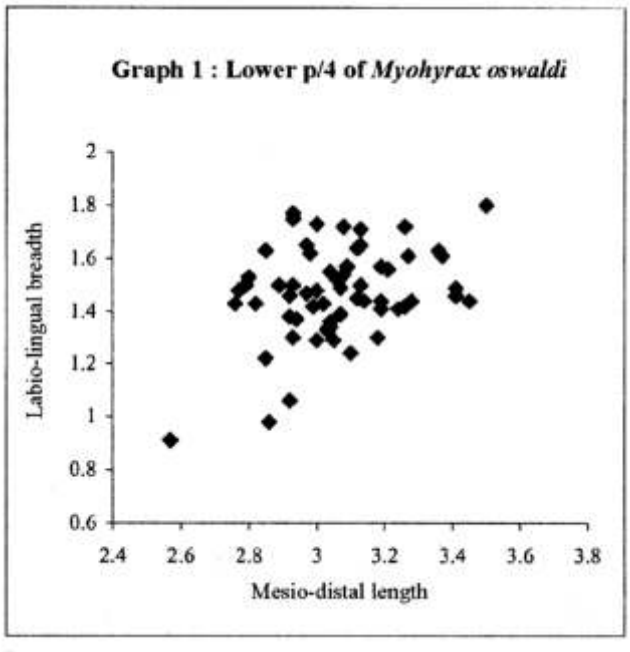
The lower canines have not been seen *in situ*, but at the front of mandible AD 421'96, the base of the broken canine is visible. Several mandible fragments show a single, very small alveolus for a canine.

Cheek teeth: The main difference between the lower premolars and molars is that the equivalent grooves in the mo-lars are displaced with respect to each other, the labial one always being anterior. This is related to the structure of the molar in which the pillars are separated into two columns united by a crest that joins the hypoconid to the metaconid. The rings corresponding to infillings of the pulp cavity are sometimes visible in worn specimens of p/3-m/3, notably in mandibles AD 647'98, AD 648'98, AD 650'98, and AD 672'99 among others.

Premolars (Tabl. 1,2,3) : In the premolars, the trigonid is triangular and the talonid more quadrangular.

p/1 : AD 569'94 from the left side is the only specimen represented in the Arrisdrift material. It is a small, low, sin-gle rooted tooth (much lower crowned than the second premolar) very spatulate and strongly inclined towards the front. It is labio-lingually flattened, and is triangular presenting low mesial and distal tubercles joined together by a rounded crest. At the mesial end there is a small tubercle; it is stretched out mesio-distally

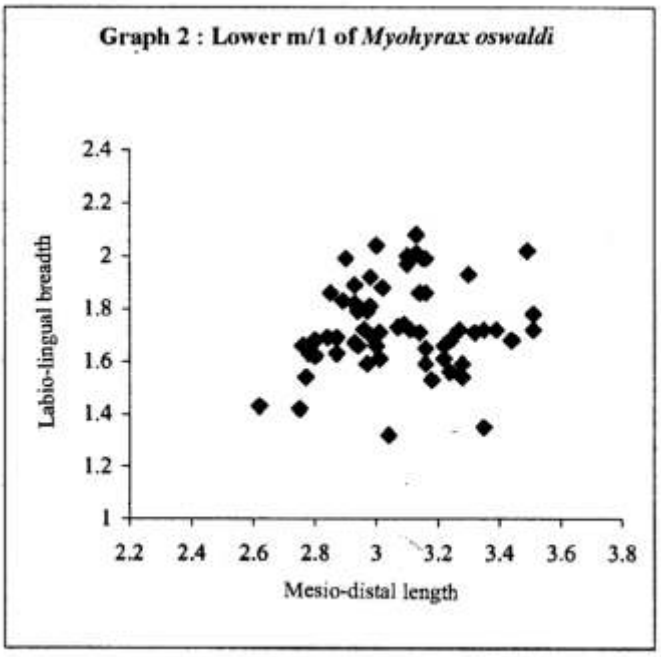
p/2 : They are well represented in mandibles PQ AD 123 (left), PQ AD 1104 (right), PQ AD 2036 (left), PQ AD 2587 (left), PQ AD 3287 (right), AD 247'94 (left), AD 566'94 (left), AD 567'94 (left), AD 59'95 (right), AD 64'95 (right), AD 181'96 (left), AD 182'96 (left), AD 249'96 (left), AD 174'97 (left), AD 579'97 (right), AD 585'97 (right), AD 882'97 (right), AD 949'97 (right), AD 124'98 (right), AD 647'98 (right), AD 648'98 (right), AD 652'98 (left), AD 124'99 (right), AD 327'99 (left), AD 329'99 (right), AD 330'99 (right), AD 331 '99 (right), AD 674'99 (right), AD 24'00 (right), AD 645'00

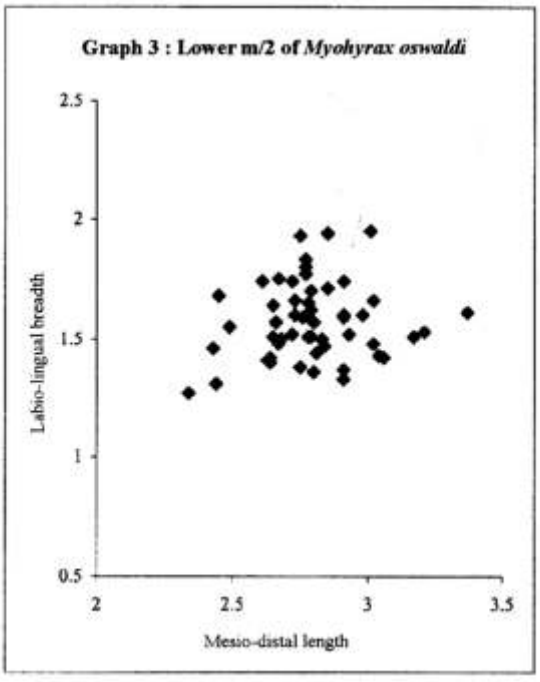


(left), AD 654'00 (left).

The second premolar is a low tooth, flattened labiolingually, with two roots. The lingual surface is usually flatter than the labial one. It consists of two tubercles one behind the other, the anterior one being higher and more pointed than the distal one. In labial view, the two tubercles are separated by a shallow gutter between two smooth crests which descend from the two tubercles (the posterior one being more marked) which come together above the root imparting a bilobed appearance to the tooth. The wear facet appears as two triangles joined to each other of which the anterior one is rounded. Because of the sectorial nature of the tooth, the wear facets slope gently lingually in lightly worn specimens, but in more deeply worn specimens it becomes a single large facet displaced lingually.

Beginning with the p/3, all the posterior cheek teeth are comprised of two prismatic columns separated by deep labial and lingual gutters. These columns or pillars are particularly well marked on the lingual side. For a list of material, which is very abundant, the reader is referred to the annex.





The p/3 are almost molariform, flattened labiolingually. The trigonid is always open and longer mesio-distally than the talonid (see table). The paraconid is located very anteriorly and is isolated from the metaconid (which appears to be the more important of the two) by a more or less well marked groove depending on the degree of wear of the tooth. The hypoconid is linked to the metaconid by a cristid obliqua. In mandible AD 750'97, the p/3 is in the process of erupting and shows the classic schema described by Butler on the basis of specimens of *Myohyrax oswaldi* from East Africa. In worn specimens, the talonid and trigonid are reduced to two prisms joined by a cristid obliqua. The entoconid and the metaconid are almost the same height.

The p/4s (Tabl. 3, Graph. 1) are molariform with a triangular trigonid and a squarer talonid. The gutter between the paraconid and metaconid is always well developed, as in the molars. In all of these hypsodont teeth, the highest cuspid in the trigonid is the metaconid.

Molars (Tabl. 4, 5, Graph. 2, 3) : The m/1s are generally larger than the p/4, the trigonid is square in the molars. In occlusal view the occlusal surface appears as two quadrangular lobes. The p/4 is sometimes the largest tooth in the dental series but it is usually the m/1,

In lightly worn teeth, in the m/1 and m/2 there is a small groove postero-lingual to the hypoconid. The two pillars are separated from each other by labial and lingual gutters which are developed through the entire height of the crown as far as the roots.

The m/3s are reduced and usually have an ovoid occlusal surface, with a single large central basin. It is com-prised of a single column with two folds, one anterior (antero-internal) is more marked than the other (postero-internal).

The m/2 and m/3 are usually strongly inclined towards the front, the m/3 even more so. Moreover, this inclination seems to be stronger in older individuals than in juveniles. The morphology of m/3 can be seen in mandibles AD 579'97 and AD 110'96 in which the tooth is in the process of erupting: it has a single anterior column corresponding to the trigonid with sharp paraconid and metaconid; the latter being more projecting. Distally, a posterior talonid is present, but is lower and very pinched labio-lingually. Wear produces a rosette shaped outline. In general the m/3 is strongly inclined towards the front of the jaw

Upper teeth (Pl. 1, III):

Anterior teeth:

Left IIIs : PQ AD 637, PQ AD 2370, PQ AD 2427, PQ AD 2594, PQ AD 3287, AD 196'95, AD 522'95, AD 422'96, AD 887'97, AD 663'98a, AD 151'99, AD 776'99.

Right IIIs: PQ AD 716, PQ AD 3460, AD 196'95, AD 422'96, AD 100'97, AD 588'97, AD 895'97, AD 663'98b, AD 776'99, AD 854'99

The IIIs (Pl. 1, Pl. 1II, fig. 1, 2) are curved and have convex labial and concave lingual surfaces. They are slightly helicoidally twisted when unworn, and have four digitations which disappear with wear. The first digitation (mesial) forms a short, almost vertical wall. The second digitation is the highest. From the mesial to the distal part, the digitations, equal in their development, are isolated from each other by weak

grooves. The distal digitation is shorter and separated from - the others by a better marked groove. The lingual wear facet is a rounded losange in the form of a burin. The root is compressed laterally

I2/: PQ AD 637 (left), AD 100'97 (right).

In premaxilla PQ AD 637, the 121 is a small tooth, with transversely convex labial surface which is strongly curved towards its base but less than in the first incisor. It has 4 digitations. The specimen in AD 100'97 is worn; because of this we do not see whether it had digitations or not. It is slightly shorter than the I1/ and is less curved than it. The tooth is labio-lingually flattened as in the preceding specimen, and it is stretched out mesio-distally. The wear facet is ovoid and oblique from front to back. The tooth has a more triangular surface in labial view, with a shorter distal end and a mesial swelling corresponding to the most projecting point of the incisor. It has a weak vertical, labial, distal depression which perhaps corresponds to the last digitation.

I3/ : AD 100'97 (right), Auchas, isolated tooth (AM without N°)

This is the best preserved specimen. It is a small tooth with a triangular crown elongated mesio-distally from the cervix to the apex and convex forwards. In addition, it has slight helicoidal torsion. The lingual wear facet is elongated. The 131 in place in the jaw is more worn (its outline is ovoid in occlusal view) with rounded margins and inclined towards the front. Its crown is convex towards 12/. It is half the size of Ill. The two incisors are covered by enamel on their labial surface

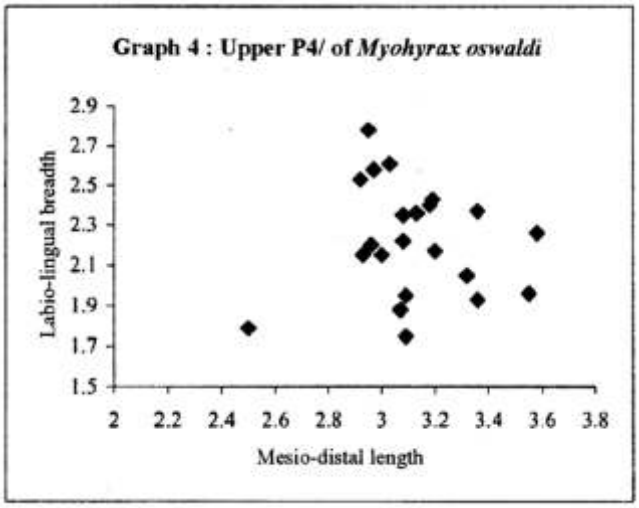
Upper canine: AD 100'97 (right)

The upper canine is the same size as the I3/, and is pointed. The wear facet is oblique towards the rear.

Cheek teeth: The premolars are usually rectangular and the molars square or trapezoidal. In lateral view, the columns are more projecting and rounder on the premolars and they are sharper and more extended mesio-distally on the molars. The labial surfaces of the cheek teeth are traversed by crests or vertical styles. The parastyle is the lowest. In the premolars, it is always lower than the main labial cusps. The ribs emanating from the metacone seem to be sharper in the molars, and the parastyle and metastyle are always more projecting in the molars than in the premolars. In labial view, the outline of the cusps and styles is more symmetrical in the molars. In the maxilla, the teeth are strongly convex labially, are usually recurved towards the base, more or less strongly depending on wear. The lingual groove is usually more oblique in the molars than in the premolars where it is more perpendicular on the labial surface of the tooth.

P1/ : two first premolars are known in right maxillae AD 251'94 and AD 100'97. The former is the most worn and is reduced to a small remnant. The one in AD 100'97 is less used and reveals its morphology: The tooth is elongated mesio-distally, and is the same size as the canine. But whilst the canine is inclined anteriorly, the first premolar is clearly inclined towards the rear. It is two-rooted and its wear facet is ovoid, underlined by a margin of thickened enamel. It is slightly pinched mesially and distally, corre-sponding to an anterostyle and a posterostyle.

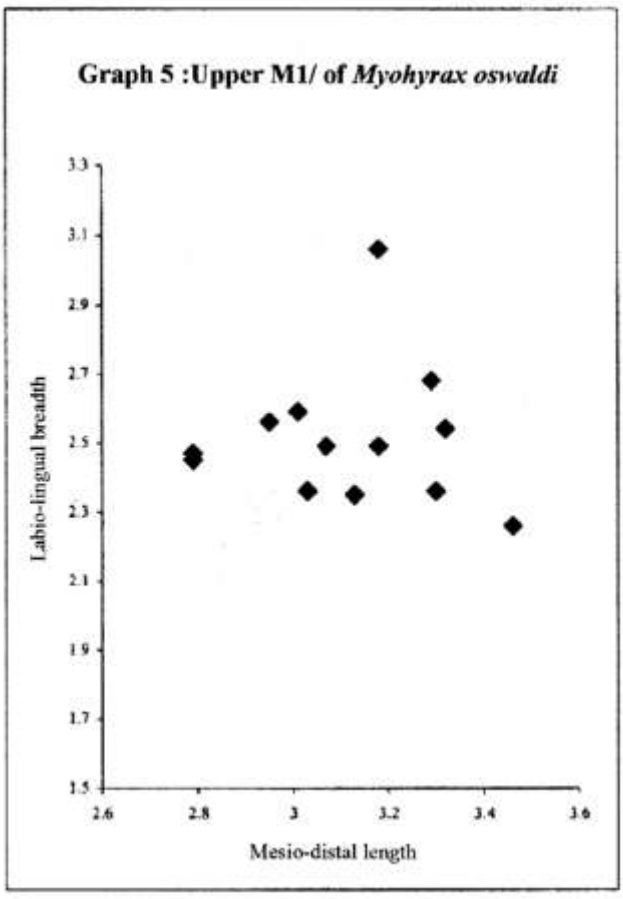
P2/ (Tabl. 6) : PQ AD 1021 (left), PQ AD 1050 (right), PQ AD 3030 (right), AD 138'95 (right), AD 100'97 (right), AD 870'97 (right and left), AD 265'98 (right), AD 665'00 (right),



AM 2'93 (left).

The P2/ is a slightly asymmetrical tooth formed of two lobes of which the anterior one is the shorter mesio-distally. The tooth is elongated mesio-distally presenting two labial ribs which underlie the paracone and metacone. On the antero-external surface, an enamel fold indicates the presence of a weakly marked parastyle. The protocone is isolated from the hypocone by a shallow groove located in the axis of the gutter that separates the metacone from the paracone. The tooth has two separate labial roots and two fused lingual ones.

The fossettes are very clear in the cheek teeth. They are variable in expression depending on the stage of wear. In P2/, there are one or two fossettes. Butler (1984) reported that the posterior buccal fossette is the only one present in this tooth, but



in two specimens at least, PQ AD 3030, there is a posterior lingual fossette and in AD 870'97, the two buccal fossettes are present. The second premolar has three roots, of which the mesial ones are fused.

P3/ : PQ AD 1050 (right), PQ AD 2852 (left), PQ AD 3384 (right), AD 575'94 (left), AD 426'96 (left), AD 100'97 (right), AD 870'97 (right), AD 677'99 (right), AD 657'00 (right).

P4/ : PQ AD 1069 (right), PQ AD 1348 (left), PQ AD 2354 (right), PQ AD 2370 (left), PQ AD 2424 (right), PQ AD 2455 (left), PQ AD 2468 (right), PQ AD 2640 (left), PQ AD 2852 (left and right), AD 575'94 (left), AD 426'96 (left), AD 100'97 (right), AD 870'97 (right), AD 677'99 (right), AD 696'99 (left). Several other isolated teeth were difficult to identify and are listed in the annex with question marks.

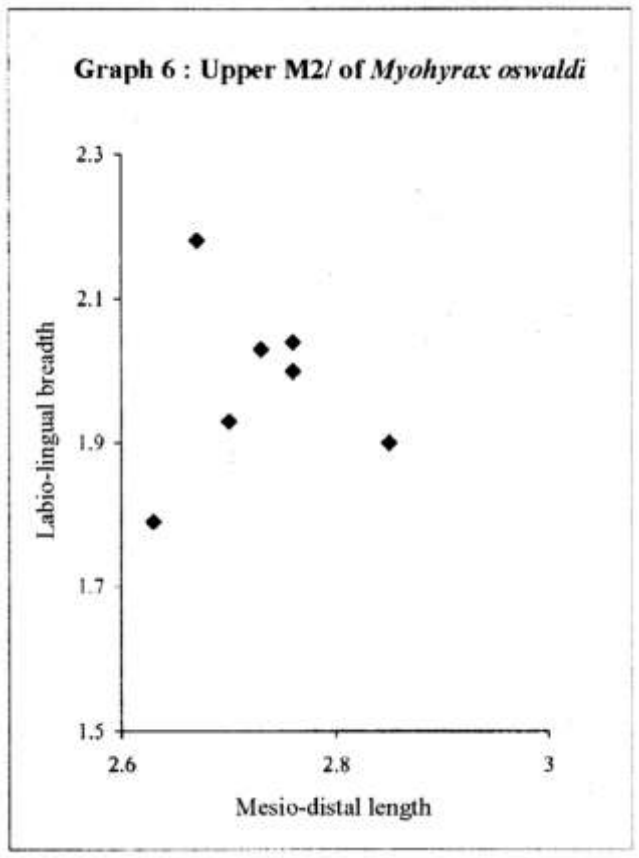
P3/ and P4/ are molariform teeth (Pl. 1, III, Fig. 4, Tabl. 7, 8, Graph. 4), the P3/ being more rectangular and the P4/ more square. The parastyle is always lower than the paracone. The P3/ is always shortest labio-lingually. It has four roots of which the two lingual ones are fused. The teeth enlarge slightly from cervix towards the apex of the tooth, which is why more worn teeth tend to be squarer in occlusal outline.

M1/ and M2/ (Pl. 1, III, Fig. 3, Tabl. 9, 10, Graph. 5, 6) : These teeth are abundant so a complete listing is provided in the annex. The occlusal features are typical of Macroscelididae as noted above. The descriptions which were provided by Andrews (1914), Stromer (1926), Whitworth (1954), Butler & Hopwood (1957), Patterson (1965), Butler (1984, 1995) and all the other characters are not repeated in this paper. They are very hypsodont teeth with projecting parastyles. They classically have two labial fossettes located between the paracone and paraconule and between the metacone and metaconule respectively, and two lingual fossettes located above the hypocone and protocone. The protocone is isolated from the hypocone by a deep groove, strongly inclined towards the front. The parastyle is shorter mesio-distally and is more pinched than the metastyle, a result of which is that a clear vertical gutter is well expressed in the M1/. The enamel in the fossettes may be crenulated depending on the stage of wear of the tooth. The anterior surface is always the longest and the M2/ is trapezoidal with the posterior surface much shorter than the anterior one.

M1/ and M2/ have four roots of which the two lingual ones are close to the M1/. Cement is not always present in the fossettes. It seems to be an inconstant feature.

In none of the Arrisdrift tooth rows is an M3/ present. A very reduced M3/ was described in specimens from East Africa by Whitworth (1954) (C.M.Hy.44 and C.M.Hy.54) and by Butler (1984) (KNM RU 3764). None of the Arrisdrift maxilla fragments possesses an alveolus for this tooth, from which we conclude that it was not present in *Myohyrax* from the site. This tooth is exceedingly reduced in the older East African specimens, so it is possible that it was suppressed completely in *M. oswaldi* at Arrisdrift which is younger.

Discussion: The dental material of Macroscelididae from Arrisdrift appears to be quite homogeneous. There are slight individual variations in the strength of the styles or the projection of the pillars, but there are no fundamental features by which we can separate the specimens from those collected in



East Africa. Metrically, the sample is homogeneous. (Tables 3, 4, 8, Graph. 1, 2, 4). The specimens from Arrisdrift do not differ either metrically or morphologically from the species of Myohyracinae described by Andrews in 1914 from Kenya, *Myohyrax oswaldi*. After comparing all the measurements for the upper and lower P4, M1 and M2, we found no difference between *M. oswaldi* and the Arrisdrift specimens (Tabl. 11). It is thus cotierent to attribute the material from the Orange River to *Myohyrax oswaldi*.

Taking into account the data published by Stromer (1926) on *Myohyrax doederleini*, it appears that the latter is not fundamentally morphologically different from the sample found in the Orange River valley. Metrically, *M. doederleini*, falls within the range of variation of *M. oswaldi*. When the species *M. doederleini* was erected, the available material was not abundant and in view of the observed variation it is possible that these closely similar species belong in fact to a single species, as Whitworth (1954), Patterson (1965) and Butler (1984) have already proposed. The presence of a smaller species, *M. doederleini* is thus not the case at Arrisdrift: In the collection, there is a size variation which encompasses the small specimens from Elisabethfeld. As for the presence of a lingual groove between the paraconid and the metaconid, there are several specimens from Arrisdrift in which it can be observed, and it thus reflects nothing more than individual variation linked to wear of the tooth and perhaps to hypsodonty. The presence of cementum in the fossettes is not constant. The deposit of cementum in the fossettes varies as a function of wear and hypsodonty. In addition, some depositional environments can lead to the solution of cementum which can thus disappear from teeth that initially bore some. Thus, in the Arrisdrift sample, out of more than 100 teeth in jaws that possess similar morphology there are many with

cementum and many without. It is thus a variable feature and cannot De used to differentiate species or genera.

Diet. The great hypsodonty of the cheek teeth suggests a diet based on hard foods, a suggestion confirmed by the cutting nature of the anterior incisors. Furthermore, the molarisation of the premolars augments the grinding sur-face of the dental battery (Butler, 1995). These features indicate that these mammals were adapted to herbivory. It is likely that they ate hard grass or seeds. This is compatible with the environmental reconstructions made on the basis of other faunal elements and plants.

Subfamily Rhynchocyoninae Gill, 1872
Genus *Miorhynchocyon* Butler 1984

Type species: *Rhynchocyon clarki* Butler & Hopwood 1957

Other species: *R. rusingae* Butler 1969, *Miorhynchocyon rusingae* (Butler 1969), *M. meswae* Butler 1984, *Miorhynchocyon gariepensis* nov. sp.

Original diagnosis of genus: "Differing from *Rhynchocyon* as follows: Oblique crest (anterior hypoconid crest) on lower molariform teeth ends midway between protoconid and metaconid, instead of joining the metaconid; metastylid absent on dp/4 and m/1; paraconid of p/4 and m/1 higher and more lingually situated; cheek teeth more brachyodont; anterior margin of ascending ramus more upright. The skull, known only in *M. clarki*, has primitive characters (Butler & Hopwood 1957).

Species *Miorhynchocyon garlepensis* nov.
(Fig. 1)

Holotype: Fragment of left mandible AD 666'00 with p/4, m/1-m/2.

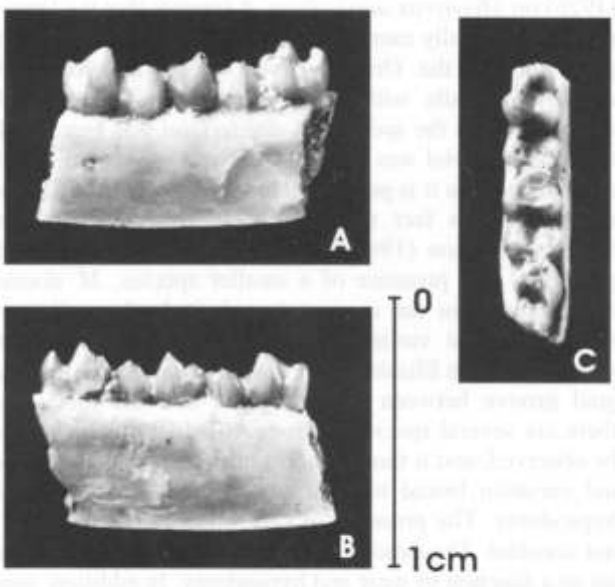


Figure 1: *Miorhynchocyon gariepensis*, Holotype : AD 660'00, left mandible with p/4, m/1-m/2, a : labial view, b : lingual view, C : occlusal view (X 3)

Paratype: Half an upper M1/, AD 167'96a, and a right m/2, AD 72'95.

Diagnosis: Brachyodont species of Rhynchocyoninae with trigonid and talonid well differentiated in the p/4, m/1 and m/2 and with relatively sharp cusps. Macroscelididae smaller than *M. rusingae*, but close to *M. clarki*. It differs morphologically from the other species of *Miorhynchocyon* by a talonid that is much lower than the trigonid and by the fact that the paraconid is not separated from the protoconid by a deep groove. In addition, the trigonid and the talonid are labio-lingually equally wide in the p/4.

Derivatio nominis: The species name derives from the local name for the Orange River - Gariep.

Type locality: Arrisdrift, Sperrgebiet (Namibia); 16°42'20"E : 28°28'30"S.

Age: Base of the Middle Miocene, correlated biochronologically with European mammal zone MN4 and Faunal Set PIII of East Africa.

Description: There is very little material known: a fragment of mandible which constitutes the holotype, an isolated m/2 and half a worn cheek tooth (probably an M1/).

Mandible. It is quite small with a tooth row (p/4-m/2) 10 mm long. The horizontal ramus is low with two parallel sides, 3.90 to 4.31 mm deep. The mental foramen is located below the p/4, as in *M. meswae*, and thus further to the rear than occurs in other Miocene Macroscelididae.

Dentition. The p/4 is larger than the m/1 which is in turn larger than the m/2 : p/4 = 3.94 mm; m/1 = 3.53 mm; m/2 = 2.73 mm. In the p/4, the trigonid (2.19 mm) is practically as wide as the talonid (2.12 mm). The paraconid is as high as the protoconid and a little lower than the metaconid and well in advance of it. In the p/4, the paraconid is smaller than the metaconid and well mesial to it. It is isolated from the protoconid by a weak notch thereby differing from *Miorhynchocyon rusingae*. The entoconid is as high as the hypoconid. The hypoconulid is very close to the entoconid and almost as well developed.

In the m/1 and m/2s there is a clear groove between the paraconid and the metaconid; the latter is not as deep as in *M. clarki* and the cusps appear less detached. In m/1, the entoconid crest englobes the hypoconulid and ends slightly behind the hypoconid. In m/1, the talonid is almost the same size as the trigonid (mesio-distal length 1.70 versus 1.66 mm), but in the m/2, the talonid is very reduced in comparison with the trigonid (mesio-distal length 1.26 versus 1.41 mm) and very short labio-lingually and the paraconid is much lower than the metaconid. In comparison with *M. rusingae* the talonid is more elongated vestibulo-lingually and the trigonid and talonid squarer than in the Arrisdrift fossil. An antero-labial cingular fold is clear in the m/1 and a cingulum is visible behind the hypoconid. It seems that there was an alveolus for an m/3. The cheek teeth are close in size to those of *M. clarki* (Butler, 1984) (Table 12): p/4 = 3.6-3.8 mm; m/1 = 3.0-3.5 mm; m/2 = 2.2-2.8 mm.

The upper molar from Arrisdrift differs from that of *M. clarki* by having sharper paracone and metacone and the metacone as high as the paracone. The metacone is pinched mesio-distally. The paracone and the metacone are triangular : the labial sur-

face is flatter than in *M. clarki* and *M. rusingae*. As in *M. clarki*, the upper molar has three roots of which the lingual one is the strongest.

Species cf *Miorhynchocyon gariepensis*
(Pl. 1V)

At Arrisdrift there are four additional specimens which are clearly Macroscelididae, but which pose particular problems. They are not Myohyracinae, but possess features which indicate affinities with Miorhynchocyoninae. They comprise a skull with right III and a remnant of cheek tooth (PQ AD 1639), and three upper Il/s, one without number (left), PQ AD 2965, a broken right incisor, and AD 399'96 (left). This material is referred provisionally to *Miorhynchocyon gariepensis*.

Descriptions: Dentition. The only teeth known from Arrisdrift are upper IIIs. PQ AD 1639 is the only *in situ* tooth. The most complete specimen is PQ AD 1639 but it is quite worn. The upper IIIs are mesio-distally curved teeth and convex anteriorly and inferiorly. Unbroken teeth have 6 main digitations. In AD 339'96, which is large, there are six digitations of which the first two are accentuated by a vertical crest which descends to the base of the crown and a strong fold on the mesial surface of the first digitation. The other four digitations are reinforced by short low crests. The fragment of incisor PQ AD 2965 has wrinkled enamel on all the digitations. The incisors are covered in enamel on the labial and lingual surfaces, differing in this respect from Myohyracinae where it is not present on the lingual surface.

The presence of digitations in the upper III suggests that these specimens belong to Macroscelididae. In the Myohyracinae, these teeth are smaller and have only four digitations, which are more like lobules. No upper incisors have been described for *Protypotheroides beetzi* from the Early Miocene of the Sperrgebiet. In most respects, the dentition of this species is typical of Myohyracines, so it would be difficult to imagine that its incisors would be very different.

Skull. The skull PQ AD 1639, found during the 1976 excavations, has never been described. Unfortunately it was severely damaged during mechanical preparation at the time of discovery. All the teeth save for the upper right central incisor which is erupting, were lost. The individual was therefore not yet adult at the time of death. The skull is flat, elongated and widens regularly from front to back, giving a form to the skull intermediate between those of *Rhynchocyon* and *Petrodromus*. The temporal fossae are clearly delimited. The fronto-parietal suture is visible at the back of the skull; it ends in the zygomatic arch. The occipital is rounded; the bone being broken in the left side, where several circumvolutions of the brain cast can be seen. On the right rear part there is part of the occipital crest visible.

The skull is almost complete, 90.5 mm long and a width of at least 42.2 mm; the two zygomatic arches being broken, this measurement is not the maximal. Whatever the case, it is much longer than any extant Macroscelididae. The muzzle is relatively short in comparison with the total length of the skull: 36.4 mm from the fronto-parietal suture to the ends of the nasals. The naso-maxillary sutures are not visible; it is thus not possible to make out their form. But the fronto-parietal suture is almost transversal and thus differs from extant *Rhynchocyon*.

In superior view, the muzzle is narrow (12.4 mm) the lacrymal foramina are not visible, nor are the orbital foramina, and there is no sagittal crest, but the lambdoid crest is preserved on the left side of the skull. A doubled supraorbital foramen is present on the two sides of the skull. It is prolonged forwards as a groove which curves progressively laterally along the fronto-maxillary suture.

In palatal view, the anterior part in front of the orbits forms a wide triangle, and is quite short antero-posteriorly, and thus differs from most of the modern Macroscelididae except for *Rhynchocyon*. All the posterior part of the skull is damaged so it is not possible to estimate the position or development of the auditory bullae. The palatine is destroyed, so we are unable to know if the palate was fenestrated or not.

In lateral view, the flattening of the skull is clear. On the left side, there is a strong post-orbital process and a small lacrymal foramen which opens laterally; it is prolonged by a groove over a distance of 14.2 mm. Towards the front, a broken tooth is present behind the I/1. It is unidentifiable, but it is quite large (4.5 mm in mesio-distal length) and it is inclined forwards.

Discussion: The morphology of the skull and the III with distinct digitations, suggest that these specimens belong to a Macroscelididae. Several skull characters indicate closeness to Rhynchocyoninae, but there remains some uncertainty about its attribution to a particular taxon on account of its poor preservation. It appears to be intermediate in morphology between *Rhynchocyon* and *Elephantulus* with its elongated low skull which is ovoid in overall outline.

The only Macroscelididae of this size known in Namibia is *Protypotheroides beetzi*, described from Elisabethfeld by Stromer in 1923. But for the reasons evoked above, it seems difficult to assign the Arrisdrift material to this genus. In addition, the cheek teeth of *Protypotheroides* are very hypsodont, and it would be difficult to lodge then in a skull that has such a low cranial roof. The material clearly does not belong to *Myohyrax oswaldi*. The only other Macroscelididae present at the site is *Miorhynchocyon gariepensis*, but this species is known only by a lower jaw and an isolated upper molar. In the absence of other remains from Arrisdrift, it is prudent to assign the specimens to cf. *Miorhynchocyon gariepensis*.

Postcranial skeleton: Several postcranial remains of Macroscelididae are represented in the collections. Those attributed to *Myohyrax* are the most abundant.

Humerus: PQ AD 305 (right), AD 445'96 (left), AD 588a'94 (left), AD .588b'94 (left), AD 588c'94 (right), AD 588d (left), AD 883'97 (left), AD 667'00 (right) (Fig. 2 : 3a, b)

The small humeri have the classic morphology of elephant shrews with a clear entepicondylar foramen, a humeral trochlea that projects strongly medially which is followed laterally by a globular *capitulum* stretched out medio-laterally and a perforated olecranon *fossa*. The diaphysis in the few specimens in which it is preserved, is straight overall.

Distal breadth (medio-lateral) : PQ AD 305, 5.2 mm; AD 445'96, 5.6 mm; AD 584a'94, 5.2 mm; AD 584b'94, 5.4 mm;AD 584c'94, 5.0 mm; AD 584d'94, 5.0 mm; AD 883'97, 5.1 mm; AD 667'00, 5.4 mm. These measurements are com-

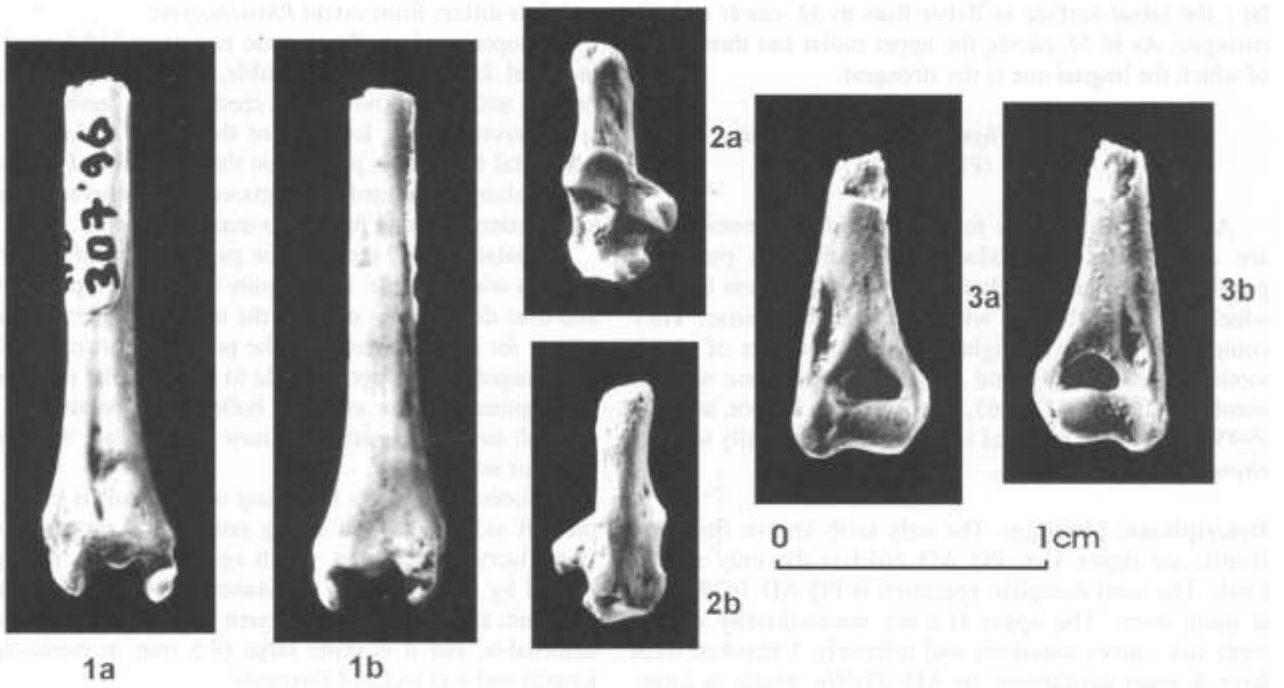


Figure 2: Postcranial remains of *Myohyrax oswaldi* ; 1 : distal end of right tibio-fibula AD 307'96, a : anterior view, b : posterior view ; 2 : right calcaneum PQ AD 2454 a : superior view, b : inferior view ; 3 : distal end of right humerus PQ AD 305, a : posterior view, b : anterior view

patible with those given by Stromer (1926) concerning *Myohyrax oswaldi* to which we attribute all these humeri.

Proximal tibia and fibula: PQ AD 3017 (left), AD 445'96 (right), AD 668'00 (left), AD 669'00 (left). PQ AD 3017 consists of a proximal tibia and .fibula in connection. The tibial plateau has two convex articulations for the distal femur, and the anterior tibial crest, which projects strongly anteriorly, is markedly curved towards the exterior. The fibula is fused to the tibia for a distance of about 17 mm from the tibial plateau. This piece is larger than the others and cannot belong to the same group. The medio-lateral breadth of the tibial diaphysis just above the junction tibia / fibula is 29 mm in PQ AD 3017 and 20 mm in AD 669'00. In AD 668'00, the fusion between the fibular and tibial diaphyses occurs about 3 cm above the distal articulation. In AD 669'00, the proximal part has been badly stuck together (it is missing a fragment of diaphysis) and it is not possible to estimate the fusion point. The small specimens are attributed to *Myohyrax oswaldi* and the large to *Miorhynchocyon gariepensis*.

Distal tibio-fibula: PQ AD 196 (right), PQ AD 1368 (right), PQ AD 2310 (right), PQ AD 2454 fragment of distal diaphysis, PQ AD 2554 (left), PQ AD 3250 (left), AD 171'96 (right), AD 307'96 (right), AD 246'97 (right), AD 302'97 (left), AD 255'98 (left), AD 256'98 (left), AD 503'99 (left), AD 718'99 (left), AD 668'00 (left), AD 669'00 (left), AD 670'00 (left), AD 671 '00 (left), AD 672'00 three fragments which lack the articular region (Fig. 2 : 1 a, b) (Table 13).

The distal tibia-fibula is by far the best represented part of the skeleton. The tibia and the fibula are fused distally, as is classically the case in the elephant shrews. Proximally, the tibial plateau is triangular with an anterior tibial crest that is quite strong, projecting anteriorly and strongly excavated medio-laterally. It extends for almost 25 mm, then at this level the fibula fuses with the tibial diaphysis.

The distal end is elongated medio-laterally and the two malleoli project a long way distally and are gently recurved towards the interior. The articular facets for the calcaneum and talus are deeply depressed, suggesting a well constrained articulation. Specimen PQ AD 1368, differs clearly from the rest by its large size (the medio-distal distance would be even more as the external and internal malleoli are broken) and probably belong to a different taxon from the other macroscelidids in the sample. The morphology of the distal articulation is also different. In the small specimens, the two malleoli are strongly recurved downwards, and the external one is medio-laterally short. In PQ AD 1368, the distal articulation is wider and the external malleolus more elongated antero-posteriorly. The tibio-otalar articulation is more deeply excavated in the small specimens and their diaphysis appears flatter antero-posteriorly. The smaller specimens are attributed to *Myohyrax oswaldi* and the larger ones to *Miorhynchocyon gariepensis*.

Talus: AD 717'99 (right). This is quite a large complete specimen (5.9 mm) which is at the upper limit of the range of variation of East African *Myohyrax oswaldi* (Butler, 1984). The bone is flattened supero-inferiorly. Its morphology is typical of Macroscelididae : The talar neck is long and is half the length of the bone (total length: 5.9 mm, length of the neck: 3.2 mm), as already noted by Butler in the East African specimens. It has a medio-laterally enlarged talar head with clear articular surfaces for the navicular and cuboid, the latter being the smaller of the two. The two malleolar facets are rounded and very deep. The tibial facette is more abrupt and the fibular one is strongly excavated laterally and posteriorly. At the base of the trochlea, which is in the shape of a pulley of which the lateral lip is higher than the medial one, there is a deep depression. By its size (breadth of the trochlea: 2.2 mm in its middle),

Table 13: Measurements of the tibio-fibula of Arrisdrift, Namibia, Macroscelididae (mm).

N° specimen	Length	Breadth
PQ AD 196	60	32
PQ AD 1368	67	38
PQ AD 2310	53	27
PQ AD 2554	56	28
PQ AD 3250	52	25
AD 171'96	58	32
AD 307'96	50	25
AD 246'97	55	27
AD 302'97	58	30
AD 255'98	57	28
AD 256'98	55	30
AD 503'99	54	25
AD 718'99	52	26
AD 668'00	53	27
AD 669'00	53	26
AD 670'00	57	27
AD 671'00	55	26

it agrees perfectly with the tibio-fibulae attributed to *Myohyrax oswaldi*.

Calcaneum: PQ AD 2454 (right), PQ AD 3089 (left), AD 588'94e (right), AD 258'95 (left) which lacks the *sustentaculum tali*, AD 266'98 (right) (Fig. 2: 2 a, b).

The calcaneum is clearly macroscelidid by the important projection of the *sustentaculum tali*. The *tuber calci* is very elongated, and it constitutes by itself more than half the length of the specimen (6 mm for 9.7 mm in PQ AD 2039). The posterior talar facet is triangular and anterior to it, there is a deep, circular ligamentary depression. The anterior talar facet corresponding to the *sustentaculum tali* is well detached from the body of the calcaneum and makes a strong projection medially. The calcaneum is quite long: 9.7 mm in PQ AD 2039,9.1 mm in PQ AD 2454, 10.1 mm in AD 588'94, 10.3 mm in AD 258'95 and 10 mm in AD 266'98. The last one agrees well in size and morphology with the talus described above. It is identified as *Myohyrax oswaldi*.

Metatarsals: PQ AD 2795, four left metatarsals stuck to the median cuneiform which is quite elongated. The metatarsals are slender and elongated, but it is not possible to estimate their total length as they are broken.

Phalanx: a distal phalanx AD 41'00 shows a very peculiar feature, typical of macroscelidids : it is bifid at its extremity.

Figure 3: Terminal phalanx attributed to *Myohyrax oswaldi* AD41'00
a : superior view; b: lateral view; c : medial view; d : inferior view.

Conclusions

The Macroscelididae from the Proto-Orange deposits fill a gap in the history of this African group. Whereas the early Miocene sites in the northern Sperrgebiet are dominated by *Protypotheroides*, it is *Myohyrax* which is by far the commonest in the middle Miocene of the Orange River Valley. *Protypotheroides* is not yet known in the younger deposits. It is not a collecting artefact, because the micro-mammal fauna is abundantly represented, the Macroscelididae particularly so. The vast majority of specimens belong to very hypsodont Macroscelididae, *Myohyrax oswaldi*. The Miorhynchocyoninae described are very rare and are known only by a few brachyodont specimens attributed to a new species *Miorhynchocyon gariepensis*. Finally, a skull and some isolated upper central incisors are tentatively assigned to this latter taxon. For the moment, it is difficult to explain the major imbalance between the representation of these two macroscelidids. Was it ecological in nature? or was it competition between the brachyodont species and other mammals? It is delicate to reply to these questions, but further study of the East African species and those from earlier localities in the northern Sperrgebiet, of which the skeleton is well known, may throw light on the matter.

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Appendix 1: Catalogue of Macroscelididae from Arrisdrift (Namibia)

PQ AD without n°	M1/ upper right
PQ AD without n°	I1/ upper right digitate
PQ AD 66	P3/ or P4/ upper left
PQ AD 67	M1/ upper right
PQ AD 89	Cheek tooth lower
PQ AD 123	Left mandible with p/2-4, m/1
PQ AD 124	Fragment of left mandible with p/4, m/1-2
PQ AD 125	Fragment of left mandible with p/4, m/1-2
PQ AD 126	Fragment of left mandible with p/4, m/1-3 + one isolated tooth (p/4 ?)
PQ AD 152	M1/ upper left
PQ AD 196	Tibio-fibula
PQ AD 256	Fragment of tooth
PQ AD 305	Right humerus
PQ AD 335	Molar in poor condition
PQ AD 626 a	Fragment of right mandible with m/1-3 + 4 isolated teeth
PQ AD 626 b	Lot of upper teeth
PQ AD 626 c	Isolated M3/
PQ AD 633	Lower p/4 and m/1
PQ AD 637	Fragment of premaxilla with I1-2/
PQ AD 673	Fragment of right mandible with p/3-4
PQ AD 680	2 damaged upper teeth
PQ AD 710 a	Fragment of mandible with m/1-3 + isolated teeth
PQ AD 710 b	2 upper teeth
PQ AD 716	Upper left I/
PQ AD 742 a	Fragment of left mandible with p/4-m/1 + an isolated tooth
PQ AD 742 b	3 upper teeth
PQ AD 752	M1/ upper left and M2/ upper right
PQ AD 766	Lot of premolars and upper molars
PQ AD 767 a	Lot of mandible fragments with cheek teeth
PQ AD 767 b	2 upper teeth
PQ AD 788	M1/ upper left
PQ AD 803 a	Fragments of mandible
PQ AD 803 b	M1/ upper right
PQ AD 860	Fragment of left mandible with p/4-m/1
PQ AD 880	Fragment of left mandible with m/1-2
PQ AD 887	Mandible fragment + isolated teeth
PQ AD 900	Fragment of right mandible with p/4, m/1-2
PQ AD 918	P3/ or P4/ upper right worn
PQ AD 966	3 lower teeth
PQ AD 971	Mandible
PQ AD 984	p/3 lower right
PQ AD 996	Upper molar in poor condition
PQ AD 1005 a	Fragment of left mandible with p/3-4
PQ AD 1005 b	2 upper teeth
PQ AD 1021	P2/ upper left and p/4 lower right
PQ AD 1040 a	Fragment of right mandible with p/3-4, m/1 + p/3 lower left
PQ AD 1040b	P4/ left+ M1/ right
PQ AD 1043	Lower I
PQ AD 1050	Fragment of right maxilla with P2/-P3/
PQ AD 1069	P4/, M1/, M2/ upper right
PQ AD 1094	Mandible fragments right (one with p/4-m/2, alveoli of p/3 and p/2 ; one with m/1 and m/2.
PQ AD 1104	Fragment of right mandible with p/2-3-4, m/1 and perhaps m/2
PQ AD 1122	Lot of lower teeth
PQ AD 1123	Lot of upper teeth
PQ AD 1124	Fragment of left mandible with p/2
PQ AD 1152	p/4 or m/1 lower
PQ AD 1162	p/4 lower left
PQ AD 1189	Fragment of right mandible with p/4, m/1-2
PQ AD 1348	P4/ upper left
PQ AD 1368	Tibio-fibula distal
PQ AD 1416	Mandible in matrix
PQ AD 1563	Fragment of right mandible with m/1-2
PQ AD 1610	M2/ upper left
PQ AD 1622	Fragment of right mandible with p/4 ?
PQ AD 1627	Fragment of left mandible with p/4, m/1-2
PQ AD 1639	Skull
PQ AD 1655	Fragment of maxilla in matrix
PQ AD 1685	Fragment of left maxilla with P4/, M1-2/
PQ AD 1726	M1/ upper left + M2/ upper left rolled + p/3 lower ?
PQ AD 1754	p/4 lower right
PQ AD 1774	Distal femur
PQ AD 1777	Fragment of left mandible with p/4 ?
PQ AD 1872	p/4 lower left ?
PQ AD 1944	Fragment of left mandible with p/4, m/1-3
PQ AD 2001	2 fragments right mandibles with p/3-4, m/1 and p/4, m/1-2
PQ AD 2035	Fragment left mandible with m/1-2-3
PQ AD 2036	Fragment of left mandible with p/2-3 + p/4 right + fragment distal metatarsal
PQ AD 2127	Fragment of left mandible with p/3-p/4-m/1
PQ AD 2188	Fragment of maxilla in matrix
PQ AD 2214	Mandible
PQ AD 2218	2 lower teeth
PQ AD 2231	= 2436 catalogue upper tooth
PQ AD 2243	Scapula fragment
PQ AD 2248	Fragment of right mandible of a young individual with p/1 and i/1
PQ AD 2249	Fragment of left mandible with p/3
PQ AD 2254	Tibio-fibula left
PQ AD 2310	Tibio-fibula right
PQ AD 2354	M1/ upper left + P4/ upper right + p/4 lower left
PQ AD 2370	Upper teeth : I1/ left, P4/ left + p/4 lower right
PQ AD 2373	M1/ left + 1 Hyracoidea
PQ AD 2376	p/4 lower left
PQ AD 2380	Fragment of mandible with p/3-4 + 1 lower tooth + 2 upper teeth
PQ AD 2416	Upper and teeth + Hyracoidea
PQ AD 2424	P4/ upper right
PQ AD 2427	I1/ upper left
PQ AD 2436	3 lower teeth and 2 upper teeth
PQ AD 2446	Distal humerus
PQ AD 2450	M1/ upper left
PQ AD 2455	Fragment of left maxilla with P4/, M1-2/
PQ AD 2468	P4/ and M1/ upper right
PQ AD 2470	Fragment of right mandible with p/3
PQ AD 2479	Fragment of worn left mandible with p/4, m/1-3 + M2/ upper
PQ AD 2515	Fragment of left mandible with m/1-3 young
PQ AD 2554	Tibio-fibula
PQ AD 2562	1 Upper molar and 1 Lower molar
PQ AD 2566	Fragment of right mandible with p/3-4, m/1-2
PQ AD 2578	Fragment of right maxilla with M1-2/
PQ AD 2581	Pelvis
PQ AD 2586	1 upper tooth + 1 lower tooth
PQ AD 2587	2 fragments of left mandibles (same individual) with p/2-3, m/1-2 + 1 Hyracoidea
PQ AD 2594	I1/ upper left broken + 2 lower teeth
PQ AD 2610	Lot of teeth
PQ AD 2611	2 small fragments of mandible
PQ AD 2618	M1/ upper left and p/4 lower right
PQ AD 2640	P4/, M1/ upper left (associated)
PQ AD 2666	2 small mandible fragments left : one with m/2 and the others with p/4 ?
PQ AD 2675	Mandible fragments
PQ AD 2690	Fragment of left mandible with p/3-p/4
PQ AD 2710	Fragment of mandible with p/3-4 + m/1 upper right + P4/ (?) right
PQ AD 2720	Upper and lower teeth
PQ AD 2794	Fragment of left mandible with p/3-4, m/1 young individual + anterior tooth alveoli
PQ AD 2795	Metatarsals in connection
PQ AD 2838	M1/ upper right
PQ AD 2852	P3/, P4/, M1/ upper left associated + P4/ and M2/ upper left + p/3 or p/4 lower right
PQ AD 2865	M1/ upper left + M2/ upper left
PQ AD 2897	Fragment of right mandible with p/4, m/1-3
PQ AD 2964	Fragments of mandible : left with p/4, m/1-2 ; left with m/2-3 right with p/4-m/1
PQ AD 2965	I1/ upper left
PQ AD 3012	Fragment of right mandible with p/4, m/1-2 + m/1 left
PQ AD 3017	Tibio-fibula proximal
PQ AD 3030	Fragment of right maxilla with P2-4/, M1-2/
PQ AD 3038	p/4 lower ?
PQ AD 3065	Mandible
PQ AD 3089	Calcaneum
PQ AD 3191	P4/ upper right ?
PQ AD 3241	2 lower teeth
PQ AD 3250	Calcaneum + tibio-fibula distal
PQ AD 3251	Lot of upper teeth and lowers
PQ AD 3263	3 mandible fragments + upper teeth and lowers isolées

PQ AD 3268	4 upper teeth and a lower tooth
PQ AD 3278	1 upper tooth and 1 lower tooth
PQ AD 3287	3 mandible fragments right : one with p/2 ; one with p/3-4 ; one with p/4, m/1-2 + isolated teeth upper and lower including one I1/ upper left
PQ AD 3384	Fragment of right maxilla with P3-4/, M1-2/
PQ AD 3398	Fragment of left mandible with m/2
PQ AD 3460	I1/ upper right and p/3 (?) lower left
PQ AD 23400	Fragment of left mandible with m/1-2 + M1/ upper right ?
AD 236'94	Fragment of right mandible with p/3-4, m/1-3
AD 237'94	Mandible
AD 238'94	Mandible in poor shape with p/4, m/1-2 (?)
AD 239'94	Fragment of right mandible with m/1
AD 240'94	Fragment of left mandible with p/3 ?
AD 241'94	Fragment of left mandible with p/4, m/1-2
AD 242'94	Fragment of mandible
AD 243'94	Left mandible with p/3-4, m/1-3
AD 244'94	Mandible
AD 245'94	Mandible
AD 246'94	Fragment of mandible
AD 247'94	Front of left mandible with i/1, i/2 and p/2
AD 248'94	Fragment of left mandible with i/1-2, p/3-4
AD 249'94	Fragment of mandible with p/4, m/1-3 (broken)
AD 250'94	Left mandible with alveoli of anterior teeth, p/3-4, m/1-3
AD 251'94	Fragment of maxilla with P1-2/
AD 252'94	Fragment of maxilla
AD 253'94	Lower incisors
AD 254'94	Upper incisors
AD 255'94	Molars lowers
AD 256'94	Upper molars
AD 257'94	Mandible
AD 258'94	Fragment of mandible (large)
AD 259'94	Fragment of mandible (small)
AD 260'94	Isolated teeth
AD 566'94	Front of left mandible with alveoli i/1, i/3, c/1, p/1 and base i/2, p/2-3
AD 567'94	Front of left mandible with alveoli front teeth, p/2-4.
AD 568'94	Left mandible with i/1, p/3-4, m/1
AD 569'94	Front of mandible with i/1-2, alveoli i/3, c/1, and p/1-4
AD 570'94	Fragment of mandible with p/4, m/1-2
AD 571'94	Left mandible broken with p/4, m/1-2
AD 572'94	Fragment of left mandible with p/4, m/1-3
AD 573'94	Fragment of right mandible with p/4, m/1-2
AD 574'94	4 mandible fragments
AD 575'94	Fragment of left maxilla with P3-4/ plus an upper tooth in poor condition
AD 588'94	4 distal humeri and 1 calcaneum
AD 59'95	Right mandible with p/2-4, m/1-3 and base i/1
AD 61'95	Mandible
AD 62'95	Mandible
AD 64'95	Fragment of right mandible with fragment p/2, p/3, m/1-3
AD 72'95	m/2 lower right of *Miorhynchocyon*
AD 76'95	Fragment of mandible with m/1-3 (young)
AD 77'95	Fragment of mandible with 2 teeth
AD 78'95	Fragment of right mandible with p/4
AD 79'95	Fragment of mandible with p/4 (?)
AD 90'95	Lot of lower teeth
AD 91'95	Lot of upper teeth
AD 92'95	Mandibular condyle
AD 126'95	Left mandible with p/3-4, m/1-3
AD 127'95	Fragment of left mandible with m/1-3 (worn)
AD 137'95	Fragment of left mandible with p/4, m/1
AD 138'95	Fragment of right maxilla with P2-3/
AD 183'95	Mandible with alveoli front teeth and p/4, m/1-3
AD 196'95	Lot of upper incisors
AD 476'95	2 fragments of mandible : 1 with p/3-4, m/1 and 1 with m/1-2
AD 482'95	Fragment of right mandible with p/4-m/1
AD 484'95	Fragment of right mandible in poor condition
AD 522'95	Upper I1/ and I3/
AD 534'95	Fragment of mandible with m/1-2
AD 110'96	Left mandible young with p/3-4, m/1-3
AD 111'96	Left mandible with alveoli i/1-2, p/1-3, and p/4, m/1-2
AD 167'96	Lot of upper molars
AD 168'96	Fragment of left mandible worn with p/3-4, m/1-3
AD 169'96	Lot of lower molars
AD 170'96	Right mandible with p/3-4, m/1-2
AD 171'96	Tibio-fibula
AD 172'96	Right mandible very worn with p/3-4, m/2-3
AD 173'96	Fragment of right mandible with alveoli p/1, and p/4 and roots p/2, m/1-3
AD 174'96	Fragment of right mandible with p/4, p/1
AD 175'96	Several mandible fragments
AD 176'96	Fragment of left mandible with roots p/3, alveoli p/4 and m/1-3
AD 177'96	Fragment of left mandible with m/2-3
AD 180'96	i/2 lower
AD 181'96	Left mandible with p/2-4, m/1-3
AD 181'96 bis	Fragment of right mandible with m/3
AD 182'96	Fragment of left mandible with alveoli i/1, i/2, c/1, p/1 and p/2-3
AD 183'96	Mandible
AD 200'96	Left mandible gypsified with p/3-p/4, m/1-m/2
AD 201'96	Right mandible with p/3-4, m/1-2
AD 202'96	Right mandible with p/3-4, m/1-3
AD 246'96	Mandible pulverised
AD 247'96	Mandible
AD 249'96	Fragment of left mandible with p/2-4
AD 307'96	Tibio-fibula right
AD 328'96	I2 left and 2 P1
AD 330'96	Fragment of mandible with m/2-3
AD 399'96	Upper digitated I/
AD 420'96	Fragment of right mandible with i/1, p/3-4
AD 421'96	Front of mandible with i/1-3, c/1
AD 422'96	2 upper I1/
AD 426'96	Associated upper P3-4/, M1/ left
AD 429'96	Fragment of mandible with p/3-4
AD 445'96	Tibio-fibula in matrix
AD 449'96	Distal humerus
AD 450'96	Fragment of left mandible young with m/1-2
AD 7'97	Left mandible with p/3-4, m/1-3
AD 8'97	Right mandible with p/3-4, m/1-3
AD 25'97	Lot of lower teeth
AD 51'97	Lot of upper teeth
AD 99'97	Fragment of left mandible with p/3-4, m/1-2
AD 100'97	Right maxilla with I1-3/, C/, P1-4/
AD 106'97	Fragment of left mandible with p/4, m/1-3
AD 107'97	Fragment of right mandible with p/3-4, m/1-2
AD 109'97	Lot of upper teeth
AD 110'97	i/1 lower right
AD 111'97	Fragment of left mandible with p/4, m/1
AD 112'97	Fragment of right mandible with m/1-2
AD 120'97	Fragment of left mandible with m/1-3
AD 174'97	Left mandible with p/2-4, m/1-3
AD 246'97	Tibio-fibula
AD 293'97	Fragment of left mandible with m/2 worn
AD 294'97	Fragment of left mandible with m/1-2
AD 302'97	Tibio-fibula
AD 368'97	Fragment of right mandible with p/4, m/1-2
AD 369'97	Fragment of maxilla with P4/, M1-2/
AD 372'97	i/2 lower right
AD 394'97	Fragment of left mandible with m/1-2
AD 577'97	Fragment of mandible with m/1-3
AD 578'97	Right mandible with p/3-4, m/1-3
AD 579'97	Right mandible with alveoli two incisors, c/1, p/1 and p/2-4, m/1-3
AD 580'97	Right mandible young with p/4, m/1-3
AD 581'97	Right mandible with p/3-4, m/1-2
AD 582'97	Fragment of mandible with 2 teeth in poor condition
AD 583'97	Fragment of left mandible quite worn with p/4, m/1
AD 584'97	Fragment of right mandible with p/3-4, m/1
AD 585'97	Fragment of right mandible with i/1, p/2-3 slightly worn
AD 586'97	Fragment of left mandible in poor condition with 2 teeth
AD 587'97	Fragment of right mandible, fresh with p/3-4
AD 588'97	I1/ upper right and P1/ upper (?)
AD 589'97	Ulnas
AD 729'97	Left mandible with p/3-4, m/1-2
AD 730'97	Left mandible with p/3-4, m/1-2
AD 749'97	Left mandible with p/3-4, m/1-3
AD 750'97	Left mandible with alveoli c/1, p/1-2, and i/1-2, p/3-4, m/1-2
AD 752'97	Fragment of right mandible with m/2-3
AD 870'97	Skull with P2-4/, M1-2/ right and P2/ left
AD 882'97	Right mandible with p/2-4, m/1-3
AD 883'97	Humerus
AD 885'97	Fragment of left mandible with alveoli of p/1, roots p/2 and p/3
AD 886'97	Fragment of mandible in poor condition

AD 887'97	Premaxilla with I1 /left
AD 895'97	I1/ upper right
AD 949'97	Right mandible with i, alveoli c/1, p/1 and p/2-4
AD 1000'97	Mandible preserved on a pebble
AD 17'98	Fragment of left mandible with p/3-4, m/1-2
AD 19'98	Upper molar
AD 124'98	Fragment of mandible with p/2-4, m/1
AD 129'98	Upper molar
AD 255'98	Tibio-fibula left
AD 256'98	Tibio-fibula left
AD 257'98	Fragment of left mandible with p/4, m/1-3
AD 258'98	Left mandible with alveoli of anterior teeth and p/3-4, m/1-3
AD 259'98	Right mandible with p/3-4, m/1-3
AD 260'98	Fragment of left mandible with p/4, m/1-3
AD 261'98	Fragment of right mandible with m/1-2
AD 262'98	Fragment of left mandible with p/4, m/1 (?)
AD 263'98	Fragment of left mandible with p/3-4, m/1-2
AD 264'98	Fragment of right mandible with p/4-m/1 and m/2 pulverised
AD 265'98	Right maxilla with P1-4/, M1-2/
AD 266'98	Calcaneum
AD 267'98	Lot of upper teeth
AD 268'98	Lot of lower teeth
AD 645'98	Right mandible with p/3-4, m/1-3 + front of mandible in matrix
AD 646'98	Mandible in matrix in poor condition
AD 647'98	Right mandible with i/2, p/2-4, m/1-3
AD 648'98	Right mandible with i/1-2, p/2-4, m/1-3
AD 649'98	Fragment of right mandible with alveoli c/1, p/1, p/2 and p/3-4, m/1-2
AD 650'98	Left mandible with edentulous front part and p/3-4, m/1-2
AD 651'98	Fragment of left mandible with p/3-4 fresh
AD 652'98	Left mandible with p/2-4, m/1-2
AD 653'98	Fragment of left mandible with alveoli p/2, and p/3-4, m/1
AD 654'98	Fragment of right mandible with p/4, m/1-3
AD 655'98	Fragment of left mandible quite worn with m/1-3
AD 656'98	Mandible broken
AD 657'98	Fragment of left mandible with p/3 unworn, p/4, m/1-3
AD 658'98	Fragment of left mandible with alveoli p/1-2, and p/3-4 and m/1 fragment
AD 659'98	Fragment of left mandible with p/4, m/1-3 + fgt md left with p/3-4
AD 660'98	Fragment of right mandible with p/3-4, m/1-2
AD 661'98	Fragment of mandible with p/3-4
AD 662'98	Small fragment of right mandible with p/3-4
AD 663'98	Upper I1-2/
AD 668'98	Fragment of right mandible with p/3-p/4, and m/1
AD 687'98	Fragment of left mandible broken with m/2
AD 46'99	Right mandible with alveoli of i/1-2, c/1, p/1-2, and p/3-4, m/1-3
AD 78'99	M1/ upper right
AD 97'99	Fragment of right mandible with p/3-4, m/1-2
AD 124'99	Fragment of right mandible with alveolus of p/1, and p/2-4, m/1
AD 149'99	Lot of upper teeth
AD 150'99	Lot of lower teeth
AD 151'99	I1/ upper left
AD 327'99	Left mandible with i/1-2, p/2-4, m/1-3 + portion of ascending ramus
AD 328'99	Left mandible with alveoli i/2-3, c/1, p/1-2 and p/3-4, m/1-3
AD 329'99	Right mandible with bases i/1-2, p/2-4, m/1
AD 330'99	Right mandible with alveoli i/1-3, c/1, p/1 and p/2-4, m/1-3
AD 331'99	Right mandible juvenile with p/2-4, m/1-2
AD 332'99	Right mandible with p/3-4, m/1-3
AD 333'99	Fragment of right mandible with p/4, m/1-2
AD 334'99	Fragment of right mandible with p/4, m/1-2
AD 335'99	Fragment of right mandible with p/4, m/1-2
AD 336'99	Front of mandible with alveoli i/1-3, c/1, p/1-2 and p/3
AD 337'99	Fragment of right mandible with m/1-3 (m/3 slightly worn)
AD 338'99	Fragment of left mandible with m/1-2
AD 339'99	Fragment of left mandible with alveoli p/4, and m/3
AD 388'99	Fragment of right mandible with m/3
AD 503'99	Tibio-fibula distal
AD 672'99	Left mandible with ascending ramus, gonion, p/3-4, m/1-2
AD 673'99	Fragment of right mandible with p/3-4, m/1-2
AD 674'99	Right mandible with p/2-4, m/1
AD 675'99	Fragment of right mandible with p/3-4, m/1 broken
AD 676'99	Fragment of right mandible with p/4, m/1-3
AD 677'99	Right maxilla with P3-P4/, M1-2/
AD 678'99	Fragment of left mandible with p/3-4, m/1-3
AD 683'99	Fragment of left mandible with p/4, m/1-3
AD 685'99	Calcaneum
AD 687'99	Fragment of right mandible with m/1
AD 688'99	Fragment of left mandible with p/3-4, m/1-3
AD 696'99	Fragment of left maxilla with P4/, M1/
AD 712'99	Fragment of maxilla young adult with M1-2/
AD 717'99	Astragalus
AD 718'99	Tibio-fibula distal
AD 719'99	Fragment of left mandible with p/3-4
AD 720'99	Fragment of left mandible with m/1-2 (?)
AD 721'99	Fragment of left mandible with m/2-3
AD 722'99	Fragment of left mandible with p/3-4, m/1-2
AD 776'99	Lot of upper incisors
AD 854'99	I1/ upper left
AD 857'99	Fragment of left mandible with m/1-3
AD 25'00	Front of right mandible with alveoli of i/1-3, c/1, p/1 and p/2 in place
AD 34'00	Fragment of right mandible with p/3-4, m/1
AD 35'00	Lot of lower teeth
AD 36'00	4 upper teeth
AD 40'00	Fragment of left mandible with m/1-2
AD 41'00	Distal phalanx
AD 93'00	½ right mandible in block
AD 349'00	Right mandible with p/3-4, m/1-3
AD 641'00	Lot of upper teeth
AD 642'00	Lot of lower teeth
AD 643'00	Fragment of right mandible with p/3-4, m/1-2
AD 644'00	Fragment of left mandible with p/3-4, m/1-3
AD 645'00	Left mandible with alveoli of i/1-3, c/1, p/1 and p/2-4, m/1-2
AD 646'00	Fragment of right mandible with p/4, m/1-3
AD 647'00	Fragment of right mandible with m/1-3
AD 648'00	Fragment of left mandible with p/4-m/1-3
AD 649'00	Fragment of left mandible with p/3-4, m/1-3
AD 650'00	Fragment of right mandible with p/4, m/1-2
AD 651'00	Fragment of left mandible with p/4, m/1-3
AD 652'00	Front of mandible edentulous with alveoli of i/1-3, c/1, p/1-3
AD 653'00	Left mandible in two pieces with p/3-4, m/1-3
AD 654'00	Front of left mandible with alveoli of i/1-3, c/1, p/1 and p/2-4
AD 655'00	Fragment of right mandible with p/3-4
AD 656'00	Fragment of right mandible pulverised
AD 657'00	Fragment of maxilla with P3-4/, M1-2/
AD 658'00	Fragment of right mandible with m/1-2
AD 659'00	Fragment of left mandible with alveoli p/2 and p/3 in place
AD 660'00	Fragment of mandible with p/3-4
AD 661'00	Fragment of left mandible with p/3-4
AD 662'00	Fragment of right mandible with p/3-4, m/1-2
AD 663'00	Fragment of right mandible with m/3
AD 664'00	Fragment of left mandible pulverised with p/3-4
AD 665'00	Right maxilla with P2-4/, M1-2/
AD 666'00	Fragment of mandible de *Miorhynchoncyon* with p/4, m/1-2
AD 667'00	Distal humerus
AD 668'00	Tibio-fibula distal
AD 669'00	Tibio-fibula distal
AD 670'00	Tibio-fibula distal
AD 671'00	Tibio-fibula distal
AD 672'00	3 fragments of tibio-fibula distal
AD 674'00	Upper I1/, i/2 lower + 1 unidentified tooth
AD 675'00	Condyle of mandible ?
AD 725'00	Metapodial
AD 726'00	Mandible
AD 729'00	Fragment of right mandible with p/4-m/1

Table 1 : Lower p/2 of *Myohyrax oswaldi*

Specimen	Mesio-distal length	Labio-lingual breadth
Holotype Andrews	1.7	1.1
AD 568'94	1.71	0.75
AD 181'96	1.95	0.74
AD 249'96	1.58	0.99
AD 174'97	1.77	0.62
AD 585'97	1.87	0.59
AD 882'97	1.83	0.52
AD 949'97	1.86	0.61
AD 647'98	1.73	0.6
AD 652'98	1.7	0.74
AD 124'99	1.82	0.56
AD 674'99	1.64	0.57

Table 2 : Lower p/3 of *Myohyrax oswaldi*

Specimen	Md length	Trigonid md	Talonid md	Trigonid breadth	Talonid breadth
Holotype Andrews	3.1			1.3	
AD 568'94	2.85	1.55	134	1.03	1.11
AD 168'96	2.87	1.51	1.5	0.9	0.97
AD 170'96	2.85	1.49	1.33	1.09	1.26
AD 172'96	2.54	1.29	1.3	1.19	1.18
AD 181'96	2.81	1.36	1.51	1.15	1.26
AD 182'96	2.85	1.35	1.54	0.92	1.09
AD 200'96	2.86	1.45	1.49	1.01	1.14
AD 201'96	2.83	1.42	1.32	1.08	1.03
AD 202'96	2.69	1.3	1.36	0.87	0.95
AD 249'96	2.76	1.42	1.38	1.1	1.05
AD 7'97	2.66	1.36	1.27	0.98	1.14
AD 8'97	2.76	1.42	1.34	1.18	1.17
AD 99'97	2.58	1.06	1.35	0.77	0.79
AD 107'97	2.87	1.5	1.36	1.13	1.23
AD 174'97	2.8	1.49	1.3	1.03	1.21
AD 578'97	2.8	1.35	1.47	0.97	0.93
AD 579'97	1.66	0.8	0.66	0.57	0.62
AD 581'97	2.77	1.54	1.21	0.91	1.1
AD 584'97	2.59	1.48	1.13	1.12	1.38
AD 585'97	2.67	1.47	1.21	1.25	1.08
AD 587'97	3.05	1.56	1.53	1.18	1.15
AD 729'97	2.58	1.4	1.1	1.04	0.98
AD 749'97	2.52	1.42	0.97	0.87	1.08
AD 750'97	2.75	1.46	1.28	1.36	1.33
AD 882'97	2.83	1.56	1.4	1.03	1.08
AD 885'97	2.23	1.1	1.1	0.96	0.88
AD 949'97	2.88	1.47	1.43	1.09	1.28
AD 17'98	2.58	1.29	1.22	1.02	1.13
AD 647'98	2.66	1.41	1.22	1.01	1.22
AD 648'98	2.88	1.55	1.35	1.25	1.25
AD 649'98	2.74	1.49	1.15	0.92	1.03
AD 650'98	2.81	1.35	1.39	1.08	1.2
AD 652'98	2.61	1.38	1.18	0.74	1.22
AD 653'98	2.51	1.3	1.22	0.81	1.01
AD 657'98	2.99	1.5	1.51	1.13	1.2
AD 658'98	2.57	1.39	1.08	0.98	1.01
AD 668'98	2.66	1.32	1.31	0.83	0.82
AD 46'99	2.84	1.54	1.31	1.08	1.22
AD 97'99	2.64	1.42	1.23	1.01	1.13
AD 124'99	2.72	1.53	1.24	0.88	1.09
AD 328'99	2.97	1.47	1.33	1.03	1.16
AD 332'99	2.82	1.53	1.28	1.19	1.29
AD 672'99	2.63	1.49	1.22	1.15	1.37
AD 673'99	2.65	1.2	1.39	0.93	1.03
AD 674'99	2.9	1.31	1.67	1	1.23
AD 675'99	2.8	1.39	1.41	0.98	1.05
AD 678'99	2.79	1.37	1.33	0.98	1.14
AD 688'99	2.8	1.52	1.45	1.08	1.29
AD 722'99	2.56	1.28	1.28	1.1	1.16

Table 3 : Lower p/4 of *Myohyrax oswaldi*

Specimen	Md	Md trig	Md tal	Breadth
Holotype Andrews	3.5			1.8
AD 110'96	2.92	1.51	1.47	1.06
AD 111'96	2.93	1.59	1.41	1.75
AD 168'96	3.41	1.55	1.87	1.46
AD 170'96	3.09	1.54	1.57	1.57
AD 172'96	2.85	1.36	1.4	1.63
AD 173'96	3	1.42	1.58	1.73
AD 174'96	2.93	1.37	1.55	1.77
AD 181'96	3.13	1.46	1.68	1.71
AD 200'96	3.19	1.43	1.71	1.57
AD 201'96	3.12	1.42	1.71	1.45
AD 202'96	3.28	1.7	1.63	1.44
AD 249'96	3.18	1.52	1.65	1.3
AD 429'96	3.24	1.65	1.57	1.41
AD 7'97	2.86	1.54	1.46	0.98
AD 8'97	3.08	1.58	1.44	1.54
AD 99'97	3.04	1.48	1.43	1.34
AD 107'97	3.21	1.56	1.64	1.56
AD 111'97	3.1	1.41	1.64	1.24
AD 174'97	2.93	1.58	1.31	1.5
AD 368'97	2.76	1.29	1.42	1.43
AD 578'97	3.05	1.34	1.53	1.29
AD 579'97	2.57	1.34	1.13	0.91
AD 580'97	2.99	1.51	1.46	1.42
AD 581'97	3.45	1.86	1.58	1.44
AD 583'97	3.26	1.69	1.57	1.72
AD 584'97	2.92	1.52	1.42	1.46
AD 587'97	3.37	1.65	1.75	1.61
AD 729'97	3.26	1.61	1.61	1.42
AD 730'97	3.19	1.49	1.57	1.44
AD 749'97	2.94	1.43	1.48	1.37
AD 750'97	3.12	1.49	1.66	1.64
AD 882'97	3.04	1.47	1.61	1.55
AD 949'97	3.41	1.77	1.6	1.49
AD 17'98	2.82	1.39	1.43	1.43
AD 257'98	3.02	1.58	1.56	1.43
AD 264'98	2.97	1.53	1.46	1.47
AD 647'98	3.06	1.51	1.56	1.52
AD 648'98	3.13	1.41	1.6	1.65
AD 649'98	3.14	1.64	1.52	1.44
AD 650'98	3.07	1.51	1.57	1.49
AD 652'98	2.94	1.4	1.49	1.37
AD 653'98	2.93	1.43	1.5	1.3
AD 657'98	3	1.51	1.47	1.48
AD 658'98	2.89	1.4	1.54	1.5
AD 659'98	2.77	1.49	1.31	1.48
AD 668'98	2.85	1.45	1.36	1.22
AD 46'99	3.04	1.53	1.44	1.36
AD 97'99	2.79	1.5	1.3	1.5
AD 124'99	2.93	1.5	1.45	1.3
AD 328'99	3.36	1.68	1.64	1.63
AD 332'99	3.08	1.6	1.53	1.72
AD 333'99	2.8	1.51	1.31	1.53
AD 334'99	3	1.39	1.64	1.29
AD 672'99	2.98	1.5	1.48	1.62
AD 673'99	2.92	1.34	1.54	1.38
AD 674'99	3.13	1.5	1.61	1.5
AD 675'99	3.07	1.41	1.64	1.39
AD 676'99	3.03	1.46	1.55	1.33
AD 678'99	3.19	1.58	1.57	1.41
AD 688'99	3.27	1.59	1.65	1.61
AD 722'99	2.97	1.52	1.46	1.65

Table 4 : Lower m/1 of *Myohyrax oswaldi*

Specimen	Md length	Breadth
Holotype Andrews	3.1	2
AD 110'96	3.18	1.53
AD 111'96	3.16	1.99
AD 168'96	3.22	1.66
AD 170'96	3.3	1.93
AD 174'96	3.15	1.99
AD 176'96	2.96	1.72
AD 181'96	3	2.04
AD 200'96	3.01	1.71
AD 201'96	3.35	1.72
AD 202'96	3.51	1.78
AD 450'96	3.35	1.35
AD 7'97	2.87	1.69
AD 8'97	2.93	1.82
AD 99'97	3.28	1.54
AD 106'97	3	1.66
AD 107'97	3.28	1.59
AD 111'97	2.97	1.59
AD 112'97	2.62	1.43
AD 120'97	3.16	1.59
AD 174'97	3.02	1.88
AD 294'97	2.94	1.66
AD 368'97	2.94	1.8
AD 394'97	2.76	1.66
AD 578'97	3.51	1.72
AD 579'97	3.04	1.32
AD 580'97	3.01	1.61
AD 581'97	3.44	1.68
AD 583'97	3.49	2.02
AD 584'97	3.16	1.86
AD 729'97	3.27	1.72
AD 730'97	3.24	1.56
AD 749'97	2.98	1.7
AD 750'97	3.13	2.08
AD 882'97	3.24	1.68
AD 17'98	2.78	1.63
AD 257'98	2.94	1.79
AD 264'98	3.13	2.01
AD 647'98	3.07	1.73
AD 648'98	2.93	1.89
AD 649'98	3.39	1.72
AD 650'98	2.93	1.67
AD 652'98	2.8	1.68
AD 653'98	2.8	1.62
AD 655'98	2.75	1.42
AD 657'98	2.98	1.81
AD 659'98	2.89	1.83
AD 668'98	2.87	1.63
AD 46'99	3.09	1.74
AD 97'99	2.84	1.69
AD 124'99	2.77	1.54
AD 328'99	3.14	1.86
AD 332'99	2.98	1.92
AD 333'99	2.97	1.79
AD 388'99	3.14	1.71
AD 672'99	2.9	1.99
AD 673'99	3.11	1.72
AD 674'99	3.32	1.71
AD 676'99	3.22	1.61
AD 678'99	3.16	1.65
AD 688'99	3.1	1.97
AD 722'99	2.85	1.86

Table 5 : Lower m/2 of *Myohyrax oswaldi*

Specimen	Md length	Breadth
AD 110'96	2.64	1.4
AD 111'96	3.01	1.95
AD 168'96	3.02	1.48
AD 170'96	2.85	1.71
AD 176'96	2.91	1.74
AD 181'96	2.85	1.94
AD 200'96	2.79	1.62
AD 202'96	3.21	1.53
AD 330'96	2.91	1.33
AD 450'96	2.8	1.36
AD 7'97	2.68	1.5
AD 8'97	2.75	1.38
AD 99'97	2.91	1.37
AD 106'97	2.79	1.51
AD 120'97	3.04	1.43
AD 174'97	2.61	1.74
AD 193'97	2.49	1.55
AD 294'97	2.8	1.57
AD 368'97	2.67	1.48
AD 394'97	2.73	1.66
AD 578'97	3.17	1.51
AD 579'97	2.72	1.52
AD 580'97	2.84	1.47
AD 581'97	3.37	1.61
AD 729'97	2.93	1.52
AD 730'97	3.06	1.42
AD 749'97	2.73	1.6
AD 750'97	2.77	1.77
AD 752'97	2.34	1.27
AD 882'97	2.91	1.6
AD 17'98	2.43	1.46
AD 257'98	2.65	1.64
AD 647'98	2.76	1.59
AD 648'98	2.77	1.83
AD 649'98	2.81	1.44
AD 650'98	2.66	1.57
AD 652'98	2.65	1.51
AD 655'98	2.44	1.31
AD 657'98	2.79	1.7
AD 659'98	2.72	1.74
AD 668'98	2.64	1.42
AD 46'99	2.83	1.5
AD 97'99	2.79	1.62
AD 328'99	3.02	1.66
AD 332'99	2.78	1.65
AD 333'99	2.67	1.75
AD 388'99	2.98	1.6
AD 672'99	2.75	1.93
AD 673'99	2.63	1.41
AD 676'99	2.91	1.59
AD 678'99	2.78	1.51
AD 688'99	2.77	1.8
AD 722'99	2.45	1.68

Table 6 : Upper P2/ of *Myohyrax oswaldi*

Specimen	Md length	Breadth
PQ AD 3030	2.06	1.68
AD 100'97	1.95	1.76
AD 870'97	2.07	1.48
AD 265'98	2.18	1.44
AD 661'00t	1.85	1.42
AD 665'00	2.07	1.49

Table 7 : Upper P3/ of *Myohyrax oswaldi*

Specimen	Md length	Breadth
PQ AD 3030	3.01	1.68
AD 100'97	2.77	2.29
AD 870'97	3.28	1.87
AD 265'98	2.78	2.01
AD 677'99	2.9	1.79
AD 665'00	3.15	2.16
AD 661'00u	2.84	1.58

Table 8 : Upper P4/ of *Myohyrax oswaldi*

Specimen	Md length	Breadth
PQ AD 3030	3.03	2.61
PQ AD 2578	2.97	2.58
AD 100'97	2.95	2.78
AD 369'97	2.93	2.15
AD 870'97	3.08	2.22
AD 265'98	3.13	2.36
AD 677'99	3.2	2.17
AD 696'99	3.32	2.05
AD 665'00	3.18	2.4
AD 641'00g	3.36	2.37
AD 641'00h	3.19	2.43
AD 641'00i	3.58	2.26
AD 641'00j	3.55	1.96
AD 641'00k	3.08	2.35
AD 641'00l	2.5	1.79
AD 641'00m	3.36	1.93
AD 641'00n	3	2.15
AD 641'00o	3.09	1.75
AD 641'00p	3.07	1.88
AD 641'00q	3.09	1.95
AD 641'00r	2.92	2.53
AD 641'00s	2.96	2.2

Table 9 : Upper M1/ of *Myohyrax oswaldi*

Specimen	Md length	Breadth
PQ AD 3030	3.18	2.7
PQ AD 2578	2.57	2.13
AD 369'97	3.03	2.36
AD 870'97	3.18	2.49
AD 265'98	3.01	2.59
AD 677'99	3.07	2.49
AD 696'99	3.29	2.68
AD 712'99	3.3	2.36
AD 665'00	3.32	2.54
AD 641'00a	2.95	2.56
AD 641'00b	3.13	2.35
AD 641'00c	2.79	2.47
AD 641'00d	2.79	2.45
AD 641'00e	3.46	2.26
AD 641'00f	3.18	3.06

Table 10 : Upper M2/ of *Myohyrax oswaldi*

Specimen	Md length	Breadth
PQ AD 3030	2.67	2.18
AD 369'97	2.63	1.79
AD 870'97	2.85	1.9
AD 265'98	2.76	2.04
AD 677'99	2.73	2.03
AD 712'99	2.76	2
AD 665'00	2.7	1.93

Table 11 : Length of the lower cheek teeth of *Myohyrax* (after Butler, 1984)

		Lower p/3			Lower p/4			Lower m/1			Lower m/2		
M. oswaldi													
	Chamtwara	4	2.6-3.1	2.8	5	3.0-3.6	3.3	7	3.1-3.6	3.36	5	2.7-3.1	2.9
	Songhor				1	3.4		1	3.1		1	3	
	Mfwangano				1	3		1	3.2		1	3	
	Rusinga	4	2.7-3.1	2.9	11	3.0-3.5	3.24	13	3.0-3.5	3.26	13	2.7-3.0	2.88
	Karungu	9	2.6-3.1	2.91	23	3.1-3.6	3.34	17	3.0-3.6	3.27	17	2.7-3.2	2.91
	Fort Ternan										1	2.9	
M. doederleini													
	(Stromer 1926)	1	2.3		2	2.6, 3.0		1	2.9		2	2.5, 2.6	
	Napak	1	2.4		1	2.9		1	3.2		1	2.7	

Table 12 : Measurements of the teeth of *Miorhynchocyon* (after Butler, 1984)

	Lower p/4						Lower m/1						Lower m/2		
	Length			Breadth			Length			Breadth			Length		
	N	variation	m	N	variation	m	N	variation	m	N	variation	m	N	variation	m
M. clarki	5	3.6-3.8	3.68	4	1.8-2.2	2	12	3.0-3.5	3.27	8	1.8-2.2	2.08	7	2.2-2.8	2.51
cf. *M. clarki*	4	4.0-4.5	4.33	5	2.2-2.5	2.34	1	3.4		2	2.3-2.4	2.35	3	2.5-2.9	2.77
M. rusingae	1	5.1		1	2.6		3	4.1-4.7	4.5	3	2.8-3	2.93	1	3.65	

Table 13 : Distal tibio-fibula of Macroscelididae from Arrisdrift

	Md length	AP width
PQ AD 196	60	32
PQ AD 1368	67	38
PQ AD 2310	53	27
PQ AD 2554	56	28
PQ AD 3250	52	25
AD 171'96	58	32
AD 307'96	50	25
AD 246'97	55	27
AD 302'97	58	30
AD 255'98	57	28
AD 256'98	55	30
AD 503'99	54	25
AD 718'99	52	26
AD 668'00	53	27
AD 669'00	53	26
AD 670'00	57	27
AD 671'00	55	26

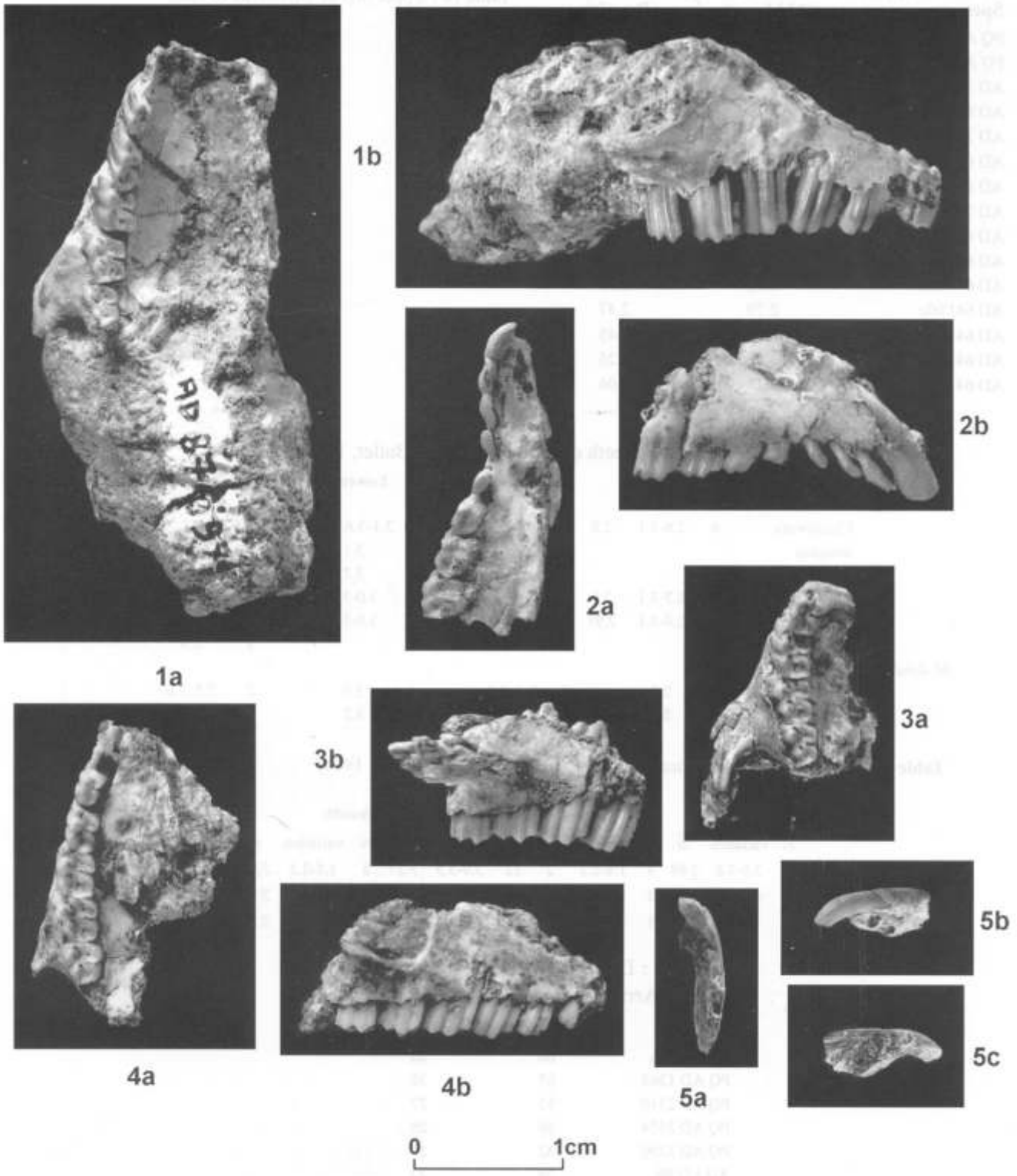

Plate I: Maxillae of *Myohyrax oswaldi* (a : occlusal view (x), b : labial view (x 3), c : lingual view (x 3)).
Figure 1 : Maxilla AD 870'97 with P2/-P4/, M1/-M2/ right and P2/ left.
Figure 2 : right maxilla AD 100'97 with I1/-I3/, C/, P1/-P4/.
Figure 3 : maxilla AD 677'99 with P3/-P4/, M1/-M2/.
Figure 4: right maxilla with P1/-P4/, M1/-M2/.
Figure 5 : left premaxilla AD 887'97 with I1/ in place and alveoli I2/-I3/.

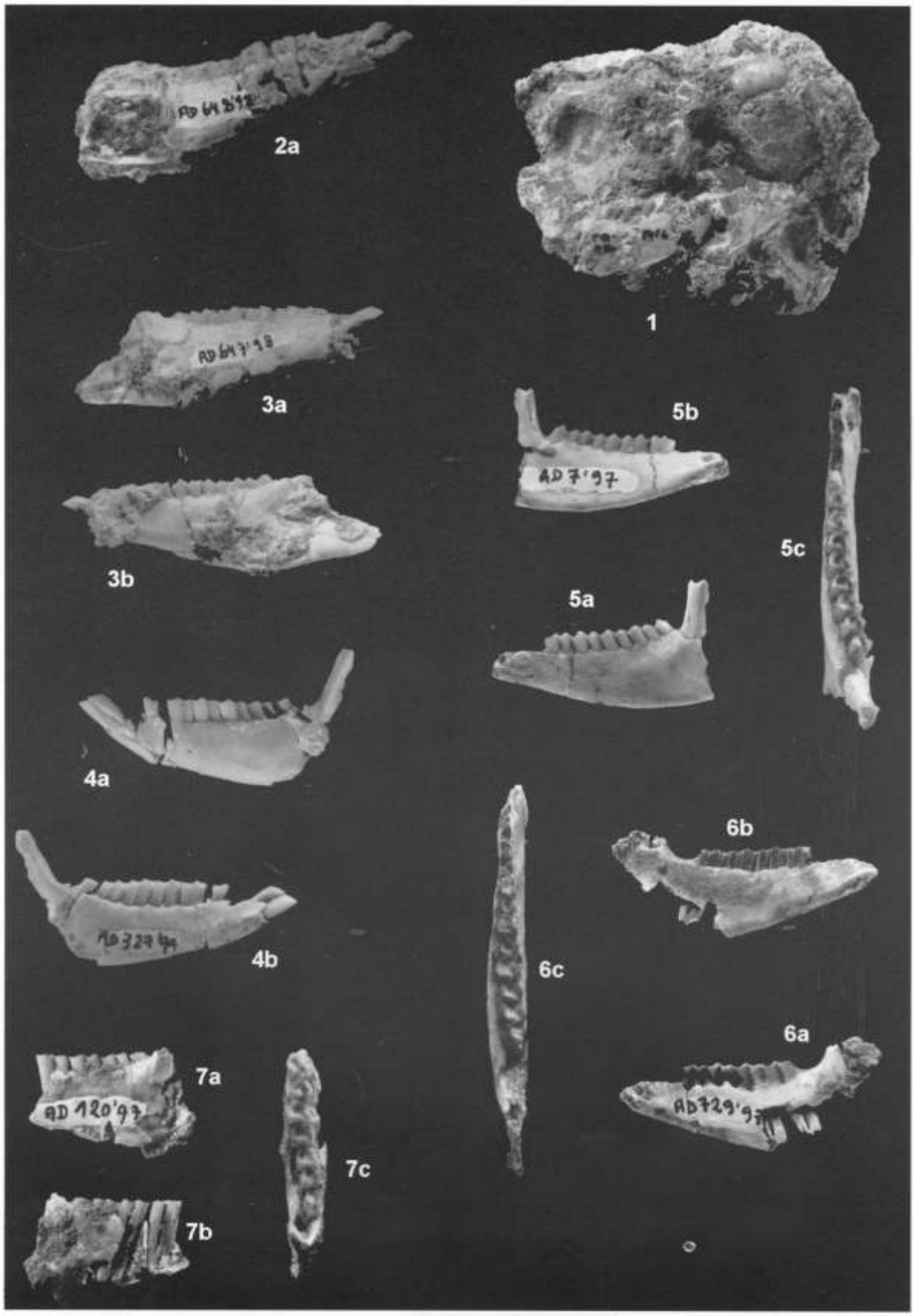

Plate II: Mandibles of *Myohyrax oswaldi* (a : labial view (x 2) ; b : lingual view (x 2) ; c : occlusal view (x 3))
Figure 1 : mandible PQ AD 1416 in its block of breccia (x 1,5);
Figure 2 : right mandible AD 648'98 with i/1-i/2, p/2-p/4, m/1-m/3.
Figure 3 : right mandible AD 647'98 with i/2, p/2-p/4, m/1-m/3.
Figure 4 : left mandible AD 327'99 with /1-i/2, p/2-p/4, m/1-m/3.
Figure 5 : left mandible AD 7'97 with p/3-p/4, m/1-m/3.
Figure 6 : left mandible AD 729'97 with p/3-p/4, m/1-m/2.
Figure 7 : left mandible AD 120'97 with m/1-m/3.

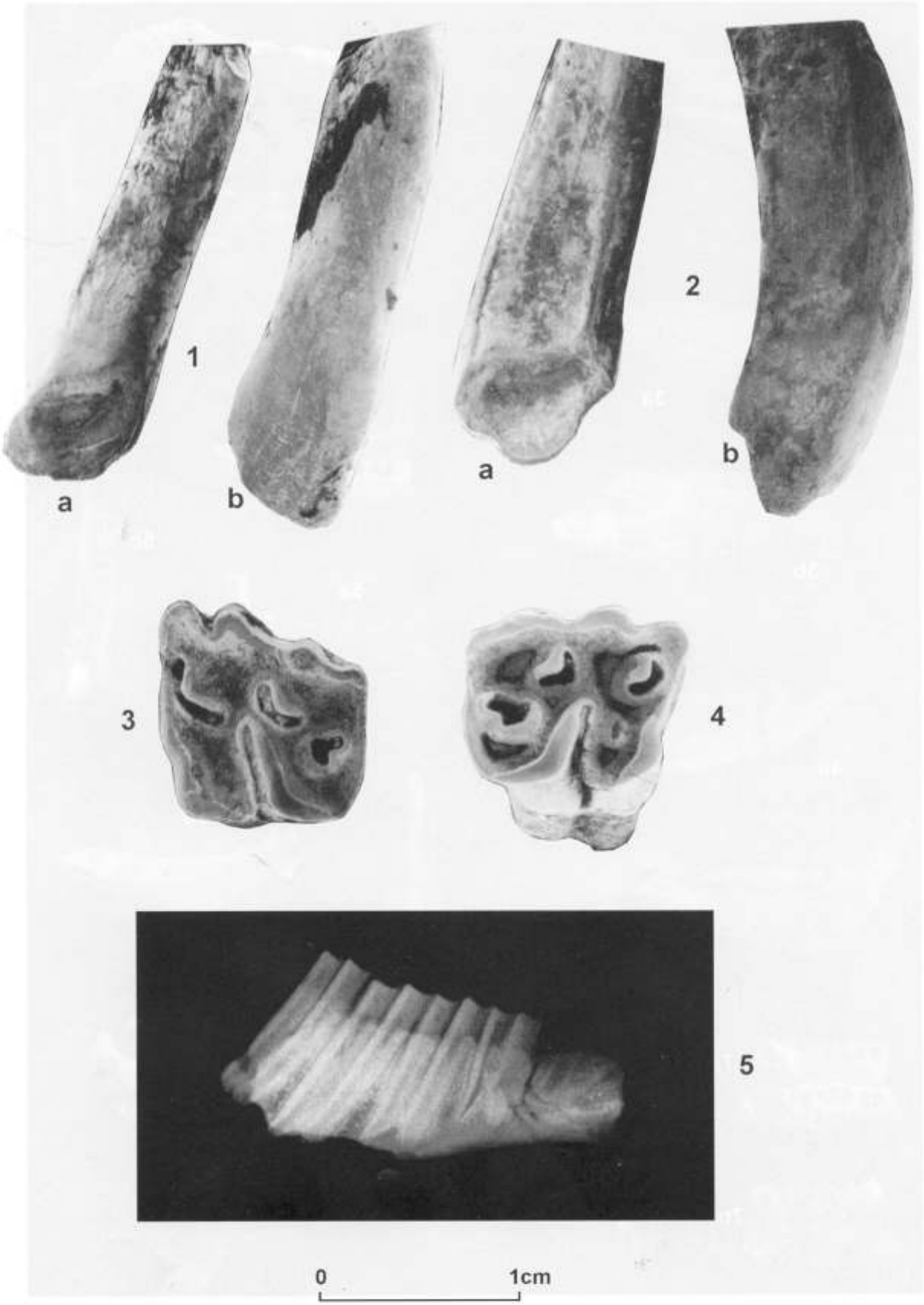

Plate III: Teeth of *Myohyrax oswaldi*.
Figure 1 : I1/ right AD 895'97, (a : lingual view (x 15) , b : labial view (x 15)).
Figure 2 : I1/ right AD 588'97 (a : lingual view (x 15) , b : labial view (x 15)).
Figure 3 : AD 91'95, M1/ left, occlusal view (x 15).
Figure 4 : AD 91'95, P4/ right, occlusal view (x 15).
Figure 5 : X-ray of teratologic mandible AD 170'96 showing the supernumerary tooth stuck to the base of the m/2 (x 4).

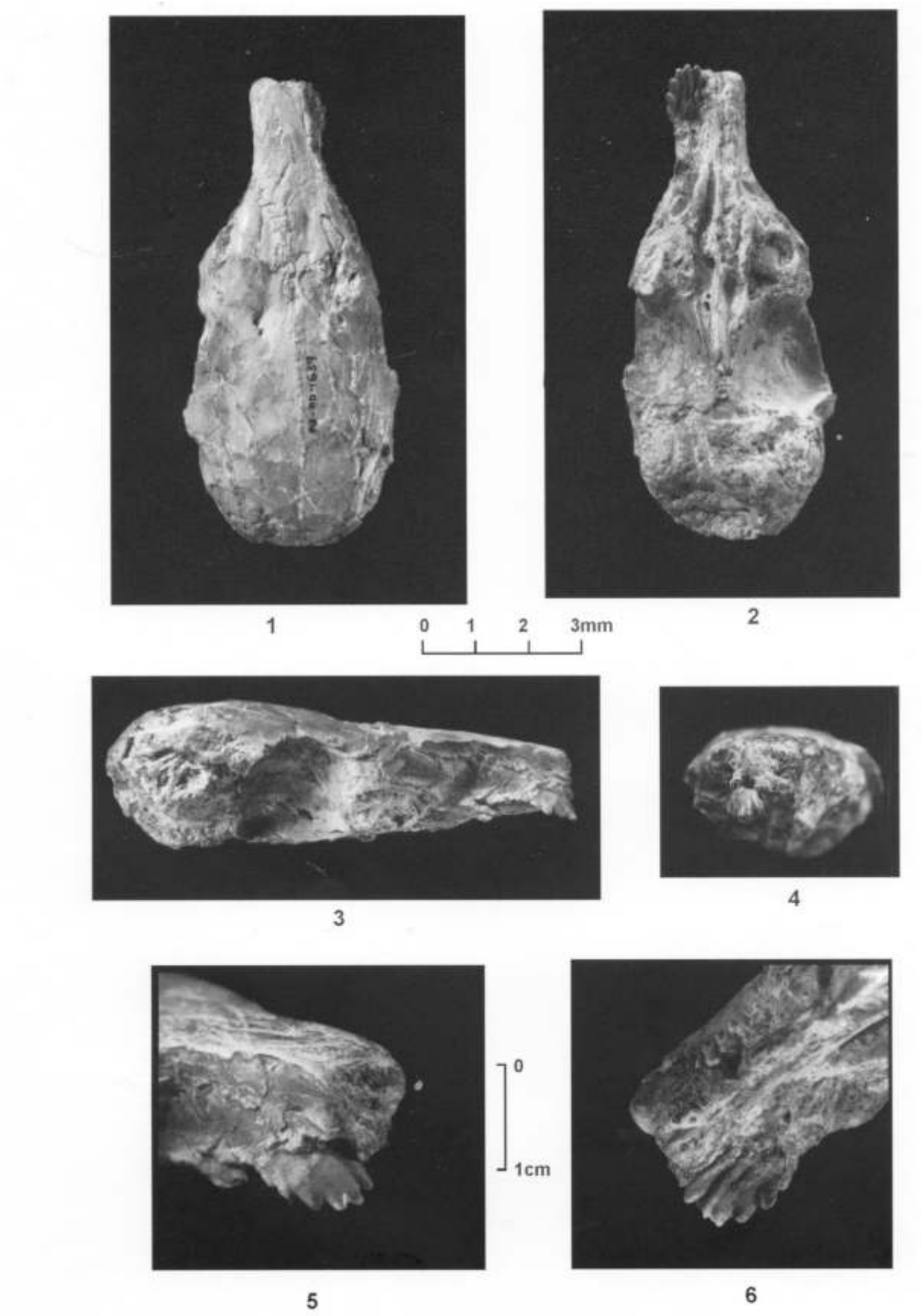

Plate IV: Skull attributed to cf *Miorhynchocyon gariepensis* PQ AD 1639.
Figure 1 : superior view.
Figure 2 : inferior view.
Figure 3 : right lateral view.
Figure 4 : anterior view.
Figure 5 : detail of the digitate I1/ in lateral view.
Figure 6 : detail of the digitate I1/ in lingual view.