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**GEOLOGY AND PALAEOBIOLOGY OF THE CENTRAL AND  
SOUTHERN NAMIB**

**VOLUME 2:  
PALAEOONTOLOGY OF THE ORANGE RIVER VALLEY,  
NAMIBIA**

by

**Martin Pickford and Brigitte Senut**



*Orangemeryx hendeyi*

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## The Pedetidae from the Miocene site of Arrisdrift (Namibia)

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The fossil springhares from the Miocene of the Orange River (Namibia) are well represented at Arrisdrift but there is only one specimen from older strata at Auchas Mine. At Arrisdrift it is known by dental and postcranial material which is comparable to the East African genus *Megapedetes*. Two new species are identified, a larger one *Megapedetes gariensis* and a smaller one *M. pickfordi* (smaller by 25% than *M. gariensis*) both of which are smaller than the type species *M. pentadactylus* from Kenya and Uganda. It is the first time that two species of *Megapedetes* have been found together in a single site.

### Version abrégée française

Les Pedetidae fossiles de Namibie ont été classiquement attribués au genre *Parapedetes*, décrit pour la première fois dans des dépôts fluvio-lacustres miocènes du nord de la Sperrgebiet (Stromer, 1924, 1926). Toutefois, les localités du Miocène inférieur et moyen de la vallée de l'Oranje ont livré une faune riche de Pedetidae qui peuvent être rapprochés au niveau générique de *Megapedetes* connu dans des sites comme Songhor au Kenya (MacInnes, 1957; Lavocat & Michaux, 1966). Deux nouvelles espèces provenant de couches du Miocène moyen à Arrisdrift sont décrites (Pickford *et al.*, 1996). Une phalange isolée provenant de niveaux du Miocène inférieur à Auchas Mine est attribuée au même genre, mais son identification spécifique n'est pas certaine.

Pour la première fois, deux espèces de *Megapedetes* sont décrites dans le même site. Le - genre était connu auparavant sur le site d'Arrisdrift (Senut, 1997), mais il est mieux connu dans les dépôts est-africains (Denys & Jaeger, 1992; Ishida & Ishida, 1982; Lavocat, 1977; MacInnes, 1957, 1962; Winkler, 1992) et il a été signalé en Afrique du nord, en Turquie, à Chios en Grèce et au Moyen-Orient (Batic & Fejfar, 1990; Lavocat, 1961; Sen, 1977; Tobien, 1968; Wood & Goldsmith, 1968). Le genre a donc été très largement répandu en Afrique et dans les basses latitudes de l'Europe et au Moyen-Orient.

### Introduction

The fossil spring hares of Namibia were classically attributed to *Parapedetes*, first described from fluvio-lacustrine deposits of the Northern Sperrgebiet (Stromer, 1924, 1926). However, early Miocene and basal Middle Miocene localities in the Orange River Valley have yielded a rich pedetid fauna which compares favourably at the generic level with *Megapedetes* from sites such as Songhor, Kenya (MacInnes, 1957; Lavocat & Michaux, 1966). Two new species are described from Middle Miocene strata at Arrisdrift (Pickford *et al.*, 1996). An isolated phalanx from Auchas Mine, slightly older than Arrisdrift (Pickford *et al.*, 1995; Pickford & Senut, 1999) is attributed to the same genus, but its specific identification is not certain.

### Systematic Descriptions

#### Order Rodentia Bowdich, 1821

#### Genus *Megapedetes* MacInnes, 1957

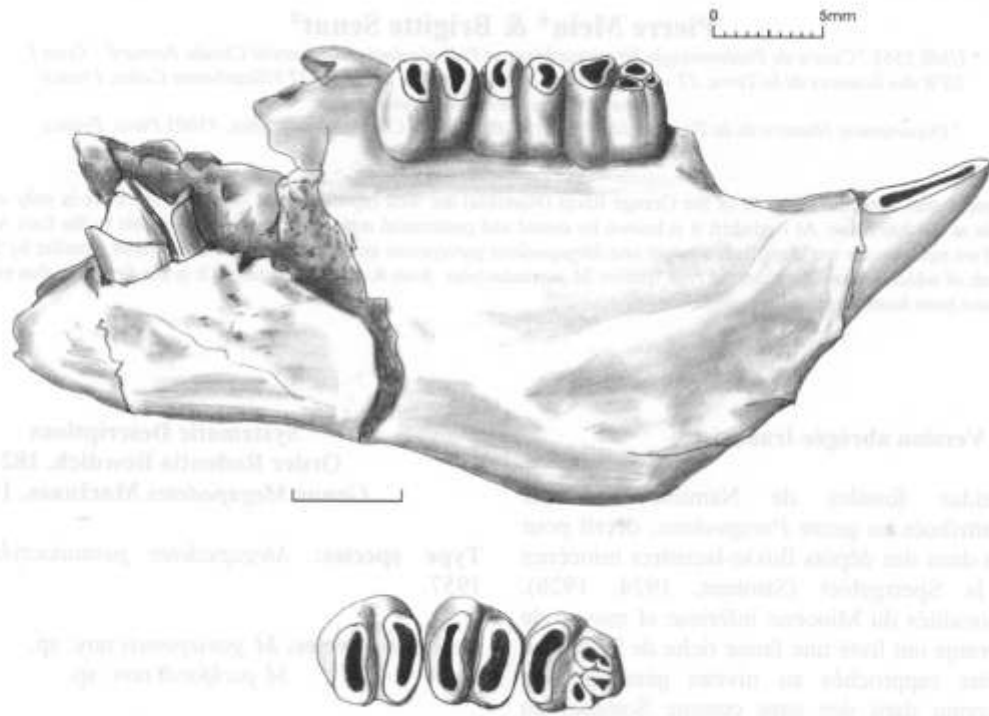
**Type species:** *Megapedetes pentadactylus* MacInnes, 1957.

**Referred species:** *M. gariensis* nov. sp.  
*M. pickfordi* nov. sp.

**Original diagnosis of the genus:** "A large pedetid in which the cheek-teeth were of limited growth, each with a median transverse fold not extending throughout the whole vertical height of the crown; hind foot with fully developed hallux."

**Emended generic diagnosis:** Large Pedetidae with weak hypsonty; height of the crown always less than twice the mesiodistal length; cheek teeth with short roots, more or less fused together. Not noted by MacInnes : dental morphology varies with age, the juvenile teeth show a median valley between the two transverse crests which, on the lateral surfaces, form grooves called stria (following the nomenclature of Stirton for the Castoridae). These grooves are moderately unequal; quite short, they tend to disappear as the teeth wear down. There is no cement in the cheek teeth. In the upper cheek teeth, the mesostria (labial groove) is larger than the hypostria (lingual groove); in the lower cheek teeth, the mesostriid (lingual groove) is slightly larger than the hypostriid (labial groove). In the lower molars, the two roots are elongated transversely, the anterior one being narrower than the posterior one. The upper molars possess a more or less bifid root but with the lingual wall always continuous. The ventral surface of the maxilla is flat and the gutter surrounding the incisive foramen (or anterior palatine foramen) present in the other genera of Pedetidae is completely absent. The premaxillo-maxillary suture forms a slight arc concave towards the rear on the ventral (or palatine) surface. The anterior palatine foramina are separated in front and coalesce at the back.

Regarding the skeletal elements, the bones are generally more robust than those of *Pedetes* and *Parapedetes*. The depression for the insertion of the *ligamentum teres* is well developed. The greater trochanter projects less proximally above the



**Figure 1:** AD 410'00, *Megapedetes gariepensis* sp. nov. paratype left mandible, lingual and occlusal views. (Scale bar = 5 mm).

femoral head than in *Pedetes* and is thicker in its median part than in the latter, but more than in *Parapedetes*. The anterior talar facet of the calcaneum is

very salient, being different from *Pedetes* and *Parapedetes*. We also note the presence of a 1<sup>st</sup> metatarsal, as in *M. pentadactylus*, but different from *P. laetoliensis* and extant Pedetidae.

**Species *Megapedetes gariepensis* nov.**  
(Tables 1,2,3)

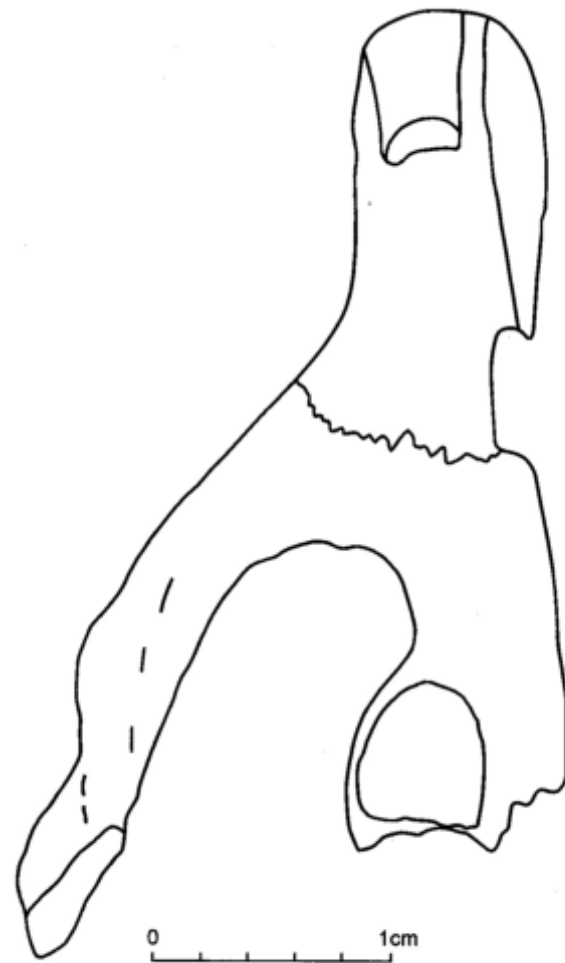
**Holotype:** Right mandible AD 407'97 with I, P<sub>4</sub>, M<sub>2</sub>, M<sub>3</sub>. (Pl. 1, Fig. 1)

**Paratypes:** AD 333'98, fragmentary right upper jaw with pre-maxilla, maxilla, I, alveolus of P<sup>4</sup> and base of the zygomatic arch (Fig. 2; Pl. 1, Fig. 4); AD 410'00, left mandible with I, P<sub>4</sub> and M<sub>1,2</sub> (Fig. 1); AD 331'97, right distal tibia (Pl. 1, Fig. 2).

**Diagnosis:** Form that is about 15% smaller than *Megapedetes pentadactylus* from Songhor (Kenya) and with much less massive incisors; grooves in molars always less than half the height of the crown; anterior lophid of the P<sub>4</sub> narrower with deeper distal groove; posterior lophid of M<sub>3</sub> shortened; greater hypsodonty (ratio of height / mesio-distal length of the upper teeth greater than 1 and close to 1,3; morphology of the postcranial skeleton similar, better adapted to springing and which shows a difference in size related to a lesser robustness.

**Derivatio nominis:** The species name derives from the local name of the Orange River, Gariiep.

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



**Figure 2:** AD 333'98, fragment of right maxilla of *Megapedetes gariepensis* sp. nov. palatine view. (Scale bar = 1 cm).

**Table 1:** Dental measurements of *Megapedetes garipeensis* Arrisdrift (in mm)

(L = length, la = width of the 1st loph, lp = width of the 2nd loph, H = height of the crown, S = mesostria (or mesostriid), s = hypostria (or hypostriid).

	L	la	lp	H	S	s	H-s/L	H-S/L	S-s	H/L
<b>P<sub>4</sub></b>										
PQ AD 2974 rt	4,40	-	4,42	5,37	1,15	1,38	0,9	1,0	- 0,23	1,2
AD 155'97	4,20	-	3,86	3,60	0	0	0,9	0,9	0	0,9
AD 225'97	4,53	-	4,20	4,70	0,95	1,13	0,8	0,8	- 0,19	1,0
AD 407'97	3,85	-	3,70	4,25	1,00	0,55	1,0	0,8	0,45	1,1
AD 410-00	4,37	-	4,20	?	1,55	2,15			- 0,60	
<b>M<sub>1,2</sub></b>										
PQ AD 2344 (1rt)	3,84	4,17	4,30	4,60	1,15	0,90	1,0	0,9	0,25	1,2
AD 582c'94 (1rt)	4,28	4,13	4,25	4,22	0,20	0,45	0,9	0,9	- 0,25	1,0
AD 494'95 (1rt)	4,42	4,75	4,25	4,70	1,00	1,25	0,8	0,8	- 0,25	1,1
AD 407'97 (2lt)	3,72	4,42	3,85	4,00	1,45	0,90	0,8	0,7	0,55	1,1
AD 950'97 (2lt)	3,89	-	4,28	2,00	0	0				0,5
AD 969'98 (1lt)	4,25	4,70	4,70	5,65	1,25	1,36	1,0	1,0	- 0,11	1,3
AD 410'00 (1lt)	4,04	4,50	4,65	-	1,90	2,25			- 0,35	
AD 410'00 (2lt)	4,29	4,60	4,40	-	2,25	2,39			- 0,14	
AD 5'00 (1lt)	6,80	-	4,70	-	-	-				
AD 5'00 (2lt)	4,00	-	4,70	-	-	-				
<b>M<sub>2</sub></b>										
AD 407'97 lt	3,63	3,70	3,37	3,20	1,75	0,90	0,8	0,4	0,35	0,9
AD 214'95 rt	4,01	3,80	2,57	3,75	1,09	0,55	0,8	0,7	0,54	0,9
PQ AD 1646 rt	4,00	4,38	3,80	6,20	1,52	1,47	1,2	1,2	0,5	1,5
<b>M<sub>1</sub></b>										
AD 214'95 rt	2,10	2,57	1,75	3,00	0,90	0,53	1,2	1,0	0,32	1,4
<b>M<sup>1-2</sup></b>										
PQ AD 1747 (1lt)	4,03	4,57	4,34	5,40	1,55	1,22	1,0	1,0	0,33	1,3
PQ AD 2564 (rt)	4,14	4,50	4,30	6,00	1,75	1,75	1,0	1,0	0	1,4
AD 582a'94 (1rt)	3,88	4,25	3,95	5,75	1,45	0,98	1,2	1,1	0,47	1,5
AD 582b'94 (2 lt)	3,60	3,80	3,60	4,85	1,78	1,55	0,9	0,9	0,23	1,3
AD 414-00 (2lt)	3,52	4,22	3,79	5,00	0,97	1,00	1,1	1,1	0,3	1,4
<b>M<sup>1</sup></b>										
AD 149'99	2,85	3,48	-	4,25	0	0				2,5
<b>Lower Incisors</b>	<b>Ap x Tr</b>			<b>Upper Incisors</b>			<b>Ap x TR</b>			
PQAD 1024 rt	5.0 x 2.9			PQAD 141 lt			5.3 x 3.4			
PQAD 1745 rt juv.	4.3 x 2.7			PQAD 2534 lt			4.3 x ---			
PQAD 1769 ?	--- x 3.0			PQAD 2562 lt			4.6 x 3.1			
PQAD 2455 lt	5.0 x 3.0			PQAD 2584 lt			5.0 x 3.0			
PQAD 2822 rt	4.3 x 2.9									
AD 191'95 lt	4.7 x 3.1			AD 265'94 rt			4.9 x 3.0			
AD 273a'96 lt	4.4 x ---			AD 591'97 lt			5.4 x 3.3			
AD 155'97 lt	4.6 x 3.0			AD 333'98 rt			5.5 x 3.6			
AD 407'97 rt	4.5 x 3.0			AD 334'98 rt			5.3 x 3.2			
AD 568'97 rt	--- x 2.9			AD 121'99 lt			4.8 x 3.4			
AD 751'97 ?	--- x 3.1			AD 42'99 lt			5.5 x 3.1			
AD 830'97 rt	4.6 x 3.1			AD 412'00 lt			5.3 x 3.2			
AD 898'97 ?	--- x 3.4									
AD 125'98 rt	4.4 x 3.0									
AD 406'99 lt	--- x 3.5									
AD 5'00 lt	4.5 x 3.0									
AD 410'00 lt	4.5 x 2.8									
AD 411'00 lt	4.5 x 2.8									
AD 413'00 ?	4.1 x 3.0									

**Age:** Base of the Middle Miocene which can reasonably be correlated to MN4 in the European scale and Faunal Set P1/ (Rusinga) of East Africa.

**Other material:** 5 incomplete mandibles PQ AD 1745 Guvenile right mandible with I and alveoli for 3 cheek teeth); AD 214'95 (right mandible with M<sub>3,4</sub>) (Pl. 1, Fig. 3); AD 155'97 (left mandible with I, P<sub>4</sub>); AD 225'97 (left mandible with P<sub>4</sub>); AD 950'97 (left mandible with M2 and ascending ramus); AD 830'97 (fragment of right mandible with I); two fragments of edentulous mandibles AD 335'98 and AD 336'98; AD 5'00 (left mandible with I and worn M<sub>1,2</sub>); AD 411'00 (left mandible with I).

Isolated teeth: right P<sub>4</sub>, PQ AD 2974; right M<sub>1</sub>, PQ AD 2344; right M<sub>1</sub> or M<sub>2</sub>, AD 582c'94; left M<sub>1</sub> or M<sub>2</sub>, AD 669'98; right M<sub>2</sub>, AD 494'95; right M<sub>3</sub>, PQ AD 1646; right M<sub>1</sub> or M<sub>2</sub>, PQ AD 2564; left M<sup>1</sup>, AD 414'00; left M<sup>2</sup>, PQ AD 1747; right M<sup>2</sup>, AD 582a'94; right M<sup>2</sup>, AD 582b'94; left M<sup>3</sup>, AD 414'00; lower I: PQ AD 1024 (right), PQ AD 1578 (right), PQ AD 2455 (left), PQ AD 2822 (right); PQ AD 3249 (right), AD 191'95 (left), AD 273a'96 (left); AD 125'98 (right), AD 406'99 (left), AD 898'97 (?); AD 413'00 (left); upper I: PQ AD 141 (left), PQ AD 2534 (left), PQ AD 2562 (left), PQ AD 2584a (left), AD 265'94 (right); AD 334'98 (right), AD 591 '97 (left), AD 121 '99 (left), AD 42'99 (left), AD 751 '97

**Table 2:** Measurements of the mandible of *Megapedetes garipeensis*

(Symphysis length x width; L = length; H/P4 = depth of the mandible at the level of P4 taken on the lingual side, Hr = height of the ramus mandibularis, Lt = total length of the mandible, (or) when the measurement is made on the alveolus; tm = masseter tubercle, length x width. Measurements of the length of the tooth row in parentheses indicate a measurement taken on the alveoli).

Specimen	Symphysis	Diastema	H/P4	H/M2	H/M3	LP4-M3	tm	Hr	Lt
PQ AD 1745 lt	21,4 x 78	/8	/				6,5 x 3,1		
AD 155'97 lt	22,7	9,2	17,5	17,0	15,0	(18,6 (P4M4))	4,5 x 2,5		> 52
AD 225,97 lt	23,3	7,6	17,6	13,6	15,5	17,9)	6,4 x 2,1	33,5	~ 50
AD 407'97 rt	24,0 x 7,5	10,6	14,8	16,2	16,8	16,3	4,3 x 3,1		
AD 335'98 rt	24,6	9,0	16,8	-	-	-	4,4 x 2,5		
AD 336'98 rt	23,8	8,8	16,6						
AD 214'95 rt	20,0	5,5	16,5	13,4	14	(17,1	5,1 x 3,0	34,0	51,6
AD 950'97 lt	/	/	/	14,7	16,4			35,0	
AD 5'00 lt	-	~ 6,5	19,0	19,4	-	(20)	5,8 x 2,4		
AD 830'97 rt	> 18,6	6,4	17,2	-	-				
AD 410'00 lt	21,4 x 7,3	8	15,9?	14,9			4,9 x 1,6		
AD 411'00 lt	20,7 x 6,2	6,8	15,7	12,0		(20,3)	4,7 x 2,1		
<i>M. pentadactylus</i>	30	12	26					47	
<i>P. capensis</i>	22							31,6	

(left), AD 412'00 (left).

Postcranial material: AD 331 '97 (distal end of right tibia).

No p<sup>4</sup> has been recognised, because, despite the morphological similarity between it and the M<sup>1</sup>, the p<sup>4</sup> can be identified by the absence of a contact facet on the mesial surface and by the antero-labial root which leans forwards (observed in *M. pentadactylus* from Napak).

**Description:** Upper jaw. Only one maxilla is known, the paratype AD 333'98 (Fig. 2, Pl. 1, Fig. 4). The concavity of the anterior part of the ventral surface of the zygomatic arch juxtaposes the alveolus of the p<sup>4</sup>. The muzzle is narrower than that of *Megapedetes pentadactylus* as evidenced by the width of the palate just in front of the p<sup>4</sup> (*M. pentadactylus* : 13 mm - measurement given by MacInnes 1957, p. 7; the Arrisdrift specimen: 11,0 mm) and approaches extant *Pedetes* in this feature (11,4; 10,8 and 11,5 mm in MacInnes).

Mandible. The general form of the mandible is similar to that of *Megapedetes pentadactylus*. In lateral view, the lower masseteric crest, as in *M. pentadactylus*, gives rise to a prominent masseteric tubercle (the strength of which is quite variable), just in front of P<sub>4</sub>. This smooth crest forms a continuous curve the trajectory of which is parallel to that of the symphysis, descending from below the incisor to the level of M<sub>2</sub>, but in inferior view the masseteric tubercle does not produce a clear swelling of the mandibular body as was drawn in *M. pentadactylus* and as occurs in extant *Pedetes*. The superior masseteric crest, which is very slight and located high on the mandibular body rapidly blends into the alveolar margin whereas in *Pedetes*, this crest is lower and more obvious.

The result is that the mandibular body is higher labially than lingually. The intercrest surface is smooth, while in *Pedetes*, it is rugose and bumpy, because of the great hypsodonty and incurving of the M<sub>2</sub> and M<sub>3</sub>. The ascending branch of the jaw preserved in AD 214'95 (Pl. 1, Fig. 3) and AD 950'97 shows a condyle whose summit is recurved upwards and backwards as in *Pedetes capensis* and not horizontal as suggested by MacInnes (1957, p. 8). It is extremely narrow and the coronoid apophysis is missing, but seems to have been weak, possibly inexistent. The lingual surface of the ascending ramus has a very high *foramen dentale*, located just below the condyle. The deep groove extending from the incisive alveolus reaches almost to the condyle. The height of the ascending ramus is 37,1 mm, estimated to be 47,0 mm in *M. pentadactylus* and 31,6 mm in *Pedetes capensis*. The height of the mandible at the level of P4 ranges from 14,8 mm to 17,7 mm with a mean of 17,0 mm (5 measurements). This height is estimated to be 25,0 mm in *M. pentadactylus* (MacInnes, 1957, p. 9); this greater reduction is linked to the reduction of the incisor (see later). The mandibular symphysis has the shape and the same orientation as that of *M. pentadactylus*; its mean length is 23,7 mm for 5 measurements against 30 mm in *M. pentadactylus* and 22 mm in the extant form (MacInnes 1957, p. 9). The length of the diastema in the holotype is 10,6 mm; 12,9 mm in *M. pentadactylus* and 8,8 mm on average in the extant ones (Davies, 1987).

Juvenile mandible. Mandible PQ AD 1745 is thought to be juvenile for two reasons: 1. the antero-posterior diameter of the incisor increases from 4,2 mm at the level of its tip to 4,6 mm at the level of the break in the ascending ramus, 2. the alveoli reveal the presence of three cheek teeth, and thus the M<sub>3</sub> had not erupted. The mandibular symphysis is relatively wide (7,8 mm) for a width of 21,4 mm (range of variation from 20,0 mm to 24,6 mm) whereas in adult specimens that

can be measured (AD 411'00 = 6,2 mm; AD 407'97 = 7,2 mm) it is narrower.

**Pathological mandible.** Specimen AD 2]4'95 (Pl. 1, Fig. 3), for which we described the ascending ramus, reveals a particular weakness of the masseteric crests; in addition, it also has a supernumerary tooth, interpreted as an  $M_4$  (see figure). Its diastema is shorter than it is in all the other mandibles.

#### Upper teeth

**Incisors.** The most striking difference between this new species and *M. pentadactylus* resides in the reduced dimensions of the upper incisor: considering that on average the species is 15% smaller, the surface of the incisor (mesio-distal diameter x transverse diameter) is about 50% smaller (17 mm) compared to the Kenyan specimen (35 mm). Apart from this major difference in size, the upper incisor in the two species resemble each other closely in morphology.

**Cheek teeth.** Only six upper cheek teeth were collected, mainly represented by  $M^1$  and  $M^2$ . They have contact facets on their mesial and distal surfaces. The roots, which are shorter than the crowns, are confluent and have a lingual root. The anterior loph is slightly lower than the posterior one and its mesio-distal length is slightly greater (see figure). The mesostria is a bit deeper than the hypostria, and the mesoflexus wider than the hypoflexus. The anterior loph is more curved than the straighter posterior one. It is interesting to calculate the hypsodonty (ratio of the height over the mesio-distal length of the tooth) but because this measurement varies with the wear stage of the crown, which biases the measurement of the height, it is necessary to use the height of the tooth from the depth of the grooves. This method greatly augments the comparative sample.

The only  $M^3$  known (AD 140'99) (Pl. 2, Fig. D) is noticeably smaller than the other cheek teeth. Its length is 1/3 less than its width (2,85 x 3,48 mm). The wear surface is in the outline of a horse-shoe with a wide anterior branch and a short oblique posterior one. Between the two branches, on the labial side, a small fossette is present, but the mesostria has disappeared, whereas on the lingual side there is neither a fossette nor a hypostria. In contrast, in lateral view, distolingually, there is a small groove on the crown between the first and second loph. The tooth has a root that is slightly subdivided into two at the apex.

No  $M^3$  of *Megapedetes pentadactylus* has been described. Nevertheless there is an  $M^3$  (Napak V 64) preserved at the Uganda Museum in Kampala, which is clearly smaller than the other molars of this species (measuring: 3,25 mm x 3,47 mm) and having the same structure as that of *M. garipeensis*, but with the length less reduced in comparison with the breadth and with more pronounced brachyodonty. The Arrisdrift specimen is thus the first attributed to the genus; however, a tooth (KNM ME 10525) reported from the Early Miocene of Meswa Bridge in Kenya (Winkler, 1992, Fig. 3) as Pedetidae indet. could belong to a *Megapedetes*.

#### Lower teeth:

**Incisors.** The lower incisor which is better represented (7 specimens) than the upper incisors are also reduced in size to the same proportion relative to *M. pentadactylus* as the upper incisors (14 mm for the Arrisdrift specimens and 32 mm for *M. pentadactylus*), corresponding to a reduction of nearly 50%. Extant Pedetidae show a slight reduction (11,5 mm for

*Pedetes capensis*).

**$P_4$ .** They are not molariform and have a narrow anterior margin. In lightly worn teeth, the anterior lophid appears to be composed of three elements (or four in the holotype AD 410'00) in which we recognise the protoconid, metaconid and anteroconid, as had already been reported for *M. pentadactylus* by Lavocat & Michaux (1966). In specimen PQ AD 2974, these 3 cuspids are well isolated from each other and are separated by small longitudinal valleys; but in worn specimens they fuse together and form an arched lophid with a posterior indentation due to the more mesial position of the anteroconid. All the structures disappear in extreme wear, only a ring of enamel encircling dentine remains. The posterior root is longer than the anterior one, and is much enlarged (which could be due to the fusing of two roots which might have existed in the ancestral state). Wear of the posterior lophid is more severe than in the anterior one; this phenomenon of differential wear is not known in *M. pentadactylus* in which it is uniform.

In the paratype AD 410'00, the  $P_4$  retains the juvenile structures of the anterior lophid (metalophid) which is subdivided into three cusplets that we interpret as the anteroconid, metaconid and protoconid. This tooth can be compared with a germ of  $P_4$  of *M. pentadactylus* from Songhor (SO 809) from which it differs in the following details: more triangular outline, clearer separation of the three cusplets, even though the wear is greater, protoconid more mesial than the metaconid, and the anteroconid/ protoconid pair in a more mesial position. There is a deep continuous valley, separating the anterior and posterior lophids which does not exist in the Songhor specimen.

**$M_1 - M_2$ .** These are teeth in which the posterior half is slightly higher than the anterior one. The anterior lophid is mesio-distally longer than the posterior one. The mesoflexid is wider than the hypoflexid and the anterior lophid is more arched than the posterior one and straighter than it. When the roots are visible, it appears that the anterior one is more gracile than the posterior one in the  $M_1$  but the two are equally strong in the  $M_2$ . In addition, it appears from the median transverse constriction of the roots (both anterior and posterior) that they each result from the fusion of two roots, which means that the ancestral condition probably consisted of four roots. Worn teeth have a circular outline, whereas at Songhor, the outline is more square; which in the Arrisdrift specimens is due to the presence of a more important interdental space.

**$M_3$ .** Three specimens of  $M_3$  are known: one on the holotype AD 407'97, one on the pathological mandible AD 214'95 and an isolated germ PQ AD 1646. It is the absence of a posterior facet which permits us to determine the  $M_3$ . The posterior lophid is narrower than the anterior one. Contrary to the  $M_1$  and  $M_2$  which are straight, the tooth is slightly inclined towards the rear. It is the most hypsodont tooth in the collection because it is the least worn. Wear between the two lophids is the same, but because it is weak, one can observe two clear cusplets (hypoconid and entoconid) on the posterior lophid and three cusplets on the anterior one. The  $M_3$  in the pathological mandible is abnormally small, in particular its posterior lophid which is greatly reduced vestibulo-lingually.

**$M_4$ .** It has a morphology which is similar to but smaller than that of  $M_3$  described above and its posterior lophid is much lower than the anterior one.

**Skeleton.** Morphologically, the tibia is similar to that of *M.*

**Table 3:** Comparative measurements of the postcranial elements of *Pedetidae*

Anatomy	<i>Megapedetes gariensis</i>	<i>Megapedetes pickfordi</i>			<i>Megapedetes pentadactylus</i>	<i>Pedetes laetoliensis</i>	<i>Pedetes capensis</i>	<i>Pedetes capensis</i>
<b>Femur</b>		<b>AD 215'95</b>				<b>LT 79.5514</b>	MNHN	FSL
Total length		95,2			130,0	85,3	108,0	110,5
A-p length of head		7,5			11,0	6,5	9,0	8,2
Width m-l head		8,2			12,0	7,4	9,0	8,6
Width bicondylar		18,3			27,0	15,6	21,0	18,5
<b>Tibia</b>	<b>AD 331'97</b>	<b>AD 216'95</b>	<b>AD 265'97</b>	<b>AD 270'98</b>				
Total length				120,0	150,0	108,0	135,0	131,9
A-p length of head				19,0	28	17,5	23,0	23,0
Width m-l head				18,5	27	18,5	23,0	23,3
Width a-p distal	11,1	9,6	8,6	8,9	13,2		10,0	9,6
Width distal m-l	14,8	11,8	12,5	11,8	18,1	9,9	15,0	14,2
<b>Calcaneum</b>		<b>PQ AD 845</b>	<b>PQAD 2018</b>	<b>AD 540'94</b>				
Total length			29,5	30,0	42,0	29,4	39,0	37,4
Width total		10,7	10,0	10,2	15,6	7,3	9,5	10,0
Length <i>tuber calcis</i>			10,3	15,1	23,7	12,5	18,0	16,0
<b>Metatarsal I</b>		<b>AD 322'99</b>						
Total length		26,3			34	-	-	
length a-p. prox.		6,3						
Width m-l prox.		3,9						
Width m-l dist.		3,9						
<b>Metatarsal II</b>		<b>AD 322'97</b>	<b>AD 567'97</b>					
Total length		39,2	38,6		50	38	45	
Width a-p. prox.		7,8	7,1		13		8	
Width m-l prox.		4,7	4,4		6,5		4,5	
Width m-l dist.		5,6	5,2		7,8		6,25	
<b>Metatarsal IV</b>	<b>AD 566'97</b>							
Total length	38,5				46	33,5	38,5	
Length a-p. prox.	6,5				10		7,5	
Width m-l prox.	5,8				8,5		7	
Width m-l dist.	4,7				6		6	
<b>Metatarsal V</b>	<b>AD 279'96</b>							
Total length	30,7				37,0	25,8	28,0	30,6
<b>Phalanx IIIrd digit</b>	<b>AD 325'00</b>							
Total length	22,0				25,0		20,0	
<b>Phalanx IVth digit</b>	<b>AM 44'98</b>							
Total length	18,2				22,0		17,5	
<b>Phalanx Vth digit</b>		<b>AD 269'98</b>						
Total length		16,0			-			

*pentadactylus*, but it is on average 20% smaller (see the table).

**Species *Megapedetes pickfordi* nov.**  
(Tables 3, 4)

**Holotype:** p<sup>4</sup> AD 715'99 (Pl. 2, Fig. A).

**Paratype:** M<sub>2</sub>, tooth germ AD 583a'94.

**Diagnosis:** Smaller by 25% than *M. gariensis* from Arrisdrift; slightly more hypsodont (ratio of height over length = 1,9 in the least worn tooth, the paratype germ of M<sub>2</sub>). The difference in height between the mesostriid and hypostriid is greater than in *M. gariensis*. The root of the P<sub>4</sub> is concave towards the front and is slightly bifid at its tip.

**Derivatio nominis:** The name of the species is given in honour of Martin Pickford, co-director of the Namibia Palaeontology Expedition.

**Type locality:** Arrisdrift (Sperrgebiet, Namibia).

**Age:** Base of the Middle Miocene which is reasonably correlated to European Land Mammal zone MN4 and Faunal Set

P1/ of East Africa (Rusinga).

**Other material:** right M<sub>1</sub>, AD 583b'94 (Pl. 1, Fig. 6); left M<sub>2</sub>, AD 273b'96 (Pl. 1, Fig. 5); right M<sub>2</sub>, AD 536'95; right M<sub>1</sub><sup>1</sup>, AD 405'99 (Pl. 2, Fig. B); left M<sub>2</sub><sup>2</sup>, AD 414'00 (Pl. 2, Fig. C); lower I, PQ AD 2584b (left), AD 668'99 (right); upper I; AD 404'99 (right).

Postcranial material: AD 215 '95 (complete right femur); AD 216'95 (right distal tibia); AD 269'97 (distal left tibia); AD 270'98 (complete left tibia).

**Descriptions:** Dentition Upper teeth

P<sup>4</sup>. Specimen AD 715'99 is interpreted as a P<sup>4</sup> because of the following features: The crown is higher distally than mesially. The mesial loph is longer and lower than the distal loph and the latter is wider than the former. The root, which is slightly bifid at its tip is concave towards the front.

M<sup>1</sup>. AD 405'99 has a mesial loph which is wider than the distal one; the root which is bifid only on the labial side is weakly concave towards the rear. The hypostria is very reduced and the tooth is therefore at a stage of wear comparable to that of the P<sup>4</sup>.

Upper incisor. AD 404'99 right incisor is comparable to *M.*



**Table 4:** Dental measurements of *Megapedetes pickfordi* (in mm)

(L = length, la = Width of first loph, lp = Width of 2nd loph, H = crown height, S = mesostria (or mesostriid), s = hypostris (or hypostriid))

	L	la	lp	H	S	s	H-s/L	H-S/L	S-s	H/L
M <sub>1,2</sub>										
AD 583a'94 (2 lt)	2,55	2,80	2,80	4,88	3,25	1,98	1,1	0,6	1,27	1,9
AD 583b'94 (1 lt)	2,73	3,13	3,05	3,85	1,53	0,66	1,2	0,8	0,87	1,4
AD 536'95 (2 rt)	2,80	3,00	2,80	3,70	1,34	0,35	1,2	0,8	0,99	1,3
AD 273b'96 (2 lt)	2,65	3,00	2,65	3,78	1,53	1,10	1,0	0,8	0,43	1,4
P <sup>4</sup>										
AD 715'99 (rt)	2,84	2,60	2,73	3,80	1,16	0,14	1,3	0,9	1,02	1,3
M <sup>2</sup>										
AD 405'99 (1rt)	2,90	2,72	2,95	4,00	1,34	0,60	1,2	0,9	0,74	1,4

Lower incisors	Ap x Tr
PQ AD 2584 b (lt)	4,0 x 2,6
AD 668'99 (rt)	4,0 x 2,8
Upper incisors	Ap x Tr
AD 404'99 (rt)	4,6 x 2,6

*gariensis* with 20% smaller diameters.

#### Lower teeth

M<sup>1</sup>. The distal loph is slightly narrower than the mesial one (wider at the front than at the back); which confirms its identification as an M<sub>1</sub>. The hypostrid is weak, showing that the tooth is deeply worn. It is broken at the level of the root.

M<sup>2</sup>. AD 536'95 is a heavily worn tooth with a very reduced hypostrid and a distal lophid much shorter than the mesial one. AD 273b'96 is less worn than the previous specimen and clearly shows the two roots elongated transversely of which the mesial one is narrower than the distal one.

A left dental germ, AD 583a'94 is an M<sub>2</sub> on the basis of the lateral inclination of the spout which makes the lingual surface convex. The breadth of the two lophs is the same and they are separated by a transverse groove whereas in worn M<sub>2</sub>, it is inclined linguo-distally.

**Lower incisor.** PQ AD 2584b left incisor; AD 668'99 a right one. These teeth show a transverse diameter which is smaller than that of *M. gariensis*.

**Skeleton.** The distal end of the tibia (the only part preserved) has a morphology close to that of *Megapedetes gariensis*, but is on average 20% smaller. In anterior view, the femur has a straight diaphysis and not inclined as in *M. pentadactylus*. The skeleton recalls strongly those of extant Pedetidae and *Megapedetes pentadactylus*. In anterior view the femur has a tubercle, as is the case in *Pedetes laetoliensis* and extant Pedetidae, but it is strongly marked; the femoral trochlea is wide and not deep whereas in *Pedetes*, it is narrow and deep. The tibia has a tibial plateau which is shorter antero-posteriorly than it is in *Pedetes*. The distal tibial articulation is quite wide medio-laterally, deep and oblique. In the tibia, the lateral talar facet is widened, shallow and oblique, whereas in extant Pedetidae, it is narrow, deep and very oblique. The postero-medial process does not project much, differing in this respect from *Pedetes*. The more recently excavated material includes specimens still being studied comprising several phalanges and metatarsals which will be published later.

**Bones of uncertain attribution.** Certain foot bones are difficult to identify to species, but based on the bone proportions, we can estimate which one they belong to. A left metatarsal I AD 332'99, two left metatarsals II (AD 322'97, AD

567'97) could belong to *M. pickfordi*. A left metatarsal IV (AD 566'99) and a metatarsal V (AD 279'96), a distal end of left metatarsal III (PQ AD 64) and a distal end of metatarsal IV (PQ AD 220) could belong to *M. gariensis*. Several phalanges were discovered at Arrisdrift (PQ AD 302, PQ AD 327, AD 269'98 and AD 325'00) and only one at Auchas (AM 44'96). AD 269'98, a first phalanx of right digit V could belong to *M. pickfordi*, whereas AD 325'00, a first phalanx of the left digit III would belong to *M. gariensis*, as would the specimen from Auchas AM 44'98. The metatarsals, like the phalanges are more gracile than those of *Megapedetes pentadactylus*, but more robust than those of other Pedetidae. Finally, the phalanx from Auchas Mine is the only specimen indicating the presence of Pedetidae at this site.

The presence of a first metatarsal, the strength of metatarsal IV, like the proportions of the different segments of the limb, suggest that the springing adaptations in *Megapedetes* were different from those of Pliocene and Pleistocene to Recent Pedetidae.

## Conclusions and discussion

For the first time, two species of *Megapedetes* are described from a single site and it is the first time that *Megapedetes* has been reported from southern Africa (as evoked by Senut, 1997), whereas they are classically known in eastern Africa (MacInnes, 1957, 1962). During the Middle Miocene a form named *Megapedetes aegeus* described by Sen (1977) is known from Turkey, and other pedetids are known from Maroc at Beni Mellal (Lavocat, 1961) and from the Isle of Chios in Greece (Tobien, 1968). Another *Megapedetes* is mentioned from Israel (Wood & Goldsmith, 1968). *Megapedetes* from North Africa persisted until the early Pliocene in Tunisia (Batak & Fejfar, 1990). In East Africa, less common remains are known from Kirimun (Ishida & Ishida, 1982), Fort Ternan (Denys & Jaeger, 1992), Maboko and Kipsaraman (Winkler, 1992). In the former 3 sites, on the basis of size the *Megapedetes* could be attributed to *Megapedetes* cf. *gariensis*. At Kipsaraman, the *Megapedetes* is comparable in size to *M. pickfordi*, but it is much more brachyodont. This morphology correlated to tooth size has already been mentioned at Rusinga

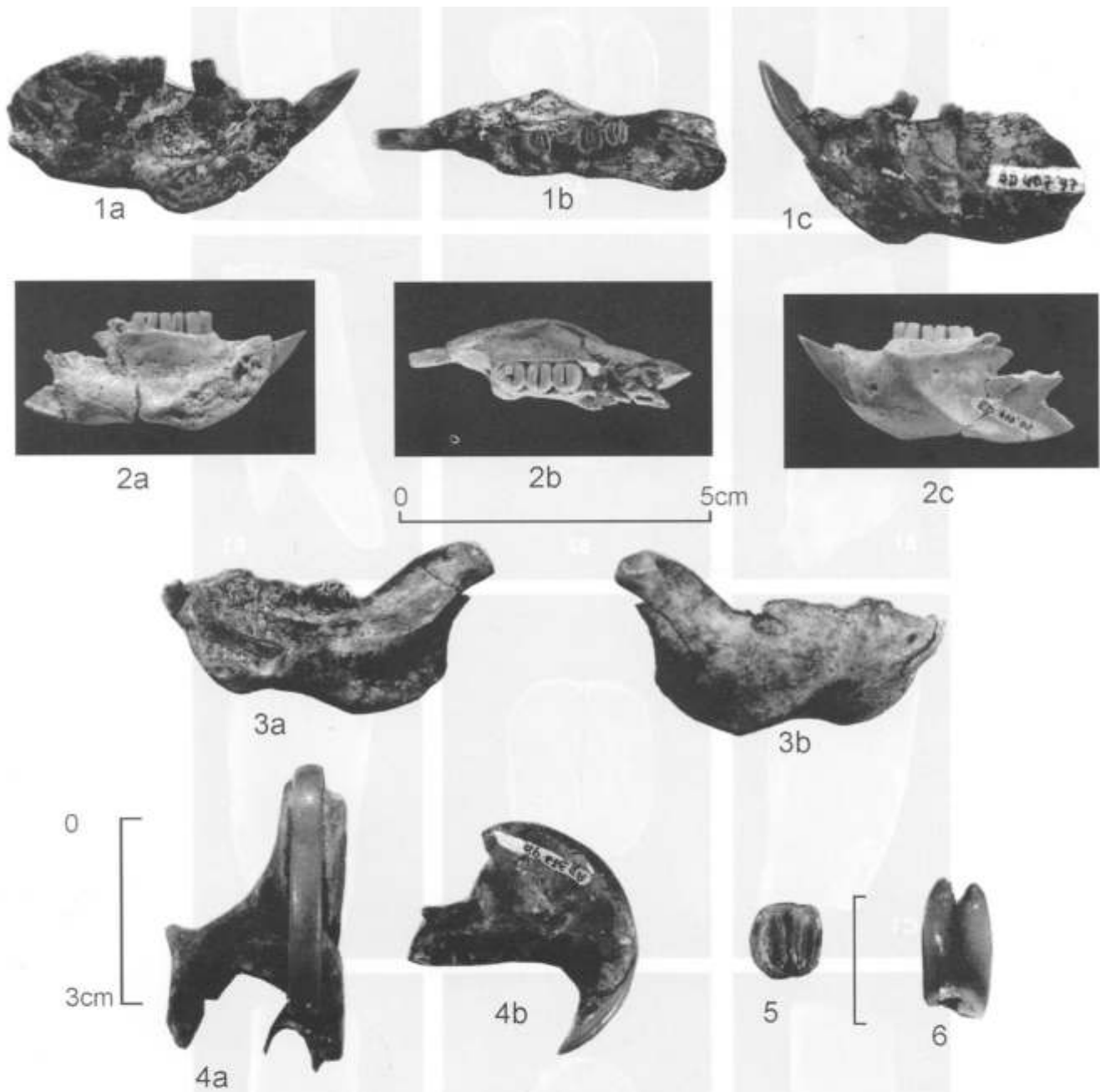
(Lavocat, 1977).

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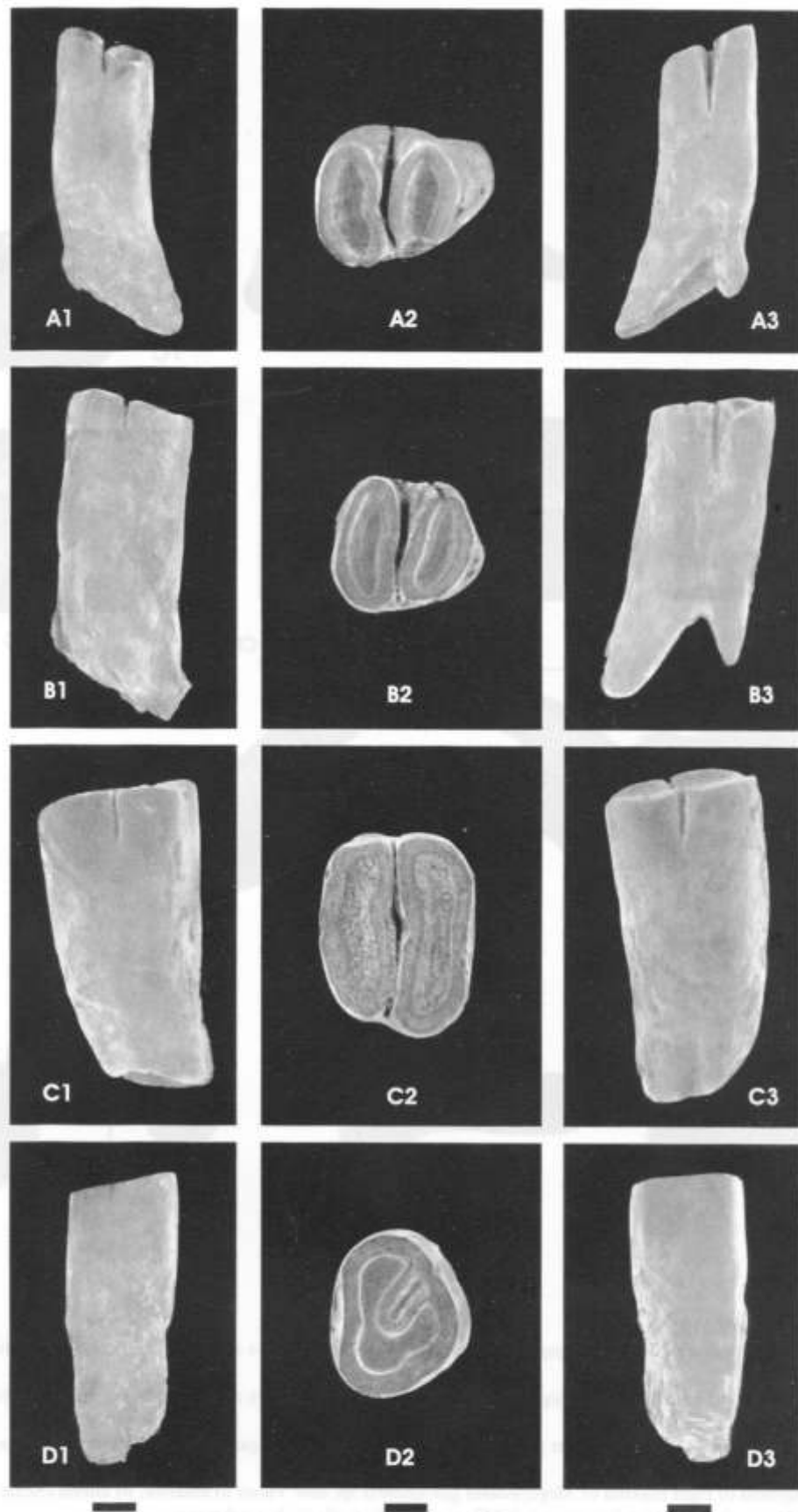
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**Plate 1:** *Megapedetes* from Arrisdrift, Namibia

- Figure 1: AD 407'97, holotype left mandible of *Megapedetes gariensis* sp. nov., views a) lingual, b) occlusal, c) labial (Scale bar = 5 cm).
- Figure 2: AD 410'00, paratype left mandible of *Megapedetes gariensis* sp. nov., views a) lingual, b) occlusal, c) labial (Scale bar = 5 cm).
- Figure 3: AD 214'95, right mandible of *Megapedetes gariensis* sp. nov. Teratogenic specimen showing the presence of an M4, views a) lingual, b) labial (Scale bar = 5 cm).
- Figure 4: AD 333'98, fragment of right maxilla of *Megapedetes gariensis* sp. nov. views a) anterior, b) lateral (Scale bar = 3 cm).
- Figure 5: AD 273b'96, *Megapedetes pickfordi* sp. nov. left M2, occlusal view (Scale bar = 5 mm).
- Figure 6: AD 583b'94, *Megapedetes pickfordi* sp. nov. right M1, lingual view (Scale bar = 5 mm).



**Plate 2:** *Megapedetes* from Arrisdrift, Namibia. (Scale bars = 1 mm).  
 Figure A: AD 715'99, *Megapedetes pickfordi* sp. nov. holotype right P<sup>4</sup>, views 1) lingual, 2) occlusal, 3) labial.  
 Figure B: AD 405'99, *Megapedetes pickfordi* sp. nov. right M<sup>1</sup>, views 1) lingual, 2) occlusal, 3) labial.  
 Figure C: AD 414'00, *Megapedetes pickfordi* sp. nov. left M<sup>2</sup>, views 1) lingual, 2) occlusal, 3) labial.  
 Figure D: AD 140'99, *Megapedetes gariepensis* sp. nov. left M<sup>3</sup>, views 1) lingual, 2) occlusal, 3) labial.