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Martin Pickford and Brigitte Senut

Orangemeryx hendeyi

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Tragulidae from Arrisdrift, basal Middle Miocene, Southern Namibia

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Medium sized tragulid remains are relatively common at Arrisdrift, being represented by good samples of mandibles, two maxillae and many postcranial elements. Comparison of the fossils with East African species and fossils from France and Spain as well as extant *Hyemoschus* reveals that there is only a single species present which, apart from some details of the dentition, is close morphologically and metrically to *Dorcatherium pigotti*.

Resume français

Les chevrotains (Tragulidae) sont des petits ruminants sans come, de taille petite à moyenne, à dentitions primitive et aux métapodes partiellement fusionnñs. Les mandibules, les maxillaires, les dents isolées et les os post-crâniens de Tragulidae sont assez fréquents à Arrisdrift (17-17,5 Ma) en Afrique australe. Métriquement, le matériel est proche de *Dorcatherium pigotti* décrit pour la première fois dans le Miocène inférieur de Rusinga en Afrique orientale (Whitworth, 1958). Toutefois, des différences mineures dans la morphologie dentaire entre les piéces d'Afrique orientale et celles d'Arrisdrift permettent d'attribuér les dernières à *Dorcatherium* aff. *pigotti*. La dentition est typiquement brachyodonte avec un pli de type "*Dorcatherium*" aux molaires inférieures. Les prémolaires inférieures sont allongées mésio-distalement et d'apparence sectoriale. Les os postcrâniens ressemblent fortement à ceux des *Dorcatherium* européens et à ceux des chevrotins d'eau actuels, *Hyemoschus*, et diffèrent fortement de ceux des Tragulidae asiatiques, *Siamotragulus* et du genre actuel *Tragulus*.

Introduction

Tragulids were reported from Arrisdrift by Corvinus & Hendey (1978) and Hendey (1978) on the basis of a few mandible fragments with partial dentitions. The Namibia Palaeontology Expedition has excavated many more remains of the same species, a lot of which are more complete. This paper is designed to complete the description of the Arrisdrift tragulid, and to compare it with material from other parts of Africa and Europe. It is a medium sized tragulid, being smaller than *Dorcatherium chappuisi* (Arambourg, 1933), larger than *Dorcatherium songhorensis* (Whitworth, 1958) and appreciably larger than *Dorcatherium parvum* (Whitworth, 1958) and *Dorcatherium moruorotensis* (Pickford, 2001).

Systematic description

Suborder Ruminantia Scopoli, 1777
Family Tragulidae Milne-Edwards, 1864
Genus *Dorcatherium* Kaup, 1833
Species *Dorcatherium* aff. *pigotti* Whitworth, 1958

Synonymy: *Dorcatherium* cf. *pigotti* Whitworth, Hendey, 1978.

Diagnosis: A species of *Dorcatherium* of medium size; length of lower molar series (m/1-m/3) about 30 mm (after Whitworth, 1958).

Type locality: Rusinga, Kenya.

Material from Arrisdrift: Cranial and dental. AD 226'95, mandible fragment with m/3; AD 227'95, mandible with broken m/2 and complete m/3; AD 150'95, m/3; AD 328'95, mandible with p/4-m/1; AD 353'96, mandible with m/2-m/3; AD 712'97, m/3; AD 424'97, mandible with p/3-m/3 (Pl. 1, Fig. 5); AD 621'97, mandible with m/1-m/3; AD 68'97, mandible p/2-m/3; AD 530'98, mandible with m/2-m/3 (Pl. 1, Fig. 3); AD 434'98, mandible with m/2; AD 180'00, mandible with d/2-m/1 (Pl. 1, Fig. 4); AD 463'00, mandible with d/2-d/3; PQAD 104, d/2-d/3; PQAD 910, d/4; PQAD 1696, m/3; PQAD 1819, m/3; PQAD 2225, m/3; PQAD 262, m/1-m/2; AD 95'95, maxilla with P2/-P3/, M2/-M3/ (Pl. 1, Fig. 1); AD 400'00, right maxilla with M1/-M2/ (Pl. 1, Fig. 2).

Postcranial. PQAD 465, right distal humerus; AD 426'98, left humerus (Pl. 2, Fig. 1); AD 57'96, left humerus lacking proximal epiphysis (Pl. 2, Fig. 2); AD 316'97, left *proximal ulna* (Pl. 3, Fig. 3); AD 471 '99, left *proximal ulna* (Pl. 3, Fig. 2); AD 570'99, left *proximal ulna* (Pl. 3, Fig. 1); AD 223'00, ulna; PQAD 2358, left magnum; PQAD 1694, right metacarpal III; AD 600'99, right metacarpal IV (Pl. 3, Fig. 4); AD 451 '00, right metacarpal III (Pl. 3, Fig. 5); AD 597'97, right femur (Pl. 3, Fig. 6); AD 139'97, left distal femur; AD 541 '98, right femur; PQAD 2696, right tibia (Pl. 4, Fig. 1); PQAD 3127, left distal tibia; PQAD 646, right distal tibia; PQAD 1567, left distal tibia; AD 704'94, right proximal tibia; AD 32'97, right tibia; AD 599'97, left juvenile tibia; AD 301 '98, right tibia; AD 89'98, left proximal tibia; PQAD 1114, right talus; AD 706'94, left talus; AD 386'99, left talus (Pl. 4, Fig. 2); AD 707'94 left navicular-cuboid (Pl. 4, Fig. 3); AD 189'97, left navicular-cuboid (Pl. 4, Fig. 4); PQAD 50, left metatarsal; AD 357'99, left metatarsal III (Pl. 4, Fig. 5).

Description: Mandible (Pl. 1, Figs 3-5). AD 424'97, mandible with lower dentition.

The mandibular foramen is located higher than the m/3. The ascending ramus is not as high as it is in the Arrisdrift bovid and begins just behind the posterior margin of m/3 and the horizontal ramus, although robust, is also not as well developed as in the bovid.

Lower dentition (Table 1). Lower m/3. The internal cusps are conical, the external ones half-moon shaped. The anterior cristid of the metaconid is low, and joins the anterior cristid

Table 1: Measurements (in mm) of the teeth of Arrisdrift Tragulidae.

PERMANENT LOWER TEETH

m/3	Length	Breadth
AD 530'98	14	5.5
PQAD 2225	14	6.2
AD 621'97	14.5	6
PQAD 1696	14.5	6.5
AD 424'97	14.7	6.7
PQAD 1819	15	6.2
AD 227'95	15.1	6.5
AD 150'95	15.1	6.9
AD 68'97	15.1	7.1
AD 226'95	15.3	6
AD 353'96	15.6	6.9
AD 712'97	15.8	6.9

m/2	Length	Breadth
AD 434'98	8.8	6
AD 621'97	8.9	5.8
AD 353'96	9.2	5.3
AD 68'97	9.2	6
PQAD 262	9.4	6
AD 424'97	9.7	6.9
AD 530'98	10.2	6.9

p/4	Length	Breadth
AD 68'97	8.2	4.3
AD 424'97	8.6	4.1

m/1	Length	Breadth
AD 68'97	7.2	5
AD 621'97	7.8	5.8
AD 424'97	8.4	5.7
AD 180'00	8.9	5.4
PQAD 262	9	5.5
AD 328'95	9.2	5.6

p/3	Length	Breadth
AD 68'97	7.8	3.8
AD 424'97	8.8	3.5

p/2	Length	Breadth
AD 68'97	5.9	2.9

DECIDUOUS LOWER TEETH

dm/4	Length	Breadth
AD 180'00	10.1	4.3
PQAD 910	10.2	4.3

dm/3	Length	Breadth
AD 180'00	8.4	3
AD 463'00	8.4	2.7
PQAD 104	8.3	2.6

dm/2	Length	Breadth
AD 180'00	7.2	2.4
AD 463'00	6.7	2.2
PQAD 104	6.7	2.1

PERMANENT UPPER TEETH

M3/	Length	Breadth
AD 95'95	9.8	12

M2/	Length	Breadth
AD 95'95	9.9	10.6

P3/	Length	Breadth
AD 95'95	8.3	4.9

P2/	Length	Breadth
AD 95'95	9.1	4.1

of the protoconid which is higher and better developed. The posterior cristids of .the metaconid and protoconid are doubled, thereby forming the so-called "*Dorcatherium* fold". The internal cristids of these two cusps join each other and touch the anterior cristid of the entoconid. However, the labial cristid of the protoconid (equivalent to the "palaeomerycid fold") joins the anterior cristid of the hypoconid. The anterior cristid of the entoconid is small and low, whereas the anterior cristid of the hypoconid is higher and better developed. The entoconid does not possess a posterior cristid, but there is a small, low entoconulid. The posterior cristid of the hypoconid is doubled such that the internal branch touches the entoconulid low down (almost forming a repetition of the "*Dorcatherium* fold"). The hypoconulid is located centrally, the labial cristid contacts the anterolabial cristid of the hypoconid and the lingual one leads towards the entoconid, but stops short of its base, leaving a strong lingual opening. There is a small ectostylid and a clear anterior cingulum.

Lower m/1 and m/2. The lower first and second molars possess anterior and posterior cingula. The basic morphology of these teeth is similar to that of m/3, but without the hypoconulid. In m/2 the most obvious difference is the absence of the doubled posterior cristid of the hypoconid and the lack of an entoconulid, which in any case is very small in the m/3.

Lower p/4. The lower p/4 has a slightly bifurcate anterior wing which disappears with light wear. The oblique central cristid is very long, almost reaching the posterior margin of the tooth. The postero-labial conid is U-shaped, and is separated from the mesio-labial conid by a vertical incision.

Lower p/3. The lower third premolar repeats the basic structure of the p/4, but the anterior conid is proportionally more developed, and the oblique cristid much less developed.

Maxilla (Pl. 1, Figs 1-2). AD 95'95, maxilla with upper dentition.

Upper M3/. The paracone is pyramidal with low crests, which are well marked externally. The strong parastyle joins the paracone at its base. The mesostyle is very strong and the metastyle weak. The metacone is less well marked externally than the paracone, and also possesses low crests. The union between the external and internal cusps occurs low down, almost at the base of the crown. The internal cusps are separated from each other and there are no folds in the lingual crests. There are smooth anterior and posterior cingula. The labial cusps are aligned with each other and there is no ectostyle.

Upper dentition (Table 1). Upper M2/. The upper second molar is similar in morphology to the M3/ but it is smaller. The M1/ and P4/ have been lost.

Upper P3/. The P3/ has a low, poorly developed lingual cusp which joins the labial cusp, with no development of crests, but with smooth cingula. In the external wall the labial cusp is high and sharp and is located in the middle of the tooth, reaching the lingual cusp in a somewhat posterior position. The anterior and posterior styles are narrow, being more compressed posteriorly than anteriorly and about equal in size.

Upper P2/. The second upper premolar is constructed on the same morphological plan as the P3/, but differs from it by having a less well developed lingual cusp, here reduced to a small swelling, and by the better developed posterior style.

Discussion

The dentition of the Arrisdrift tragulid is comparable in size (Table 1) to that of *Dorcatherium pigotti*, particularly in the lower molars which are the best represented teeth in the sample from the site as well as in the Kenyan species. Morphologically the dentition is closely comparable, being less bunodont than those of *Dorcatherium chappuisi*, and more like those of *D. pigotti* (Whitworth, 1958). With a limited sample of premolars it is difficult to appreciate the small metric differences between the Arrisdrift form and *D. pigotti* from Kenya. The impression is that the p/4 and p/2 could be slightly larger in the Namibian form, as could be the case with the m/3.

Major morphological differences occur in the P3/, but this tooth is only represented by a single specimen at Arrisdrift, which has a more primitive morphology with a low, poorly developed lingual cusp. In contrast, in the P3/ of *D. pigotti* (Whitworth, 1958, Fig. 5) the lingual cusp is clearly better developed. This is reflected in the dimensions of the two teeth, the Arrisdrift one being somewhat longer and narrower than those of *D. pigotti* from East Africa.

The few dental differences pointed out between the Arrisdrift tragulid and *D. pigotti* could be interpreted in terms of the Namibian form being at a less primitive evolutionary stage, but considering the limited sample it does not seem possible to separate the two forms at the specific level. We thus classify the Arrisdrift species as *Dorcatherium* aff. *pigotti*.

Postcranial skeleton (anatomical terms and orientation of post cranial bones are based on Barone, 1989).

Vertebrae. No tragulid vertebrae have been positively identified in the Arrisdrift collection.

Scapula. No tragulid scapulae have been recognised at Arrisdrift.

Humerus (Table 2; Pl. 2, Figs 1-2). The sample includes a complete humerus, a specimen lacking the proximal epiphysis, possibly juvenile, and a distal fragment. The morphology of these humeri is closely similar in general features to that of *Hyemoschus aquaticus*. In AD 426'98, the only specimen with its proximal epiphysis, the greater and lesser tubercles and the lateral border of the articular head are somewhat damaged. However, from what is preserved, it appears that it does not differ greatly from the extant species, and the diaphysis is comparable with its similarly compressed section. The lesser tubercle is low, as in *Dorcatherium crassum* (Morales & Sanchez, in press); the tuberosities for the greater teres muscle and the tricipital line are quite strong, as in extant *Hyemoschus*. The tuberosity for the lesser teres muscle is quite well marked in the tragulid from Arrisdrift; in contrast, the deltoid tuberosity is not discernible, as in *D. crassum*, in which it has no appreci-

Table 2: Measurements of the humerus, metacarpal III, metacarpal IV, tibia and metatarsal III+IV of Arrisdrift Tragulidae. (* = length of a subadult individual lacking the proximal epiphysis. ** diaphysis measurements (DAP, DT) were taken 34 mm from the distal extremity and the pulley measurements (DAP dist. and DT dist.) were taken on only one pulley. *** diaphysis measurements (DAP, DT) were taken 32 mm from the distal end). (Abbreviations : DAP – Anteroposterior diameter; DT – Transverse diameter; prox. – proximal; dist. – distal; max. – maximal; func. – functional).

HUMERUS	Length	DAP prox. max.	DT prox. max.	DAP diaphysis	DT diaphysis	DAP dist. max.	DT dist. max.	DAP distal func.	DT distal func.
PQAD 465						12.8	16.9	8.3	13.8
AD 57'96				10	8.3	13.1	17.3	7.6	15
AD 426'98	95.4	26.2	21	10.5	8.2	13.4	19	8	17
METACARPAL III									
PQAD 1694	43.5	7.6	6.8	3.9	6.6	7.2	7.2		
AD 451'00	45.2	7.7	6.8	4.2	6.3	6.4	6		
METACARPAL IV									
AD 600'99	42.7	5.1	7.2	3.5	5.3	6	6.4		
TIBIA									
PQAD 2696	131.5	24.2	25.2	14	13	11.8	15.8		
PQAD3127						12.3	15.3		
PQAD 646						11.8	15.2		
PQAD 1567						12	15.8		
AD 704'94		24.3	23.7						
AD 32'97	128.3	25.5	24.6	10.7	11		15.7		
AD 599'97*	118.6					11.4	15		
AD 301'98	>128.5	26.1	25.3	13.2	11.5	12.6	15.8		
AD 89'98			24.8						
METATARSAL III+IV									
PQAD 50**			c.a. 13.3	6.3	13.7	8.5	8.2		
AD 357'99***		c.a. 11.9		5.8	11.7				

able relief. In the distal epiphysis the trochlea has a lateral condyle which is more prominent than in *H. aquaticus* and *D. crassum*, whilst the *capitulum* is smaller, both transversely and vertically, than in these two taxa.

Ulna (Table 3; Pl. 3, Figs 1-3). There are four specimens in which two preserve the proximal epiphysis, but there is no complete specimen and the longest fragment measures 55 mm (*H. aquaticus* length is 100 mm). In this case, as in the rest of the postcranial skeleton, the overall morphology is close to that of *H. aquaticus*, the diaphysis is not fused to the radius, is likewise flat, but with a relatively greater DAP measurement and the lateral surface has a strong crest which does not occur in the extant African species, nor in *D. crassum*. The olecranon of the fossil from Arrisdrift has a slightly less quadrangular aspect because the anterior process is not as well developed and the proximal margin is somewhat more convex. The proximal lateral crest is preserved but is less developed than in the extant species and which doesn't exist in *D. crassum*. The lateral facet for the radius is flat, as in *Hyemoschus*, not presenting the slight central crest that is present in *D. crassum*, whilst the central facet which is subquadrangular and concave does not differ from the other two species.

Radius. No tragulid radii have been identified at Arrisdrift.

Magnotrapezoid (Table 4). The only tragulid carpal bone found at Arrisdrift is a magnotrapezoid. A specimen from the left side, PQAD 2358, is characteristic in having the lateral posterior condyle, where the facet for the semilunar is located, greatly elevated, as in *Hyemoschus*, *Dorcatherium naui* and *D. crassum*. Posteriorly, there is a distal process which articulates with the IIIrd metacarpal, whilst in *Hyemoschus* there is a second process in a medial position. In *D. naui* (Morales & Soria, 1981) there is a single process of large size which reaches its greatest extent in its central zone, and extends almost from one side of the bone to the other. The distal surface is quadrangular, anteriorly flattened and concave in the posteromedial region, similar to *D. naui*. In *Hyemoschus* and *D. crassum* it is triangular and much more concave, although the concavity is not as profound in this species as it is in the extant one. The lateral face has a flat and quadrate anterior facet and a semicircular posteroproximal one, which in *Hyemoschus* projects greatly laterally. As a whole, the morphology of this bone in *D. naui* and *D. crassum* is most similar to that of PQAD 2358.

Metacarpal III (Table 2; Pl. 3, Figs 4-5). Tragulid metacarpals from Arrisdrift are short and are not fused to each other, as in *Hyemoschus* and *Dorcatherium*. Two metacarpal IIIs in the Arrisdrift collection have the diaphysis somewhat more compressed antero-posteriorly and the section more constant than in *H. aquaticus*, *D. naui* and above all *D. crassum*. In this species the diaphysis is very robust with a triangular section, more similar to the extant tragulid, gradually increasing in width and anteroposterior diameter towards the distal end.

The proximal articular surface is quadrangular and flat, a feature that it shares with *D. crassum* whilst in *D. naui* and *H. aquaticus* it is more rectangular and in the latter species quite concave. The unciform facet is smaller and is located on a lower process than occurs in *Hyemoschus*. In the articulation for the Mc IV, there are differences between the species from Arrisdrift, *D. crassum*, *D. naui* and *Hyemoschus*. In *D. crassum*, the articulation for Mc IV is by way of a flat rectangular facet,

Table 3: Measurements (in mm) of the ulna of Arrisdrift Tragulidae. (Abbreviations : DAP – Anteroposterior diameter; DT – Transverse diameter; olec. – olecranon; proc. – process; anc. – anconeal; max. – maximal).

ULNA	H olecranon	DAP tuber olec.	DT tuber olec.	DAP proc.anc.	DT proc.anc.	H sigmoid	DT max.sigmoid	DAP diaphysis
AD 316'97	18	15	6.7	14.4	5	10.2	8.8	7.3
AD 471'99					5.3	10.2	9	
AD 570'99	18.6	14.5	5.3	15.9	5.8	10.5		8
AD 223'00					6		10.4	

Table 4: Measurements (in mm) of the magnotrapezoid, navicular-cuboid and astragulus of Arrisdrift Tragulidae. (Abbreviations : DAP – Anteroposterior diameter; DT – Transverse diameter; L – Length; prox. – proximal; max. – maximal).

MAGNOTRAPEZOID	DAP max.	DT anterior	DT posterior	H anterior	H posterior	
PQAD 2358	7.8	6.2	7.7	3.5	7.7	
NAVICULAR-CUBOID	DAP max.	DT max.		H anterior	H posterior	
AD 707'94	12.6	15		10.8	13.5	
AD 189'97	13.9	15.7		11.2	13.9	
ASTRAGALUS	DAP medial	DAP lateral	DT prox.	DT distal	L medial	L lateral
PQAD 1114		10.2	10.7			
AD 706'94		9.3	9.1	10.1		18.9
AD 386'99	10.4	10.9	10.9	11	19.6	21.3

which continues distally in a flat surface with a well marked insertion scar for the interosseous ligament, meaning that the union between the two metacarpals was for the most part ligamentary. In the Arrisdrift tragulid, the facet is larger, more rounded and more markedly concave and terminates distally in a small osseous process (which is in reality the distal margin), without it having important ligamentary insertion scars in this proximal part of the articulation. In *D. naui* the articulation for the Mc IV is similar to that seen in *Hyemoschus*, having a rectangular facet that inclines, thereby forming a fossette, and which exhibits a distal trapezoidal facet. In *Hyemoschus* it is almost the same, but the metapodial has a facet for the unciform which projects more laterally (a feature that occurs only in *Hyemoschus*), such that the proximal union between the central metacarpals is the strongest in this morphological sequence.

In the distal extremity, the sagittal crest is restricted to the flexor region of the facet for the first phalanx, and in this zone it is well developed, as is usual in Tragulidae, although its development is proportionally less than it is in *Hyemoschus*. Likewise the medial condyle is less developed.

Metacarpal IV (Table 2). There is only one specimen of tragulid Mc IV in the collection from Arrisdrift which shares with the Mc III a diaphysis which is antero-posteriorly compressed and a small distal condyle. In the proximal end the articular surface is triangular in outline but with a smaller anteroposterior diameter relative to *H. aquaticus* and *D. crassum*, but closer to that of *D. naui* from Los Valles de Fuentidueña, Spain. The facet for the Mc III is large, convex and elongated distally. In *Hyemoschus*, this facet forms an articular apophysis that slots tightly into the corresponding fossette of the Mc III. In *D. crassum* the morphology of the facet for Mc III is much simpler, forming a triangular, convex articular surface which contacts the facet for the unciform. The shape of this facet in *D. naui* is close to that observed in *Hyemoschus*, but the projection does not have marked crests. Similar to what occurs in the Mc III, the distal sagittal keel is restricted to the flexor zone of the distal facet, where it is well developed.

In summary, taking into account the morphology of the central metacarpals, it is possible to propose a morphological sequence in which the extremes occur in *D. crassum* (the most primitive) and *Hyemoschus* (the most derived); in this succession there is a tendency to develop a series of structures which impart rigidity to the proximal articulation of the two metacarpals.

Pelvis. No tragulid pelvis has been identified at Arrisdrift.

Femur (Table 5; Pl. 3, Fig. 6). Two well preserved femora and a distal fragment can be attributed to this species. The morphological characters correspond to a tragulid similar to *Hyemoschus* or *Dorcatherium crassum* although appreciably less robust, and clearly different from that of the bovid *Namacerus gariepensis* (Morales *et al.*, this vol.) which is about the same size and is also present at the site.

In the proximal epiphysis of the tragulid femur the head is more rounded and smaller and the greater trochanter is lower and narrower, barely extending beyond the top of the head. The lesser trochanter, as in *D. crassum*, is less developed than in *Hyemoschus*. The ilio-psoas muscle inserts onto this trochanter, participating in abduction and lateral rotation of the femur.

The diaphysis is gracile, and as in *D. crassum* and *Hyemoschus*, quite a bit straighter than in bovids. Its section is also distinct from that of bovids, being subtriangular rather than almost circular, with the posterior surface quite flat, limited by two crests and the anterior surface is relatively sharp.

In the distal end there are also differences from bovids such as *Namacerus*. The anterior trochlea is narrow and short with parallel lips. The distal two posterior condyles are not so different in size and the intercondylar *fossa* is wide and deep.

Tibia (Table 2; Pl. 4, Fig. 1). The tibia is the best represented tragulid postcranial bone in the Arrisdrift collection. There are 9 specimens which can clearly be assigned to this ruminant, three right tibia which are complete and belong to adult individuals, one left tibia belonging to a sub adult which lacks the proximal epiphysis, two proximal ends (one left, the other right) and three distal ends (one right, two left). The minimum number of individuals is thus four adults and a subadult.

The tragulid tibiae from Arrisdrift are considerably shorter than those of *Namacerus* and differences in the proximal end consist of the smaller size of the anterior tuberosity, the straight medial border, and weaker groove for the extensor and incision for the popliteal. The tibial crest, however, is strong and longer, extending to the middle of the diaphysis. The articular surface and the lateral eminence are more elevated than the medial ones, as in *D. naui*, but different from *H. aquaticus* and *D. crassum*, in both of which the eminences are the same height. These two species have slightly more curved diaphyses and flatter surfaces than the Arrisdrift fossils.

The distal epiphysis is small and rectangular with almost flat surfaces. There is not much difference in size or in the section of the diaphysis from those of *Namacerus* but the orientation of the cochlear facets is more oblique with respect to the sagittal axis than in the bovid. In *Hyemoschus* the distal diaphyseal section is triangular while the epiphysis is trapezoidal with concave faces and more prominent facets, especially the

Table 5: Measurements (in mm) of the femur of Arrisdrift Tragulidae. (Abbreviations : DAP – Anteroposterior diameter; DT – Transverse diameter; prox. – proximal; dist. – distal; max. – maximal; l. troch. – lesser trochanter; diaph. – diaphysis).

FEMUR	Length	DAP head	DT head	DAP l.troch.	DT prox.max.	DAP diaph.	DT diaph.	DAP dist. max.	DT dist. max.
AD 139'97								30.3	24.9
AD 597'97	120	12	18	12.7	26.9	12	10.6	28.5	23.1
AD 541'98	125			16		12.3	11.1	29.4	23.1

medial one. The morphology of the distal end is similar to that of *D. naui* from Los Valles de Fuentidueña (Spain), sharing a very small and blunt medial maleolus lower than the anterior process, which is also poorly developed. Nevertheless the anterior process is more weakly developed in *D. naui* than in the Arrisdrift tragulid. There is no maleolar incision and the facet which is narrow and concave, is not subdivided. The fibular groove is shallow without bony margins and the hollow for the dorsomedial part of the maleolar is weakly marked. In all these features it differs from both *Hyemoschus* and *D. crassum*. All of them have a well developed groove for the tendon of the medial digital flexor muscle.

Astragalus (Table 4; Pl. 4, Fig. 2). Contrary to the usual situation, astragali are not very abundant at Arrisdrift, only three specimens being known, of which AD 285'99 is the best preserved. The size is the same as the specimen figured by Whitworth (1958, fig. 6) which he attributed to *Dorcatherium pigotti*. The length is similar to that of *Namacerus gariepensis* the other small ruminant present at the site.

The inclination of the proximal trochlea with respect to the distal one is less marked than in *D. naui*, *D. crassum*, or *Hyemoschus*, resembling more closely the angle in extant *Tragulus*. Also, in its narrowness and compression it is more like *Tragulus* than *Hyemoschus*, and is thus similar to *D. naui* in which the values for DT and DAP are small relative to the length.

In the proximal trochlea the lateral condyle is quite a bit wider than the medial one. Distally the valley is narrow and deep, as in *Hyemoschus* but the lateral condyle has a weaker plantar development, a feature that it shares with *D. naui* together with the presence of a plantar surface which is more concave than in the extant African species.

Navicular-cuboid (Table 4; Pl. 4, Figs 4-5). Two left navicular-cuboids from Arrisdrift are well preserved and the same size as specimen 738'52 from Rusinga, Kenya (Whitworth, 1958, fig. 6, measurements on page 11 : DT 13.5 and DAP 12.8 mm) which the author assigned to *D. pigotti*. As with the talus, its size is similar to that of the small bovid *Namacerus gariepensis*.

Of the two facets for the astragalus, the lateral one is wider and dorsally more prominent. The two proximal posterior processes are low but differ from the situation in bovids by having the lateral one higher than the medial one. In this it is similar to *Hyemoschus* and more markedly so to *D. naui*. In *D. crassum* and *Tragulus* the posterior processes are subequal in height. The calcaneal facet is long, almost reaching the distal border and the lateral groove does not contact it, the same as in *D. naui*. However, in *H. aquaticus* this groove limits distally the calcaneal facet, the length of which is more reduced.

The ectomesocuneiform is fused to the navicular-cuboid as in *D. crassum*, *D. naui* and *Hyemoschus*. In the distal surface the anterior facets are strongly curved and apart from the smaller size of the posterior one for the IVth metatarsal, is not very different from that of *H. aquaticus*, *D. crassum* or *D. naui*, neither are they different on the posterior surface, which is flat with the distal lateral process very pronounced. As for its proportions, it has lower values relative to DAP than the above species and, as in *Hyemoschus* differs from *D. naui* by its relatively greater height.

Metatarsals III+IV (Table 2; Pl. 4, Fig. 5). There is no complete specimen so we do not know the total length. PQAD 50 is broken into two fragments which are missing a piece of bone between them. The proximal fragment is small and poorly preserved, the distal one measures 37.5 mm long. AD 357'99 is from a smaller individual and has lost the distal extremity.

Its morphology is similar to that of *Hyemoschus aquaticus*. The two metatarsals are fused for the proximal two thirds of each bone and preserve independent cavities. The conjoined diaphysis is very straight with the plantar surface flat and the section antero-posteriorly compressed. In *D. crassum* and *H. aquaticus* the section is less compressed, especially in the former, and the plantar surface is concave. The metatarsal sulcus is proportionally narrower than in *Hyemoschus* and *D. crassum* being especially wide in the latter. The sulcus for the lateral extensor tendon runs more parallel to the metatarsal sulcus in the Arrisdrift tragulid than it does in *D. crassum*, in which its trajectory is oblique. The metatarsals of *D. naui* from Los Valles de Fuentidueña (Spain) are not well preserved, and although they have a more compressed section than in *D. crassum* and the plantar surface is slightly concave, they do not reach the extreme of *D. pigotti*.

In the proximal end of AD 357'99 there are two anterior kidney-shaped facets with a regular diameter and rounded anterior border. The anteromedial facet is concavo-convex. In *Hyemoschus* however, they are dorsally augmented with an angular border which continues onto the diaphysis, thereby forming a keel. This is particularly visible on the medial facet, which is strongly concave. In this *D. crassum* is similar to *Hyemoschus* although more moderately.

The fossette for articulation with the Mt II is weaker in *Hyemoschus* and in the tragulid from Arrisdrift than in *D. crassum*, being large in the latter species. In the case of the Mt III-IV of the Arrisdrift species, a small remnant of the proximal end of Mt II can be seen fused to the Mt III.

Phalanges. No tragulid phalanges have been recognised in the Arrisdrift collection.

Discussion and conclusions

The tragulid postcranial bones described and figured by Whitworth (1958) show the same type of morphology that occurs at Arrisdrift, corresponding to that known in the European tragulid *Dorcatherium naui*. It differs somewhat from *Dorcatherium crassum* and *Hyemoschus*. The talus from Arrisdrift falls close to the size mean of *Dorcatherium pigotti*. Thus the postcranial and dental remains both suggest close morphometric affinities with *D. pigotti*. Until now, none of the African tragulids show a close relationship to the extant Asian genus *Tragulus*.

From *Dorcatherium crassum* to *Hyemoschus aquaticus* we observe a progressive accumulation of structures in the proximal articular zone between the central metacarpals, and between the central elements of the distal carpal line, which tend to reduce the capacity for movement in this articulation. The departure point is the articular morphology observed in *D. crassum* from which it is easy to derive the morphologies of *D. naui* and *H. aquaticus*. It progresses from a more lax union which permits relatively great movements of the joint (the ligamentous union of *D. crassum*) to a more stable joint, comprising the original facet but with additional apophyses and fossettes which slot together perfectly to the extent that they restrict movements in the proximal articulation (the case in *D. naui* and *H. aquaticus*). Besides, in *Hyemoschus* the lateral extension of the unciform facet in McIII effectively limits intercarpal and intermetacarpal movements. *Dorcatherium pigotti* has developed its own blocking structures (large and rounded facet in the McIII, with a small distal apophysis, and the articular process also large in the McIV), such that the proximal intermetacarpal articulation, without being as rigid as in *D. naui* and *H. aquaticus*, was more restricted in its movements than in *D. crassum*.

In the tarsal articulation, the greater development of the medial maleolus of the tibia seen in *D. crassum* and *H. aquaticus* indicates greater power in the colateral ligament in these two taxa, and therefore a greater rigidity of the tarsus, which depends greatly on the action of this ligament.

Overall, each of the structures related to the digital flexor ligaments are strong, not only in *D. pigotti*, but also in tragulids in general, which indicate great power in these ligaments, and probably a lower capacity for "automatic response" of the tendons involved in the suspensory apparatus than occurs in the Pecora.

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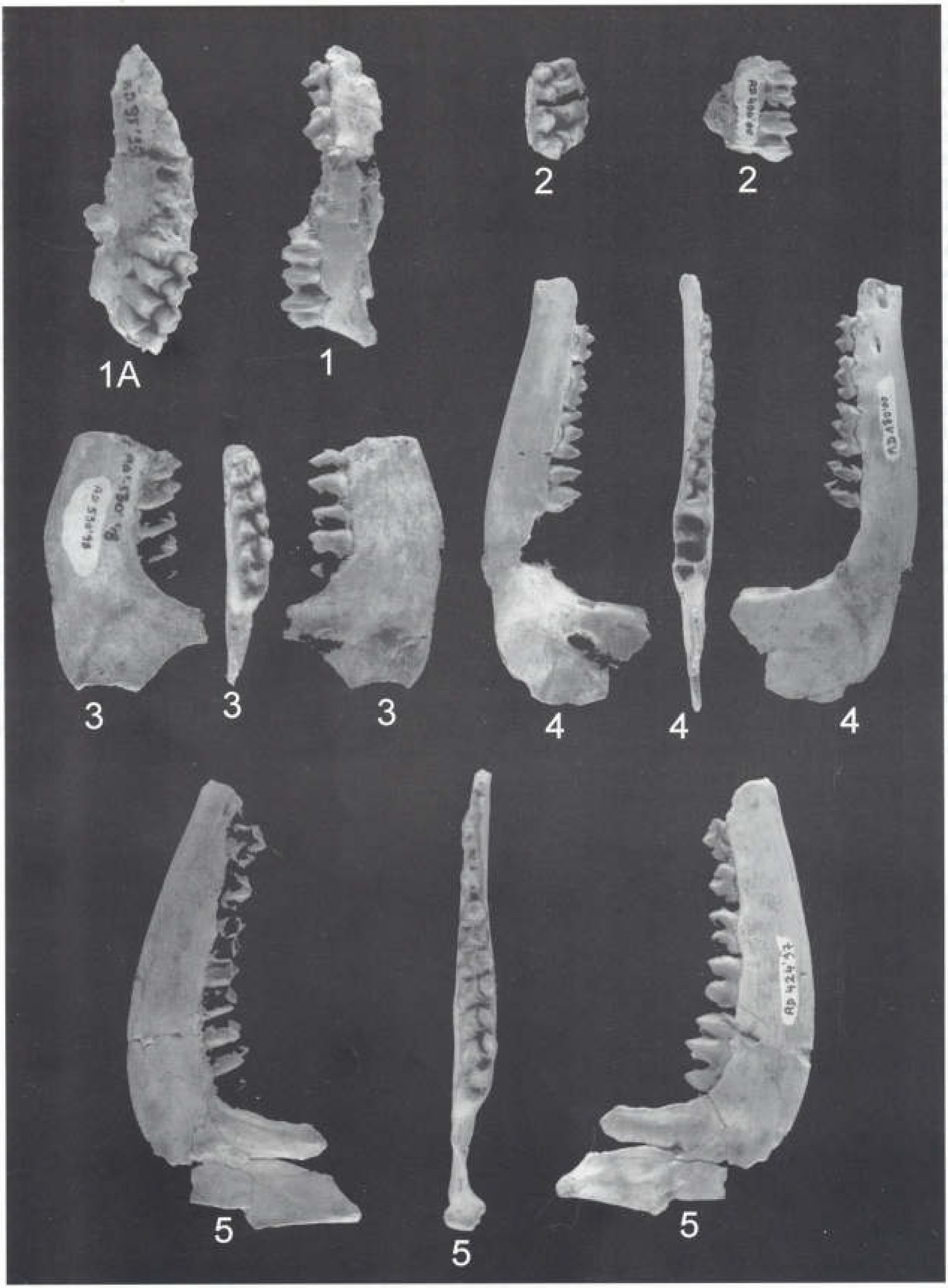

Plate 1: *Dorcatherium* aff. *pigotti* (natural size)

Figure 1, AD 95'95, left maxilla with P3/-P4/, M2/-M3/, a) occlusal; b) buccal view.
Figure 2, AD 400'00, right maxilla with M1/-M2/, a) occlusal; b) bucal view.
Figure 3, AD 530'98, left mandible with m/2-m/3, a) buccal; b) occlusal; c) lingual view.
Figure 4, AD 180'00, right mandible with d/2-d/4, m/1, a) lingual; b) occlusal; c) buccal view.
Figure 5, AD 424'97, left mandible with p/3-m/3, a) buccal; b) occlusal; c) lingual view.

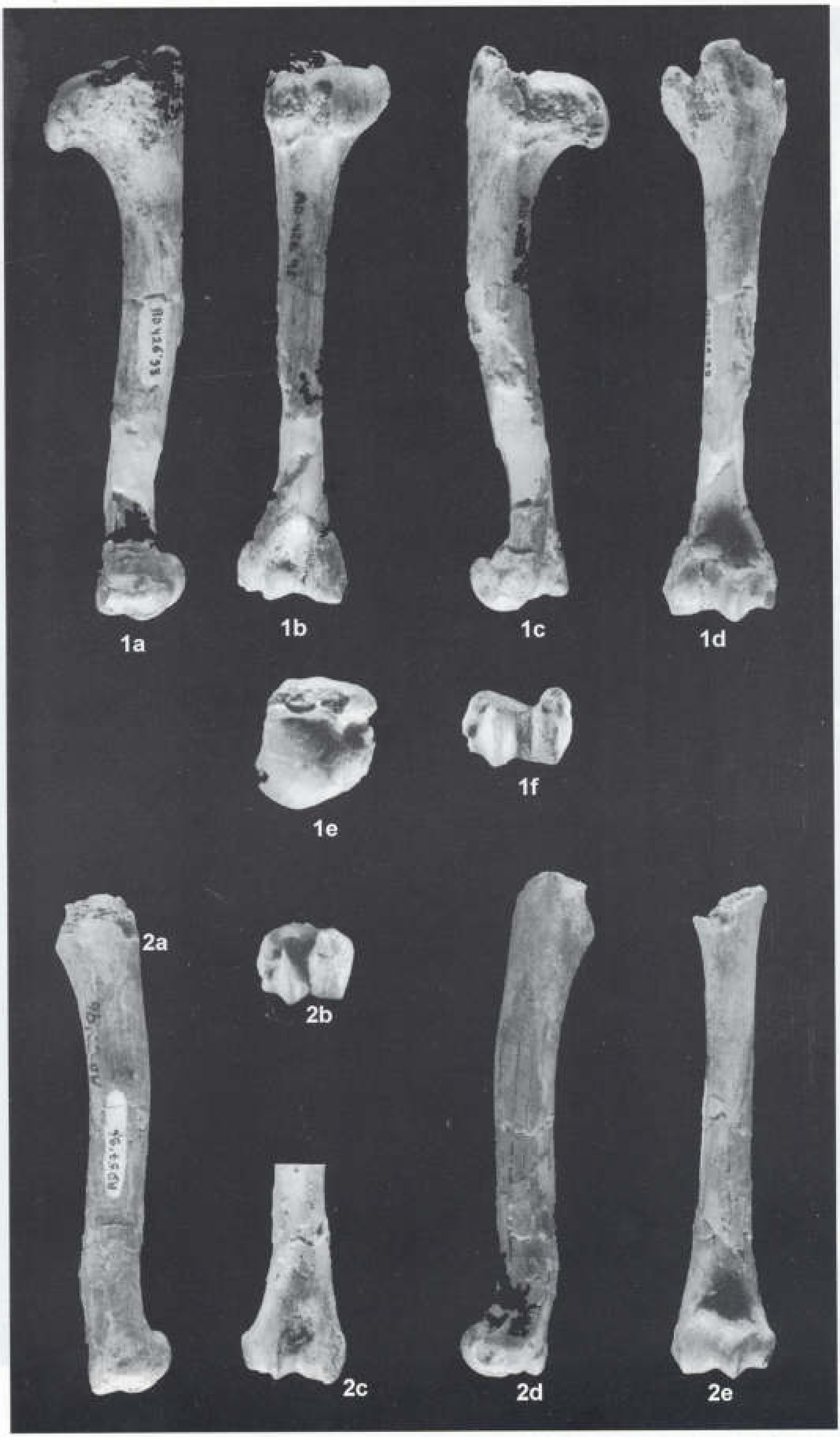

Plate 2: *Dorcatherium* aff. *pigotti* (natural size)
Figure 1, AD 426'98, left humerus, a) medial; b) posterior; c) lateral; d) anterior; e) proximal; f) distal views.
Figure 2, AD 57'96, left humerus lacking proximal epiphysis, a) medial; b) distal; c) posterior; d) lateral; e) anterior views.

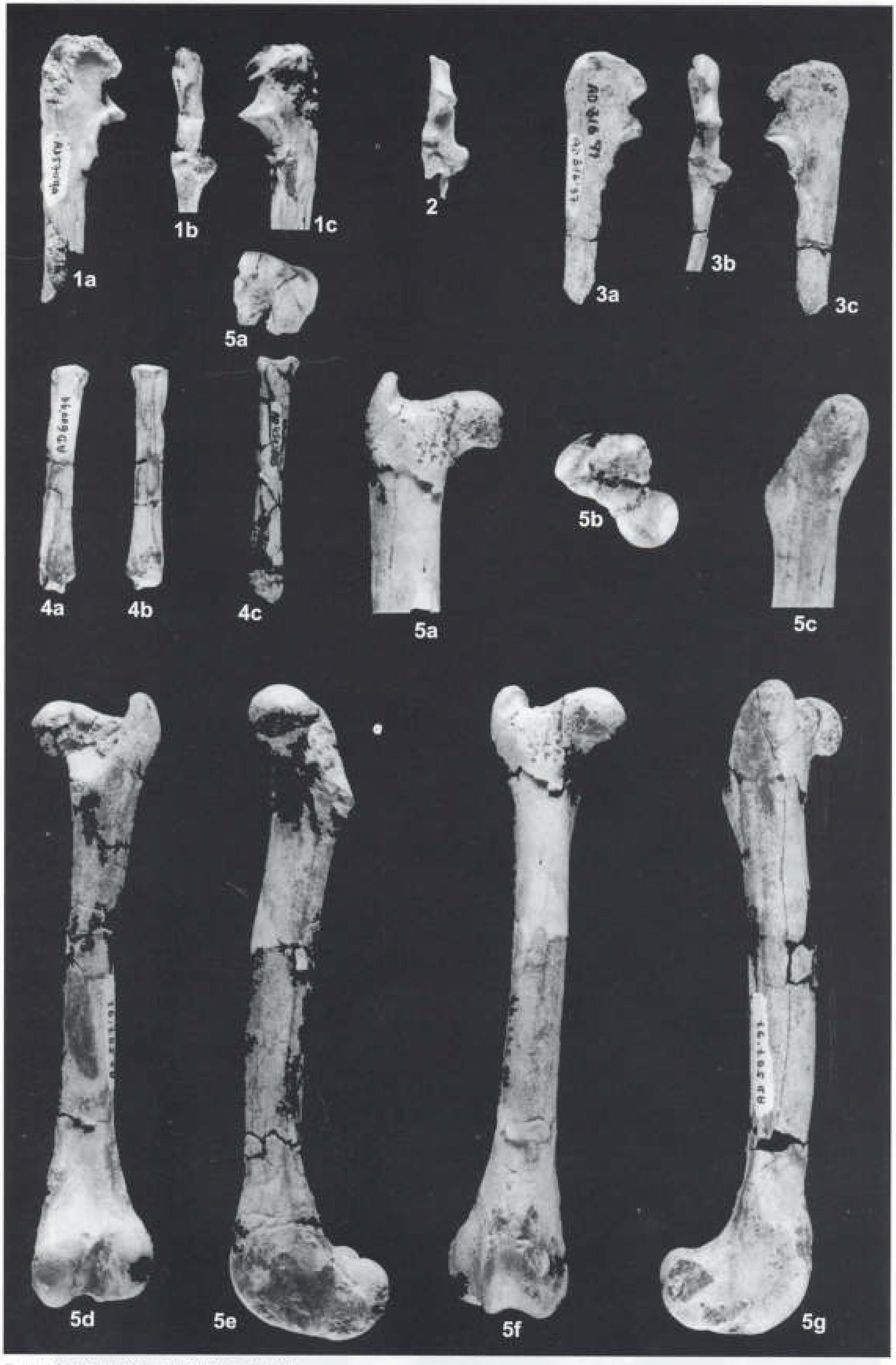

Plate 3: *Dorcatherium* aff. *pigotti* (natural size)
Figure 1, AD 570'99, left proximal ulna, a) medial; b) anterior; c) lateral views.
Figure 2, AD 471'99, left proximal ulna.
Figure 3, AD 316'97, left proximal ulna, a) medial; b) anterior; c) lateral views.
Figure 4, AD 600'99, right metacarpal III, a) volar; b) dorsal views
Figure 5, AD 451'00, right metacarpal III, a) proximal view (enlarged); b) dorsal view.
Figure 6, AD 597'97, right femur, a) anterior; b) proximal; c) lateral; d) posterior; e) medial; f) anterior; g) lateral views.

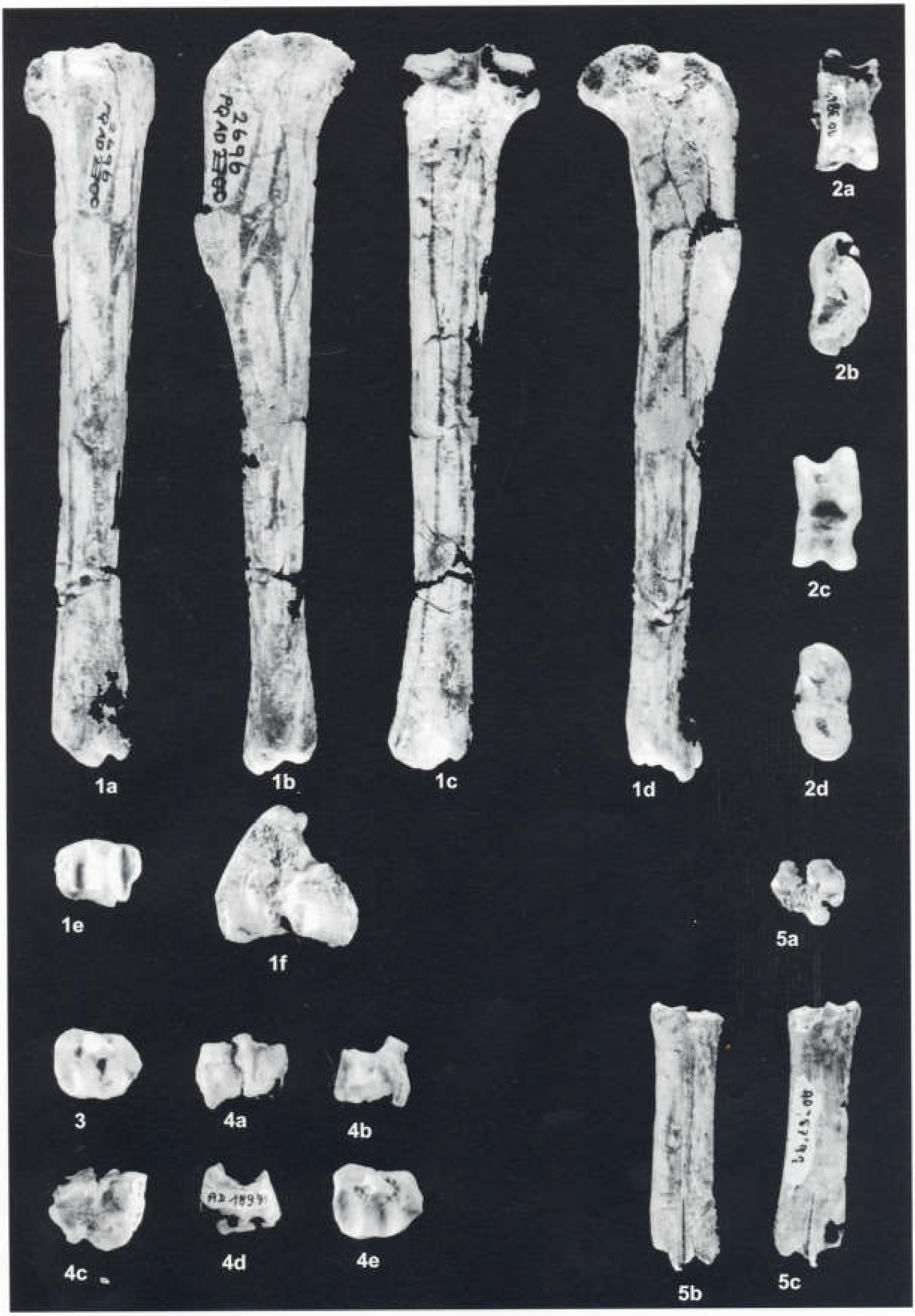

Plate 4: *Dorcatherium* aff. *pigotti* (scale bar 10 mm)

Figure 1, PQAD 2696, right tibia, a) anterior; b) medial; c) posterior; d) lateral; e) distal; f) proximal views.
Figure 2, AD 386'99, left astragalus, a) posterior; b) lateral; c) anterior; d) medial views.
Figure 3, AD 707'94, left navicular-cuboid, proximal view.
Figure 4, AD 189'97, left navicular-cuboid, a) posterior; b) lateral; c) distal; d) medial; e) proximal views.
Figure 5, AD 357'99, left metatarsal III, a) proximal; b) dorsal; c) volar views.