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GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

Dr Martin Pickford[1,2] and Dr Brigitte Senut[2]

[1]Collège de France, and [2]Département Histoire de la Terre, UMR 5143 du CNRS,
Case postale 38, 57, rue Cuvier, 75005, Paris

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Pecoran ruminants from the Early Miocene of the Sperrgebiet, Namibia

[1]J. Morales, [1]D. Soria and [2]M. Pickford
[1]*Departamento de Paleobiología, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal, 2, E-28006 Spain (e-mail:- mcnm166@mncn.csic.es)*
[2]*Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS, Case postale 38, 57 rue Cuvier, F-75005, Paris (e-mail:- pickford@mnhn.fr)*

Ruminant fossils are extremely common in the Early Miocene deposits of the Northern Sperrgebiet, but they are not very diverse. Five species of pecorans and three of tragulids are now recorded from the various sites. Among the pecorans there are two primitive climacoceratids which lack cranial appendages, and there are three species of hornless bovoids, one of which is new.

Pecoran taxa outnumber traguloids in the Namibian sites by 5:3, whereas in East African sites of similar age, the opposite is the case, with the ratio of pecorans to traguloids being 4:6. This difference reflects the more open, more arid palaeoenvironments of the Sperrgebiet compared to the more humid tropical Early Miocene palaeoenvironments of East Africa. As a guild, the Sperrgebiet ruminants show a greater propensity for a grazing component in their diet than do those from deposits of comparable age in East Africa, with fossils of folivores and omnivores present but scarce in the Sperrgebiet, but dominant and common in East Africa. In contrast, selenodont fossils, often with a light cementum cover are very common in the Sperrgebiet but in East Africa are much less common then traguloid fossils.

Introduction

Fossil ruminants have been described from the Northern Sperrgebiet on several previous occasions (Cooke, 1955; Hamilton and Van Couvering, 1977; Hopwood, 1929; Morales *et al.*, 1995, 1999; Stromer, 1923, 1924, 1926; Van Couvering and Hamilton, 1983). The predominance of pecorans over tragulids has been noted by most authors, and was used from the earliest studies as evidence in support of the idea that the region was open savannah or steppe at the time of deposition (Stromer, 1926; Braestrup, 1935).

Stromer (1924, 1926) described what he considered to be early Antilopidae, cfr *Strogulognathus sansaniensis* from Langental and *Propalaeoryx austroafricanus* from Elisabethfeld. Both of these fossil species are here attributed to the Climacoceratidae.

The first report of tragulids in the Northern Sperrgebiet was by Hopwood, 1929, on the basis of a mandible housed in the American Museum of Natural History, from "South of Lüderitz" (probably Langental). Morales *et al.*, (1995, 1999) described the new genera and species *Namibiomeryx senuti* and *Sperrgebietomeryx wardi* on the basis of fossils from Elisabethfeld. The former was attributed to Bovidae and the latter to Climacoceratidae, but these attributions are modified in this paper after more detailed study and more wide ranging comparisons with other African and European ruminants.

Methods : We describe many of the postcranial remains of Sperrgebiet ruminants in detail. This approach leads to some repetition, but we make no apologies for this, since we consider that there has been a regrettable tendency among palaeontologists to undervalue, and therefore to ignore, evidence concerning the postcranial skeleton of ruminants. As was pointed out more than a century ago (Kowalevsky, 1873) an understanding of the postcranial skeleton is essential for throwing light on artiodactyl systematics and phylogeny. In the detailed descriptions of postcranial bones, we have numbered the features described in order to facilitate comparisons between specimens. In specimens which lack parts, we simply omit the corresponding numbers, but keep the same numbers for the same parts described in other fossils. Thus number 3 in the humerus will always refer to the same feature, in this case the relative elevation of the medial lip with respect to the lateral one.

It is now no longer defensible to interpret African Early Miocene ruminants in isolation, without taking into account contemporaneous material from Europe. This is because there appear to be pervasive compositional, morphological and metric similarities between Early Miocene ruminant assemblages from Europe and Africa. This is apparent not only in different lineages, but also in assemblages of ruminants, as well as in the range of dental and postcranial adaptations exhibited by the various groups (traguloids, pecorans). We fully realise that the analysis presented here has its limitations, and that one of the major areas of weakness is related to the fact that a general revision of the Early Miocene ruminants of East Africa needs to be done before the meaning of the Sperrgebiet ruminants can be better understood. For example, there are serious questions that need to be investigated concerning the genus *Walangania* Whitworth, 1958 (Janis and Scott, 1987). The juvenile condition of the holotype of *Walangania gracilis* Whitworth, 1958, continues to pose problems, and in our opinion, until adult material from Mfwangano, Kenya, and contemporaneous deposits on Rusinga Island, Kenya, are published, doubts will persist about the proposed synonymy between *W. gracilis* and *Palaeomeryx africanus* Whitworth, 1958 (Hamilton, 1973, 1978a, 1978b; Pickford, 2002) the latter species being defined on material from older deposits at Songhor, Kenya. For the purposes of this study we accept the presence of two species of *Walangania* in East Africa, *W. africanus* in Faunal Set I (Koru, Songhor, Napak) and *W. gracilis* in Faunal Set II and IIIa (Mfwangano, Rusinga, Moroto, Moruorot).

Abbreviations : The following abbreviations are used throughout this paper:- AP – antero-posterior; BU – Bristol University; DT – Transverse diameter; DAP – antero-posterior diameter; EF – Elisabethfeld; FS – Fiskus; GT – Grillental; LT – Langental; SAM – South African Museum. Other abbreviations are explained in the legends of each appendix.

Material : Fossils collected by the Namibia Palaeontology Expedition include abundant cranial, dental and postcranial remains of pecorans, but relatively few of tragulids. The range of variation in the skeleton of *Propalaeoryx* can now be re-assessed on the basis of many specimens.

Systematic descriptions

Part 1 : *Propalaeoryx* Stromer, 1924

Suborder Ruminantia Scopoli, 1777
Superfamily Giraffoidea Simpson, 1931
Family Climacoceratidae Hamilton 1978
Subfamily Propalaeorycinae nov.

Diagnosis : Climacoceratidae without cranial protuberances, brachyodont-mesodont dentition with elongated premolars and presence of p/1.

Genus *Propalaeoryx* Stromer 1924
Species *Propalaeoryx austroafricanus* Stromer 1924

Type locality : Elisabethfeld, Sperrgebiet, Namibia.
Age : Early Miocene.

Holotype : 1926x507, right mandible with p/2-m/2 and alveolus of p/I (Stromer, 1926).

Diagnosis : In Stromer (1926, p. 118).

Material examined :

Cranial. Elisabethfeld. EF 34’01 (Pl. 1, Figs 1 A-B) occipital part of skull including the basioccipital with the occipital condyles and part of the supraoccipital. There are no great differences between this specimen and the same region in the skull of *Sperrgebietomeryx*. If the muscle insertions of the basioccipital appear to be less strong, it could be due to the state of preservation of the fossil which is not very good.

EF 35’09 (Pl. 1, Fig. 2) right temporal condyle. The articular tubercle is shorter than the one in *Sperrgebietomeryx*, but the retro-articular process in the new fossil is higher and more prominent.

Upper dentition : EF 22’01 (Pl. 1, Fig. 6; Text-fig. 1, A1-2) upper left canine is a high crowned tooth with no separation between the crown and the root. Its transverse section is subtriangular. The external wall is concave at the root but becomes convex on the crown. The internal wall has two planar surfaces well defined by a small keel located in quite an anterior position.

EF 91’01, right upper canine, is somewhat lower crowned than the previous tooth. It is reasonably well preserved, and appears to be similar in morphology to it.

EF 19’01 (Pl. 1, Figs 5A-C) a right maxilla with P2/-M3/. The M3/ has a strong parastyle united basally with the external rib of the paracone. The very strong mesostyle is as big as the metastyle, the two being almost united basally. The anterior crista of the protocone is separated from the parastyle and short posterior crista without joining the anterior crista of the metaconule. The central valleys remain joined with each other. The posterior crista of the metaconule is united to the metastyle. The ectostyle is medium sized. There is a strong anterior basal cingulum and a weaker posterior one. In the M2/ the metastyle is very weak, and the metaconule is better developed, but the rest of the tooth is similar to the M3/.

The M1/ is similar to the M2/ but is smaller and more worn to the stage where the posterior crista of the protocone and the anterior crista of the metaconule have fused. The P4/ is subtriangular. The very strong anterior style is joined basally to the buccal cusp. The posterior style is quite weak, and the buccal cusp is well marked externally. The lingual cusp is centrally positioned and its crests unite with the styles of the external wall and it possesses a small internal fold. It has a relatively strong and high basal cingulum.

The P3/ is an elongated tooth, with a strong anterior style united basally to the buccal cusp that has an external rib better developed than in the P4/. The posterior style is weak. The lingual cusp is located in a very posterior position, and possesses a small internal fold, joining the anterior style by a long crest and its anterior crest remains separated by a vertical inflexion of the internal wall of a small cusplet in an anterior position - which joins the anterior style - forming an individualised lobule of the main body of the tooth.

The P2/ is close in size and morphology to the P3/, but is narrower. The elements of the external wall are well marked, especially the robust anterior style. The lingual cusp is smaller than that of the P3/ and is more individualised.

EF 4’93 fragment of right maxilla with P4/-M/3.

EF 12’03, fragment of maxilla with M1/-M3/ in poor condition.

EF 47’94 (Pl. 1, Figs 4 A-B) right P4/ and EF 48’94 (Pl. 1, Figs 3A-B) left P3/ were found together and are of similar wear stage. The P4/ is subtriangular, being morphologically similar to specimen EF

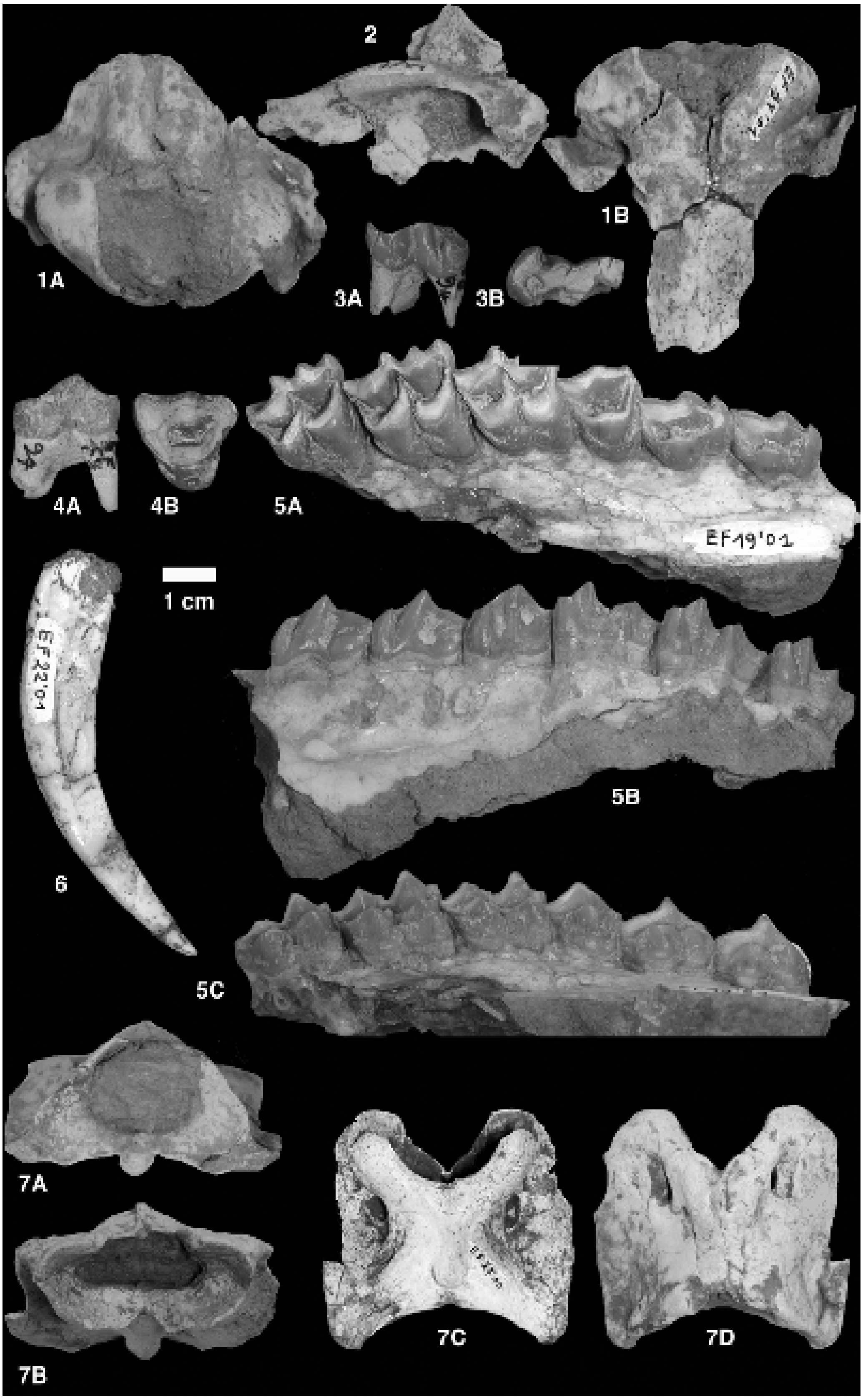
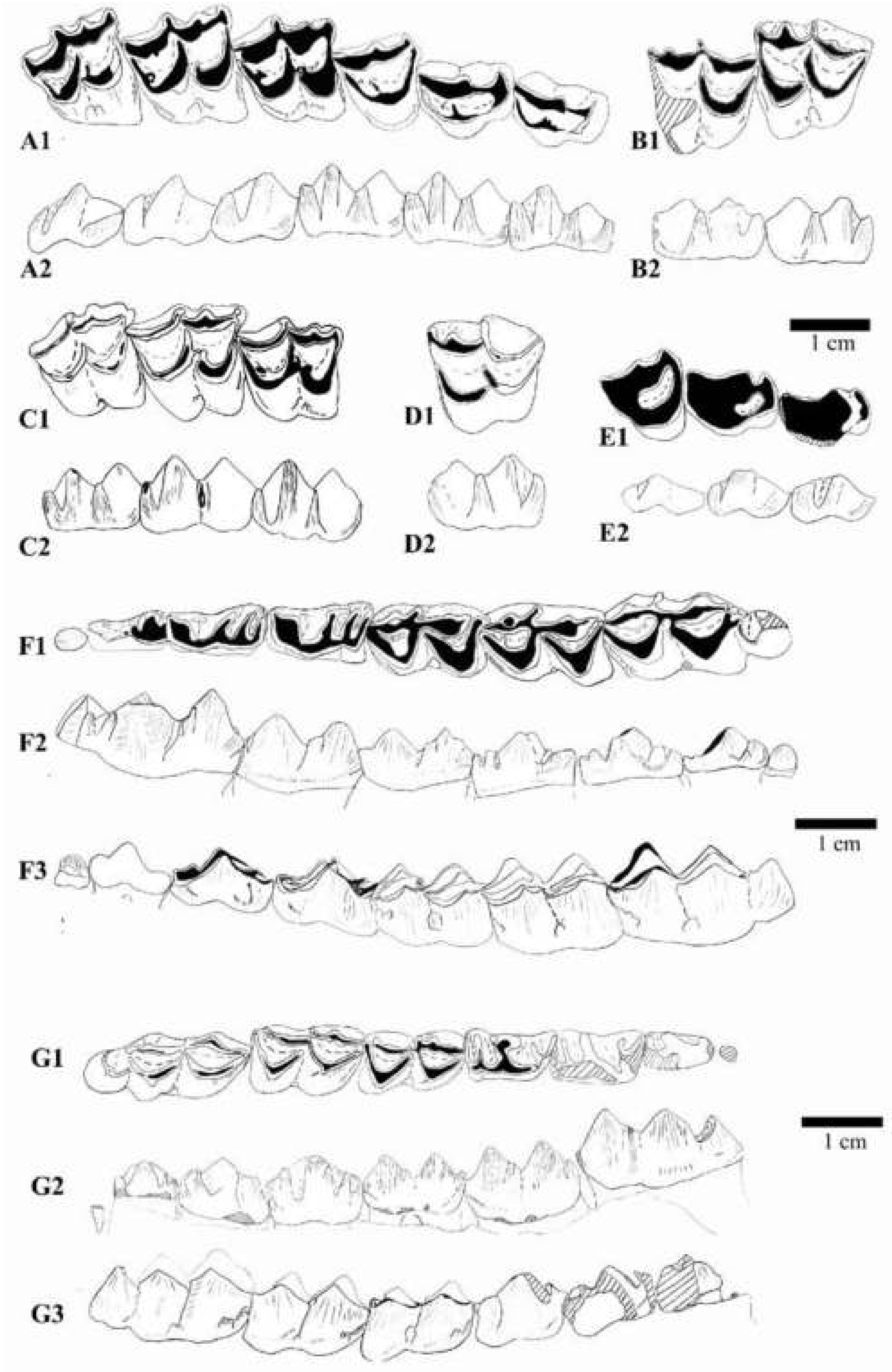


Plate 1: *Propalaeoryx austroafricanus* from Elisabethfeld. 1) EF 34’01, occipital part of skull. A) nuchal view, B) basal view. 2) right temporal condyle, basal view. 3) EF 48’94, left P3/. A) buccal view, B) occlusal view. 4) EF 47’94, right P4/. A) buccal view, B) occlusal view. 5) EF 19’01, right maxilla with P2/-M3/. A) occlusal view, B) buccal view, C) lingual view. 6) EF 22’01, upper left canine in buccal view. 7) EF 27’00, atlas. A) caudal view, B) cranial view, C) ventral view, D) dorsal view.



Text figure 1: Dentition of *Propalaeoryx austroafricanus* from Elisabethfeld (EF) and *Propalaeoryx stromeri* nov. sp. from Langental (LT) and Grillental (GT). A) EF 19'01 *Propalaeoryx austroafricanus*, right maxilla with P2/-M3/. A1) occlusal view, A2) buccal view. B) LT 199'03, left M3/-M2/ *Propalaeoryx stromeri*, B1) occlusal view, B)2 buccal view. C) LT 59'96, *Propalaeoryx stromeri* right M3/-M1/ (holotype) C1) occlusal view, C2/ buccal view. D) LT 376'96, *Propalaeoryx stromeri* left M3/, D1) occlusal view, D2) buccal view. E) LT 191'96, *Propalaeoryx stromeri* right P4/-P2/, E1) occlusal view, E2) buccal view. F) EF 30'00, *Propalaeoryx austroafricanus* left mandible with m/3-p/1, F1) occlusal view, F2) lingual view, F3) buccal view. G) GT 175'04, *Propalaeoryx stromeri* right mandible with m3/-p/2 and a small root for the p/1. G1) occlusal view, G2) lingual view, G3) buccal view.

19'01. The P3/ has lost its internal wall, but what remains is similar to EF 19'01.

Lower dentition : EF 31'01, a fragment of ascending ramus of a mandible, is poorly preserved. The height from the base of the jaw to the condylar process is 69 mm. The condylar process is eroded.

EF 28'04, a fragment of ascending ramus of a mandible, is very poorly preserved, but similar in size to EF 31'01. Outstanding is the great width of the anterior part of the ramus.

EF 3'93 (Pl. 2, Figs 2A-C) a mandible has lost the ascending ramus and the symphyseal portion. The horizontal ramus is robust and preserves the alveolus for p/1 which is uniradiculate. The lower molars possess a moderate *palaeomeryx*-fold, most marked in the m/1. The metastylid is strong and isolated. The posterior wing of the hypoconid is well separated from the entoconid. The basal pillar is of moderate size. The hypoconulid of the m/3 is simple and of moderate size. The p/4 presents a bifurcate anterior wing and complex metaconid positioned in front of the protoconid and forming an incipient internal wall. There is a deep vertical incision in the posterior part of the external wall. The p/3 is much smaller and simpler. It also has a bifurcate anterior wing, but the metaconid is a simple crest directed backwards. The p/2 is smaller than the p/3 and has a simple anterior wing.

EF 30'00 (Pl. 2, Figs 1A-C; Text-fig. 1, F1-3) a left mandible has a broken ascending ramus, but the articular condyle is preserved. It is short and robust. The mandibular foramen is well developed. The angle of the jaw is broken. The mental foramen is strong and the alveolar process for the canine and incisors is damaged. The m/3 has a lingual wall with imbricated cusps, and both the metaconid and entoconid are externally convex. The metastylid is very strong. The cristids of the protoconid unite with those of the metaconid, completely enclosing the anterior lobe. The anterior cristid of the hypoconid also unites with the anterior one of the entoconid whereas the posterior cristid of the hypoconid joins a columnar hypoconulid - weakly separated from the entoconid - and to the anterior cristid of the hypoconulid. The ectostylid is moderate and there is a strong cingulum at the base of the protoconid. The m/2 differs from the above tooth by the separation between the anterior cristids of the protoconid and metaconid and the absence of an entoconulid. That is to say that the posterior cristids of the hypoconid and the entoconid remain well separated. The ectostylid and the anterior cingulum are weaker than in the m/3. The m/1 is more deeply worn than the other molars and presents a strong union between the anterior cristids of the metaconid and protoconid. In contrast, the anterior cristid of the hypoconid does not fuse with the anterior cristid of the entoconid.

In the p/4, there is a strong vertical incision postero-buccally, the cusp and postero-lingual stylids are oblique and are practically united together and with the posterior cristid of the mesio-lingual cusp. The anterior wing is bifurcate. The p/3 is simpler than the p/4, differing from it by the absence of the meso-lingual cusp (only a cristid obliquid) and the absence of the vertical incision in the external wall.

The p/2 is like the p/3 but is somewhat shorter and narrower with more bunodont cusps. There is a small p/1 with a rounded crown.

EF 31'00, a left mandible in poor condition, is slightly smaller than EF 30'00. The most obvious difference is in the m/2 which has a better separation between the posterior cristids of the hypoconid and entoconid.

SAM PQN 50, a right mandible in relatively poor condition, has the m/3 which shows a moderate metastylid and a closed hypoconulid. The anterior cristid of the hypoconid is isolated, and the entoconulid is of moderate size. In the m/2 the advanced stage of wear results in the union of the anterior cristids of the metaconid and protoconid closing the front of the lobe. The ectostylid is strong in the three molars. The premolars are poorly preserved.

Postcranial skeleton :

Atlas. EF 27'00 (Pl. 1, Figs 7A-D) is an atlas which is somewhat bigger than the type material of *S. wardi* (Morales *et al.*, 1999) and is morphologically similar to it. It differs significantly from the atlas LT 21'00 attributed to *Propalaeoryx stromeri*, even though both present a typical quadrangular morphology.

1.- Almost perfectly quadrangular, its cranio-caudal length of 46.5 mm is similar to the greatest distance between the borders of the wings 45.9 mm.

2.- Laterally the wings are very straight.

3.- In dorsal view the alar and intervertebral foramina are located in the same depression. The dorsal tubercle is high and sharp. The dorsal angle is sharp, triangular, equal to the incisure which is well marked.

4.- In ventral view, the ventral tubercle is well developed, located relatively close to the caudal margin, and a long way from the cranial border. The wings which are well differentiated from the vertebral body, are x-shaped. The alar foramina are relatively big. The ventral arch is also acute, but not as much as the dorsal one, and there is a ventral incisure.

5.- In cranial view, the vertebral foramen is elliptical, compressed dorso-caudally. The articular facets for the occipital condyles, are big and quite vertical.

6.- In caudal view, the caudal articular surfaces are wide. The caudal tubercle of the wing is barely developed. The vertebral foramen is almost circular.

Scapula: EF 22'00 (Pl. 3, Figs 1A-B) a very eroded right scapula, has two bite marks.

1.- The supraglenoid tuberosity which is eroded

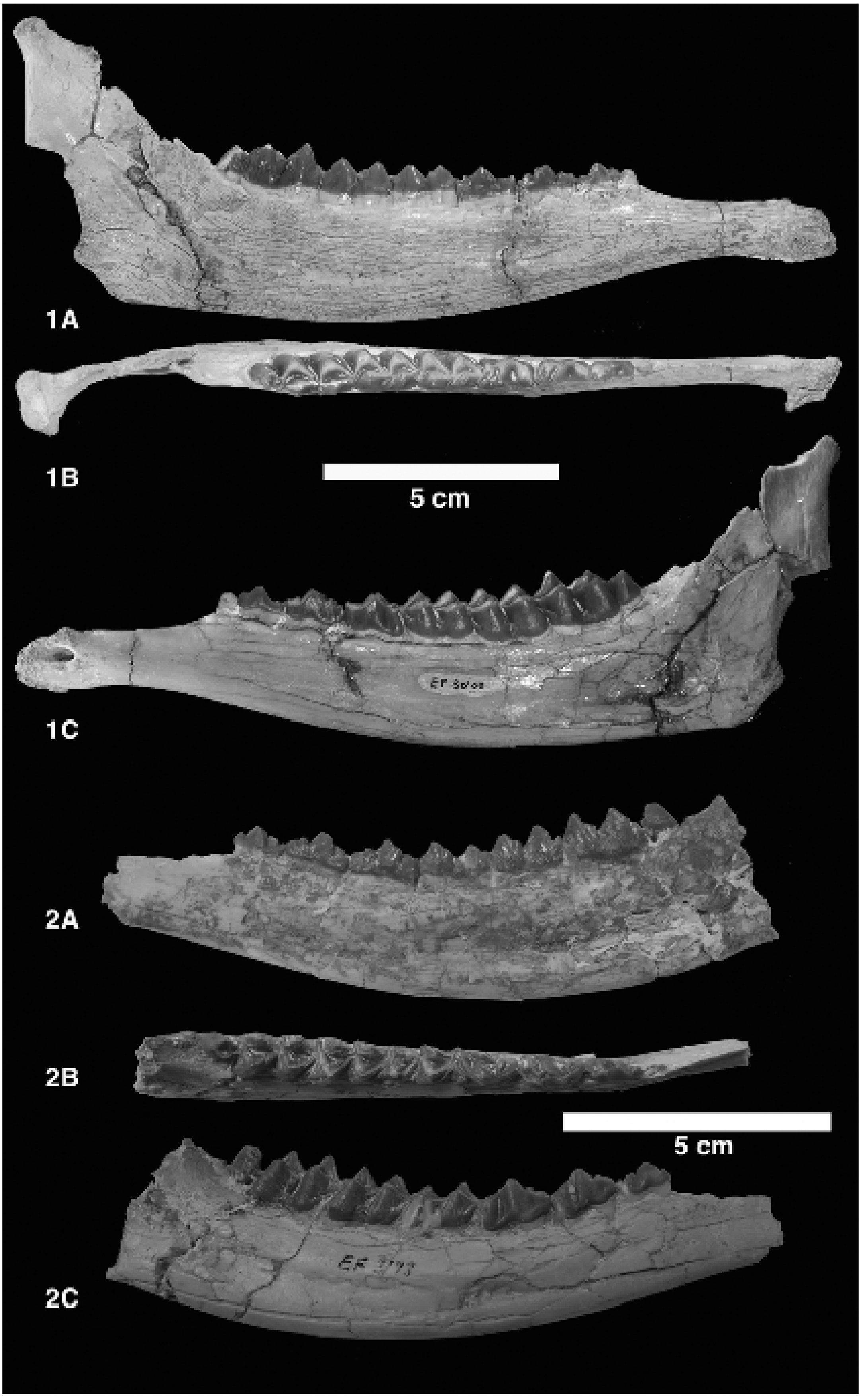


Plate 2: *Propalaeoryx austroafricanus* from Elisabethfeld. 1) EF 30'00, left mandible. A) lingual, B) occlusal view, C) buccal view. 2) EF 3'93, right mandible. A) lingual view, B) occlusal view, C) buccal view.

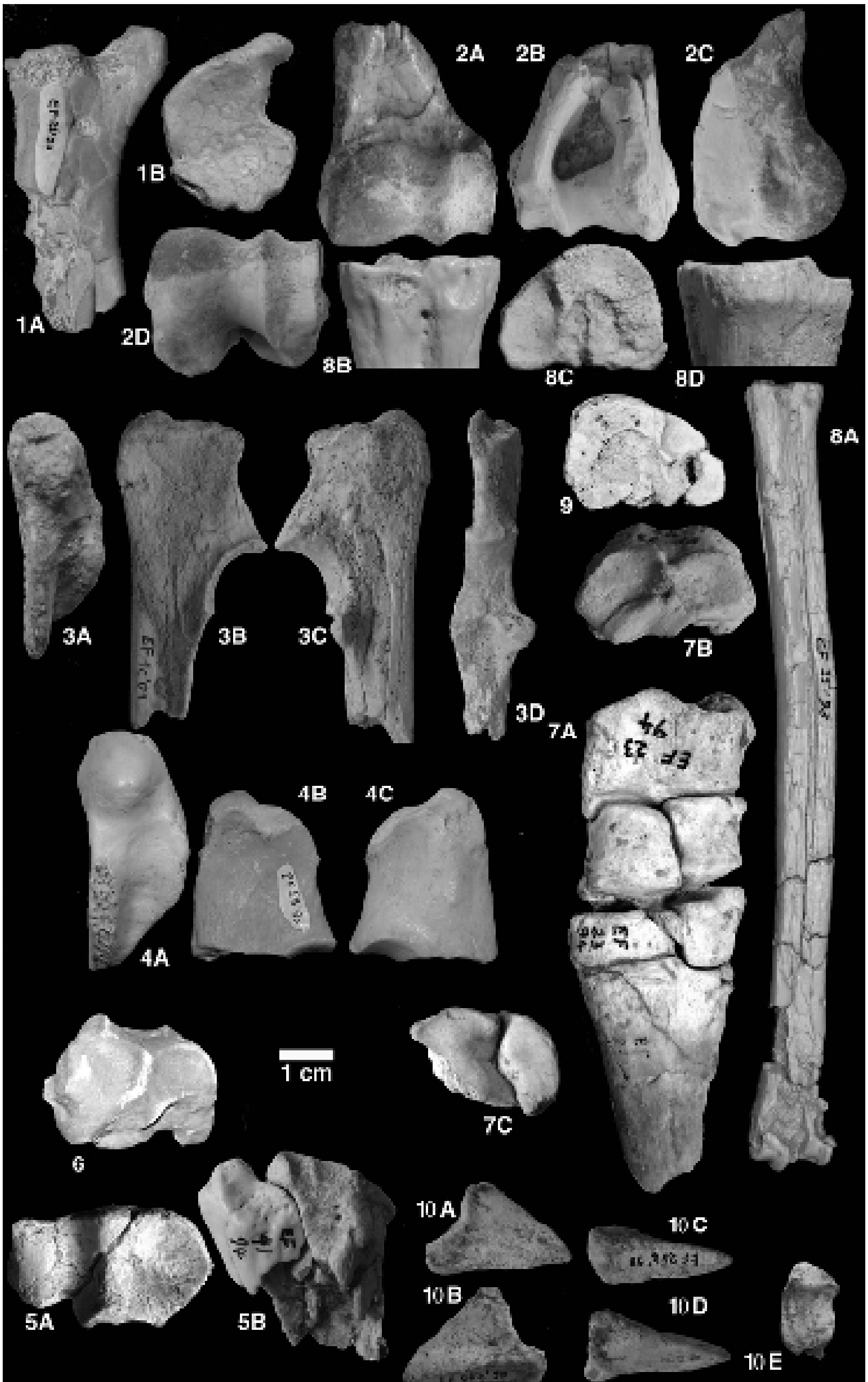


Plate 3: *Propalaeoryx austroafricanus* from Elisabethfeld. 1) EF 22’00, right scapula. A) medial view, B) proximal view, glenoid cavity. 2) EF 22’93, distal right humerus epiphysis. A) cranial view, B) caudal view, C) medial view, D) distal view. 3) EF 1c’04, proximal left ulna fragment. A) proximal view, B) lateral view, C) medial view, D) dorsal view. 4) EF 59’96, proximal left ulna fragment. A) proximal view, B) lateral view, C) medial view. 5) EF 41’94, proximal left radius epiphysis. A) proximal view, B) palmar view. 6) EF 24’94, distal left radius epiphysis, distal view. 7) EF 23’94, associated distal radius epiphysis, carpals and proximal fragment of metacarpal III-IV (left side). A) dorsal view, B) radius distal view, C) scaphoid and semilunar proximal view. 8) EF 35’93, left metacarpal III-IV. A-B) palmar view, C) proximal view, D) dorsal view. 9) EF 66’01, proximal right metacarpal III-IV fragment. in proximal view. 10) EF 25c’98, IIIrd phalanx. A) medial view, B) lateral view, C) plantar view, D) dorsal view, C) proximal view.

has a pedicle that is narrower than in LT 68'96 but is more similar to LT 45'00.

3.- There is no coracoid process. The lateral profile of the glenoid cavity is similar to that of LT 45'00, and distinct from LT 68'96.

5.- The acromion is broken, but the base is very close to the glenoid cavity (as in the other two fragments from Elisabethfeld). This specimen from Elisabethfeld is the same size as LT 68'96 and is much smaller than LT 45'00, taking into account the erosion.

EF 68'01 left scapula.

4.- There is no infraglenoid tubercle, but there is a long fossa. Between the caudal border and the base of the acromion there are two lines for muscle insertion that start at the lateral margin of the glenoid cavity, the more caudal one joins the caudal border of the scapula. In the most ventral part a zone of muscle insertions is developed (medial side eroded).

EF 67'01, right scapula. In this specimen the zone of muscle insertion of the caudal border is displaced towards the medial side.

EF 13'94, left scapula, small but poorly preserved.

Humerus : EF 22'93, distal epiphysis.(Pl. 3, Figs 2A-D; Text-fig. 1, A1-5).

1.- The trochlea is subquadrangular.

2.- The medial epicondyle, of moderate size, and is somewhat higher than the lateral margin of the trochlea.

3.- The medial lip is more elevated than the lateral one.

4.- The medial lip is quite wide and symmetrical.

5.- The capitulum is long and rises laterally.

6.- Nevertheless its projection reaches slightly beyond the gully of the trochlea.

7.- The gully is quite symmetrical.

8.- The lateral epicondyle is low and weakly developed.

9.- The crest of the lateral epicondyle is divergent with respect to the medial epicondyle, making the olecranon fossa markedly asymmetrical.

10.- The medial surface has strong relief centrally.

11.- The lateral surface has a deep circular fossa.

12.- In the lateral surface a strong protuberance is developed in contact with the radial fossa.

EF 8a'93, distal right epiphysis. (Text-fig. 3, B1-5).

1.- The trochlea is subquadrangular.

2.- The medial epicondyle, of moderate size, is a little higher than the lateral border of the trochlea.

3.- The medial lip is not very elevated, almost at the same height as the lateral lip.

4.- The lateral lip is quite wide and symmetrical.

5.- The capitulum is long and rises laterally.

6.- The projection of the capitulum remains slightly above the gully of the trochlea.

7.- The gully of the trochlea is quite symmetrical.

8.- The lateral epicondyle is low and little developed.

9.- The crest of the lateral epicondyle is almost parallel to the crest of the medial one, which makes the olecranon fossa symmetrical and very deep.

10.- The medial face has gentle central relief, but the zone has been somewhat eroded.

11.- The lateral surface has a deep circular fossa.

12.- In the lateral surface there is a weak protuberance in contact with the radial fossa.

Other specimens : EF 1e'04 distal left humeral epiphysis with eroded capitulum. EF 36'94 distal epiphysis, similar morphology to EF 8a'93, but smaller (wind eroded).

Ulna : EF 1c'04 (Pl. 3, Fig. 3A-C) is a well preserved left ulna associated with a distal humerus and an eroded fragment of proximal radius. The diaphysis is broken about 1.5 cm from the lateral radial facet. It is narrow with small transverse diameters (in the summit and the middle of the olecranon).

1.- The olecranon is quadrangular, moderately high.

2.- The olecranon has two crests, the medial one is high and long, but narrow, its proximal border is at right angles to the sagittal axis, whereas the lateral one is lower and shorter. The valley is moderately deep. The palmar tuberosity is a bit higher than the apex.

3.- The anconeal process extends further dorsally than the dorsal proximal process. The dorsal border of the olecranon is curved.

4.- The radial notch is shallow and wide.

5.- The medial facet is stepped.

6.- The lateral radial facet is conical with two proximal crests.

EF 59'96 (Pl. 3, Figs 4A-C) a left ulna broken in the middle of the sigmoid notch.

1.- The olecranon transverse diameter is bigger and there is a medial tuberosity. The postero-lateral proximal zone is a bit eroded as is the olecranon tuberosity.

2.- The olecranon has two crests, the medial one is eroded and the lateral one is shorter and lower, but a bit stronger than in EF 1c'04 but of the same shape, including the valley, save for the greater breadth. The transverse diameters are greater (more robust) and in the medial side there is strong relief for muscle insertion in a proximal position, a feature that is absent in EF 1c'04.

EF 33'00, a fragment of left diaphysis.

6.- This specimen preserves the lateral facet for the radius which is conical with two crests, the rugose area for the radius is very small.

Radius : EF 41'94, proximal left epiphysis (Pl. 3, Figs 5A-B and Text-fig. 1, E1-3).

1.- Trapezoidal outline, with the medial border wider than the lateral one. The medial border is subtriangular, the lateral one straight. The palmar and dorsal borders are straight, the palmar being slightly higher than the dorsal. The dorsal edge has quite a well developed process that passes beyond the lateral border.

2.- The articulation for the trochlea of the humerus is trapezoidal, its surfaces are deep especially that for the articulation with the lateral lip.

3.- The articular surface for the humeral capitulum is subquadrate and the lateral protuberance is not well developed although is clearly visible proximally.

4.- The notch is strong, the lateral articular surface for the ulna is located in two planes, without subdivision. The medial facet appears to be large and slightly subdivided.

EF 10'01, proximal epiphysis (Text-fig. 3, F1-3). Similar morphology to EF 41'94, but the lateral articular surface for the ulna is located in a single quite curved plane. However, its state of preservation limits its observation. The medial facet is not visible.

Other specimens : EF 21'94, proximal epiphysis partially eroded. EF 137'01, juvenile radius without distal epiphysis. EF 7'97, wind-eroded proximal epiphysis. EF 137'01, proximal epiphysis.

EF 23'94, distal left epiphysis (Pl. 3, Figs 7A-B and Text-fig. 1, G), EF 24'94, distal left epiphysis (Pl. 3, Fig. 6).

1.- The articular surface for the scaphoid is limited by high medial and lateral crests, its dorsal part is wide and deep, and its palmar area is broken.

2.- The lateral ridge of the articular surface for the scaphoid is damaged on the palmar part.

3.- The articulation for the semilunar is delimited by a high dorsal ridge and a smoother lateral one, the dorsal part is also deep and on the palmar side continues like a toboggan track.

4.- The facet for the pyramidal is relatively big, disposed parallel to the medio-lateral axis, is inclined with respect to the facet for the semilunar, forming a step with respect to the articular surface for the distal epiphysis of the ulna. The line that separates the semilunar and pyramidal facets reaches laterally forming a small projection on the lateral side.

5.- The palmar border has a deep groove between the articular facets for the semilunar, pyramidal and distal ulna.

Carpals : EF 197'01, left scaphoid with the lateral side eroded.

1.- In the proximal surface the dorsal part is elevated and separated by a valley from the palmar part.

3.- In lateral view the form is rectangular, due to its moderate proximo-distal height.

EF 23'94 (Pl. 3, Figs 7A and C) articulated with the left distal radius described above, there is the carpus, the elements of which are held solidly together by sediment. Our descriptions are therefore limited.

Scaphoid :

1.- In the proximal side the dorsal part is elevated and separated from the palmar side by a valley.

2.- The external distal facet for the lunate is very prominent. The shape, in lateral view is quadrangular, quite high proximo-distally.

Semilunar :

1.- The palmar prominence is well developed.

2.- On the distal side the two dorsal facets are unequal (medial is more developed than the lateral) and are located in different planes, the lateral facet being rather inclined.

Pyramidal :

2.- The dorsal side is well developed.

Metacarpal III-IV : EF 35'93, left metacarpal (Pl. 3, Figs 8A-D) is long and gracile.

1.- The proximal surface is quite flat and compressed transversely, making an obovoid outline. The magnum facet is much larger than that for the unciform.

2.- The two facets are separated by a strong ridge.

3.- The line fades out posteriorly where the facets are separated by the sinovial fossa.

4.- The sinovial fossa is oval and open on the palmar border.

5.- There is a strong rugosity in the articular facet for the magnotrapezoid which contacts the sinovial fossa.

6.- The anterior medial tuberosity is smooth (possibly gnawed by rodents and chewed by other small animals on the lateral part beneath its margin).

7.- The posterior side of the diaphysis is moderately concave in the proximal half. The dorsal groove is fine and visible throughout the diaphysis. The distal extremity is poorly preserved.

EF 24'94, a left Mc III-IV associated with various phalanges is missing the lateral half of the proximal epiphysis and diaphysis. The distal extremity is eroded.

EF 23'94, a proximal left fragment of Mc III-IV in connection with the carpus and distal radius of a juvenile. We can only affirm that the articular facets for the magnotrapezoid and unciform lie in different planes, the former being the higher.

EF 66'01, right proximal fragment of Mc III-IV, 14.5 cm long. The proximal surface is wider and more compressed antero-posteriorly than EF 35'93. The facet for the magnotrapezoid is strong and the postero-medial border rises into a point. In the posterior side, right on the lateral side there is a flat facet for the Mc V. The fossae and tuberosities are similar to those in LT 1'96.

EF 5'03, proximal epiphysis of McIII-IV, has rodent gnawing marks on the proximal end which have altered its outline.

EF 66'01, right proximal fragment of Mc III-IV.

1.- In dorsal view there is a major difference in the heights of the two facets, the magnotrapezoid one being the higher of the two.
2.- The line separating the facets is very strong.
3.- The line of separation follows the sinovial fossa.
4.- The sinovial fossa is large and opens into the palmar border.
5.- There is a strong rugosity in the articular facet for the magnotrapezoid which contacts the sinovial fossa.
6.- The medial tuberosity is strong.
7.- The diaphysis is deformed, but the posterior side has a moderately concave proximal part while the rest is flat. The damage does not permit assessment of the dorsal grooves.

EF 5'03, proximal epiphysis of Mc III-IV.
1.- The carpal facets are in distinct planes, that for the magnotrapezoid being the highest.
2.- The line separating the facets is strong.
3.- The line of separation follows the sinovial fossa.
4.- The sinovial fossa is oval and opens into the palmar border.
5.- There is a strong rugosity in the articular facet for the magnotrapezoid which is separated from the sinovial fossa.
6.- The dorso-medial tuberosity appears to have been strong.
7.- The palmar surface of the diaphysis is broken.

IIIrd phalanx (Pl. 3, Figs 10A-E)

Pelvis : EF 42'01, poor preservation and EF 21'00, right pelvis (Pl. 4, Fig. 1).

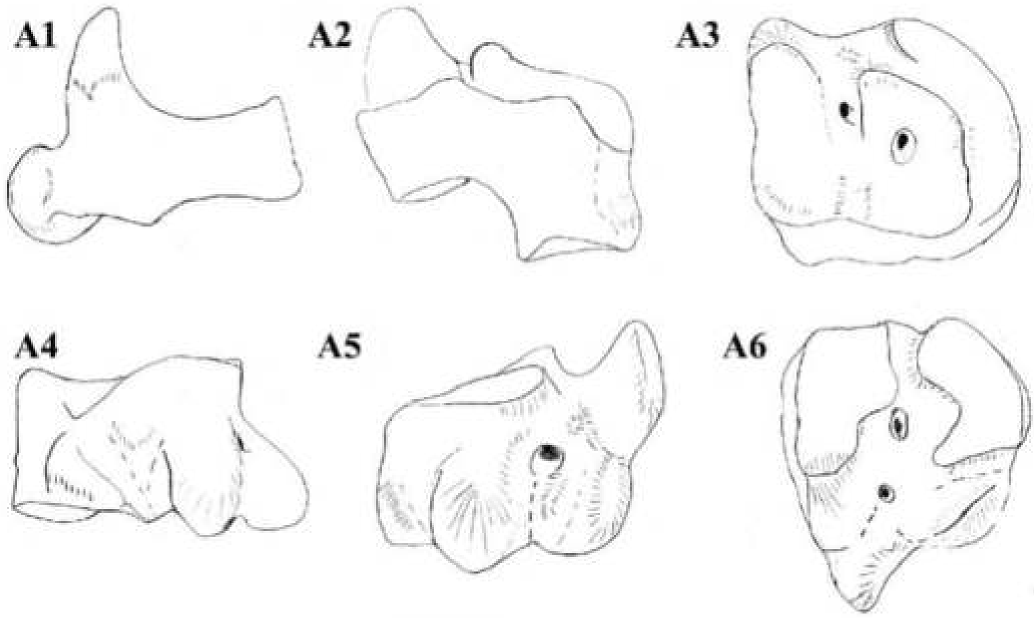
Tibia : EF 152'01, left tibia distal fragment (Pl. 4, Figs 2A-C).
1.- The epiphysis is subquadrangular in outline without antero-posterior compression.
2.1- The anterior border is straight due to the slight projection of the medial maleolus.
2.2- The posterior border is concave due to the fact that the central keel that separates the two gullies of the cochlea is narrow (AP) and because the projection of the palmar medial border of the cochlea is strong.
3.- The medial maleolus is slightly higher than the central process.
4.- The central process is wide, equalling the keel that separates the tibial cochlea.
5.- The lateral gully is narrow and is separated by a keel (somewhat eroded) from the maleolar facets.
6.- The maleolar groove is well marked.
7.- The medial protuberance is moderately marked.
8.- The fibular incision is well marked, dividing the maleolar facets into two parts which are united, with the posterior one bigger than the anterior one. Between the anterior facet and the central process there is a deep incision with well defined borders.
9.- The cochlea has a medial fossa similar in DAP to the lateral one.

EF 46a'00, has undergone antero-posterior compression. The maleolus is fused to it. In general morphology it is close to EF 152'01, but its preservation prevents clear observation of all the characters.
3.- The medial maleolus is similar in height to the central process.
4.- The central process is very wide, equalling the keel of separation of the tibial cochlea.
6.- The maleolar groove is well marked.
7.- The medial protuberance is moderately marked.

EF 208'01, articulated distal tibia, astragalus, calcaneum, navicular-cuboid and proximal fragment of metatarsal (Pl. 4, Figs. 7A-C) poorly preserved.

Astragalus : EF 46'00, right astragalus (Pl. 4, Figs 3A-F).
1.- Proximal view, the medial condyle is narrow and the lateral one a bit wider, and parallel to it. In the medial condyle, there is a strong proximal plantar process.
2.- In the dorsal side, there is a process that blocks very strong flexion (medial side) and the fossa for the medial process of the tibia is circular and deep. This means that sliding between the calcaneum and astragalus is difficult due to the interlocking mechanism between the lateral surface of the astragalus, the maleolar facet, and the groove of the calcaneum. The trajectory is small.
3.- The plantar side is very asymmetrical, the medial part is flatter and the lateral gently convex, its profile is gently concavo-convex.

Navicular-cuboid : EF 8c'01, right navicular-cuboid. Even though it is slightly eroded, it differs slightly from EF 32'01 by having the development of a medial crest parallel to the internal posterior ridge, which delimits the ligamentary fossa. EF 32'01, left navicular-cuboid (Pl. 4, Figs 5A-F and Text-fig. 2, A1-6).
1.- Proximal view, the proximal processes are high, especially the medial one, the lateral one is higher than the calcanear facet.
2.- Distal view, the anterior facet for the metatarsal is subtriangular, with a strong internal notch. The posterior facet for the metatarsal is small and sits on a strong protuberance. The facet for the ectocuneiform is elongated. Outstanding is the strong development of the postero-internal bulge almost the same size as the postero-external protuberance and almost forming a continuous crest.
3.- In plantar view, outstanding is the swelling of the base of the posterior facet for the metatarsal which occupies a major part of the plantar surface of the navicular-cuboid. The postero-internal



Text figure 2: EF 32'01, left navicular-cuboid of *Propalaeoryx austroafricanus* from Elisabethfeld. A1) medial view, A2) lateral view, A3) proximal view, A4) plantar view, A5) dorsal view, A6) distal view.

bulge forms a prominent crest between the plantar and medial sides, but is separated by a wide groove from the base of the internal tenon. Between these crests there develops just beneath the medial tenon, a relatively deep fossa perforated by a strong foramen.

Calcaneum : EF 208'01, right calcaneum.

1.- the tuber is asymmetrical, with the medial lobe high and narrow. The fossa is deep with strong lateral and medial insertions.

2.- the anterior margin of the neck is convex, the posterior is straight except for a slight concavity in the middle.

EF 46'00, right calcaneum lacking its tuber.

3.- the sustentaculum tali is well developed due to its strong medial projection. The tendinal groove is small but well defined.

4.- there are signs of the presence of a small dorsal articular facet.

5.- the maleolar facet has the proximal part very prominent in the medial sense. The distal part is long, with the cuboid facet uneven, very widened distally.

EF 36'93 left calcaneum. (Pl. 4, Fig. 4).

1.- The tuber is asymmetrical, with the medial lobe higher and narrower. The fossa is deep, with strong lateral and medial insertions.

2.- The anterior border of the neck is straight, the posterior one is similar save for a slight concavity in front of the tuber.

3.- The sustentaculum tali is noticeably developed, due to its strong medial projection. The tendinal groove is weakly defined.

4.- There is no indication of a dorsal articular facet.

5.- The maleolar facet has a very prominent proximal part medially. The distal part is long, with the facet for the cuboid irregular, somewhat widened in its middle.

Metatarsal : EF 4'03, right Mt III-IV (Pl. 4, Figs 6A-C).

1.- There is complete fusion of Mt III-IV.

2.- Mt III (articulates with the cuneiform) the proximal anterior facet is kidney-shaped and concave, delimited by two weak tuberosities, one dorso-medial, the other plantar medial.

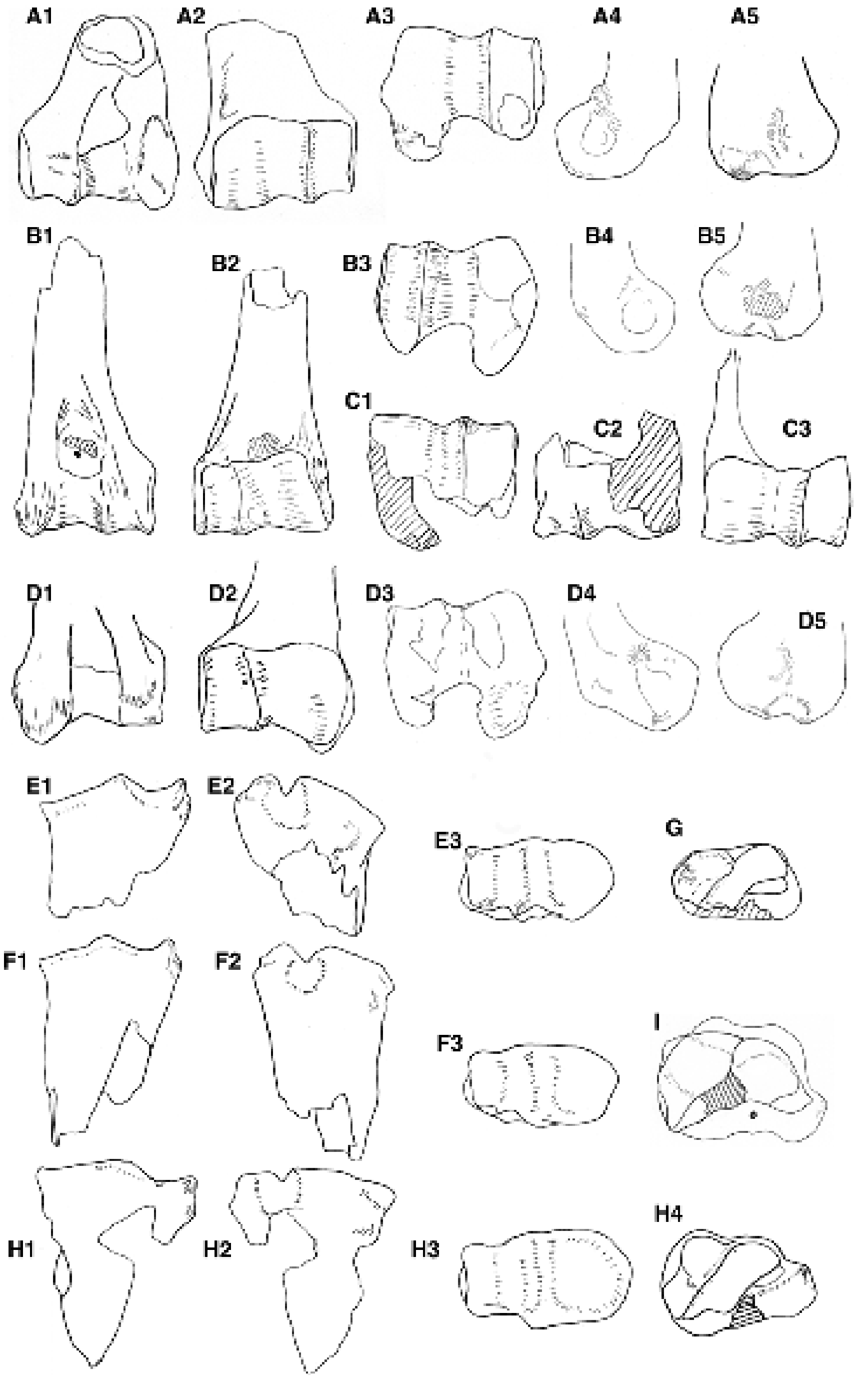
3.- The proximal posterior facet for the ectocuneiform is rounded, and is marked on its plantar side with a sesamoid facet.

4.- Mt IV (articulates with the cuboid) has a proximal anterior facet which is subquadrangular and gently convex.

5.- The posterior proximal facet is subtriangular, small, inclined and very elevated. It is separated by a canal from the posterior proximal facet for a small sesamoid.

6.- The lateral-plantar prominence is very weakly developed, the medial-plantar one almost as weak is a small protuberance.

7.- The proximal canal of the metatarsal is very



Text figure 3: Humerus and radius of *Propalaeoryx austroafricanus* from Elisabethfeld and *Propalaeoryx stromeri* from Langental. A) EF 22'93, *Propalaeoryx austroafricanus*, Elisabethfeld, distal epiphysis of left humerus. A1) caudal view, A2) cranial view, A3) distal view, A4) lateral view, A5) medial view. B) EF 8a'93, *Propalaeoryx austroafricanus*, Elisabethfeld, distal epiphysis of right humerus. B1) caudal view, B2) cranial view, B3) distal view, B4) lateral view, B5 medial view. C) LT 261'99, *Propalaeoryx stromeri*, Langental, distal epiphysis of left humerus. C1) cranial view, C2) distal view, C3) caudal view. D) LT 239'03, *Propalaeoryx stromeri*, Langental, distal epiphysis of right humerus. D1) caudal view, D2) cranial view, D3) distal view, D4) lateral view, D5) medial view. E) EF 41'94, *Propalaeoryx austroafricanus*, Elisabethfeld, proximal epiphysis of left radius. E1) palmar view, E2) dorsal view, E3) proximal view. F) EF 10'01, *Propalaeoryx austroafricanus*, Elisabethfeld, proximal epiphysis of left radius. F1) palmar view, F2) dorsal view, F3) proximal view. G) EF 23'94, *Propalaeoryx austroafricanus*, Elisabethfeld, distal epiphysis of radius in distal view. H) LT 261'99, *Propalaeoryx stromeri*, Langental, proximal epiphysis and distal epiphysis of left radius. H1) palmar view, H2) dorsal view, H3) proximal view, H4) distal view. 8) EF 23'94, *Propalaeoryx austroafricanus*, Elisabethfeld, distal epiphysis of left radius. I) LT 38'00, *Propalaeoryx stromeri*, Langental, distal epiphysis of radius.

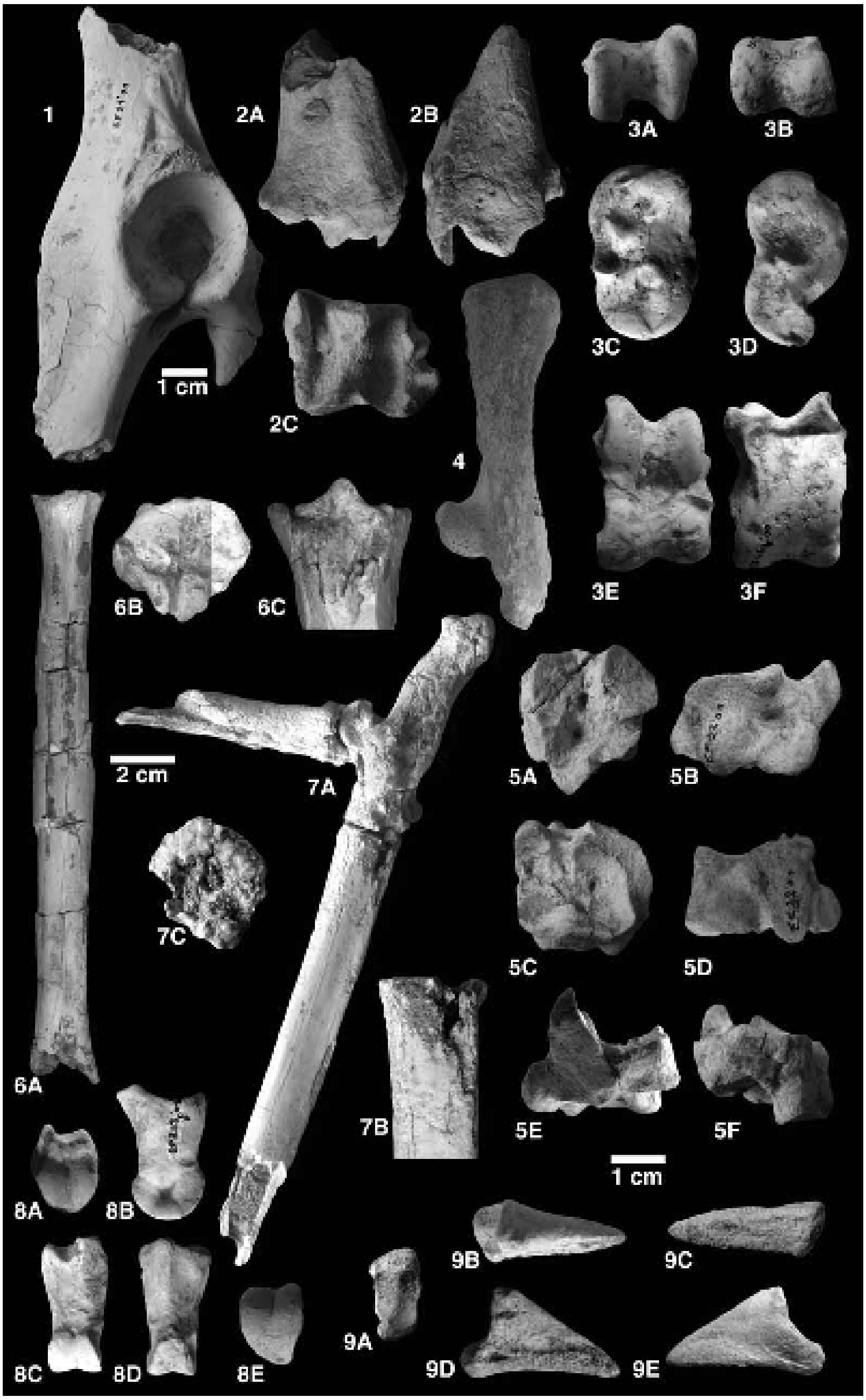


Plate 4: *Propalaeoryx austroafricanus* from Elisabethfeld. 1) EF 29'00, right coxal fragment in lateral view. 2) EF 152'01, distal left tibia epiphysis, A) dorsal view, B) plantar view, C) distal view. 3) EF 46b'00, right astragalus, A) proximal view, B) distal view, C) medial view, D) lateral view, E) dorsal view, F) plantar view. 4) EF 36'93, right calcaneum in dorsal view, 5) EF 32'00, left navicular-cuboid. A) distal view, B) plantar view, C) proximal view, D) dorsal view, E) medial view, F) lateral view. 6) EF 4'03, right metatarsal III-IV, A) dorsal view, B) proximal view, C) plantar view. 7) EF 208'01, articulated association of distal tibia, astragalus, calcaneum, navicular-cuboid and metatarsal (left side) A) lateral view, B) proximal metatarsal epiphysis in lateral view, C) proximal metatarsal epiphysis in proximal view. 8) EF 208f'01, right IInd phalanx, A) lateral view, B) proximal view, C) distal view, D) plantar view, E) dorsal view. 9) EF 208g'01, right IIIrd phalanx, A) proximal view, B) dorsal view, C) plantar view, D) medial view, E) lateral view.

big on the proximal surface, apparently its contact with the plantar side is very reduced.

8.- The dorsal canal is weakly marked on its dorsal proximal border.

9.- Backing onto the dorsal canal on the medial side, there is a well marked groove.

10.- Mt II fused, very reduced, Mt V fused but preserving its wedge shape. In proximal view it resembles a small conical process.

11.- The distance between the lateral and medial sides diminishes along the bone, right to the distal epiphysis.

12.- The dorsal groove is moderately pronounced.

14.- The plantar groove is moderately marked.

The Mt III-IV is characterised by several features : the medial plantar prominence which is generally a weak protuberance. The proximal canal of the metatarsal has a large proximal surface, apparently its contact with the plantar surface is very reduced, the Mt V is fused. but preserves its wedge-like shape. In proximal view it appears as a small conical process. The lateral and medial sides diminish in size along the length of the bone as far as the distal epiphysis. The dorsal groove is moderately pronounced as is the plantar one. In the Mt III-IV of *P. austroafricanus* the medial plantar prominence is a sharp protuberance that projects outwards. The fused Mt II is wedge-shaped but is not so clearly marked proximally. The Mt V is unfused, there is a triangular articular facet in the Mt IV. The dorsal groove is quite pronounced in the proximal part of the diaphysis, equal to the plantar groove which is very marked on the proximal part of the diaphysis.EF 208a'01, metatarsal with poorly preserved proximal surface.

1.- There is complete fusion between Mt III-IV.

2.- Mt III (articulates with the cuneiform) The proximal facet is kidney-shaped and concave, limited by two tuberosities, one dorso-medial the other a weak plantar-medial.

3.- The proximal facet for the ectocuneiform is damaged, but on the plantar side there is marked an articulation for a sesamoid.

4.- The proximal anterior facet of the Mt IV is damaged.

5.- The proximal posterior facet is damaged.

6.- The lateral plantar prominence is weakly developed, the medial plantar protuberance is sharp and projecting to the rear.

7.- The proximal canal of the metatarsal is large on the proximal surface, apparently its contact with the plantar side is very reduced.8.- The dorsal canal is very weakly marked on the proximal dorsal border.

9.- Backing onto the dorsal canal in the medial side, there is a weakly defined groove.

10.- The Mt II is fused and very reduced. Mt V is not fused, but its facet has a trianglular outline.

12.- The dorsal groove is moderately pronounced.

14.- The plantar groove is evenly marked.

EF 3'04 metatarsal.

10.- Mt II is fused and very reduced. Mt V is not fused but its triangular facet is present.

<u>*IInd phalanx*</u> : EF 208'01 (Pl. 4, Figs 8A-E) IInd phalanx articulated with IIIrd phalanx EF 208'01.

1.- Robust.

2.- In proximal view one can see that the post-articular platform is well developed and asymmetrical.

3.- The dorsal extensor process is moderately high.

4.- The outline of the distal articular facet is quite triangular.

5.- The articulation extends greatly dorsally.

<u>*IIIrd phalanx*</u> : EF 208'01 (Pl. 4, Figs A-E) IIIrd phalanx articulated with IInd phalanx EF 208'01.

1.- The dorsal ridge is straight.

2.- There is strong dorsal process for the insertion of the extensor.

3.- The articular surface is well rounded but not deep.

4.- There is a medium sized plantar process for the insertion of the deep flexor tendon.

5.- Dorsal view : the ridge is long and in a lateral position.

6.- The plantar surface is well defined by two ridges (medial and external).

Species *Propalaeoryx stromeri* nov.

Synonymy :

v1924 cfr *Strogulognathus sansaniensis* Filhol, 1851 Stromer, 1924.

v1926 cfr *Strogulognathus sansaniensis* Filhol, 1851 Stromer, 1926.

v1977 *Propalaeoryx austroafricanus* Stromer, 1924 Hamilton and Van Couvering, 1977

Holotype : LT 59'96, upper molar series left M1/-M3/.

Type Locality : Langental, Sperrgebiet, Namibia.

Other localities : Grillental, Fiskus, Sperrgebiet, Namibia.

Age : Early Miocene.

Diagnosis : *Propalaeoryx* with tendency towards microdonty. Lower molars with flattened lingual wall, lingual cusps weakly marked (low relief). Upper molars with moderately tall buccal styles, M3/ with weakly developed metastyle, almost absent in some individuals. Premolar series with tendency to be reduced.

Differential diagnosis : *Propalaeoryx stromeri* differs from *P. austroafricanus* by its slightly smaller dimensions for its dentition but greater size of the postcranial skeleton. The dentition of *P. stromeri* is somewhat more hypsodont with weaker buccal styles in the upper molars than in *P. austroafricanus*. The lower molars of *P. stromeri* have flatter lingual walls such that the lingual cusps have lower relief. The upper premolars of *P. stromeri* (although the sample is quite small) are narrower than those of *P. austroafricanus* and the P2/ is reduced in *P. stromeri*. The postcranial skeleton of both species is strongly variable, but that of *P. stromeri* is generally larger than that of *P. austroafricanus*, being especially clear in the dimensions of the IIIrd phalanges which are well represented at the various localities. *P. stromeri* differs from *Propalaeoryx nyanzae* by it lesser size and greater hypsodonty.

Langental:

Cranial. LT 194'96, occipital (Pl. 5, Figs 1A-D).

4.- The sagittal crest is strongly marked.

6.- The nuchal zone is massive, and is greatly widened.

7.- The muscle insertions on the occipital are weak.

8.- The nuchal border is straight. The nuchal crest projects strongly to the rear extending amply beyond the occipital condyles.

16.- The basioccipital has strongly developed muscle insertions.

Upper dentition : SAM PQN 49, an upper canine is high with a compressed transverse section in the shape of an almond (ovaloid).

LT 4'06 left upper canine with a broken base (Pl. 5, Figs. 4A-B). The tooth has a subtriangular transversal section with sharp anterior and posterior crests, and a smooth antero-lingual keel. The external wall is almost flat, gently convex. The internal wall is formed of two planes that meet at the antero-lingual keel.

LT 159'96, is a poorly preserved upper canine. (Pl. 5, Figs. 5A-B).

LT 125'00, upper canine with broken base and tip.

SAM PQN 57, M1/-P3/ (Janis and Scott, 1987, fig. 12B). The M1/ has a strong parastyle united basally to the external rib of the paracone. The mesostyle is strongly united by a smooth cingulum to a moderate metastyle. The anterior crista of the protocone, which is relatively high, is narrowly joined to the parastyle, the posterior crista contacts the anterior crista of the metacone making a central islet. There is no contact between these two cristae and the buccal cusps, thereby not interrupting the central valleys. The ectostyle is weak.

The P4/ is subtriangular, with the strong anterior style united basally to the buccal cusp.There is a small medial fold. The lingual cusp is centrally positioned and its cristae are moderately high.

The P3/ is elongated, with a strong anterior style united basally to the buccal cusp, which has a strong external rib, more developed than in the P4/. The posterior style is weak. It has a medial fold. The lingual cusp is displaced posteriorly, and joins the anterior style via a lingual crista.

SAM PQN 58, M3/-M1/. The M1/ is similar to the one in PQN 57. The M2/ has the two internal cusps connected to each other, but the internal valley, although still continuous is at the point of subdividing. The M3/ is characterised by the presence of an enormous metastyle united basally to the mesostyle by a strong cingulum. The metaconule is clearly smaller than the protocone. The cristae of the lateral unions between the four cusps are high in all three molars.

SAM PQN 59, right M1/-D3/. The unworn M1/ shows clear separation between the anterior crest of the protocone and the posterior one of the metaconule. The D4/ is badly damaged. The D3/ is elongated, and the external wall shows a weak style, a strong main cusp, a strong medial style, an ample and prominent posterior cusp and a weak posterior style. Lingually, in front of the external cusp there is a strong cusplet which joins the anterior style via a long crest. A second crest runs parallel to the external wall and ends by uniting with the posterior style.

LT 59'96, fragment of right maxilla with M3/-M1/ (Pl. 5, Figs 2A-C; Text-fig. 1, C1-2). The M2/ is bigger than the M3/ and the M1/. The M3/ has a strong parastyle, joined basally to the paracone which is clearly marked on the external wall. The mesostyle is columnar and of moderate size. The metacone is flattened and the metastyle weak. The protocone is simple, its anterior crista is long but decreases in height as far as the parastyle. The posterior crista is short and contacts the anterior crista of the metaconule which is long and which reaches the base of the junction of the paracone and metacone. The posterior crista of the metaconule is short and low, contacting the metastyle low down. There is a weak cingulum at the base of the protocone and a minute ectostyle.

The M2/ differs from the M3/ by the greater separation of the posterior protocone crest from the anterior metaconule crest. However, these crests are not simple as in the M3/ but bifurcate slightly at their termination.

The M1/ is similar to the M2/, but has a strong mesostyle, and because of its greater wear the posterior protocone crista and the anterior metaconule crista, both with bifurcate ends, are joined together. The three teeth have a moderate cingulum at the base of the anterior crista of the protocone.

LT 376'96, a left M3/ (Text-fig. 1, D1-2) has a strong parastyle joined basally to the paracone. The mesostyle is columnar and as strong as the parastyle and projects externally to quite a degree. The metacone is flat and the metastyle strong but low. The protocone is simple, its anterior crest is long and contacts the parastyle. The posterior crest is short and is clearly separated from the anterior crest of the metaconule which is long and leads to the base of the junction of the paracone and the metacone. The pos-

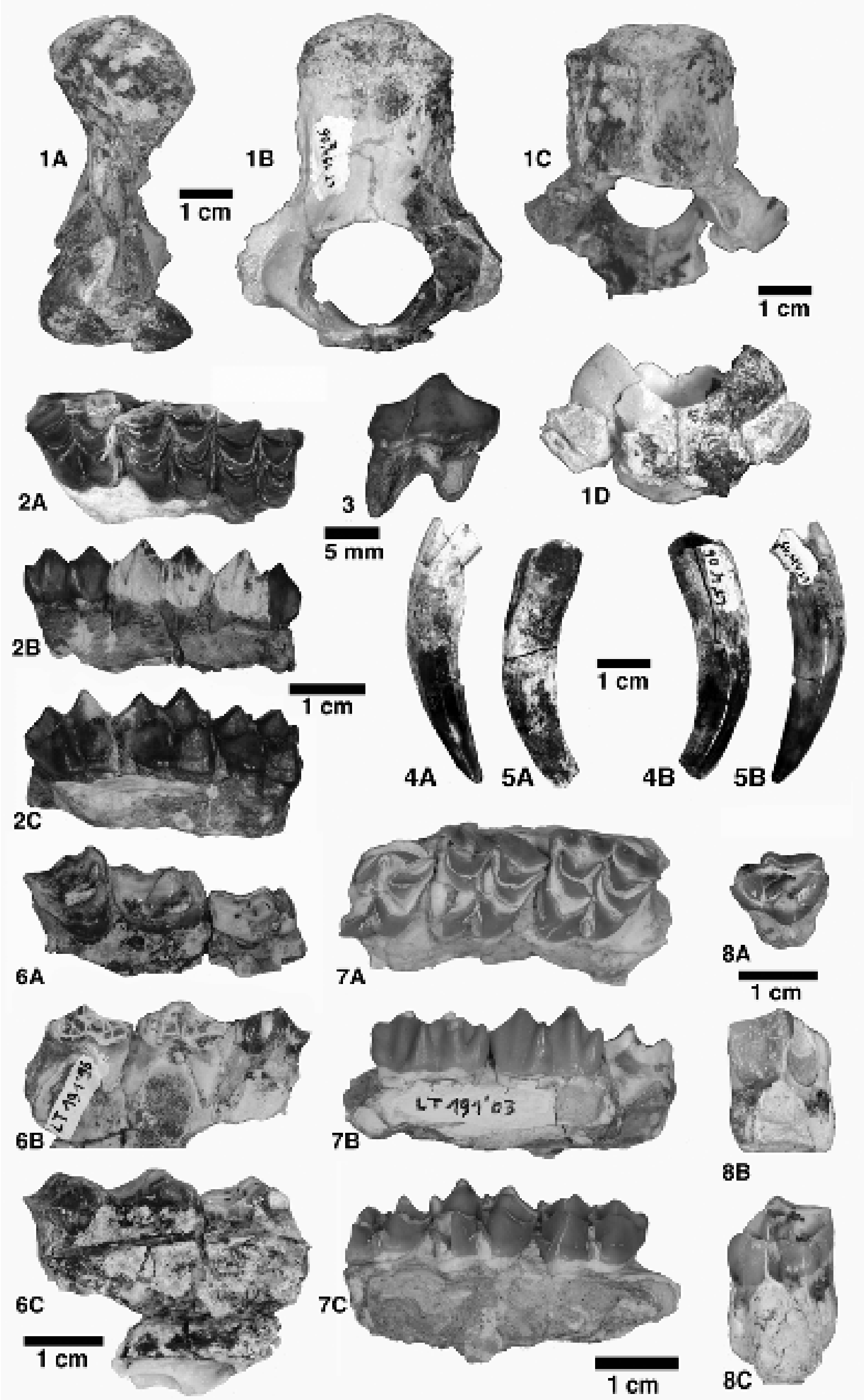


Plate 5: *Propalaeoryx stromeri* nov. sp. from Langental. 1) LT 194'96, occipital, A) lateral view, B) nuchal view, C) dorsal view, D) basal view. 2) LT 59'96 (holotype), fragment of right maxilla with M3/-M1, A) occlusal view, B) buccal view, C) lingual view. 3) LT 64'96, left P4/ in buccal view. 4) LT 4'06, left upper canine, A) buccal view, B) lingual view. 5) LT 174'99, left upper canine, A) buccal view, B) lingual view. 6) LT 191'96, fragment of right maxilla with P4/-P2, A) occlusal view, B) buccal view, C) lingual view 7) LT 191'03, left maxilla with M3/-M1/, A) occlusal view, B) buccal view, C) lingual view. 8) LT 172'99, left P3/, A) occlusal view, B) buccal view, C) lingual view.

terior crest of the metaconule is short and low, contacting the metastyle low down. There is no lingual cingulum, but there is a moderate one at the base of the anterior crest of the protocone.

LT 64'96, is a deeply worn left P4/ (Pl. 5, Fig. 3). The tooth is subtriangular, elongated and with a strong basal cingulum.

LT 168'99, a worn right M3/ has a strong parastyle joined basally to the external rib of the paracone, which is well marked on the outer wall. The mesostyle is very strong, and is joined by a well developed cingulum to a large metastyle. The anterior crest of the protocone is weakly joined to the parastyle, the weakly bifurcate posterior crest is clearly separated from the anterior crest of the metaconule. Neither of these two crests contact the buccal cusps, leaving the central valleys in contact. The posterior crista of the metaconule is low and only contacts the metastyle close to its base. The ectostyle is weak and the anterior cingulum is strong.

LT 122'00, left M2/-M1/. The molars are quite worn and broken. Only measurements can be taken.

LT 175'99, fragment of right maxilla with M3/ and part of M2/. The M3/ has a strong parastyle joined basally to the well developed external rib of the paracone. The mesostyle is very strong and prominent, and is joined by a moderate cingulum to a medium sized metastyle. The anterior crista of the protocone is weakly joined to the parastyle, the posterior crista is clearly separated from the anterior crest of the metaconule. Neither of these crests contact the buccal cusps, leaving the central valleys open. The posterior crista of the metaconule is low and only contacts the metastyle near its base. The ectostyle is weak and the anterior cingulum is moderate sized. The M2/ is quite broken, and differs from the M3/ by the virtual absence of the external cingulum at the base of the metacone and by the weakness of the metastyle. The ectostyle is weak.

LT 191'96, fragment of right maxilla with P4/-P2/ (Pl. 5, Figs 6A-C; Text-fig. 1, B1-2). The deeply worn P4/ is subtriangular. The strongly developed anterior style is united basally to the buccal cusp. The posterior style is weak, and the buccal cusp is well marked externally. The lingual cusp is centrally positioned and its crests join the styles of the external wall.

The P3/ is elongated, with strong anterior style which joins the buccal cusp at its base, the outer surface of which sports a well marked rib although it is smaller than in the P4/. The posterior style is weak. The lingual cusp is very posteriorly positioned and joins the anterior style via a long crest. The P2/ is morphologically close to the P3/ although it is smaller. The elements of the external wall are well marked, especially the robust anterior style. The lingual cusp is smaller than that of the P3/ and is separated by an inflexion from the internal wall of a small anterior cusplet, which joins the anterior style, forming a small cusplet isolated from the main body of the tooth.

LT 172'99, left P3/ (Pl. 5, Figs 8A-C). The anterior part of the external wall is broken. The buccal cusp is strong with a well marked external rib. The posterior style is weak. The lingual cusp which is in a posterior position joins the anterior style by a long crest and its anterior crest remaining separated from the small anterior cusplet by a vertical inflexion of the internal wall. There is a small internal fold.

LT 191'03, left M1/-M3/ (Pl. 5, Figs 7A-C; Text-fig. 1, B1-2). The M1/ is damaged, but has a strong ectostyle and the elongation of the anterior and posterior crests of the metaconule are evident. The M1/ possesses a strong parastyle joined basally to the external rib of the paracone. The mesostyle is strong. The protocone is partly broken, its posterior crest ending in a weak bifurcation, but remaining well separated from the anterior crista of the metaconule. Neither of these two crests contact the buccal cusps leaving the central valleys open. The posterior crista of the metaconule makes contact with a smooth metastyle, but without fusing with it. The ectostyle is strong.

The M3/ has a strong parastyle joined basally to the external rib of the paracone. The mesostyle is strong and joined by a smooth cingulum to a medium sized metastyle. The anterior crest of the protocone, which is relatively high, is narrowly joned to the parastyle, the simple posterior crista is clearly separated from the anterior crest of the metaconule. Neither of the two crests make contact with the buccal cusps, leaving the central valleys in contact. The posterior crista of the metaconule contacts the metastyle, closing the wall posteriorly. The ectostyle and anterior cingulum are strong.

<u>Lower dentition</u> :

<u>Incisor</u> (Pl. 6, Figs 4A-B). SAM PQN 51, right mandible (Pl. 6, Figs 1A-C) Hamilton and Van Couvering (1977, fig. 1) Janis and Scott (1987, fig. 12B). The horizontal ramus is robust, widened behind the m/3, the mandibular foramen is above the level of the m/3. The metaconid and protoconid of the m/3 have very long crests, but without closing the lobe anteriorly. The metastylid is of moderate size, but is vertically marked dividing the external wall into two parts. The posterior cristids of the metaconid and protoconid are shorter than the anterior ones, and contact each other, closing the anterior loph, and uniting with the metastylid and the anterior wing of the entoconid. As in the anterior loph, the anterior cristids of the entoconid and hypoconid are longer than the posterior ones and do not contact each other. The posterior cristid of the entoconid is weakly developed, that of the hypoconid is bigger and contacts the two cristids of the hypoconulid, which is thus closed, and with a low entoconulid. There is no palaeomerycid fold nor ectostylid. The tooth is moderately worn, and there is a small anterior cingulum.

The m/2 is morphologícally similar to the m/3,

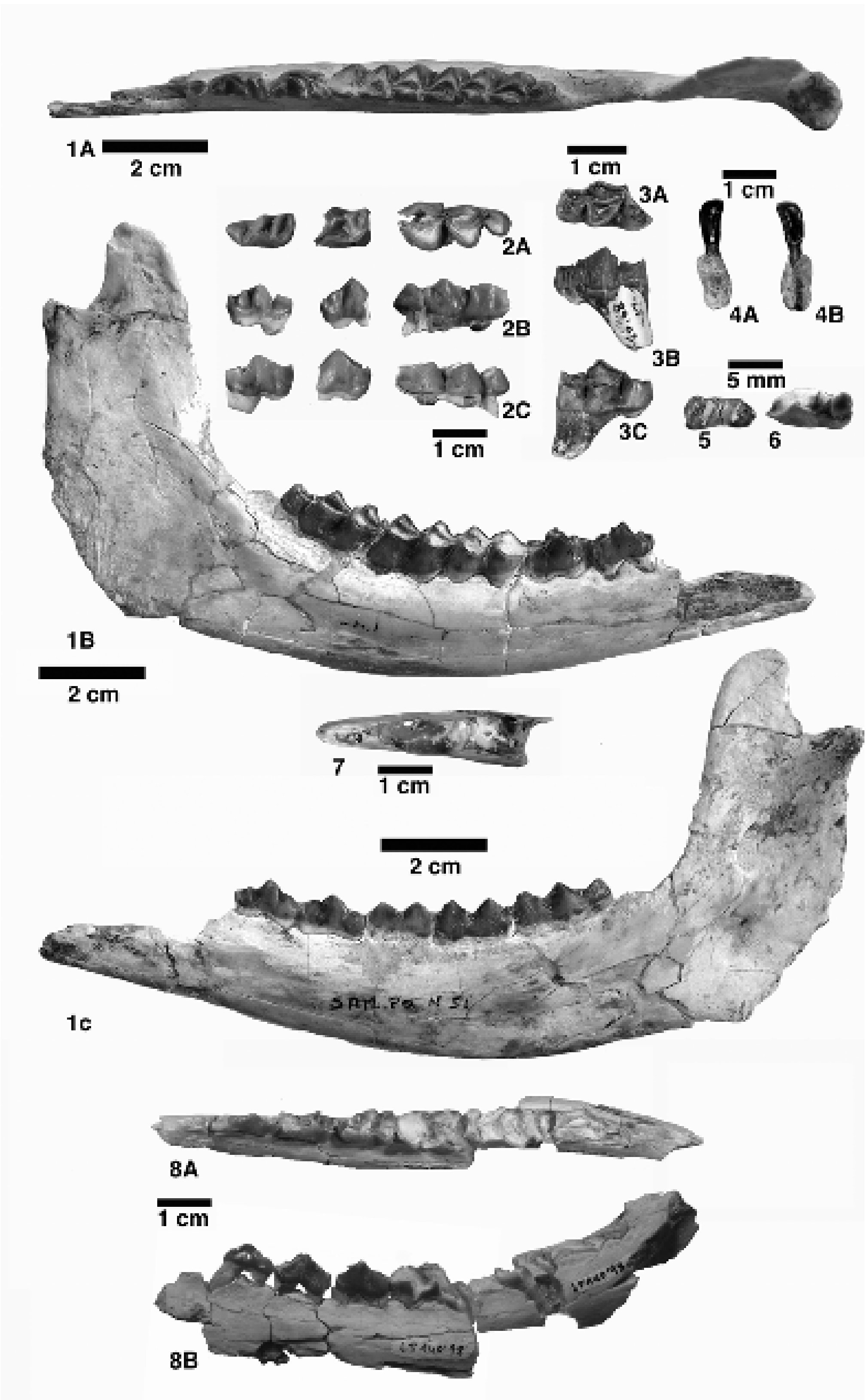


Plate 6: *Propalaeoryx stromeri* nov. sp. from Langental. 1) SAM PQ N 51, right mandible, A) occlusal view, B) buccal view, C) lingual view. 2) LT 71’04, left m/3, fragment of p/4 and p/3, A) occlusal view, B) lingual view, C) buccal view. 3) LT 89’03, right m/3, A) occlusal view, B) lingual view, C) buccal view. 4) LT 31’06 incisor, A) buccal view, B) lingual view. 5) LT 126’00, left p/2 in occlusal view. 6) LT 99’98, left p/3 in occlusal view. 7) LT 170’99, left mandible fragment with alveolus for p/1, p/2 and the anterior part of p/3 in occlusal view. 8) LT 140’98, left mandible with premolars and damaged m/1, A) occlusal view, B) buccal view.

but the posterior cristid of the hypoconid ends in an entoconulid which only contacts the entoconid basally, leaving the entoconulid separate from the posterior cristid of the entoconid. There is a small ectostylid. However, the separation between the anterior cristids of the metaconid and protoconid can be seen, but not in the deeply worn m1/. The latter tooth also has a moderate ectostylid.

The p/4 has a moderate vertical incision in the external wall. The anterior wing is bifurcate. The postero-lingual cusp and posterior stylid are horizontal. The mesio-lingual cusp has moderately developed anterior and posterior cristids.

The p/3 possesses a postero-lingual cusp which is more perpendicular to the axis of the tooth, the mesio-lingual cusp formed of a cristid obliquid. The anterior wing is bifurcate, the vertical incision in the external wall is almost imperceptible.

SAM PQN 8356, left mandible with m/3-m/1. The specimen is bigger than PQN 51. The m/3 has elongated anterior cristids of the anterior cusps which are almost parallel and not fused to each other. The hypoconulid is completely closed but lingually the wall is quite low. The posterior cristid of the hypoconid reaches the lingual position, developing a strong stylid, but remaining well separated from the anterior cristid of the entoconid. The metastylid is moderate, but is stronger in the m/1. In the m/2 the posterior cristids of the hypoconid and entoconid are strongly separated. In the three molars the ectostylid is weak.

Cast labelled cf *Strogulognathus sansaniensis* Stromer, 1926, the original of which is housed in the Iziko South African Museum, Cape Town : The morphology of the m/3 is quite strange for this group of ruminants. The anterior lophid is closed and contacts the metastylid and the anterior cristid of the entoconid. The hypoconid remains isolated, but its very well developed posterior cristid makes contact with a strong entoconulid which is ample and flat. The hypoconulid is not completely closed, its buccal cristid contacts the posterior cristid of the hypoconid and the lingual cristid is not so big, but almost contacts the entoconulid. There is an anterior cingulum and another small one on the hypoconulid. The ectostylid is moderate. There is no palaeomerycid fold. The m/2 has the same morphology, with the hypoconid isolated, its posterior cristid ending in a strong entoconid. The ectostylid is strong. The metastylid is reduced but visible.

SAM PQN 52, left m/3 is deeply worn which is why the lophs are united, except the posterior cristid of the hypoconid separated from the very small cristid of the entoconid and contacting with a large, long and flat entoconulid. The hypoconulid has its buccal cristid united to the posterior cristid of the hypoconid, and the lingual one contacts with the latter, closing the lophid which is quite elongate. The ectostylid is medium sized and there is another basal pillar in the hypoconulid.

SAM PQN 53, left m/3 is worn and damaged, differing in some details from the above tooth. The hypoconid is separated from the anterior lophid but its posterior cristid has contacted the posterior cristid of the entoconid. This gives the impression that the hypoconulid is closed, and the entostylid was big.

LT 375’96, fragment of mandible with m/3-m/2. The teeth are deeply worn, and only measurements can be taken.

LT 378’96, fragment of lower molar showing clearly the separation between the posterior cristid of the entoconid and the union entoconulid - posterior cristid of the hypoconid. The ectostylid is strong.

LT 134’96, fragment of right mandible with the posterior part of p/4. The premolar is quite damaged. The vertical incision of the buccal wall is strong and in the lingual wall the posterior cristid of the mesio-lingual conid contacts the postero-lingual conid.

LT 36’97, posterior fragment of left p/3 is damaged but shows a cristid obliquid which is quite perpendicular to the axis of the tooth, terminating in a simple cusplet. The postero-lingual cusp is strong and reaches the postero-lingual border of the tooth contacting the posterior stylid.

LT 140’98 (Pl. 6, Figs 8A-B) poorly preserved left mandible with the premolars and a damaged m/1 which nevertheless shows the anterior cristid of the hypoconid still isolated. The external wall undulates. The p/4 has a strong vertical incision in the external wall. The anterior wing is broken. The metaconid is strong and does not appear to have an antero-lingual cristid. The p/3 is elongated and gracile, the anterior wing is worn and eroded. The external wall is completely smooth. The metaconid is flat, obliquely positioned and large, but appears more like a crest than a cusp. The p/2 is also elongated, the internal wall is broken, and one can only observe a small simple cusplet anteriorly united by a crest to the main cusp. There is an alveolus for a p/1.

LT 169’99, deeply worn right m/1, which shows the presence of a strong ectostylid.

LT 173’99, external wall of a p/4 shows only the strong vertical groove on the external wall.

LT 171’99, left p/3 is a simple cusp with a cristid obliquid that does not form a mesio-lingual cusplet. The posterior cusp and posterior stylid unite to form a closed oval in occlusal view.

LT 170’99 (Pl. 6, Fig. 7) left mandible fragment with alveolus for p/1, plus the p/2 and the anterior part of p/3. The p/2 is a simple bundont tooth with a rounded mesio-lingual cusp on which a lingual fold is marked. The posterior cusplet is weak and directed as far as the contact with the posterior stylid.

LT 126’00, left p/2 (Pl. 6, Fig. 5) is simple in morphology with a sharp mesio-lingual cusp without cristid obliquid. The anterior cusplet is simple. The postero-lingual cusplet is perpendicular to the axis of the tooth and joins the posterior stylid forming an oval outline.

LT 127’00, poorly preserved m/3.

LT 71'04, a left m/3, fragment of p/4 and p/3 found together (Pl. 6, Figs 2A-C). The m/3 has a lingual wall with imbricated cusps. The metastylid is very strong, with clear separation of the hypoconid and entoconid, the latter cusp being strong and in a lingual position. Anterior cingulum is present, and the ectostylid is strong. There is no *palaeomeryx* fold. The anterior part of p/4 is preserved, and shows a moderate vertical postero-buccal incision and the formation of a continuous wall between the cusp and the postero-lingual stylid. The p/3 has a simple anterior cusplet. The cristid obliquid ends in a weak cusplet and the cusp and posterior stylid almost touch lingually to form an oval.

LT 89'03, right m/3 with broken metaconid (Pl. 6, Figs 3A-C). The mesio-lingual valley appears to have been relatively weak. The posterior cristid of the protoconid contacts the anterior cristid of the entoconid and the anterior cristid of the hypoconid, but does not fuse with them. The posterior cristid of the hypoconid is short and contacts the anterior cristid of the hypoconulid, but remains well separated from the posterior cristid of the entoconid and the entoconulid. These two elements remain separated. The entoconulid is strong and forms a small wall in the lingual part of the hypoconulid, which bears a smooth cingulum at its base. The ectostylid is almost inexistent. The morphology of the molar is very different from that of *Propalaeoryx austroafricanus*, in particular the shortness of the posterior cristid of the hypoconid and its union with the hypoconulid. In *P. austroafricanus* the posterior cristid of the hypoconid is long and unites with a strong, columnar entoconulid. A second difference is the wall-like morphology of the entoconulid.

LT 98'98, fragment of ascending ramus; LT 99'98, fragment of mandible with p/4; LT 100'98 fragment of mandible with p/3 and LT 101'98 fragment of mandible with alveoli are all from the right side and were found together. Only the p/3 (Pl. 6, Fig. 6) can be described. The anterior part seems to be simple (not bifurcate) the cristid obliquid ends in a simple cusplet and the postero-lingual cusplet is much inclined towards the rear, contacting the posterior stylid which is perpendicular to the axis of the tooth.

LT 22'04, right p/2 is poorly preserved, but is a relatively robust tooth with quite a bundont cusp.

LT 29'05, right m/1, p/4 and the posterior part of the p/3 found together.

<u>Postcranial skeleton</u> :

<u>Atlas</u>. LT 81'00, half an atlas split sagittally.

1.- The shape is quadrangular, its cranio-caudal length is 50 mm which is similar to the distance between the margins of the wings, calculated as ca. 49 mm.

2.- The part of the lateral wing preserved is quite straight.

3.- In dorsal view, the alar and intervertebral foramina lie in the same depression. The dorsal tubercle is broken. The dorsal arch is not as acute as in EF 27'00.

4.- In ventral view, the ventral tubercle is well developed, positioned close to the caudal margin and far from the cranial edge. The wings are well differentiated from the vertebral body which are developed into an X. The alar foramina are relatively large. The ventral arch is also less acute than in EF 27'00, and the ventral incisure is weak.

5.- In cranial view, the vertebral foramen is ellipsoid, compressed dorso-ventrally. The articular facets for the occipital condyles of the skull are large but less vertical than in EF 27'00.

6.- In caudal view, the articular surfaces are narrow. The caudal tubercle of the wing is better developed than it is in EF 27'00. The vertebral foramen is more circular.

<u>Scapula</u> : LT 68'96, left scapula (Pl. 7, Figs 1A-C) with carnivore bite marks.

0.- Lateral profile elevated.

1.- Glenoid cavity circular, concave.

2.- Supraglenoid tubercle high and rounded.

3.- Coracoid process vestigial, quite prominent with the glenoid notch reduced.

4.- There is no infraglenoid tubercle, but there is a long, deep triangular fossette, with the very strong medial border. Between the caudal border and the base of the acromion there are two vestigial lines of insertion which reach the lateral border of the glenoid cavity and unite at the caudal border of the scapula.

5.- The acromion is broken.

LT 45'00, right scapula (Pl. 7, Figs 3A-D) well preserved scapula.

1.- The glenoid cavity has a straighter external margin than LT 68'96.

2.- The supraglenoid tuberosity is stronger and the pedicle finer than in LT 68'96.

3.- There is no coracoid apophysis. The notch is wide and shallow, more marked (as in LT 102'04) than in the drawing of LT 68'96.

4.- In the lateral side there are two lines of insertion as described in EF 68'01 and in the caudal margin, beneath the glenoid cavity, there is a large fossa displaced medially (as in the previous specimen).

5.- The base of the acromion is close to the glenoid cavity.

LT102'04, right scapula (Pl. 7, Figs 2A-B) differs from LT 45'00 by the greater medio-lateral compression of the glenoid cavity, which is, as a consequence, less circular, almost elliptical.

SAM PQN 66. The glenoid cavity is broken medially. The shape of the notch (incisura glenoidea) of the supraglenoid tuberosity and the coracoid is like that of LT 45'00, but the pedicle of the tuberosity is narrower, the tuberosity itself bigger and with a small coracoid.

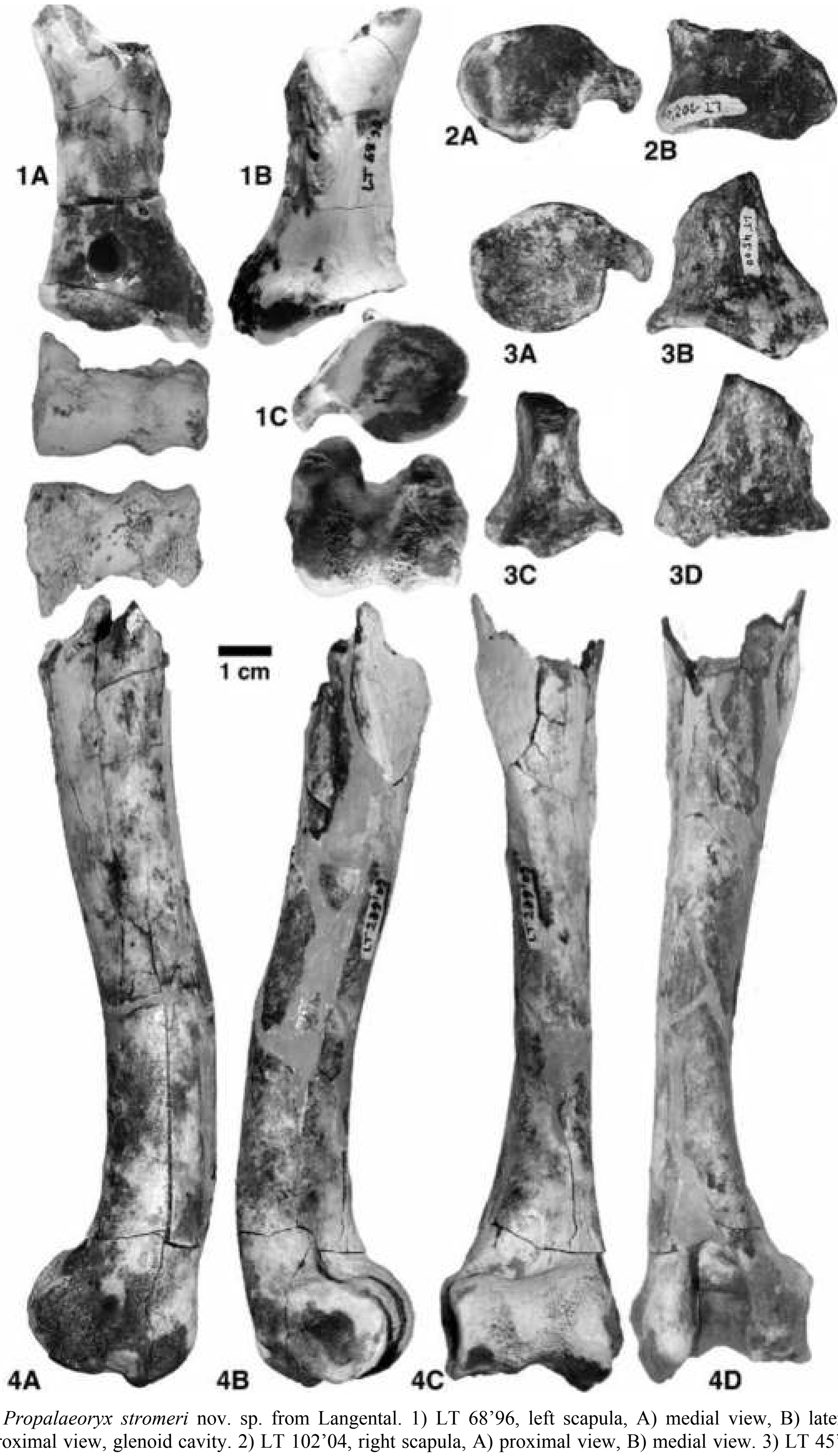


Plate 7: *Propalaeoryx stromeri* nov. sp. from Langental. 1) LT 68'96, left scapula, A) medial view, B) lateral view, C) proximal view, glenoid cavity. 2) LT 102'04, right scapula, A) proximal view, B) medial view. 3) LT 45'00, right scapula, A) proximal view, B) medial view, C) dorsal view, D) lateral view. 4) LT 239'03, right humerus, A) medial view, B) lateral view, C) dorsal view, D) cranial view, E) distal view. 5) LT 26'99, distal epiphysis of left humerus, A) cranial view, B) distal view.

Humerus : LT 239'03, right humeral diaphysis and distal epiphysis (Pl. 7, Figs 4A-E and Text.fig. 3, D1-5).

1.- The trochlea is partly eroded, but it was probably quadrangular.
2.- The medial epicondyle is relatively strong, and higher than the medial border of the trochlea.
3.- The medial lip is eroded, but one can see that it would have been higher than the lateral lip.
4.- The shape of the lateral lip cannot be made out.
5.- The capitulum is long and rises laterally.
6.- The projection of the capitulum remains slightly above the gully of the trochlea.
7.- The gully of the trochlea has eroded margins.
8.- The lateral epicondyle is low, but is well developed.
9.- The lateral pillar is parallel to the medial one, making a symmetrical olecranon fossa, which is deep.
10.- The medial side has strong central relief.
11.- The lateral side has a deep, circular fossa.
12.- The coronoid fossa is shallow.
13.- In the lateral side, a large protuberance develops in contact with the radial fossa.

LT 261'99, left distal humeral epiphysis with damaged condyles (Text-fig. 1, C1-3).

1.- The trochlea is subquadrangular, quite narrow laterally.
2.- The medial epicondyle is damaged.
3.- The medial lip was similar in height to the lateral lip.
4.- The medial lip is wide and high, asymmetrical, with its medial side more extended than its lateral one, which is more vertical.
5.- The capitulum is long and rises laterally.
6.- The projection of the capitulum remains slightly above the gully of the trochlea.
7.- The gully is quite deep and symmetrical.
8.- The pillar epicondyle is broken.
9.- Pillar is broken.
10.- The medial side is damaged.
11.- The lateral side has a deep, circular fossa.
12.- The size of the coronoid fossa cannot be determined.
13.- In the lateral side a medium sized protuberance is developed in contact with the radial fossa.

LT 02'03 (Pl. 7, Fig. 6, 5A-B) fragment of right distal humerus lacking the lateral epicondyle is too damaged to yield morphological details.

Ulna : LT 113'04, right ulna (Pl. 8, Figs 3A-D) with the diaphysis broken beneath the proximal rugosity. It is the largest specimen in the sample, but is not much different.

1.- Olecranon quadrangular, high.
2.- The crests are eroded but it is possible to see that the lateral one is longer and higher and the valleys deeper than in EF 1a'04. It has strong proximal relief and is robust, the transverse diameters are big.
3.- Anconeal process extends dorsally more than the dorsal proximal process. The dorsal border of the olecranon is curved.

LT 70'96, left ulna (Pl. 8, Fig. 4) broken at the midpoint of the sigmoid notch.

1.- Olecranon quadrangular, quite high.
2.- The crest and medial side are eroded, as is the posterior border. Only the maximal height of the olecranon can be measured. The sigmoid notch would have been narrow. The palmar tuberosity is a bit higher than the apex.
3.- The anconeal process extends further dorsally than the dorsal process. The dorsal border of the olecranon is curved.

LT 43'00, left ulna. The anterior border and part of the apex is broken. It is small.

1.- Olecranon is broken on its lateral side, and only the palmar tuberosity is preserved.
4.- The radial incisure is deep and narrow.
5.- The medial facet is not preserved.
6.- The lateral radial facet is poorly preserved.

LT 276'99, ulna fragment with the sigmoid notch and the radial facets.

4.- Radial incisura shallow and wide.
5.- Medial facet stepped.
6.- Lateral radial facet conical.

Radius : LT 261'99, proximal and distal epiphysis of radius (Text-fig. 1, H1-4).

Proximal epiphysis :

1.- Trapezoidal outline, with the medial border wider than the lateral one. The medial border is circular, the lateral one straight. The palmar and dorsal margins are straight, the palmar one being slightly higher than the dorsal one. The dorsal border has a well developed process which extends beyond the lateral border.
2.- The humeral articular facet is elliptical, its surface is deep, especially that for the lateral lip.
3.- The articular surface for the capitulum is subquadrate and the lateral protuberance is not well developed, slightly visible proximally.
4.- The notch is strong, the lateral articular surface for the ulna lies in two planes, which are not divided. The medial facet is not visible.

Distal epiphysis :

1.- The articular surface for the scaphoid is delimited by high medial and lateral ridges, its dorsal part is wide and deep, narrowing in the palmar direction.
2.- The lateral ridge of the scaphoid articulation is particularly strong on the palmar end, to the extent of forming a keel which prolongs the medial side of the radius. That is to say that its lateral profile resembles that of the metapodials.
3.- The semilunar articular facet is delimited by a high dorsal ridge and a lower lateral one, its dorsal part is deep, and continues towards the palmar side in the shape of a toboggan.

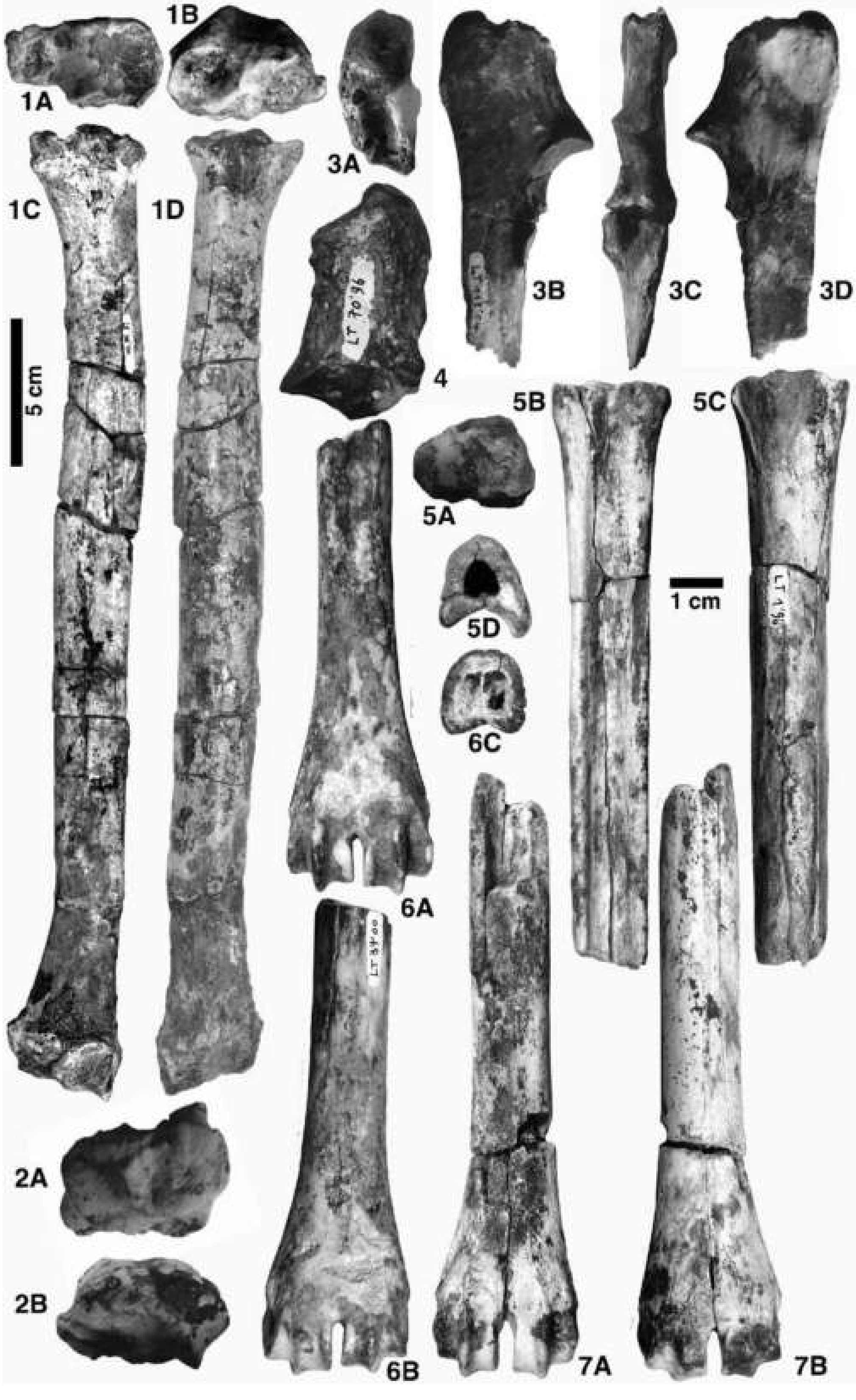


Plate 8: *Propalaeoryx stromeri* nov. sp. from Langental. 1) LT 38'00, left radius, A) proximal view, B) distal view. C) palmar view, D) dorsal view, 2) LT 02'04, distal right radius epiphysis, A) palmar view, B) distal view. 3) LT 113'04, left ulna, A) proximal view, B) lateral view, C) dorsal view, D) medial view. 4) LT 70'96, right ulna in medial view. 5) LT 1'96, left proximal metacarpal III-IV, A) proximal view, B) palmar view, C) dorsal view, D) distal diaphysis cross section. 6) LT 37'00, distal metacarpal III-IV, A) palmar view, B) dorsal view, C) diaphysis cross section. 7) LT 51'98, distal metacarpal III-IV, A) palmar view, B) dorsal view.

4.- The pyramidal facet is small, inclined to the medio-lateral axis and almost vertical to the semilunar facet, and is difficult to distinguish from the articular facet for the distal ulna. The line of separation of the semilunar from the pyramidal prolongs laterally, making a strong protuberance on the lateral side.

5.- The palmar margin between the aticular facets for the semilunar, pyramidal and distal ulna is broken. A second groove is located at the palmar base of the semilunar facet.

LT 38'00, complete left radius (Pl. 8, Figs 1A-D and Text-fig. 1, I).

Proximal epiphysis : The morphology is like that of LT 261'99, but its state of preservation is worse. Because of this the humeral articular surface appears subquadrangular rather than elliptical.

Diaphysis : Quite compressed antero-posteriorly, with the dorsal side convex and the palmar side flat or slightly concave.

Distal epiphysis :

1.- The articular surface for the scaphoid is delimited by high medial and lateral ridges, the dorsal part being wide and very deep, narrowing towards the palmar side. These two ridges prolong dorsally strongly marking the dorsal surface of the diaphysis.

2.- The lateral ridge of the scaphoid surface is broken on the palmar side, but judging from the break it was probably strong.

3.- The semilunar articulation is delimited by a high dorsal crest and a lower lateral one. Its dorsal part is deep, and on the palmar side it continues in the shape of a toboggan.

4.- The pyramidal facet is small, disposed parallel to the medio-lateral axis and almost vertical to the semilunar facet, and is difficult to distinguish from the articular facet for the distal ulna. The line of separation of the semilunar from the pyramidal prolongs laterally, making a strong protuberance on the lateral side.

5.- The palmar border has a deep groove between the semilunar, pyramidal and distal ulnar facets. A second groove occurs at the palmar base of the prolongation of the semilunar articulation.

LT 147'99, broken distal radial epiphysis.

1.- The articular surface for the scaphoid is delimited by high medial and lateral ridges, its dorsal part is wide and deep, narrowing palmarly.

2.- On the palmar side, the lateral ridge of the scaphoid facet is particularly prominent, making a ridge that prolongs the medial side of the radius. This means that the profile of the radius recalls that of the metapodials.

3.- The semilunar facet is delimited by a high dorsal ridge and a lower lateral one, its dorsal part is deep, and on the palmar side continues as a toboggan.

4.- The pyramidal facet is small, oriented parallel to the medio-lateral axis and almost vertically to the semilunar facet, making it difficult to discern the facet for the distal ulna. The line that separates the facets of the semilunar and pyramidal projects laterally forming a protuberance on the lateral side.

5.- On the palmar border there is a deep groove between the facets for the semilunar, pyramidal and distal ulna. A second groove is present on the palmar base of the prolongation of the semilunar facet.

Other specimens : LT 78'98, LT 15'97, LT 148'99 and LT 15'03, proximal radial epiphyses similar in morphology to LT 261'99. LT 02'04 distal radial epiphysis (Pl. 8, Figs 2A-B) similar in morphology to LT 147'99.

Carpals : LT 79'96, left magnotrapezoid (Text-fig. 4, A1-6).

1.- In the proximal side the lateral facet for the semilunar is weakly developed and discontinuous.

2.- The lateral palmar facet for the unciform is well developed and is visible in palmar view.

3.- The proximal lateral facet for the unciform is weakly developed.

4.- In the distal side the area that contacts the Mc III-IV is quite developed.

5.- The palmar proximal process is high.

6.- The lateral articular border of the proximal side is concave.

7.- The shape of the proximal and distal sides is quadrangular.

LT 124'98, right unciform (Text-fig. 4, B1-6).

1.- The palmar area is well developed with two prominent rounded processes.

2.- The palmar processes are low compared to the height of the unciform.

3.- The medial articular border of the proximal side is convex.

LT 48'97, left scaphoid (Text-fig. 4, C1-6).

1.- In the proximal side the dorsal part is elevated and separated by a valley from the palmar part.

2.- The external distal facet of the lunate is prominent.

3.- The shape in lateral view, is quadrangular (high disto-proximally).

LT 50'97, left semilunar (Text-fig. 4, D1-6).

1.- The palmar prominence is well developed.

2.- In the distal side, the two dorsal facets are unequal (the medial facet is better developed than the lateral one) and are in different planes, the lateral facet being very inclined.

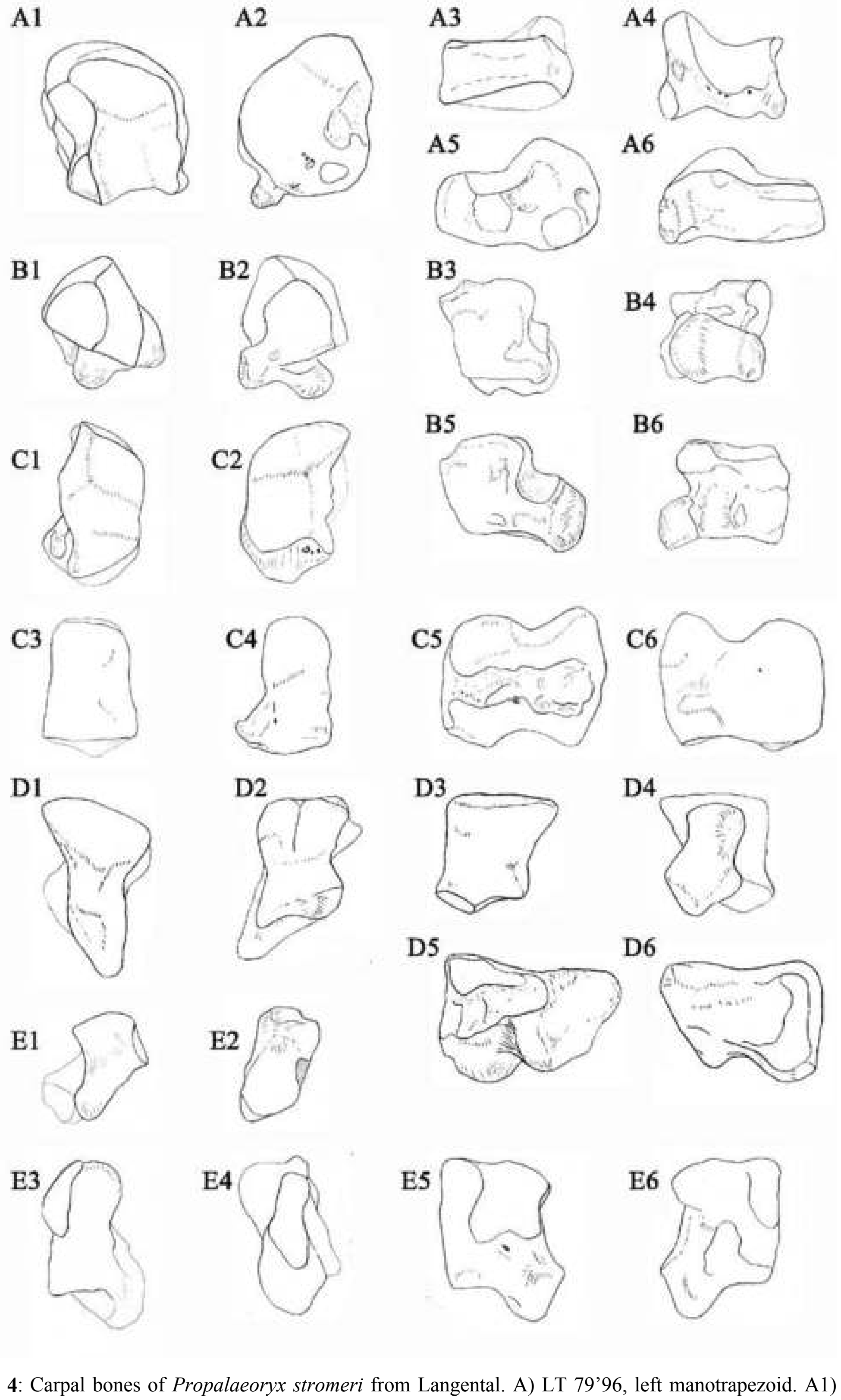
LT 242f'03, right pyramidal.

LT 200'99, left pyramidal (Text-fig. 4, E1-6).

1.- The distal side is widened.

2.- The dorsal side is well developed.

Metacarpal III-IV : LT 1'96, fragment of proximal left metacarpal (Pl. 8, Figs 5A-D) LT 52'98, proximal fragment of right metacarpal, lacking the distal extremity, the fragment measures 167 mm. LT 51'98,



Text figure 4: Carpal bones of *Propalaeoryx stromeri* from Langental. A) LT 79'96, left manotrapezoid. A1) proximal view, A2) distal view, A3) dorsal view, A4) palmar view, A5) lateral view, A6) medial view. B) LT 124'98, right unciform (reverse). B1) proximal view, B2) distal view, B3) dorsal view, B4) palmar view, B5) lateral view, B6) medial view. C) LT 48'97, left scaphoid. C1) proximal view, C2) distal view, C3) dorsal view, C4) palmar view, C5) lateral view, C6) medial view. D) LT 50'97, right semilunar (reverse). D1) proximal view, D2) distal view, D3) dorsal view, D4) palmar view, D5) lateral view, D6) medial view. E) LT 200'99, left pyramidal. E1) proximal view, E2) distal view, E3) dorsal view, E4) palmar view, E5) lateral view, E6) medial view.

distal metacarpal (Pl. 8, Figs 7A-B) of large size morphotype A (Köhler, 1993). LT 37'00, distal metacarpal (Pl. 8, Figs 6A-C) large size morphotype A, gracile diaphysis. LT 04'03, distal fragment of metacarpal, large size. LT 1a'97, is interpreted to be a very large distal metacarpal, but it could be a metatarsal.

LT 1'96, proximal metacarpal.

1.- The magnum facet is eroded, as is the dorsal medial zone which is why there is no tuberosity. The dorsal margin of the unciform facet is higher than in EF 35'93 and EF66'01 (although the latter specimen is doubtful due to damage). In the lateral posterior border there is a flat facet for the Mc V followed medially by a tuberosity and a fossa. In the medial half there is another fossa between two tuberosities, all of which are stronger than in the lateral half.

2.- The line that separates the facets is strong.

3.- The line that separates the facets borders the sinovial fossa.

4.- The sinovial fossa is oval and reaches the palmar edge.

5.- A low rugosity is visible in the magnotrapezoid facet which is separated from the sinovial fossa.

7.- The diaphysis is compressed transversely, the palmar side is extremely concave, the lateral border being the higher, and in this feature it differs from EF 66'01. The dorsal groove is fine and shallow, visible in the proximal third. The lateral extensor groove is long and shallow.

LT 52'98, proximal metacarpal fragment. The proximal outline is as in LT 1'96. The dorsal proximal profile with the medial tuberosity zone is elevated, differing from EF 35'93, more moderate in EF 66'01.

6.- The dorsal medial tuberosity is strong. In the postero-lateral corner there is a depression for the Mc V, the rest of the proximal margin is eroded.

7.- The diaphysis is very concave posteriorly, but in this case the medial border is the most prominent. The lateral extensor groove is shallow and long and the dorsal one is fine and visible throughout the fragment.

LT 51'98, distal metacarpal fragment. LT 04'03, distal metacarpal fragment.

8.- The distal canal of the metacarpal is dorsally large (LT 51'98) or very large (LT 04'03) the palmar one strong.

9.- The distal pulleys are parallel.

10.- The pulley keels are strong dorsally.

11.- The articular eminences are wide.

12.- The distal part of the diaphysis is higher than the pulley.

<u>*Femur*</u> : LT 3'03, poorly preserved left medial epicondyle of femur (Pl. 9, Fig. 1).

<u>*Tibia*</u> : LT 78'99, damaged proximal epiphysis of left tibia (Pl. 9, Fig. 2).

LT 193a'96 (Pl. 9, Figs 5A-C) distal fragment of left tibia.

1.- The epiphysis is subquadrangular without antero-posterior compression.

2.1- The anterior margin is inclined due to the strong projection of the medial maleolus.

2.2. The posterior border is concave due to the fact that the central keel that separates the gullies of the cochlea is narrow (AP) and that the projection of the plantar medial border of the cochlea is strong (maximum AP).

3.- The medial maleolus is slightly higher than the central process.

4.- The central process is very wide, equalling the keel that separates the tibial cochlea.

5.- The lateral gully is narrow and clearly separated by a keel from the maleolar facets.

6.- The maleolar groove is weakly marked.

7.- The medial protuberance is weak.

8.- The fibular incision is weak but divides the maleolar facets into two parts which are united, the posterior being bigger than the anterior. Between the anterior facet and the central process there is a groove with well defined margins.

9.- The cochlea has a wider medial fossa than the lateral one.

LT 7'01 (Pl. 9, Figs 4A-C) distal left tibia fragment.

1.- The epiphysis is subquadrangular without antero-posterior compression.

2.1- The anterior margin is moderately inclined due to the projection of the medial maleolus.

2.2. The posterior border is relatively straight, due to the slight projection of the plantar-medial border of the cochlea.

3.- The medial maleolus is slightly higher than the central process.

4.- The central process is very wide, equalling the keel that separates the tibial cochlea.

5.- The lateral gully is narrow and separated by a keel from the maleolar facets.

6.- The maleolar groove is well marked.

7.- The medial protuberance is moderately marked.

8.- The fibular incision is well marked and divides the maleolar facets into two parts which are united, the posterior being bigger than the anterior. Between the anterior facet and the central process there is a deep incision with well defined margins.

9.- The cochlea has a wider (DAP) medial fossa than the lateral one.

LT 2'01 (Pl. 9, Figs 3A-B) right distal tibia.

<u>*Astragalus*</u> : LT 193b'96 (Pl. 9, Figs 6A-F) left astragalus.

1.- Proximal view, the medial condyle is narrow and quite sharp, whereas the lateral one is wider, the two being parallel to each other. In the medial condyle there is a strong proximal plantar process, which is smaller than in EF 46'00.

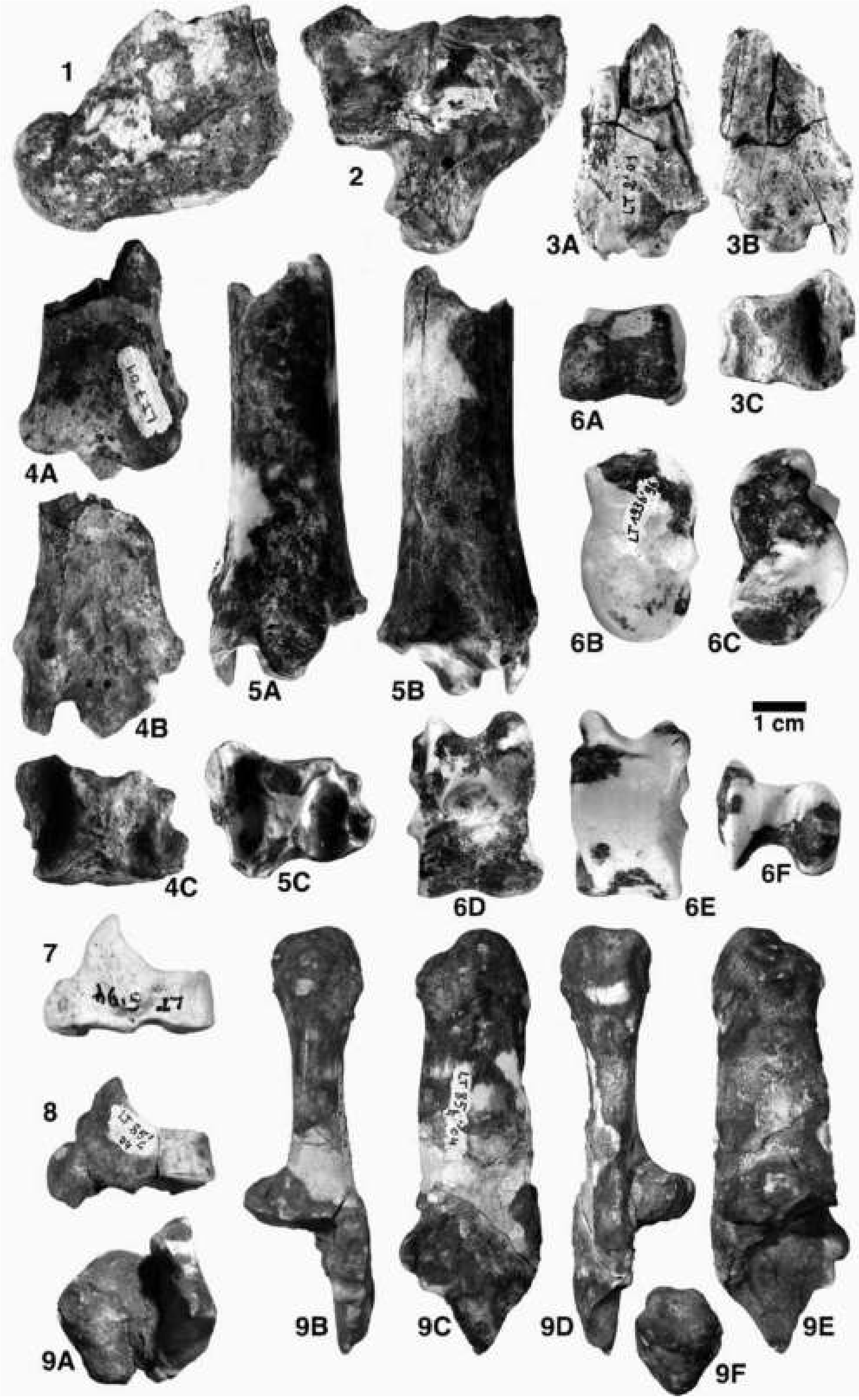


Plate 9: *Propalaeoryx stromeri* nov. sp. from Langental. 1) LT 3'03, left medial epicondyle of femur in medial view. 2) LT 78'99, right proximal epiphysis of tibia in proximal view. 3) LT 2'01, distal right tibia epiphysis, A) plantar view, B) dorsal view, C) distal view. 4) LT 7'01, distal left tibia epiphysis. A) plantar view, B) dorsal view, C) distal view. 5) LT 193a'96, distal left fragment of tibia A) dorsal view, B) plantar view, C) distal view. 6) LT 193b'96, left astragalus, A) distal view, B) lateral view, C) medial view, D) plantar view, E) dorsal view, F) proximal view. 7) LT 5'94, left navicular-cuboid in medial view. 8) LT 85c'04, left navicular-cuboid in medial view. 9) LT 85a'04, left calcaneum, A) proximal view, B) plantar view, C) lateral view, D) dorsal view, E) medial view, F) distal view.

2.- In the dorsal side there is a strong process that blocks flexion (medial side) and the fossa for the medial process of the tibia is circular and deep.
3.- The plantar side is very asymmetric, the medial part is flatter and the lateral gently concave, its profile being gently concavo-convex. This plantar side is narrower (latero-medial) than in EF 46’00.

Calcaneum : LT 118’96, left calcaneum, LT 200’96, left calcaneum, LT 137’99, left calcaneum lacking the proximal part, LT 01’03, left calcaneum with tooth marks and LT 85’04, left and right calcanea (Pl. 9, Figs 9A-F).
1.- The tuber is asymmetric with the medial lobe higher and narrower than the lateral one. The fossa is deep and there are strong lateral and medial insertions.
2.- The anterior border of the neck is slightly convex, the posterior side straight.
3.- The sustentaculum is notably developed, due to its strong medial projection. The tendinal groove is small but well defined.
4.- There are signs of a small dorsal articular facet.
5.- The proximal part of the maleolar facet is prominent medially. The distal part is long, with an irregular cuboid facet, widened in its middle.
LT 196’96 left proximal half of calcaneum.
3.- The sustentaculum tali is notably well developed, due to its strong medial projection. The tendinal groove is weakly defined.
4.- There are no signs of a dorsal articular facet.
5.-The maleolar facet has a proximal part that is very prominent in the medial sense. The distal part is long, with the cuboid facet irregular, somewhat widened in the middle (even though this part has been slightly eroded).

Navicular-cuboid : LT 50’01, right navicular-cuboid. LT 5’94 (Pl. 9, Fig. 7), LT 85c’04 (Pl. 9, Fig. 8).
1.- In proximal view, the proximal processes are high, especially the medial one, the internal one is higher than the calcaneal facet.
2.- In distal view, the anterior facet for the metatarsal is subtriangular, with a strong internal notch. The posterior facet for the metatarsal is small and sits on a strong protuberance. The facet for the ectocuneiform is elongated. Outstanding is the well developed postero-internal bulge which is almost the same size as the postero-external protuberance almost forming a continuous crest.
3.- In plantar view, the most obvious feature is the swelling of the base of the posterior facet for the metatarsal, which occupies a large part of the plantar side of the navicular-cuboid. The postero-internal bulge makes a prominent crest between the plantar and medial sides, but is separated by a wide groove from the base of the internal tenon. Between these crests just below the medial tenon, there is developed a relatively deep fossa penetrated by a strong foramen.

Metatarsal : LT 192’96, proximal fragment of left metatarsal (Plate, 10, Figs 1A-E).
1.- Complete fusion of Mt III-IV.
2.- Mt III (articulates with the cuneiform) the proximal anterior facet is kidney-shaped and concave, delimited by two tuberosities, a weak dorso-medial one, the other plantar one strong.
3.- The proximal posterior facet for the ectocuneiform is rounded, plantarly marked by a facet for the sesamoid.
4.- Mt IV (articulates with the cuboid) proximal anterior facet is subquadrangular and its surface concavo-convex.
5.- The proximal posterior facet is subtriangular, very small, inclined and somewhat elevated, and separated from the posterior proximal facet for the ectocuneiform by a canal.
6.- Lateral-plantar prominence is weakly developed, and the medial plantar prominence is a sharp protuberance projecting to the exterior.
7.- The proximal canal of the metatarsal is big on the proximal surface, but moderate sized on the plantar side.
8.- The dorsal canal is very slightly marked on the dorsal-proximal border.
9.- Backing onto the dorsal canal, on the medial side there is a well marked groove.
10.- Mt II is fused and wedge shaped, not marked proximally. Mt V is unfused, there is a triangular articular surface in the Mt IV.
12.- Dorsal groove is quite pronounced in the proximal part of the diaphysis.
14.- Plantar groove is very well developed on the proximal part of the diaphysis.
LT 209’96, proximal fragment of right metatarsal (Pl. 10, Figs. 2A-E).
2.- Mt III (articulates with the cuneiform) the proximal anterior facet is kidney-shaped and concave, delimited by two tuberosities, a weak dorso-medial one, the other plantar one strong.
6.- Lateral-plantar prominence is weakly developed, and the medial plantar prominence is a sharp protuberance projecting to the exterior.
10.- Mt II is fused and wedge shaped, marked proximally. Mt V is unfused, there is a triangular articular surface in the Mt IV.
LT 64’04, distal fragment of metatarsal (Pl. 10, Figs 3A-E) with open gully.
LT 39’05, distal fragment of metatarsal (Pl. 10, Figs 4A-B) with closed gully.

Ist phalanx : LT 44’07 (Pl. 10, Fig. 5) LT 1b’97.
1.- Long and gracile.
2.- In dorsal view the lateral side is concave.
3.- The incision for the metapodial verticillus is strong.
4.- The facet of the distal articulation is clearly

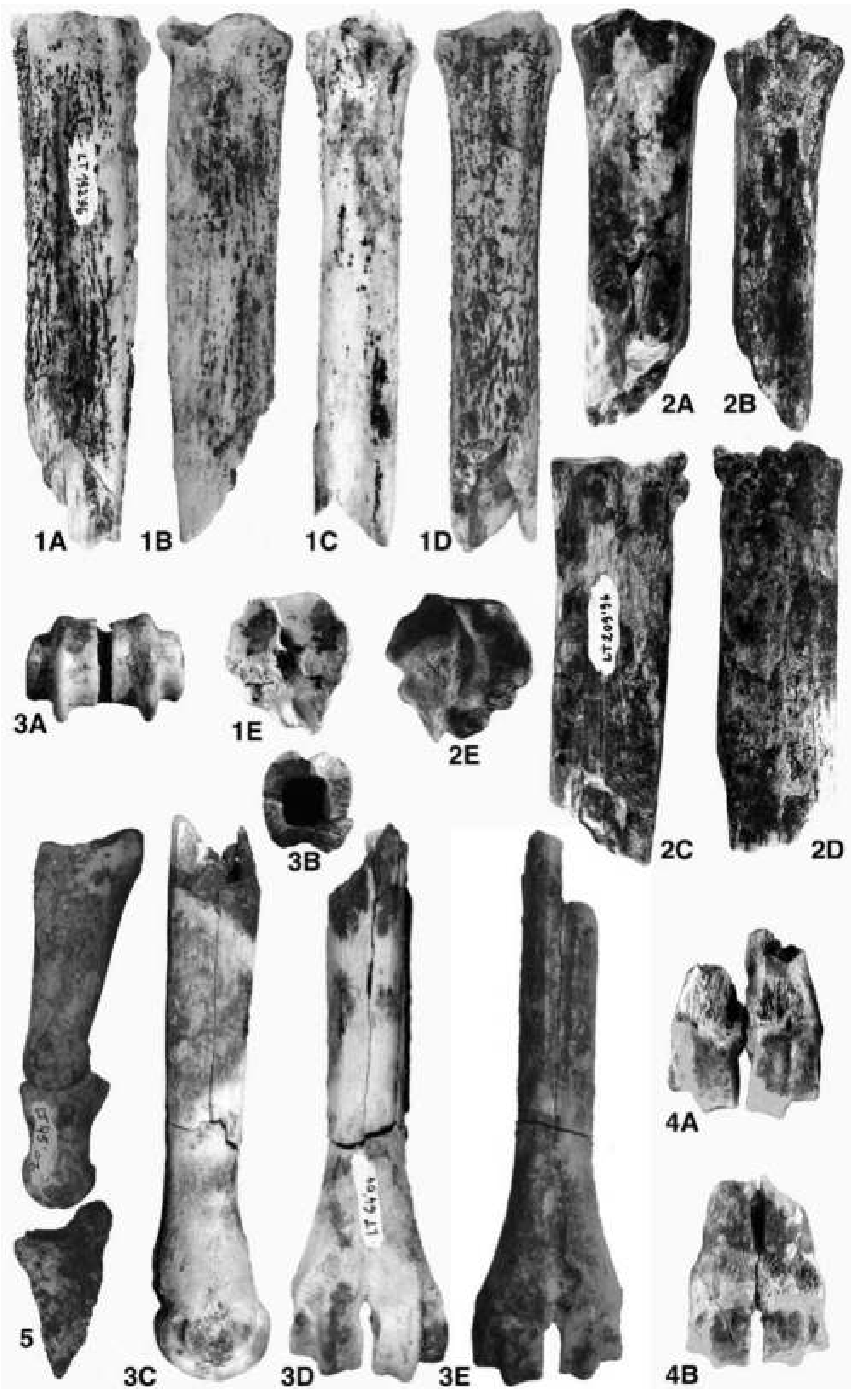


Plate 10: *Propalaeoryx stromeri* nov. sp. from Langental. 1) LT 192’96, proximal left fragment of metatarsal III-IV, A) lateral view, B) medial view, C) plantar view, D) dorsal view, E) proximal view. 2) LT 209’96, proximal right fragment of metatarsal III-IV, A) dorsal view, B) plantar view, C) medial view, D) lateral view, E) proximal view. 3) LT 64’04, distal fragment of metatarsal III-IV, A) distal view, B) diaphysis cross section, C) lateral view, D) plantar view, E) dorsal view. 4) LT 39’05, distal fragment of metatarsal III-IV, A) dorsal view, B) plantar view. 5) LT 45’07, Ist, IInd and IIIrd phalanx in lateral view.

visible in dorsal view.

5.- The facet of the distal articulation shows a well rounded outline.

LT 52’04, is more robust than LT 1b’97.

IInd phalanx : LT 45’07 (Pl. 10, Fig. 5); LT 1c’97.

1.- Robust.

2.- In proximal view the postarticular platform is elongated and asymmetric.

3.- The dorsal extensor process is short.

4.- The outline of the distal articular facet is quite triangular.

5.- The articulation extends greatly dorsally.

IIIrd phalanx : LT 46’06 (Pl. 10, Fig. 5); LT 8’98; LT 4’98.

1.- The dorsal ridge is concave (LT 8’98) or convex (LT 4’98).

2.- There is a medium sized dorsal process for the insertion of the extensor.

3.- The articular surface is well rounded but not deep.

4.- Small plantar process for the insertion of the deep flexor tendon.

5.- Dorsal view : the ridge is long and in a lateral position.

6.- The plantar surface is well defined by two ridges (medial and external).

Grillental

Lower dentition : GT 200’96, incisor (probably i/3) dimensions of the crown : L = 3.1 mm; W = 2.7 mm.

GT 82’96, right mandible, in poor condition with only the p/4 being almost complete, but lacking the postero-buccal part of the wall. The anterior wing is bifurcate. The mesio-lingual cusp is medium sized and has a small antero-lingual cristid. The posterior cusplet and the posterior stylid are worn and almost fused to each other. The m/1 has the lingual wall damaged and it is deeply worn. The ectostylid is strongly developed.

The m/2 has only the buccal wall preserved. A moderate metastylid can be discerned, and the mesio-buccal valley is well marked and there is a strong entoconid.

GT 175’04 (Text-fig. 1 and 7A-C) is a right mandible with an almost complete tooth row. In general the molars and premolars are quite narrow. The m/3 has a convex and continuous buccal wall, with the valley separating the metaconid from the entoconid weakly developed. The metastylid is extremely weak. The cristids of the protoconid are united to those of the metaconid, completely closing the anterior lophid. The posterior cristid of the metaconid is linked to the diminutive metastylid and the anterior cristid of the entoconid, such that the hypoconid is isolated from the rest of the tooth. The hypoconulid is relatively high, its lingual cristid joins without interruption the posterior cristid of the entoconid at about mid-height. The buccal cristid remains isolated close to the end of the posterior cristid of the hypoconid. There is no trace of a palaeomerycid fold. There is a small ectostylid and a moderate basal cingulum on the protoconid.

In the m/2 the posterior cristid of the hypoconid closes the tooth posteriorly, but without joining the posterior cristid of the entoconid. The posterior cristid of the entoconid is shorter than it is in the m/3 making the entoconid somewhat more bunodont. The metastylid is quite strong, equal to the valley that separates the metaconid from the entoconid in the lingual wall. The palaeomerycid fold is weakly marked. The ectostylid is extremely reduced. The m/1 is a replica of the m/2 but is smaller and its ectostylid is better developed.

In the p/4, there is a strong vertical incision postero-buccally, the cusp and postero-lingual stylids are oblique and are practically united together and with the posterior cristid of the mesio-lingual cusp. The anterior wing is bifurcate. The p/3 has a damaged buccal wall. It differs from the p/4 by the absence of the mesio-lingual cuspid. The p/2 is badly damaged. In the mandible, it is possible to make out a small root for the p/1.

GT 57’07, a fragment of left mandible with m/3-m/1, the m/1 (Pl. 11, Figs 1A-C) being quite incomplete. The dentition is more brachyodont than that of GT 175’04 (the molars are shorter and slightly broader). The m/3 differs from the one in GT 175’04 by the greater development of the basal cingulum, a stronger ectostylid and by a better development of the posterior cristid of the hypoconid which terminates in a slight bifurcation, each of which joins the corresponding cristids of the hypoconulid. The m/2 possesses a strong ectostylid, as in the m/2 of GT 175’04.

Postcranial skeleton :

Humerus : GT 75’06, right distal humerus epiphysis (Pl. 11, Figs 2A-E).

1.- The trochlea is subquadrangular.

2.- The medial epicondyle, of moderate size, is a little higher than the lateral border of the trochlea.

3.- The medial lip is not very elevated, almost at the same height as the lateral lip.

4.- The lateral lip is quite wide and symmetrical.

5.- The capitulum is long and rises laterally.

6.- The projection of the capitulum remains slightly above the gully of the trochlea.

7.- The gully of the trochlea is quite symmetrical.

8.- The lateral epicondyle is low and well developed.

9.- The crest of the lateral epicondyle is almost parallel to the crest of the medial one, which makes the olecranon fossa symmetrical and very deep.

10.- The medial face has gentle central relief, but the zone has been somewhat eroded.

11.- The lateral surface has a deep circular fossa.

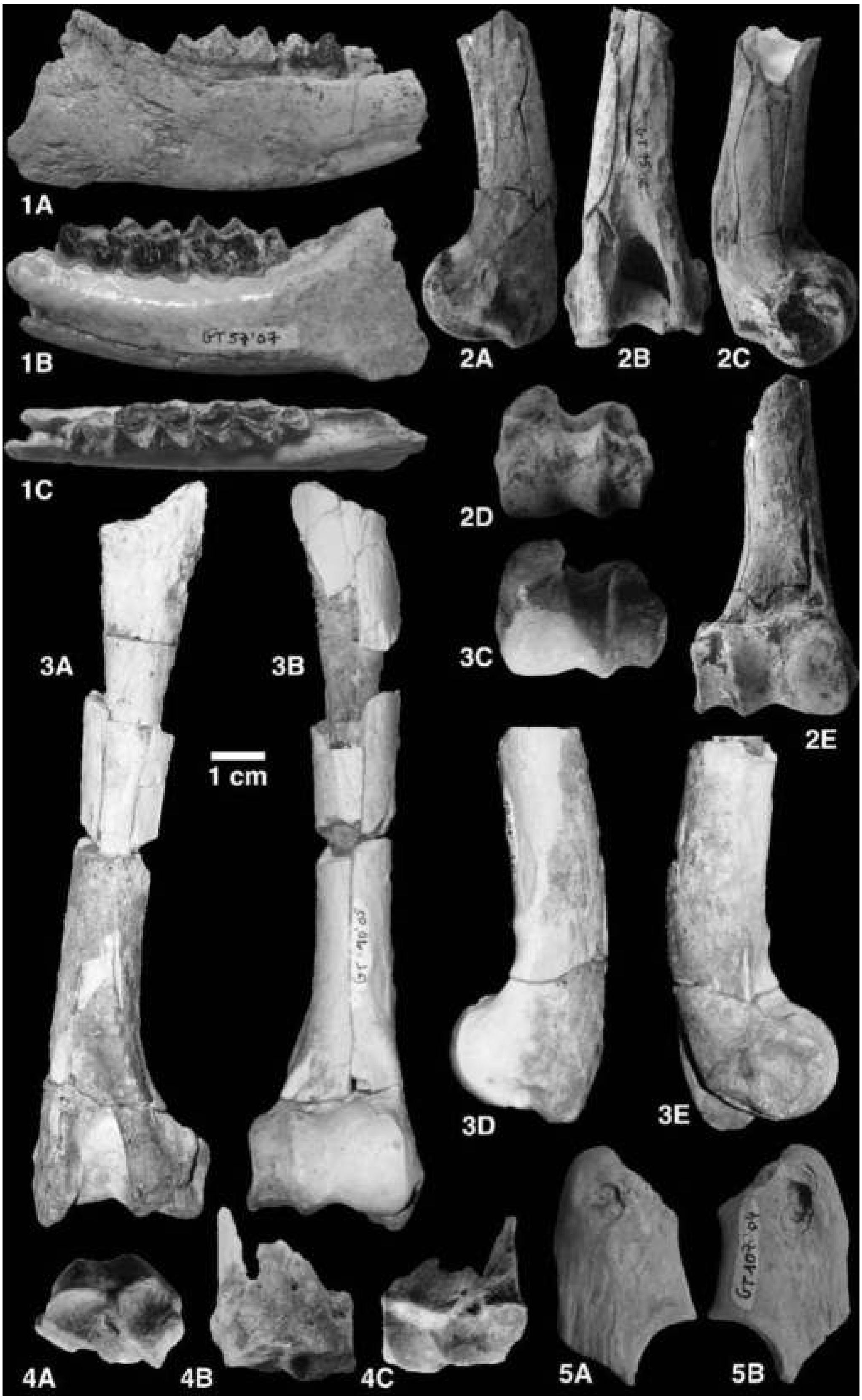


Plate 11: *Propalaeoryx stromeri* nov. sp. from Grillental. 1) GT 57'07, left mandible with m/3-m/1, A) lingual view, B) buccal view, C) occlusal view. 2) GT 75'06, distal right fragment of humerus, A) medial view, B) caudal view, C) lateral view, D) distal view, E) cranial view. 3) GT 10'05, right fragment of humerus, A) caudal view, B) cranial view, C) distal view, D) medial view, E) lateral view. 4) GT 76'06, distal right radius epiphysis, A) distal view, B) dorsal view, C) palmar view. 5) GT 107'04, right ulna, A) lateral view, B) medial view.

12.- In the lateral surface there is a strong protuberance in contact with the radial fossa.

Other specimens : GT 3'03, eroded right distal epiphysis of humerus; GT 10'05 (Pl. 11, Figs 3A-E) right distal epiphysis of humerus, same morphology as GT 75'06 but with the medial epicondyle higher.

Ulna : GT 107'04 (Pl. 11, Figs 5A-B) right ulna is broken at the middle of the trochlear incision. The olecraneon, partially eroded, is quadrangular, higher than the olecraneon of the EF 1c'04 ulna.

Radius : GT 76'06, distal epiphysis of right radius (Pl. 11, Figs 4A-C).

Scaphoid : GT 4'01, GT 14'04, GT 3'01.

Pelvis : GT 3'04, left coxal fragment (Pl. 12, Fig. 1); GT 90'06, left coxal (Pl. 12, Fig. 2).

Femur : GT 87'06, distal right femur fragment (Pl. 12, Figs 3A-C) shows several carnivore bite marks. The trochlear lips are parallel, the two lips resembling each other. The crest of the medial lip is more rounded than the lateral one. The trochlear gully is deep.

Tibia : GT 31'03, eroded distal epiphysis; GT 39'03, eroded distal epiphysis; GT 27'05, distal left tibia epiphysis (Pl. 12, Figs 4A-B).

1.- Epiphysis is sub-quadrangular.
2.1.- The anterior margin is quite straight.
2.2.- The posterior margin is concave.
3.- The medial maleolus is at the same height as the central process.
4.- The central process is wide.
5.- The keel that separates the lateral gully from the maleolar facets is quite eroded.
6.- The maleolar sulcus is well marked.
7.- The medial protuberance is moderate.
8.- The fibular incision is well marked and divides the maleolar facets into two parts.
9.- The cochlear gullies have the same width.

GT 28'00, distal left tibia, differs from the above specimen by possessing a wider keel between the cochear gullies, related to a more robust central process. The posterior side is concave. GT 185'96, damaged right distal tibia.

Astragalus : GT 7'94, left astragalus (Pl. 12, Figs 5A-F) GT 4'03, GT 5'03.

Calcaneum : GT 11'03, GT 1'07 left calcaneum (Pl. 12, Fig. 8).

Navicular-cuboid : GT 56'96, left navicular cuboid with the lateral tenon broken (Pl. 12, Figs 6A-B).

1.- in proximal view the medial proximal process (medial tenon) is high, the lateral one is higher than the calcanear facet.
2.- Distal view, the anterior facet for the metatarsal is subquadrangular, with a strong internal notch. The posterior facet for the metatarsal is almost imperceptible and sits on a strong protuberance. The facet for the ectocuneiform is elongated. Outstanding is the strong development of the postero-internal bulge, almost the same size as the postero-external bulge (which is lower) and the two form a continous crest.
3.- plantar view, outstanding is the swelling of the base of the metatarsal facet, which occupies a major part of the plantar side of the navicular-cuboid. The postero-internal bulge forms a prominent crest between the plantar and medial sides, but separated by a wide groove from the base of the internal tenon. Between these crests just beneath the medial tenon a deep fossa is developed penetrated by a strong foramen.

GT 84'96, left navicular-cuboid with the distal side damaged. GT 3'04 right navicular-cuboid (Pl. 12, Figs 7A-B).

1.- is notable for the lesser height of the medial tenon, which is not eroded.
3.- is similar to GT 56'96, but because of the slight development of the medial tenon its profile in medial view is very different.

Metatarsal : GT 54'06, metatarsal III-IV (Pl. 12, Fig. 9).

Ist phalanx : GT 7'01, GT 26'03.

IInd phalanx : GT 12'03, GT 55'06 (Pl. 12, Figs 10 A-F).

IIIrd phalanx : GT 5'01, GT 38'03, GT 44'03 very eroded, GT 6'06 (Pl. 12, Figs 11A-D).

Fiskus

Lower dentition : FS 10'04, left lower associated teeth in moderate condition of preservation. The posterior part of the m/3 shows the morphology of *Propalaeoryx*, with the posterior cristid of the hypoconid united to the entoconulid, which is broken, and well separated from the posterior cristid of the entoconid. The hypoconulid is isolated, due to the weakness of its cristids. The rest of the dental fragments preserved are not important, being poorly preserved and deeply worn. The p/4 has a strong postero-buccal vertical groove.

Postcranial skeleton :
Maleolus : FS 5'03.

Unciform : FS 31'01, FS 21'01, very damaged.

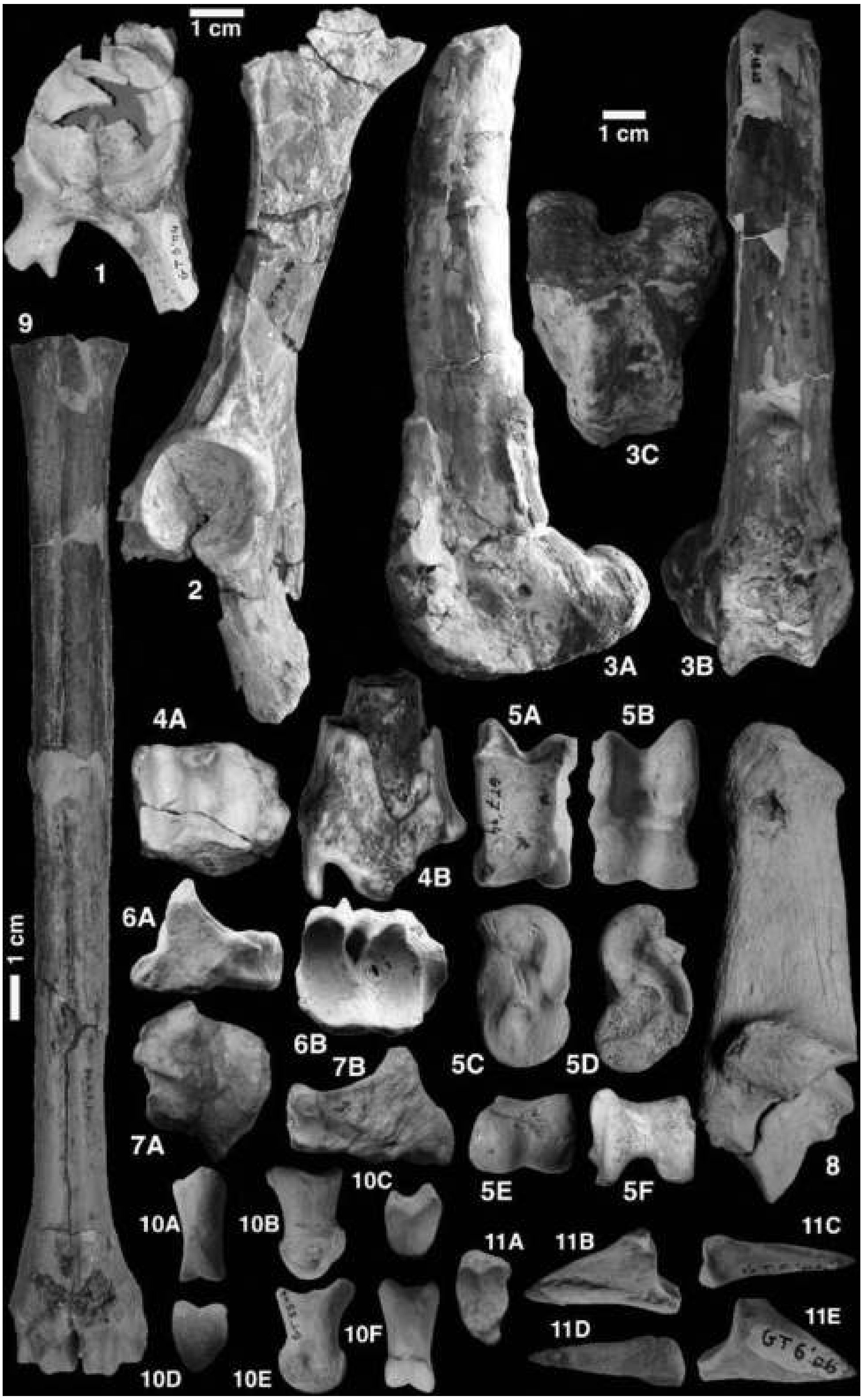


Plate 12: *Propalaeoryx stromeri* nov. sp. from Grillental. 1) GT 3'04, left coxal fragment, lateral view. 2) GT 90'06, left coxal, lateral view. 3) GT 87'06, distal fragment of right femur, A) lateral view, B) distal view, C) cranial view. 4) GT 27'05, distal left tibia epiphysis, A) distal view, B) dorsal view. 5) GT 7'94, left astragalus, A) dorsal view, B) plantar view, C) lateral view, D) medial view, E) distal view, F) proximal view. 6) GT 56'96, left navicular-cuboid, A) medial view, B) proximal view. 7) GT 3'04, right navicular-cuboid, A) distal view, B) medial view. 8) GT 1'07, left calcaneum in medial view. 9) GT 54'06, metatarsal III-IV in dorsal view.10) GT 55'06, II phalanx, A) dorsal view, B) medial view, C) proximal view, D) distal view, E) lateral view, F) dorsal view. 11) GT 6'06, IIIrd phalanx, A) proximal view, B) dorsal view, C) plantar view, D) medial view, E) lateral view.

Scaphoid : FS 18'01.

Semilunar : FS 20'01.

Pyramidal : FS 26'01.

Pisiform : FS 14'04.

Ist phalanx : FS 9'03, with damaged articulation.

IInd phalanx : FS 15'01, FS 3'03.

Discussion : The separation between the two species of *Propalaeoryx* is rendered difficult by the strong variation, especially metric, that occurs in all the samples from the various localities in the Sperrgebiet. For example at Langental there are two size groups of ruminant scapula, and in principal two morphotypes. The smaller ones possess morphology similar to *Orangemeryx*. The largest specimen LT 45'00 is less clear, but may be considered to be a different morphotype judging from the weak widening of the supraglenoid tubercle. Three specimens differ from *Orangemeryx hendeyi* by having this tubercle less developed cranio-caudally and with a shorter pedicle (see Cccg/Ccmax in Appendix 1).

When we compare the sizes of IIIrd phalanges from the different localities in the Sperrgebiet, we notice a degree of variation that greatly surpasses that documented in *Orangemeryx hendeyi* from Arrisdrift (Morales *et al.*, 2003). This great variation can be explained by the existence of size differences between the fore and hind feet, and by the possible presence of sexual bimodality (Appendices 18-20; Text-fig. 8). Nevertheless, IIIrd phalanges of *Propalaeoryx austroafricanus* from Elisabetfeld are generally smaller for each type of phalanx (anterior or posterior limb). In other postcranial bones the differences encountered in the identified species of *Propalaeoryx* is less evident, partly because there are fewer specimens, but in general bones of *P. austroafricanus* are smaller than those attributed to *P. stromeri* (Appendices 1-17). The differences between the dentitions of the two species are given in the differential diagnosis of *Propalaeoryx stromeri*.

Nevertheless the similarities between the two species in the genus are emphasized by the morphology of the navicular-cuboid. All the navicular-cuboids from the Sperrgebiet attributed to *Propalaeoryx* comprise a homogeneous morphological pattern, differing from that of Bovidae (*sensu lato*) in particular by the better development of the postero-internal bulge (which however is well developed in cervids) forming a very prominent crest. This morphological combination is present in the two morphotypes of navicular-cuboid described in *Orangemeryx hendeyi* (Morales *et al.*, 2003) and, save for the greater size, the morphological resemblances to the Sperrgebiet material are notable. The morphology of the plantar side of the navicular-cuboid in *Propalaeoryx* is similar to that of *Okapia*, but in the latter the postero-internal process is less developed, and the internal tenon is notably less high than in *Propalaeoryx* and *Orangemeryx*.

1. Relationships to Climacoceratidae

The discussion on the relations between *Propalaeoryx* and Climacoceratidae, especially with *Orangemeryx hendeyi*, the best known species of the family, modifies the results of Morales *et al.*, (1999). *Propalaeoryx* - which is now excluded from the subfamily Sperrgebietomerycinae due to the close relationship of the type genus *Sperrgebietomeryx* to the family Bovidae - can be considered as a primitive Climacoceratidae because of its lesser hypsodonty and the retention of p/1, its elongated unreduced premolars and the absence of cranial protuberances. These differences are sufficiently important to define a new subfamily, Propalaeorycinae in the family Climacoceratidae, containing *Propalaeoryx* and related genera such as *Walangania*.

2.- Climacoceratidae and Giraffidae

The systematic position of *Climacoceras* has been the subject of debate ever since the definition of the genus by MacInnes (1936) who considered it to be a deer. It was included in the Giraffidae by Hamilton (1978 a, b). The most pertinent evidence for the latter view was the possession of the same type of bilobed canine which characterises the Giraffidae. However, the presence of a bilobed canine in *Climacoceras* was contested by Churcher (1990) who did not exclude the possibility that the tooth attributed by Hamilton (1978b) to *Climacoceras gentryi* could belong the other giraffid from Fort Ternan *Palaeotragus primaevus*. In support of the absence of a bilobed canine in Climacoceratidae is the fact that in the large sample of anterior teeth of *Orangemeryx hendeyi* from Arrisdrift, Namibia (Morales *et al.*, 2003) there is no specimen of bilobed canine.

However, the relations between Climacoceratidae and Giraffidae is supported well by other characters, in particular the morphology of the navicular-cuboid. The extant Giraffidae, *Giraffa* and *Okapia* possess navicular-cuboids which are greatly modified compared to those of other pecorans. Despite the major differences between the post-cranial skeletons of the two extant species, their navicular-cuboids share a unique morphology, comprising a strong bulge and a notably well-developed and salient plantar crest. This morphology also occurs in diverse subfamilies of Giraffidae including *Bohlinia attica* or *Birgerbohlinia schaubi*.

Climacoceratidae such as *Propalaeoryx*, *Prolibytherium* or *Kenyameryx* possess a more primitive navicular-cuboid than that of Giraffidae, but share with them the strength of the bulge, and above all an incipient but clear formation of a plantar crest

(Text-fig. 5).

Navicular-cuboids which are more primitive than those of Climacoceratidae, but which are clearly derived from the primitive morphotype - characteristic of *Hyemoschus* or *Moschus*, and which vary little from the family Bovidae - are found in the majority of ruminants from the Early Miocene of Europe. This is the case with *Pomelomeryx*, *Amphitragulus* and *Bedenomeryx*, in which there is an incipient bulge, occasionally prominent on the plantar side but without forming a strong plantar crest, as in extant Cervidae and fossil forms such as *Procervulus ginsburgi*, *Heteroprox larteti* and *Dicrocerus elegans*. The plantar crest is better developed in *Dremotherium*, *Oriomeryx* and the Palaeomerycidae, but it is not as well developed in these genera as it is in the Climacoceratidae (and naturally the Giraffidae).

The correspondence of the navicular-cuboid morphology with that of nearby skeletal elements is less clear, the Climacoceratidae having a distal metatarsal III-IV in which the plantar process is strongly developed and projects towards the plantar side. In the medial surface of the astragalus it is difficult to see any corresponding derived morphology. Search for other morphological features in the postcranial skeleton that would underline the differences noted in the navicular-cuboid, is unrewarding. *Dremotherium*, *Oriomeryx*, Palaeomerycidae, Climacoceratidae and Giraffidae have clearly widened the distal trochlea of the humerus and the corresponding articular surface of the proximal radio-ulna. Likewise the distal epiphysis of the tibia of these ruminants show a clear transversal elongation (medio-lateral) when compared with genera such as *Pomelomeryx* and *Amphitragulus*, but these characters are subtle.

The dentition of all these forms differ from those of Bovidae. They are clearly more primitive, are generally more brachyodont or moderately hypsodont such that the cusps of the lower molars fuse, which makes it difficult to establish the phylogenetic relations between the genera.

But despite all these difficulties, it seems that the group Giraffidae-Climacoceratidae is clearly separated from the superfamily Bovoidea, and that, based on the available data, they are more closely related to *Dremotherium* and *Oriomeryx* – Palaeomerycidae - than with any other group of ruminants.

Part 2 : *Sperrgebietomeryx* Morales, Soria and Pickford, 1999

Superfamily Bovoidea Simpson. 1931
Family Incertae Sedis
Subfamily Sperrgebietomerycinae Morales, Soria and Pickford, 1999
Genus *Sperrgebietomeryx* Morales, Soria and Pickford, 1999

Species *Sperrgebietomeryx wardi* Morales, Soria and Pickford, 1999

Cranium : EF 37'93 (Pl. 13, Figs 1A-E) and associated mandible (Pl. 13, Figs 2A-C). Further cleaning of the holotype in 2003 permits more detailed observations than were made by Morales *et al.*, (1999) in particular concerning the auditory region and the basicranium.

1.- There are no cranial appendages.
2.- The skull is long, with the nasals located in the same plane as the frontals which are long and which form a gentle angle with the temporals.
3.- Frontal depression, near the suture with the nasals.
4.- Sagittal crest well developed.
5.- Weak temporal lines.
6.- Nuchal tubercle strong.
7.- Muscle insertions in the occipital very strong.
8.- Nuchal border is not straight. The nuchal crest projects strongly towards the rear, projecting well beyond the occipital condyles.
9.- The mastoid is not visible nuchally. Laterally it is barely developed.
10.- Paroccipital apophysis is well developed clearly surpassing the occipital condyles in height.
11.- The mastoid process contacts a bony lamina developed from the tympanic bulla separating the styloid process from the paroccipital apophysis.
12.- Tympanic bulla rounded, moderately developed with a moderately sized muscular process.
13.- External auditory meatus weakly developed not completely closed by a bony ring.
14.- Retro-articular process is elongated and is well developed.
15.- Mandibular fossa shallow, the articular tubercle (on the temporal) evenly marked.
16.- Basioccipital subquadrangular, with muscle tubercles evenly developed.
17.- Angle between the basi-occipital and the basisphenoid small, almost in the same plane.
18.- Ethmoidal fossa well developed.

Dentition : Despite the medium wear of the dentition of *Sperrgebietomeryx*, we can note the following :

1.- The enamel of the dentition of *Sperrgebietomeryx* is smooth.
2.- The metastylid of the lower molars is practically inexistant, but this could be due to the heavy wear.
3.- The internal wall is quite flat. This is a consequence as much of the flattened morphology of the lingual wall of the metaconid and entoconid, as it is due to the two cusps being positioned in the same plane without a mesio-lingual valley between them.
4.- The m/3 of *Sperrgebietomeryx* posesses a strong entoconulid that forms a continuous wall

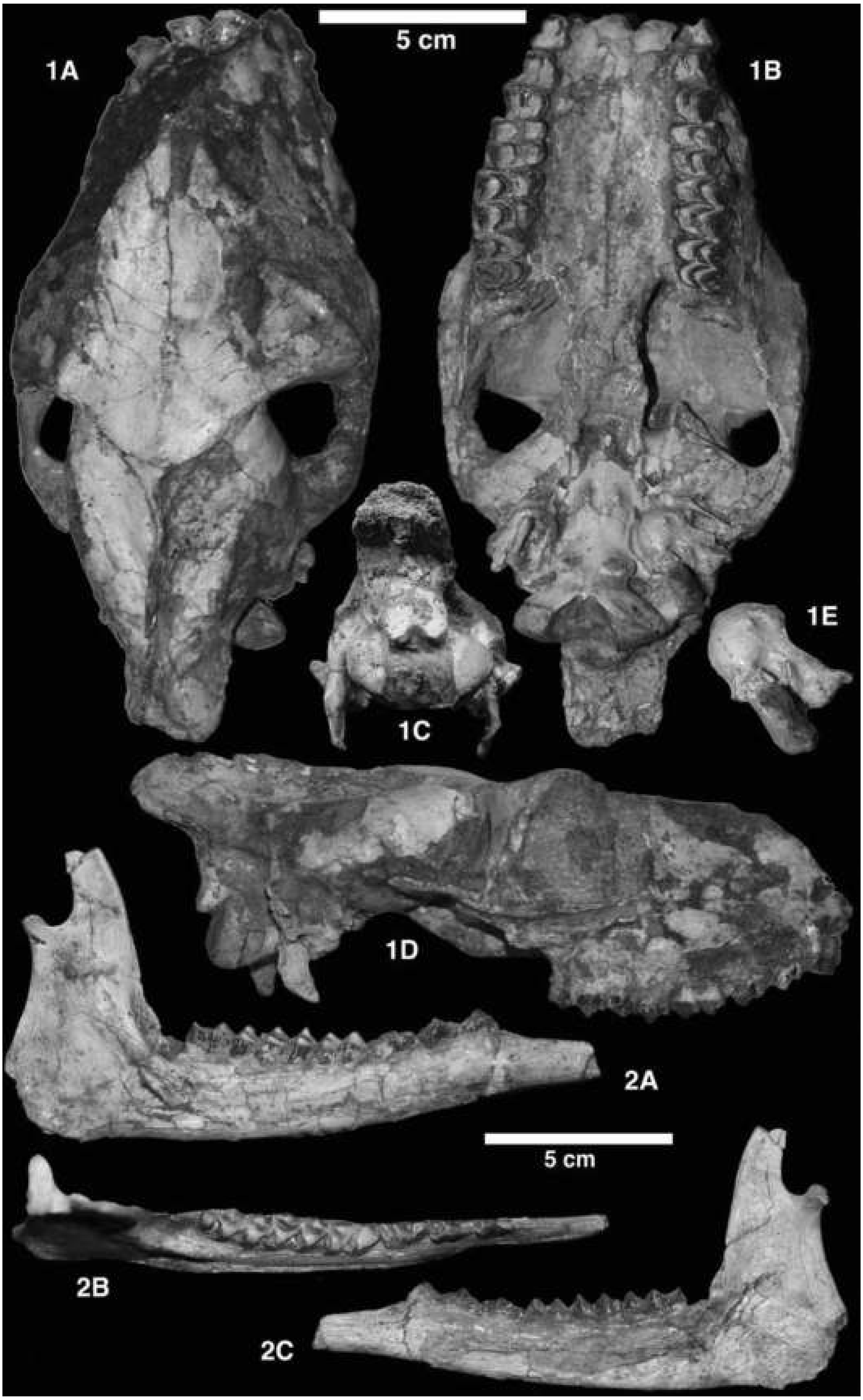


Plate 13: *Sperrgebietomeryx wardi* from Elisabethfeld. 1). EF 37'93, cranium (holotype), A) dorsal view, B) basal view, C) nuchal view, D) lateral view, E) tympanic bulla. 2) EF 37'93, right mandible, A) lingual view, B) occlusal view, C) buccal view.

in fusing with the hypoconulid, as well as fusing with the posterior cristid of the hypoconid and thus closing the posterior lobe. This morphology, which typifies Bovidae, is repeated in the m/2.

5.- The m/2 is broader than the m/3. The same size relation applies to the M2/ and M3/.

6.- There is no p/1.

7.- *Sperrgebietomeryx* presents a strong reduction in length and width of the lower (p/2 and p/3) and upper (P2/ and P3/) premolars.

Postcranial skeleton :

Vertebral column : Articulated with the holotype skull of *Sperrgebietomeryx wardi* there was the atlas (Pl. 14, Figs 1A-D) and three cervical vertebrae, the axis, V3 and V4. The atlas is notable for its elongation, being almost as long as it is wide, and in this respect resembling the atlas of several antelopes such as *Nager dama*. The borders of the wings are virtually parallel and straight. The axis and the other vertebrae are poorly preserved, only V3 being complete and revealing that it too was elongated. Associated with this assemblage was a tibia EF 37'93c, which likely belongs to the same individual.

Femur : EF 37'93, proximal epiphysis (Pl. 14, Figs 2A-C).

1.- The articular head tends to be rather cylindrical, but not as cilindrical as in *Capreolus capreolus*.

2.- The greater trochanter is damaged, but appears to have no medio-lateral compression, its lateral surface is convex.

3.- The greater trochanter is somewhat higher than the summit of the articular head.

4.- The crest of the greater trochanter is not well preserved.

5.- In dorsal view, the neck of the femur is wide, without a clear separation between the head and the diaphysis, its profile is a reclining L-shape (but not as inclined as in *Capreolus capreolus*).

6.- The lesser trochanter is broken.

7.- The trochanteric fossa is partly destroyed.

Tibia : EF 37'93, left tibia, (Pl. 14, Figs 3A-C).

Proximal epiphysis :

7.- The popliteal line is well marked.

Distal epiphysis :

1.- The epiphysis is trapezoidal and is antero-posteriorly compressed.

2.- The anterior and posterior margins are very concave due in part to the fact that the central keel which separates the two gullies of the cochlea is very short (AP) and to the projection of the medial maleolus and the plantar-medial projection of the cochlea. The latter is broken, but one can make out its plantar projection.

3.- The medial maleolus is higher than the central process.

4.- The central process is relatively narrow, and continues with moderate width between the tibial cochlea, its sinovial fossa is weakly marked.

5.- The lateral gully is slightly widened (medio-laterally) and clearly separated from the maleolar facets by a keel.

6.- The maleolar groove is marked.

7.- The medial protuberance is well marked.

8.- The fibular incision is smooth, dividing the maleolar facets into two parts which are perfectly united, the posterior one bigger than the anterior one. Between the anterior facet and the central process is a groove with well defined margins.

9.- The medial fossa of the cochlea is bigger (AP) than the lateral one.

Astragalus : EF 37'93, right astragalus (Pl. 14, Figs 5A-F).

1.- In proximal view the medial condyle is very narrow and sharp, the lateral one wider and parallel to it. In the medial epicondyle, there is a strong proximal plantar facet, that continues via a smooth keel in the medial side, without making contact with the medial process.

2.- In the dorsal side, there is a process to block very strong flexion (medial side) and another symmetrical one on the lateral side, the processes almost meeting to form a medial lateral crest. The fossa for the medial process of the tibia is subtriangular and very deep, of a form that sliding between calcaneum and astragalus is difficult due to a locking mechanism of the lateral side of the astragalus and the maleolar facet and groove of the calcaneum. It has a small trajectory.

3.- The plantar surface is very asymmetrical, the medial part is flatter and the lateral one more convex, with an axis that runs from medio-distal to proximo-lateral. The profile is concavo-convex.

Calcaneum : EF 37'93, right calcaneum (Pl. 14, Figs 4A-F).

1.- The tuber is asymmetrical, with the medial lobe higher and narrower. The fossa is deep, with strong lateral and medial insertions.

2.- The anterior border of the neck is straight, the posterior one is similar save for a slight concavity in front of the tuber.

3.- The sustentaculum tali is noticeably developed, due to its strong medial projection. The tendinal groove is weakly defined.

4.- There is no indication of a dorsal articular facet.

5.- The maleolar facet has a very prominent proximal part medially. The distal part is long, with the facet for the cuboid irregular, somewhat widened in its middle.

Discussion: The systematic position of *Sperrgebietomeryx* was previously discussed by

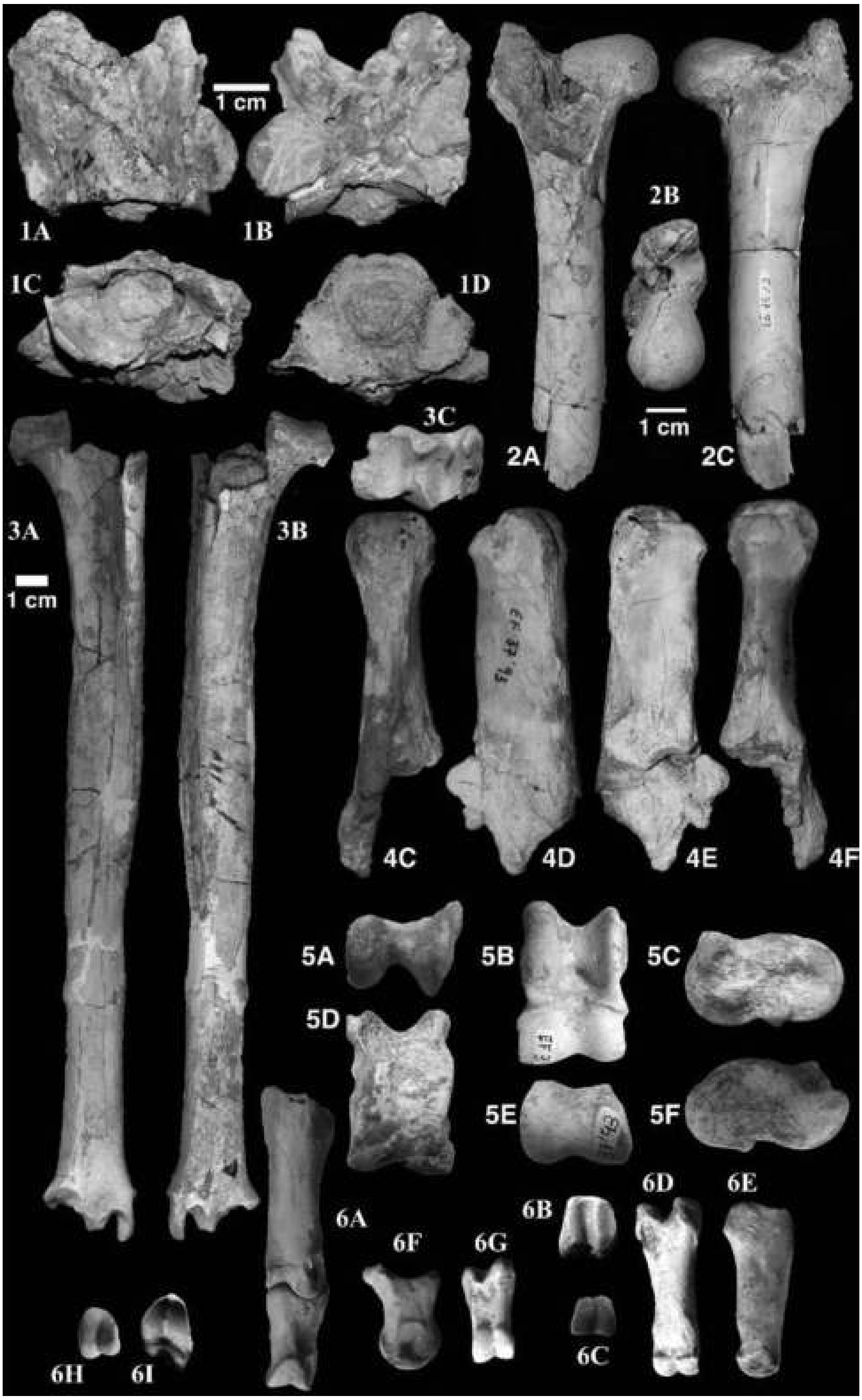


Plate 14: *Sperrgebietomeryx wardi* from Elisabethfeld (holotype). 1) EF 37'93, atlas, A) dorsal view, B) ventral view, C) cranial view, D) caudal view. 2) EF 37'93, left femur, A) caudal view, B) proximal view, C) cranial view. 3) EF 37'93 right tibia, A) dorsal view, B) plantar view, C) distal view. 4) EF 37'93, right calcaneum, A) distal view, B) proximal view, C) dorsal view, D) lateral view, E) medial view, F) plantar view. 5) EF 37'93, right astragalus, A) proximal view, B) plantar view, C) medial view, D) dorsal view, E) distal view, F) lateral view. EF 37'93 Ist and IInd phalanges, A) dorsal view, B) Ist phalanx proximal view, C) Ist phalanx distal view, D) Ist phalanx plantar view, E) Ist phalanx lateral view, F) IInd phalanx lateral view, G) IInd phalanx plantar view, H) IInd phalanx distal view, I) IInd phalanx proximal view.

Morales *et al*., (1999). The new material collected from various localities in the Sperrgebiet and which we attribute to *Propalaeoryx*, including the well preserved maxilla EF 19'01 and the mandible EF 30'00, allows us to make more detailed comparisons between these two genera from the same locality at Elisabethfeld.

1.- The enamel of the dentition of *Sperrgebietomeryx* is smooth, whereas that of *Propalaeoryx* is wrinkled.

2.- The metastylid of the lower molars of *Sperrgebietomeryx* is practically inexistent - this could be partly enhanced due to wear - whereas in *Propalaeoryx* the metastylid is well developed, and is present even in specimens as deeply worn as the *Sperrgebietomeryx* mandible.

3.- The internal wall of *Sperrgebietomeryx* molars is quite flat, whereas that of *Propalaeoryx* is clearly swollen. This is a consequence not only of the flatness of the lingual wall of the metaconid and entoconid, but also because the two cusps are oriented in the same plane and without having a mesio-lingual valley between them. In contrast, in *Propalaeoryx* the mesio-lingual valley is strongly marked and the cusps are not in the same plane, but are imbricated.

4.- The m/3 of *Sperrgebietomeryx* has a strong entoconulid that forms a continuous wall fused with the entoconid and hypoconulid, fusing with the posterior cristid of the hypoconid closing the posterior lobe. This morphology, typical of bovids, is repeated in m/2. In *Propalaeoryx* the entoconulid is in general strongly developed, but is always separated, not only from the posterior cristid of the entoconid, but also that of the hypoconulid, and as a result the posterior lobe remains open.

5.- The m/2 is broader than the m/3, the opposite of *Propalaeoryx*. The same applies to the M2/ and M3/.

6.- There is no p/1 in *Sperrgebietomeryx*, whereas it is present in all the specimens of *Propalaeoryx* that preserve the appropriate part of the mandible.

7.- *Sperrgebietomeryx* has a strong reduction of the length and breadth of the lower (p/2 and p/3) and upper premolars (P2/ and P3/).

8.- The atlas of *Sperrgebietomeryx* is proportionally longer than that of *Propalaeoryx* species.

9.- The tibia of *Sperrgebietomeryx*, has a trapezoidal distal epiphysis which is compressed antero-posteriorly. The medial maleolus is a bit higher than the central process. This central process is relatively narrow and continues in moderate width between the tibial cochlea. The lateral gully is slightly widened (lateral-medial) and clearly separated by a keel from the facets for the maleolus. The medial protuberance is well marked. The fibular incision is smooth, dividing the maleolar facets into two parts which are perfectly united, the posterior part bigger than the anterior one. Between the anterior facet and the central process there is a groove with well defined margins. The cochlea has a bigger medial fossa (AP) than the lateral one.

In the Langental specimen, the distal tibial epiphysis is subquadrangular and without antero-posterior compression. The medial maleolus is slightly higher than the central process, but lower than in *S. wardi*. The central process is very long, being equal in length to the keel that subdivides the tibial cochlea. The lateral gully is narrow and is separated by a keel from the maleolar facets. The medial protuberance is moderately marked. The fibular incision is well marked, dividing the maleolar facet into two parts which are contiguous, with the posterior one larger than the anterior one. Between the anterior facet and the central process there is a deep incision with clear borders. The cochlea has similar sized (AP) medial and lateral fossae.

10.- The astragalus of *S. wardi* shows a strong process on the medial side of the dorsal surface and another symmetrical one on the lateral side, the processes almost reaching each other to form a medial lateral crest. This morphology is present in extant *Hyemoschus aquaticus* and is quite a bit more attenuated in *Moschus moschiferus*, and differs from that of *P. austroafricanus* in which the lateral process is very weak, and does not develop a lateral medial crest.

These differences suggest to us that *Sperrgebietomeryx* and *Propalaeoryx* were phylogenetically more distantly related than thought by Morales *et al*., (1999). *Propalaeoryx austroafricanus*, not only by its dental characters, but also by its postcranial ones, is extraordinarily close to *Orangemeryx hendeyi*, differing from this species by its lack of cranial appendages (no sign of an ossicone has been found in the extensive collection in the Northern Sperrgebiet) and by other more evolved features of the Arrisdrift species, which justifies their separation into two different subfamilies within the Climacoceratidae

However, in the present state of our knowledge it does not appear to be possible to maintain *Sperrgebietomeryx* and the subfamily Sperrgebietomerycinae as part of the Climacoceratidae. In effect, the differences enumerated above are in our opinion sufficient to warrant their separation. In addition, if we take into account two features, *Propalaeoryx* falls within the range of variation of the family Climacoceratidae, save for the absence of cranial appendages, even though it retains several primitive states of certain dental characters. On the contrary, the characters that separate *Sperrgebietomeryx* from *Propalaeoryx* provide evidence that it belongs to a different group, the Bovidae *sensu lato*.

Sperrgebietomeryx is very advanced in the reduction of the anterior premolars, and this character occurs precociously in the Hypsodontidae (Köhler, 1987) but is unknown in most of the Early Miocene and most of the Middle Miocene pecoran ruminants. Closure of the posterior lobe of the m/2 and m/3 is one of the most convincing characters for defining the Bovidae, as is the morphology of the lingual wall of these molars (Text-fig. 6). The skull of *Sperrgebietomeryx* shows primitive characters, in particular the strength of the sagittal crest, its elongation, the projection of the nuchal crest etc. But these characters are also present in Hypsodontidae. In addition, the disposition of the styloid process that is separated by a weak lamina of bone – related to the tympanic bulla - of the paroccipital apophysis, approaches *Sperrgebietomeryx* to primitive bovids such as *Namacerus* (Morales *et al.*, 2003).

All these morphological characters indicate to us that *Sperrgebietomeryx* is an authentic bovid. Its inclusion in a separate subfamily is justified by the retention of a more primitive morphology (manifested by its lesser hypsodonty and the absence of a horn) than that of the Hypsodontidae of the Middle Miocene.

Part 3 : *Namibiomeryx* Morales, Soria and Pickford, 1995

Superfamily Bovoidea Simpson, 1931
Subfamily *Incertae sedis*
Genus *Namibiomeryx* Morales, Soria and Pickford, 1995
Species *Namibiomeryx senuti* Morales, Soria and Pickford, 1995

Diagnosis : Morales *et al.*, 1995.

Type locality : Elisabethfeld, Namibia.

Locality : Elisabethfeld.

Material : EF 00’93, incisor (Pl. 15, Fig. 4) and lower canine (Pl. 15, Fig. 3)
EF 00’93, left mandible with m/1-m/3 (Pl. 15, Figs 1A-D). Holotype (described in Morales *et al.*, 1995)
EF 00’93, left mandible with m/1-m/3 and EF 00’93 right mandible with m/1-m/3
EF 00’93, fragment of right mandible with p/2 (described in Morales *et al.*, 1995)
EF 00’93, left p/3 (Pl. 15, Fig. 7). Described in Morales *et al.*, 1995.
EF 00’93, left p/2 (described in Morales *et al.*, 1995)
EF 00’93, right p/2 (Pl. 15, Fig. 8). Described in Morales *et al.*, 1995.
EF 00’93, right m/3 (Pl. 15, Figs 9A-C); EF 00’93 right m/2; EF 00’93 right m/1 and EF 00’93, fragment of right mandible with p/4 (Pl. 15, Figs 5A-C). Described in Morales *et al.*, 1995.
EF 00’93, left P4/-M3/ (Pl. 15, Figs 11A-C) EF 00’93, left P3/ (Pl. 15, Fig. 12) and EF 00’93, isolated right M3/, right M2/-M1/ (described in Morales *et al.*, 1995)

New material : EF 51’96 right and left maxillae and left mandible with deeply worn teeth (Pl. 15, Figs 13A-D).
EF 00’ 94, incisor.
EF 105’94, fragment of left mandible with incomplete m/3 and m/2.
EF 252’01, right p/2.
EF 28’01, broken right m/2 (Pl. 15, Fig. 10) similar to the holotype.
EF 19’03, left p/4 (Pl. 15, Figs 6A-C).

Description : EF 00’93, left mandible with m/1-m/3 (holotype). The molars possess tall, transversely compressed cusps, which impart a tall, narrow aspect to the teeth. The m/3 shows the metaconid and entoconid aligned in the same plane, the two cusps being very compressed transversely, and their lingual walls quite swollen. The metastylid is very small and is located at the junction between the posterior cristid of the metaconid and the anterior cristid of the entoconid. The mesio-lingual valley is very weak, such that the wall is almost continuous between the lingual cusps. The anterior cusplet of the metaconid is short and joins the anterior cristid of the protoconid, which is long and located obliquely with respect to the axis of the tooth. In contrast, the posterior cristid of the protoconid is short and almost perpendicular to the axis of the tooth and is united to the posterior cristid of the metaconid, which is also short. The anterior cristid of the hypoconid is also long and oblique, and contacts the anterior cristid of the entoconid, which is short, behind the metastylid, far from the junction between the posterior cristids of the metaconid and protoconid. The posterior cristid of the hypoconid is long and, like the anterior one, is oblique. The posterior cristid of the entoconid is barely developed, but joins a low but well developed entoconulid which contacts without uniting with the postero-buccal cristid of the hypoconulid, and with the posterior cristid of the hypoconid. Nevertheless, the large size of the entoconulid and its reduced height mean that the posterior cristids of the entoconulid and hypoconid are well separated from each other. The hypoconulid is high, and its anterior cristid makes contact with the posterior cristid of the hypoconid. There is a small vertical fold in the posterior cristid of the hypoconulid. The ectostylid is reduced and there is a moderate anterior cingulum.

The m/2 shows an arrangement and morphology of the cusps like that in the m/3, save for the weaker development of the anterior cristids of the metaconid and hypoconid. The metastylid is almost imperceptible and the posterior cristid of the hypoconid is less oblique, contacting a strong entoconulid, which is clearly separated from the posterior of the entoconid. The m/1 is smaller and is quite worn, but is basically the same as the m/2, still

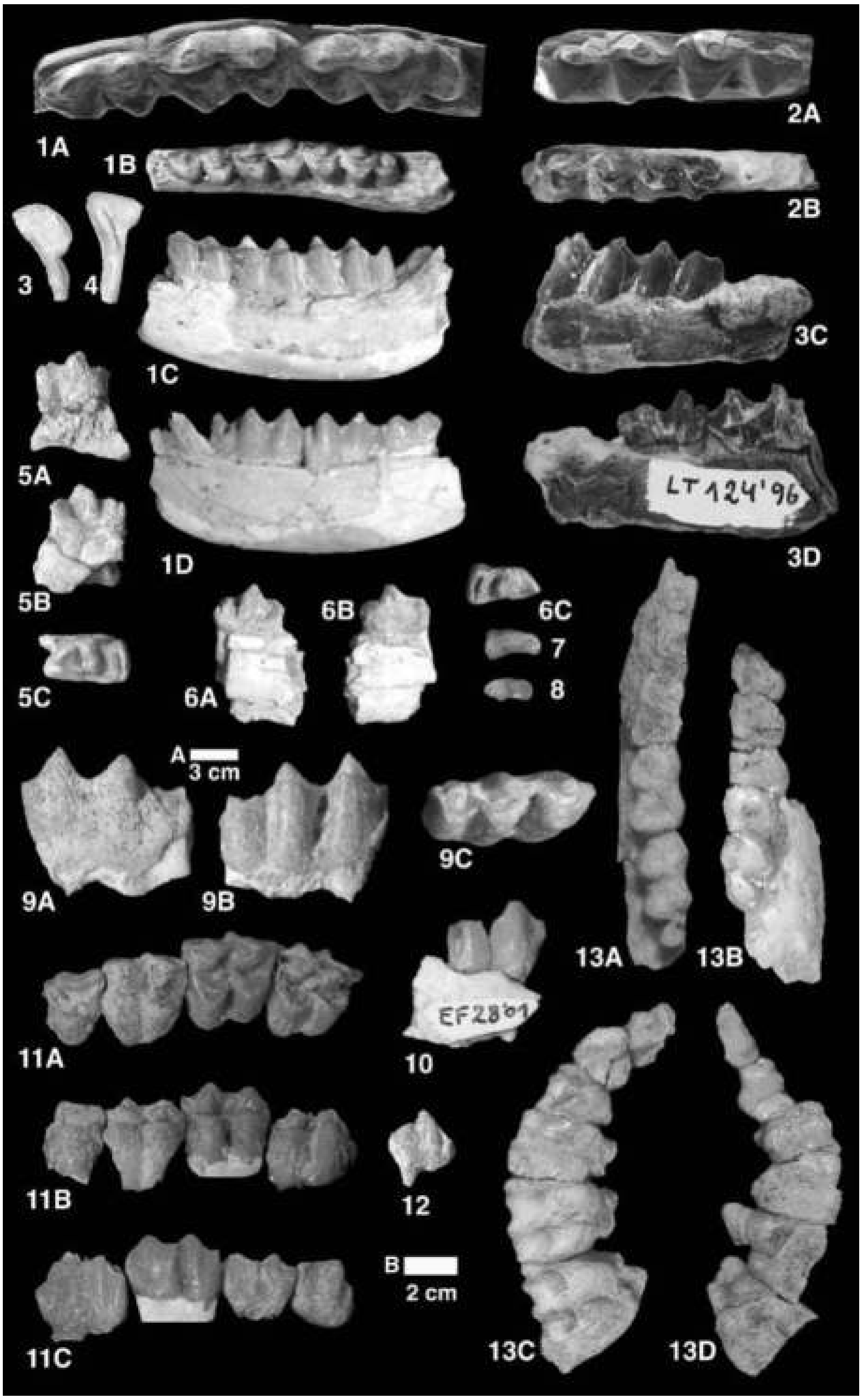


Plate 15: *Namibiomeryx senuti* from Elisabethfed (EF) and *Namibiomeryx spaggiarii* nov. sp. from Langental (LT). 1) EF 00'93, left manbible with m/1-m/3 (*Namibiomeryx senuti* holotype) A-B) occlusal view, C) buccal view, D) lingual view. 2) LT 124'96, right mandible with m/1-m/2 (*Namibiomeryx spaggiarii* nov. sp. holotype), A-B) occlusal view, C) buccal view, D) lingual view. 3) EF 00'93, right lower canine in lingual view. 4) EF 00'93, lower incisor in lingual view. 5) EF 00'93, fragment of right mandible with p/4, A) buccal view, B) lingual view, C) occlusal view. 6) EF 00'93, fragment of right mandible with p/4, A) buccal view, B) lingual view, C) occlusal view. 7) EF 00'93, left p/3 in occlusal view. 8) EF 00'93, right p/2 in occlusal view. 9) EF 00'93, right m/3, A) lingual view, B) buccal view, C) occlusal view. 10) EF 28'01, broken right m/2 in lingual view. 11) EF 00'93, left P4/-M3/, A) occlusal view, B) lingual view, C) buccal view. 12) EF 00'93, left P3/ in buccal view. 13) EF 51'96, right and left maxillae and mandible in occlusal view, A) left mandible with p/4-m/3, B) right mandible with m/1-m/3, C) left maxilla with P4/-M3/, D) left maxilla with P2/-M3/. Scale A for figures 1 and 9, scale B for the rest.

showing the separation between the posterior cristid of the entoconid on the one hand, and the entoconulid and posterior cristid of the hypoconid on the other.

EF 00'93, the right m/3, right m/2, right m/1 and a fragment of right mandible with p/4, were found with the holotype and probably come from the same individual. The size and wear stage of the dentition supports this possibility. The molars possess the same morphology observed in the holotype. The p/4, which is almost the same size as the m/1, is quite a simple premolar, with the mesio-lingual cusp devoid of crests, the anterior wing simple, the cusplet and posterior stylid strong and transversely oriented, united lingually. The postero-buccal groove is well marked.

EF 19'03, left p/4 is the same as the specimen described above.

EF 00'93, left p/3 is the only specimen of this tooth preserved. It is deeply worn and its morphology is simpler than that of the p/4. The mesio-lingual cusp is strong and voluminous. There is a cristid obliquid with a small postero-lingual cusplet. The anterior stylid is simple.

EF 00'93, right p/2 is very small with reduced anterior stylid, voluminous mesio-lingual cusp and a cristid obliquid with reduced postero-lingual cusplet.

EF 00'93, left i/1 is spatulate, asymmetric and similar to that of *Hyemoschus aquaticus*.

EF 00'93, left i/2 is spatulate, but is more symmetrical, differing from that of *Hyemoschus aquaticus*.

EF 00'93, left P4/-M3/, left P3/ and isolated right M3/, M2-M1. The M3/ has a medium sized parastyle joined basally to the external rib of the paracone which is also of moderate size. The mesostyle is small, being the same size as the metastyle. The anterior crista of the protocone joins the parastyle and the posterior crista is short and does not join the anterior crista of the metaconule, which is long, but does not close the central valleys. The posterior crista of the metaconule is joined to the metastyle. The ectostyle is tiny. There is a weak cingulum at the base of the protocone.

The M2/ is wider than the M3/, with the metaconule more developed. Its morphology is close to that of the M3/, and the union of the posterior crista of the protocone to the medial part of the anterior crista of the metaconule is clearly visible. However, the latter crista does not close the internal valleys of the tooth. The M1/ is similar in size to the M3/, and has the same morphology as the M2/.

The P4/ is subtriangular and quite asymmetric. The anterior style is strong and is joined by a high crest to the buccal cusp. The buccal cusp is close to the anterior style which is well marked on the external wall, and has a long posterior crista which joins the posterior style which is quite weak. The lingual cusp is high and its crests join the styles of the external wall. There is an internal fold and there is a very weak basal cingulum.

The P3/ is an elongated premolar, with a strong anterior style united basally to the buccal cusp, which has an external rib which is better developed than in the P4/. The posterior crista of the buccal cusp is quite long as in the P4/. The posterior style is weak. The lingual cusp is broken.

EF 51'96, comprises a left and right maxilla and a left mandible. The teeth are deeply worn preventing detailed description. It is possible to observe that the P2/ and P3/ are longer than the P4/. The P3/ has the lingual cusp less developed than in the P4/ and is in a more posterior position. The P2/ is reduced and judging from the occlusal morphology could have possessed a rudimentary lingual cusplet.

In the P3/, the lingual cusp is in a very posterior position, and possesses a small internal fold. It joins the anterior style via a long crest and its anterior crista is separated by a vertical flexure of the internal wall from a small anteriorly positioned cusplet which joins the anterior style, forming a lobe isolated from the main body of the tooth.

The P2/ is similar in size and morphology to the P3/ but is narrower. The elements of the external wall are more marked, especially the robust anterior style. The lingual cusp is smaller than that of the P3/ and is more isolated.

Postcranial skeleton :

Scapula : EF 60'03 (Text-fig. 5, A1-2) is much of the glenoid cavity of a scapula with the neck and base of the spine. The acromion is broken. Neither the coracoid nor the supraglenoid tubercle are preserved. The medial side of the neck is extraordinarily flat as is the caudal border. The lateral surface has a swelling for the insertion of the supraspinous muscle, from which extends a low rounded ridge as far as the caudal border for the deep branch of the infraspinous muscle and a fossa for the pectoralis minor. (Dimensions in mm of the neck are antero-posterior 9.4 mm; transverse 4.9 mm).

Humerus : EF 62'03, fragment of left distal humerus with the medial condyle broken, without diaphysis. EF 63'03, fragment of right medial condyle of a humerus. EF 60b'03, (Text-fig. 5, B1-4) distal humerus with part of the diaphysis. The capitulum and lateral epicondyle of the distal epiphysis are broken.

1.- The trochlea is trapezoidal.

2.- The medial epicondyle is as high as the lateral border of the trochlea.

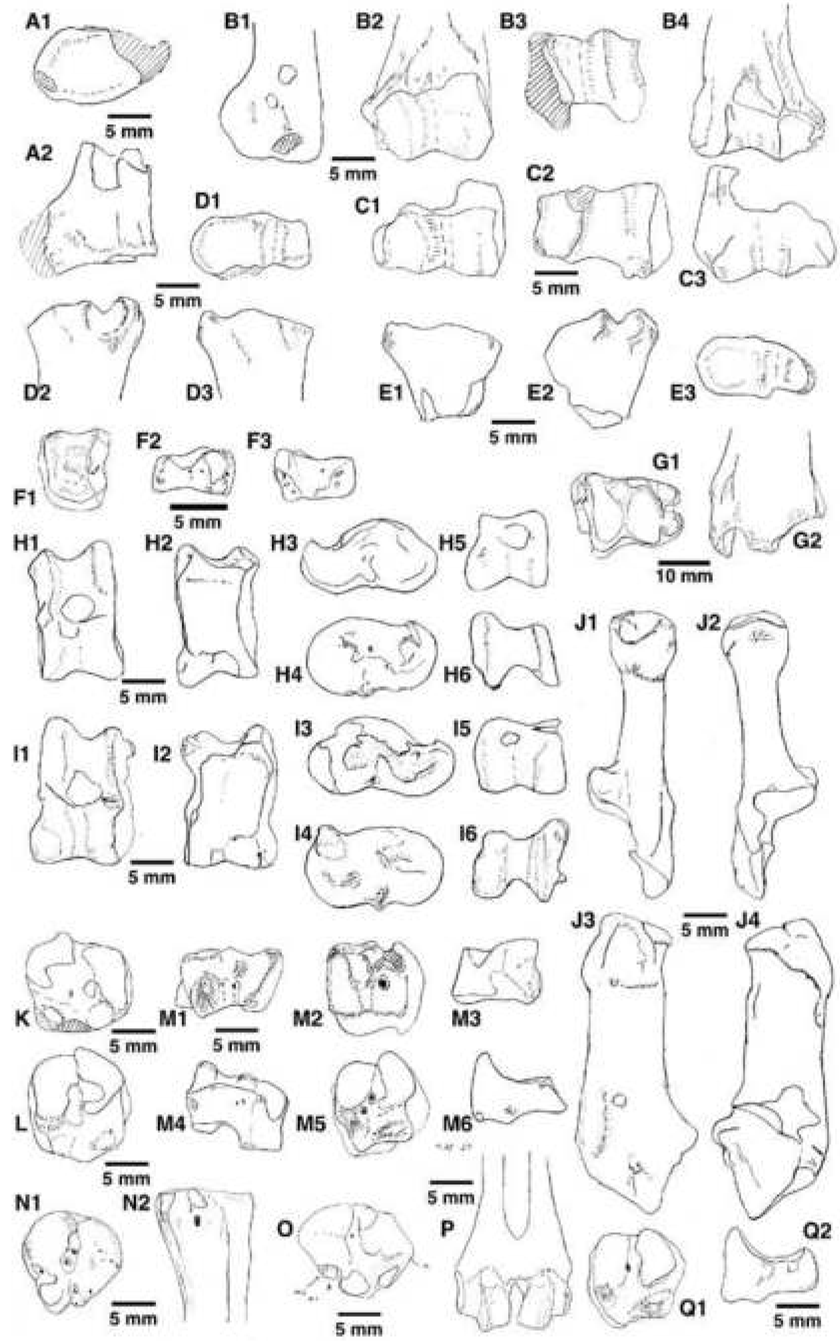
3.- The medial lip is more elevated than the lateral lip.

4.- The lateral lip is high, rounded and symmetrical.

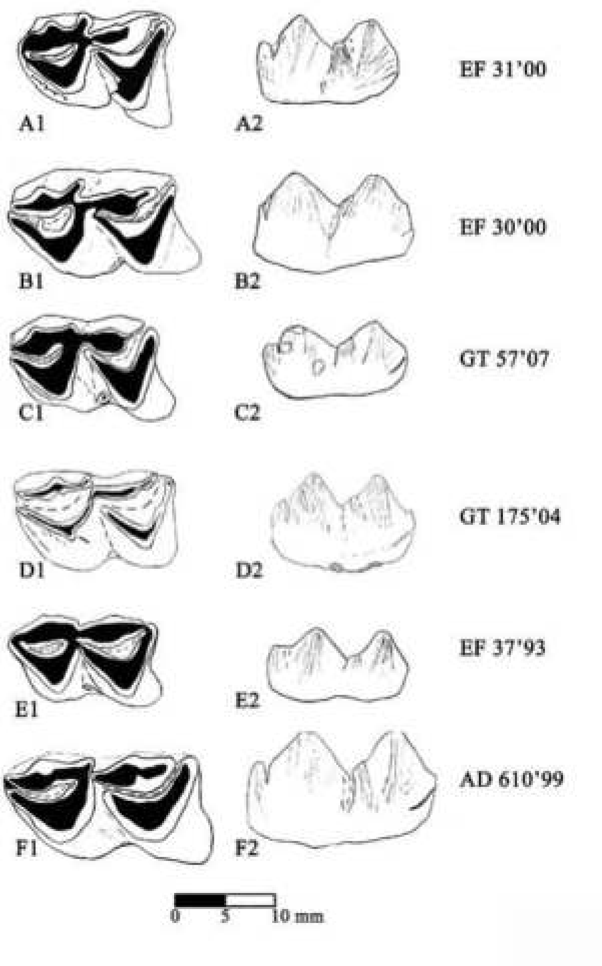
5.- The capitulum (broken in EF 61'93) is short, but with a high lateral border (EF 62'93).

6.- The projection of the capitulum stays at the same height as the gully of the trochlea.

7.- The gully of the trochlea is wide and



Text figure 5: *Namibiomeryx senuti* from Elisabethfeld (EF) and *Namibiomeryx spaggiarii* from Langental (LT). A) EF 60a'03, *N. senuti*, left scapula. A1) glenoid cavity, A2) lateral view. B) EF 60b'03, *N. senuti*, distal right humerus. B1) medial view, B2) cranial view, B3) distal view, B4) caudal view. C) LT 125'96, *N. spaggiarii* distal right humerus. C1) cranial view, C2) distal view, C3) caudal view. D) EF 66'93, *N. senuti* proximal right radius. D1) proximal view, D2) palmar view, D3) dorsal view. E) LT 127'98, *N. spaggiarii*, proximal right radius. E1) dorsal view, E2) palmar view, E3) proximal view. F) LT 204'03, *N. spaggiarii* left magnotrapezoid. F1) proximal view, F2) lateral view, F3) medial view. G) EF 57'94, distal left tibia. G1) distal view, G2) plantar view. H) LT 87'03, *N. spaggiarii*, left astragalus. H1) dorsal view, H2) plantar view, H3) lateral view, H4) medial view, H5) distal view, H6) proximal view. I) EF 60c'03, *N. senuti* right astragalus. I1) dorsal view, I2) plantar view, I3) lateral view, I4) medial view, I5) distal view, I6) proximal view. J) EF 60d'03, *N. senuti*, right calcaneum. J1) dorsal view, J2) plantar view, J3) medial view, J4) lateral view. K) EF 00'93, *N. senuti*, right navicular-cuboid in proximal view. L) EF 13'96, *N. senuti* left navicular-cuboid in distal view. M) LT 67'99, *N. spaggiarii*, left navicular-cuboid. M1) plantar view, M2) proximal view, M3) lateral view, M4) dorsal view, M5) distal view, M6) medial view. N) LT 6'05, *N. spaggiarii*, left metatarsal. N1) proximal view. N2) plantar view. O) EF 18b'04, *N. senuti*, right metatarsal in proximal view. P) LT 38'05, *N. spaggiarii*, distal epiphysis of Mt III-IV in dorsal view. Q) LT 403'96, *N. spaggiarii*, left navicular-cuboid. Q1) distal view, Q2) medial view.



Text figure 6: Lower m/2 of *Propalaeoryx*, *Sperrgebietomeryx* and *Orangemeryx* from the Sperrgebiet. A) *Propalaeoryx austroafricanus* from Elisabethfeld, A1) occlusal view, A2) lingual view. B) EF 30'00 *Propalaeoryx austroafricanus* from Elisabethfeld, B1) occlusal view, B2) lingual view. C) *Propalaeoryx stromeri* from Grillental, C1) occlusal view, C2) lingual view. D) *Propalaeoryx stromeri* from Grillental, D1) occlusal view, D2) lingual view. E) *Sperrgebietomeryx wardi* from Elisabethfeldl, E1) occlusal view, E2) lingual view. F) *Orangemeryx hendeyi* from Arrisdrift, F1) occlusal view, F2) lingual view.

asymmetrical.

8.- The lateral epicondyle (broken in EF 61'93) is weakly developed and is quite a bit lower than the height of the capitulum (EF 62'93).

9- The crest of the lateral epicondyle is divergent with respect to the crest of the medial epicondyle, consequetly the shape of the olecranon fossa is quite asymmetrical.

10.- The medial side has a weakly developed central relief.

11.- The lateral side has quite a deep fossa or depression.

12.- The coronoid fossa is shallow.

13.- On the lateral side in contact with the radial fossa there is developed a protuberance of regular size.

Radius : EF 64'03, proximal left epiphysis with part of the diaphysis. EF 32'93, proximal left epiphysis. EF 33'93, fragment of proximal left epiphysis. EF 65'03, medial fragment of proximal left epiphysis. EF 66'93, right proximal epiphysis (Text-fig. 5, D1-3).

1.- Rectangular outline with the medial border slightly wider than the lateral one. The medial border is semicircular, the lateral one straight. The palmar and dorsal margins are straight, the palmar one being higher than the dorsal one.

2.- The articular surface for the trochlea of the humerus is quite compressed in the dorso-palmar direction, with low relief. The depression for articulation with the lateral lip of the trochlea contacts the notch of the palmar side.

3.- The surface of the articulation for the capitulum is narrow and the lateral protuberance is not very well developed.

4.- The notch is small, the lateral articular surface for the ulna is large and circular and lies in one plane. The medial facet is small and triangular.

Scaphoid : EF 59'94, scaphoid.

1.- On the proximal side the dorsal part is elevated and separated by a valley from the palmar part.

2.- The external distal facet for the lunate is very prominent.

3.- The outline in lateral view is quadrangular, very high proximo-distally.

Tibia : EF 70'03, proximal right tibia fragment. EF 67'03, distal right tibial epiphysis and diaphysis. EF 68'03, left distal tibial epiphysis. EF 69'03, distal right tibial epiphyseal fragment. EF 55'00, left distal tibial epiphysis. EF 18'04, left distal tibial epiphysis with diaphysis (unfused). We include in this sample EF 51'94 (Text-fig. 5, G1-2) a distal epiphysis and part of the diaphysis of a tibia which are approximately 15% larger than but morphologically similar to the previous specimens.

1.- The epiphysis is sub-quadrangular, with slight antero-posterior compression.

2.- The dorsal side is straight and the plantar one slightly concave, the central keel which separates the two gullies of the cochlea is relatively long (AP) not very different from the maximum AP.

3.- The medial maleolus is higher than the central process.

4.- The central process is very narrow, as is its continuation between the tibial cochlea.

5.- The lateral gully is very narrow and clearly separated by a keel from the facets for the maleolus.

6.- Maleolar groove is well marked.

7.- The medial protuberance is well marked.

8.- The fibular incision is narrow, subdividing the maleolar facet into two separate parts of similar size.

9.- The cochlea has a medial fossa which is slightly bigger (AP) than the lateral one.

Maleolus : The spine is short and wide. The proximal facets are asymmetrical and are positioned at different levels, the anterior one is higher, narrower and subrectangular, the posterior one wider, concave and subcircular. In the distal side as well as the posterior part, is lower and bigger and more concave than the reduced anterior part. The posterior border is shorter than the anterior one.

Astragalus : EF 60c'93, right astragalus (Text-fig. 5, I1-6).

1.- In proximal view, the medial condyle is narrow and the lateral one a bit wider, converging proximally, also evident in the tibial cochlea, bending the articular fossae to the anterior side. The medial condyle has a strong proximal plantar process.

2.- In the dorsal side there is a strong process (medial side) to block flexion. The fossa for the medial process of the tibia is circular, relatively small and very deep that makes sliding between the calcaneum and astragalus difficult, forming a locking mechanism between the lateral side of the astragalus, the maleolar facet and the groove of the calcaneum, having a very small trajectory.

3.- The plantar side is very asymmetrical, the medial part is flatter and the lateral one more convex, with an axis that runs from medio-distal to proximo-lateral. The profile is concavo-convex.

Calcaneum : EF 18'04, right calcaneum without tuber belonging to a specimen noticeably bigger than the former one, but morphologically similar to it. EF 60d'93, right calcaneum (Text-fig. 5, J1-4).

1.- The tuber is asymmetrical, with the medial lobe higher and narrower. The fossa shallow, strong lateral and medial insertions.

2.- The anterior border of the neck is straight, the posterior one concavo-convex.

3.- The sustentaculum tali is notably well developed, because of its strong medial projection. The tendinal groove is poorly defined.

4.- In dorsal view it is possible to make out a small triangular articular facet.

5.- The maleolar facet has a prominent proximal part medially which articulates with the lateral side of the astragalus. The distal part is long, with an irregular facet for the cuboid, narrow posteriorly.

Navicular-cuboid : EF 00'93a (Text-fig. 5, K) left navicular-cuboid missing the medial half.

1.- It is missing its medial part.

2.- In distal view, the anterior facet for the metatarsal is subtriangular, with a strong internal notch. The facet for the ectocuneiform is almost circular and is located higher than the facet for the ectocuneiform. The postero-internal process appears to be weakly developed, in contrast with the strong swelling of the postero-external protuberance.

3.- In plantar view, most notable is the enlargement of the posterior facet for the metatarsal. Other morphological elements cannot be determined due to damage.

EF 00'93b, right navicular-cuboid missing the proximo-plantar portion.

2.- The distal side is reasonably well preserved and reveals that the anterior facet for the metatarsal is very narrow, due to the strength of the internal notch. The facet for the ectocuneiform is clearly separated from the anterior one, by a deep groove, and is posed on a strong protuberance. The postero-internal protuberance in this view, is not very prominent.

EF 13'96, left navicular-cuboid (Text-fig. 5, L).

1.- is missing the proximo-plantar part.

2.- shows the narrowness of the anterior facet for the metatarsal and the weak prominence of the postero-internal protuberance.

Metatarsal : EF 18'04, proximal end of metatarsal (Text-fig. 5, O). It has slight damage to the proximal surface but the morphology can be observed reasonably well.

1.- There is complete fusion of MT III-IV.

2.- In the Mt III the proximal anterior facet is large, subtriangular and concave, limited by two medial tuberosities of moderate size.

3.- The proximal posterior facet for the cuneiform is small and has a rounded shape, and dorsally there is a facet for articulation with a sesamoid. Between the two proximal facets is a small hole, one wall of which is formed by the proximal part of a tiny Mt II, which is fused with the border of the anterior proximal facet.

4.- The proximal anterior facet of the Mt IV is quite flat.

5.- The proximal posterior facet is elongated, inclined and elevated where it joins the posterior part of the Mt III. Between these two facets of the Mt IV there is a good continuity, scarcely broken by a small discontinuity due to the fusion of the Mt V.

8.- The dorsal canal is well marked.

9.- There is a small groove in the medial surface close to the dorsal canal.

10.- The Mt II and Mt V are fused and very reduced.

Ist phalanx : EF 36b'00, EF 36a'00.

1.- Long and gracile.

2.- In dorsal view the lateral side (external) is concave.

3.- The proximal articular surface is narrow with a deep groove for reception of the metapodial keel.
4.- The distal articular facet is slightly visible in dorsal view.
5.- The distal articular facet has a flattened shape.

IInd phalanx : EF 36c'00.
1.- Gracile.
2.- In proximal view the post-articular platform is very reduced. It is very developed and asymmetric in EF 54'97.
3.- Dorsally the extensor process is high.
4.- The outline of the distal articular facet is circular.
5.- The dorsal part of the articulation is greatly extended.

IIIrd phalanx : EF 36d'00.
1.- The dorsal ridge is convex.
2.- There is a small process for the insertion of the extensor.
3.- The articular surface is rounded.
4.- The plantar process for the insertion of the deep flexor tendon is small.
5.- In dorsal view the ridge is long and in a central position.
6.- The plantar surface is clearly defined by crests (medial and external).

Species *Namibiomeryx spaggiarii* nov.

Type Locality: Langental.

Age : Early Miocene.

Holotype : LT 124'96, right m/1-m/2. Geological Survey of Namibia. (Pl. 15, Fig. 2A-D).

Derivatio nominis : in honour of Renato Spaggiari, geologist.

Diagnosis : *Namibiomeryx* with hypsodont dentition, lower molars with anterior cristids of the metaconid and protoconid noticeably elongated and closed anteriorly. The anterior cristid of the hypoconid joins the anterior cristid of the entoconid, but not with the posterior cristid of the metaconid.

Differential diagnosis : *N. spaggiarii* differs from *N. senuti* by its slightly larger dentition, its more hypsodont lower molars, the greater development of the anterior cristids of the protoconid and metaconid, and by the union behind the metastylid of the anterior cristids of the entoconid and hypoconid.

Description: LT 124'96, right m/1-m/2. (Dimensions in mm; m/1 L = 8.6, W = 4.6; m/2 L = 10.3, W = 5.1). The m/1 has a broken lingual wall of the metaconid. It is a narrow, high tooth, with an incipient, but clear tendency to hypsodonty. There is no palaeomerycid fold. The protoconid cristids are high, the anterior one joins the anterior cristid of the metaconid, closing the lobe anteriorly. The posterior one joins the anterior cristid of the entoconid. The anterior cristid of the hypoconid joins the anterior cristid of the entoconid, but not the posterior cristid of the metaconid - as occurs in some species of *Hispanomeryx* (Morales *et al.*, 1981). The posterior cristid of the entoconid is weakly developed and clearly separated from the posterior cristid of the hypoconid, leaving the posterior lobe open lingually. The posterior cristid of the hypoconid could end in an entoconulid, but if this interpretation is correct, it would be barely isolated. There is a small ectostylid and weakly developed anterior and posterior cingula. The m/2 is larger and higher than the m/1 but its morphology is similar. In this molar, the metastylid is absent. The ectostylid is quite a bit smaller than it is in the m/1. The anterior cristids of the metaconid and protoconid are noticeably longer, and their union closes off the molar anteriorly.

Other dento-gnathic material : LT 415'96 and LT 416'96, edentulous mandible fragments.

Postcranial skeleton :
Humerus : LT 125'96, is the distal end of a right humerus (Text-fig. 5, C1-3) with a damaged medial epicondyle, and broken capitulum and lateral epicondyle. LT 107'04, a left distal humeral epiphysis, preserves only the medial epicondyle and part of the diaphysis. Neither of these bones differ in their preserved parts from the Elisabethfeld material described above.

Radius : LT 127'98 (Text-fig. 5, E1-3) a right proximal epiphysis has been polished by wind blown sand. The lateral facet is small and low. The anterior border is convex, not straight like in the Elisabethfeld species, and the lateral tuberosity is somewhat more developed than in *N. senuti*.

Magnotrapezoid : LT 204'03 (Text-fig. 5, F1-3) (LT 69'99 eroded by wind-blown sand).
1.- On the proximal surface, the lateral facet (external) for the semilunar is weakly developed and is discontinuous.
2.- The lateral palmar facet for the unciform is well developed and is visible in palmar view, delimited by a deep groove.
3.- The proximal lateral facet for the unciform, is weakly developed.
4.- On the distal surface, the area for contact with the Mc III-IV is eroded, but was likely to have been well developed.
5.- The proximal palmar prominence is moderately elevated.
6.- The lateral articular border of the proximal surface is moderately concave.

7.- The shape of the bone (proximal and distal surfaces) is subquadratic.

8.- On the proximal side, the lateral facet (external) for the semilunar, is very concave in its anterior part and moderately elevated and convex in its posterior part. The anterior part of the facet for the scaphoid is also concave and deep.

Astragalus : LT 396'96, LT 64'99, LT 62'99, LT 63'99, LT 81'03, LT 87'03 (Text-fig. 5, H1-6). LT 87'03, a left astragalus, is morphologically very similar to the material described from Elisabthfeld, but there are some differences such as its slightly smaller dimensions, and above all the greater medio-lateral shortening, such that the plantar surface is clearly narrower than in the astragalus of *N. senuti*.

Calcaneum : LT 409'96, lacks the tuber and the proximal part, LT 408'96 is a fragment in poor condition, LT 248'98 is a juvenile calcaneum lacking the tuber as is LT 87'03, LT 57'04 is an eroded tuber. None of these specimens is well enough preserved to allow detailed comparisons with the calcaneum from Elisabethfeld, EF 00'94.

Navicular-cuboid : LT 67'99 (Text-fig. 5, M1-6) LT 402'96, LT 403'96, LT 404'96 (Text-fig. 5, Q1-2) LT 67'99, left navicular-cuboid.

1.- In proximal view, the proximal processes (tenon) are low, especially the central one, but are a bit higher than the facet for the calcaneum.

2.- In distal view, the anterior facet for the metatarsal is subtriangular with a strong internal notch. The facet for the ectocuneiform and the posterior facet of the metatarsal are lightly eroded. The height of the postero-external protuberance is an obvious feature, as is the weakness of the postero-internal bulge, which is barely visible and without external projection, in contrast with the strong swelling of the postero-external projection. There is a clear difference in height between the two protuberances.

3.- In plantar view the most obvious feature is the swelling of the base of the posterior facet for the metatarsal which occupies a large part of the navicular-cuboid. The postero-internal bulge progressively forms a swollen ridge between the plantar and medial surfaces which sustain the strong internal process. Between these two structures, just beneath the medial process, a relatively deep fossa perforated by a foramen is developed.

LT 403'96, a left navicular-cuboid, is partly eroded on its proximal and plantar surfaces. The antero-external facet for the metatarsal is very narrow. The postero-internal protuberance is well developed, but barely projects from the body of the bone.

LT 406'96, a left navicular-cuboid, is quite eroded, but reveals a strong development of the crest that sustains the internal process.

LT 403'96, a left navicular-cuboid, has lost part of the proximal and plantar surfaces due to erosion. The antero-external facet for the metatarsal is wider and the internal notch less developed than in LT 67'99, but the protuberances in the two bones are similar in size and position.

Metatarsal : LT 6'05, proximal right metatarsal fragment (Text-fig. 5, N1-2).

1.- There is complete fusion between Mt III-IV.

2.- In the Mt III the anterior facet is big, subquadrangular and concave, limited by two sharp medial tuberosities.

3.- The proximal posterior facet for the ectocuneiform is rounded, and on the plantar side there is a facet for articulation of a sesamoid. Between the two proximal facets there is a small hole (more reduced than in EF 18b'04) partly closed by the proximal part of a tiny Mt II.

4.- In the Mt IV the proximal anterior facet is somewhat eroded, but appears to be smoothly convex.

5.- The proximal posterior facet, lies in the same plane as the proximal anterior facet, but was probably a bit more elevated at the union with the posterior part of the Mt III. Between these two facets of the Mt IV there is a good continuity, barely broken by a small discontinuity resulting from the fusion of the Mt V.

7.- The proximal canal of the metatarsal occupies a large part of the proximal surface, as well as the plantar surface.

8.- The dorsal canal is well marked, but its precise morphology cannot be made out.

9.- There appear to be no grooves on the medial side close to the dorsal canal, but this zone is eroded.

10.- The Mt II and Mt V are fused and very reduced.

LT 38'05, distal epiphysis of Mt III-IV (Text-fig. 5, P). The canal for the common digital artery is a wide, deep groove, which is completely covered in its distal part by a lamina of quite weak bone, so that the canal remains very superficial. The keels of the pulleys are dorsally moderate in size and quite rounded. Dorsally, the articular eminences are not very widened.

LT 414'96, a distal epiphysis of Mt III-IV, is reasonably well preserved. The canal for the common digital artery can be seen to be wide and deep, and that its distal part is partly closed by a lamina of bone.

Ist phalanx : LT 63a'01.

1.- Long and gracile.

2.- In dorsal view the lateral (external) side is concave.

3.- The proximal articular surface is

subquadrangular (longer than in LT 411'96) and with a deep groove for the reception of the keel of the metapodial.
4.- A small part of the distal articular facet is visible in dorsal view.
5.- The distal articular facet has a flattened outline.

IInd phalanx : LT 63b'01.
1.- Gracile.
2.- In proximal view, the post-articular platform is regularly developed.
3.- The dorsal extensor process is high.
4.- The outline of the distal articular facet is circular.
5.- There is an extension of the dorsal part of the distal articular facet.

IIIrd phalanx : LT 39'03.
1.- The dorsal ridge is straight.
2.- There is a strong process for the insertion of the extensor.
3.- The articular surface is rounded.
4.- The plantar process for the insertion of the deep flexor tendon is small.
5.- The dorsal ridge is centrally positioned.
6.- The plantar surface is clearly delimited by two ridges (medial and external).

Species *Namibiomeryx* cf. *spaggiarii*

Locality : Grillental.

Material : Only three bones from Grillental can be attributed to *Namibiomeryx*; GT 41'03, astragalus, GT 23'97, IInd phalanx and GT 14'05, calcaneum. The astragalus is lightly eroded all over, but in size and morphology it is closer to the Langental species than to *N. senuti*, but the information is too scarce for precise determination.

Calcaneum : GT 14'05.

IInd phalanx : GT 23'97.
1.- Gracile
2.- In proximal view the post-articular proximal platform is moderately developed.
3.- The dorsal extensor process is high.
4.- The outline of the distal articular facet is circular.
5.- The articulation extends greatly dorsally.

Locality: Fiskus

Material:
IIIrd phalanx: LT 39'03.
1.- The dorsal ridge is straight.
2.- There is a strong process for the insertion of the extensor.
3.- The articular surface is rounded.
4.- The plantar process for the insertion of the deep flexor tendon is medium sized.
5.- The dorsal ridge is centrally positioned.
6.- The plantar surface is clearly delimited by two ridges (medial and external).

Discussion: *Namibiomeryx* was included in the family Bovidae by Morales *et al.*, (1995) distinguished from other Bovidae and Hypsodontidae by the morphology of the posterior lobe of the lower molars in which the metastylid is barely perceptible, and the posterior cristid of the hypoconid is less oblique, contacting a strong entoconulid which is clearly separated at its top from the posterior cristid of the entoconid. In this feature *Namibiomeryx* also differs from *Hispanomeryx* (Morales *et al.*, 1981) and from *Sperrgebietomeryx wardi* (Morales *et al.*, 1999). This is a primitive character, being present in families related to Cervidae such as Giraffidae and Climacoceratidae, and even the Tragulidae. However, apart from this feature, the rest of the morphology reveals clear affinities with Bovidae, such as incipient hypsodonty, the transverse compression of the teeth, flattened internal wall of the molars and internal walls lying in the same plane (Morales *et al.*, 1995). The relatively abundant post-cranial elements show that the magnotrapezoid is extraordinarily close to that of *Eotragus sansaniensis* from Sansan, despite the great differences in size that exist between these two species. The unique difference to emerge is the greater relative size of the transverse diameter, so that in *E. sansaniensis* the anterior part of the facet for the semilunar is somewhat more elevated than in the bone from Langental. The navicular-cuboid of *Namibiomeryx* is very similar to that of *Andegameryx andegaviensis* (Ginsburg *et al.*, 1994). In particular the shared characters include the strength of the postero-external protuberance, the barely developed postero-internal protuberance (in distal view) and its development as a crest from the base of the internal process. The same morphological pattern occurs in *Eotragus sansaniensis* and *Namacerus gariepensis* (Morales *et al.*, 2003) which can therefore be considered to represent the Bovidae type. The difference from the cervid pattern resides in the fact that the latter group has a strong development of the postero-internal protuberance, which is particularly clear in distal view, in which it is very prominent. As a consequence, the articular facet for the ectocuneiform is more interior. This development of a quasi-rectilinear profile of the distal border of the navicular-cuboid (in plantar view) contrasts with the more inclined one of the bovids including *Andegameryx* and *Namibiomeryx*. Its systematic position has not changed. The family Bovidae has traditionally been based on the presence of horns and this needs profound revision. In the present state of our knowledge, there are at least three groups in this family : one comprising the bovids with horns but excluding the Hypsodontinae, which comprise a second group, and a third one which includes hornless forms such as *Sperrgebietomeryx*, *Namibiomeryx*, *Hispanomeryx* and probably *Andegameryx* (Ginsburg, 1971; Ginsburg and Morales, 1989). These hornless forms do not comprise a homogeneous group.

Part 4 : General discussion

The ruminants from the Northern Sperrgebiet comprise eight species belonging to three superfamilies.

Superfamily Traguloidea Gill, 1872
Family Tragulidae Milne-Edwards, 1864
Genus *Dorcatherium* Kaup, 1833
***Dorcatherium songhorensis* Whitworth, 1958**
***Dorcatherium moruorotensis* Pickford, 2001**
***Dorcatherium parvum* Whitworth, 1958**
Superfamily Giraffoidea Gray, 1821
Family Climacoceratidae Hamilton, 1978
Subfamily Propalaeorycinae nov.
Genus *Propalaeoryx* Stromer, 1924
***Propalaeoryx austroafricanus* Stromer, 1924**
***Propalaeoryx stromeri* nov. sp.**
Superfamily Bovoidea Gray, 1821
Family Incertae sedis
Subfamily Sperrgebietomerycinae Morales, Soria and Pickford, 1999
Genus *Sperrgebietomeryx* Morales, Soria and Pickford, 1999
***Sperrgebietomeryx wardi* Morales, Soria and Pickford, 1999**
Family Incertae sedis
Subfamily Incertae sedis
Genus *Namibiomeryx* Morales, Soria and Pickford, 1995
***Namibiomeryx senuti* Morales, Soria and Pickford, 1995**
***Namibiomeryx spaggiarii* nov. sp.**

It is interesting to compare the Early Miocene ruminants from the Sperrgebiet with those from other parts of Africa, in particular with those from the Great Rift Valley of East Africa, including hornless species from Songhor, Napak, Rusinga and Mfwangano (Whitworth, 1958; Hamilton, 1973; Janis and Scott, 1989; Gentry, 1994; Pickford, 2002, Barry *et al.*, 2005) and horned lineages from slightly younger deposits at Maboko (MacInnes, 1936; Whitworth, 1958; Thomas, 1979). The aim of this comparison is to provide a systematic approach to these ruminants.

The fossil record of the Rift Valley is extraordinarily rich, but with a few exceptions most of the palaeontological research has been focussed on primates, generally neglecting important groups such as the ruminants that can yield significant information about the environment and palaeobiogeography.

The similarities between the ruminant faunas from the Rift Valley and that of the Sperrgebiet are more than evident.

Ruminants from the Early Miocene of Kenya and Uganda.

Superfamily Traguloidea Gill, 1872
Family Tragulidae Milne-Edwards, 1864
Genus *Dorcatherium* Kaup, 1833
***Dorcatherium moruorotensis* Pickford, 2001**
***Dorcatherium parvum* Whitworth, 1958**
***Dorcatherium pigotti* Whitworth, 1958**
***Dorcatherium songhorensis* Whitworth, 1958**
***Dorcatherium iririensis* Pickford, 2002**
***Dorcatherium chappuisi* Arambourg, 1933**
Superfamily Giraffoidea Gray, 1821
Family Climacoceratidae Hamilton, 1978
Subfamily Propalaeorycinae nov.
Genus *Propalaeoryx* Stromer 1923
***Propalaeoryx nyanzae* (Whitworth) 1958**
Genus *Walangania* Whitworth, 1958
(= *Kenyameryx* Ginsburg and Heintz, 1966)
***Walangania gracilis* Whitworth, 1958**
***Walangania africanus* (Whitworth, 1958)**
Family Giraffidae
Genus *Canthumeryx* Hamilton 1973
***Canthumeryx sirtensis* Hamilton 1973**
Superfamily Bovoidea Gray, 1821
Family Incertae sedis
Subfamily Incertae sedis
Species indet. (navicular-cuboid KNM SO 1647 509'72)

Systematics of the East Africa pecorans

Family Climacoceratidae Hamilton, 1978
Subfamily Propalaeorycinae nov.

Diagnosis: Primitive Climacoceratidae lacking cranial appendages, dentition incipiently hypsodont.

Genus *Walangania* Whitworth, 1958

Type species: *Walangania gracilis* Whitworth, 1958.

Holotype: Associated elements of a juvenile skeleton (1334.51).

Type locality: Mfwangano, Kenya.

Age: Early Miocene, ca. 17.8 Ma.

Diagnosis: In Whitworth, 1958.

Differential diagnosis: *Walangania* differs from *Propalaeoryx* by the greater development of the p/1, the simpler morphology of the p/4, which is more blade-like, and a more gracile postcranial skeleton. In addition, in the navicular-cuboid of *Walangania*, the crest that joins the medial and plantar sides is less developed than it is in *Propalaeoryx*.

Species *Walangania gracilis* Whitworth, 1958

Knowledge about this species is insufficient, most authors (Hamilton, 1973; Janis and Scott, 1989; Gentry 1994 ; Pickford, 2002 ; Barry *et al.* 2005) having accented its closeness to *Palaeomeryx africanus* Whitworth (1958) and consequently proposing that the two species should be classified in the genus *Walangania*, either as two separate species as was done by Janis and Scott (1989) or as a single species, the opinion of the majority of authors mentioned. However, it is difficult to decide the issue because of a dearth of information about adult specimens of *Walangania gracilis* from Mfwangano and Rusinga, the holotype being a juvenile partial skeleton from Mfwangano, Kenya. There are certainly pervasive general morphological similarities between the two species, and the postcranial bones of the two seem to be closely similar. For example, the navicular-cuboid of *W. gracilis* shows, in dorsal view, the strong plantar projection of the bulge, and a prominent crest with an interrupted profile between the plantar and medial sides. This morphology occurs in the navicular-cuboid of *Walangania africanus* from Songhor. Without resolving the questions, we opt to keep the two species separate for the time being, noting that the only way to settle the issues would be to carry out a revsion of all the material from Songhor, Koru, Mfwangano, Rusinga and Napak.

Species *Walangania africanus* (Whitworth, 1958)

Synonymy:
v1958 *Palaeomeryx africanus* Whitworth, 1958 Whitworth.
v1965 *Kenyameryx africanus* (Whitworth) Ginsburg and Heintz, 1965.
v1970 *Palaeomeryx africanus* Whitworth Gentry, 1970.
v1973 *Walangania africana* (Whitworth) Hamilton, 1973.

Holotype: Sgr. 73.48 figured and described by Whitworth, 1958, as *Palaeomeryx africanus*.

Type locality and age: Songhor, Kenya, 19.6 Ma

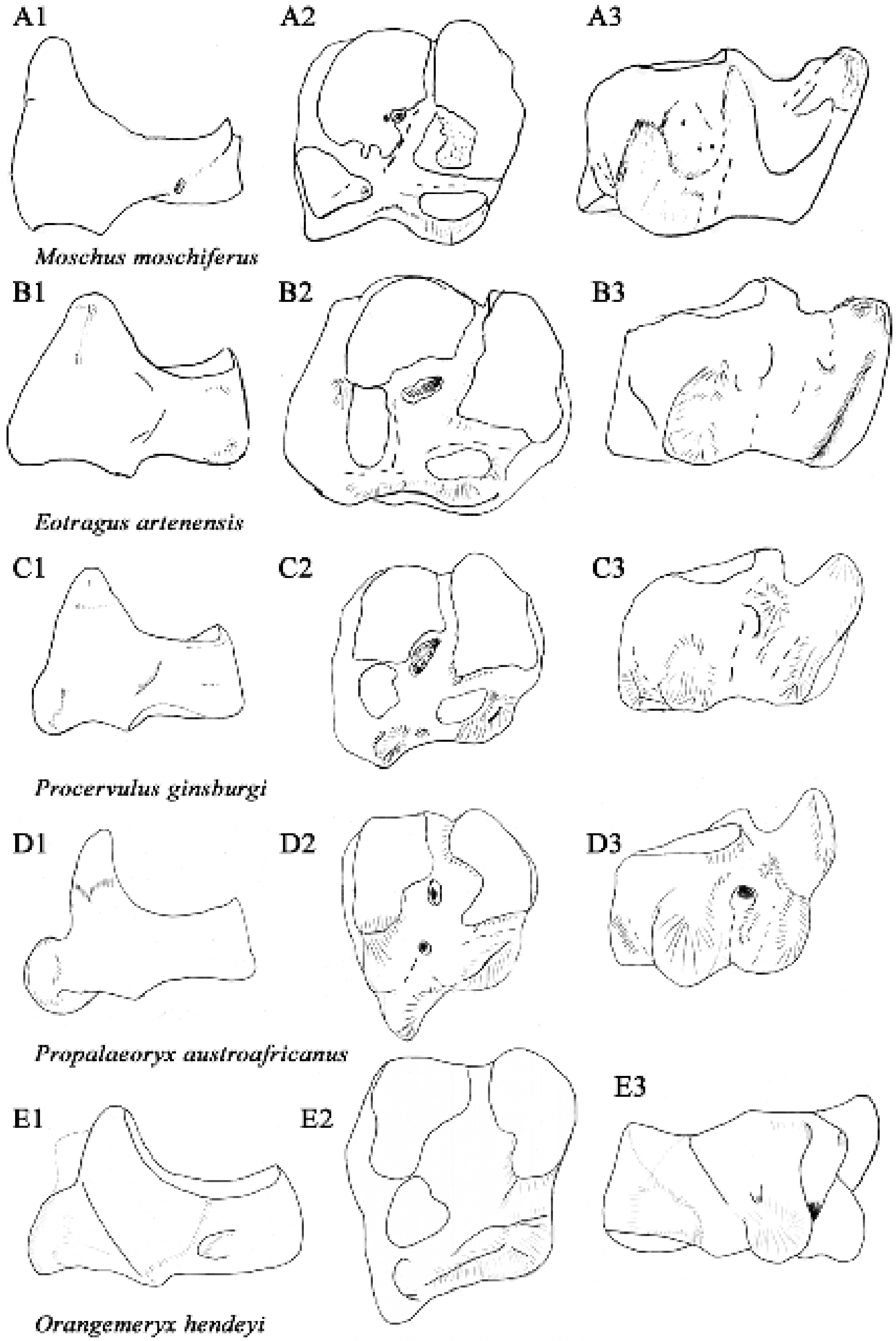
Original diagnosis: A species of *Palaeomeryx* about the same size as *Moschus moschiferus* L. probably lacking "antlers". Length of lower molar series (m/1-m/3) about 37 mm.

Emended diagnosis: in Pickford (2002) and Barry *et al.*, (2005). Medium sized Climacoceratidae, lower cheek tooth series with well developed p/1, short premolars, the p/4 with single mesio-lingual cusp, with weakly developed accessory crests. Lower molars with the lingual wall (metaconid and entoconid) quite compressed and slightly imbricated. Mesio-lingual valley moderate. Small metastylid, palaeomerycid fold present. Molars open postero-lingually. P4/ subtriangular, P3/ elongated, with lingual cusp in a posterior position and developed from an anterior lobe. P2/ more elongated than P3/. Navicular-cuboid, in distal view, has a strong development of the postero-internal bulge, that forms a prominent crest between the plantar and medial sides. The Mt II is fused and very reduced. Mt V is not fused.

Discussion: *Walangania africanus* was included by Whitworth (1958) in the genus *Palaeomeryx*. Ginsburg and Heintz (1966) separated it from this genus because of the presence of a p/1 and the more primitive morphology of the anterior premolars, and named it *Kenyameryx*. However, the latter genus loses priority to *Walangania*, which was proposed by Whitworth in 1958.

Walangania differs from *Palaeomeryx* in the morphology of the lower molars, which have compressed lingual cuspids which are not as imbricated as those in the more bunodont forms from Europe, in which the metastylid and the *palaeomeryx* fold are better developed. The dentition of *Walangania africanus* is on the whole quite primitive, and not very different from that of forms such as *Amphitragulus* or *Pomelomeryx* from the Early Miocene of Europe (Ginsburg and Morales, 1989) but is further from that of *Dremotherium*, which has lower molars characterised by more compressed lingual cuspids which are blade-like and quite similar to those in the molars of the family Cervidae (Ginsburg *et al.*, 1994)

Walangania africanus shows clear differences from *Andegameryx* (Ginsburg, 1971; Ginsburg and Morales, 1989; Ginsburg *et al.*, 1994). In the European form the lower molars are constructed on a different morphological pattern from palaeomerycids such as *Dremotherium* as well as cervids *sensu lato*, characterised by the weakness of the metastylid and the palaeomerycid fold; still residual in *Andegameryx laugnacensis* (Ginsburg and Molares, 1989) but which in *A. andegaviensis* is beginning to disappear. The lingual cuspids are compressed, but not as much as in *Dremotherium*, which gives them a slightly swollen appearance. In *A. laugnacensis* these lingual cuspids are quite imbricated, but in *A. andegaviensis* they are almost in line. The two species of *Andegameryx* show a smooth morphology of the mesio-lingual valley, not an abrupt one such as occurs in *Dremotherium* and cervids. The similarities between *Walangania africanus* and *Andegameryx* only appear in the premolars, which in *Andegameryx* are primitive, conserving a p/1 separated by a short gap from the p/2. The morphology of the postcranial skeleton and in particular the navicular-cuboid, reveals a close relationship between *Walangania* and



Text figure 7 : Navicular-cuboids of ruminants. A) *Moschus moschiferus*, B) *Eotragus artenensis* from Buñol, Spain. C) *Procervulus ginsburgi* from La Artesilla, Spain. D) *Propalaoeryx stromeri* from Langental. E) *Orangemeryx hendeyi* from Arrisdrift. 1) medial view, 2) distal view, 3) plantar view.

Propalaeoryx, and leads us to classify both in Climacoceratidae. In effect, among the postcranial fossils from Songhor there are several navicular-cuboids which show the crest with interrupted profile between the plantar and medial sides that occurs in *Propalaeoryx* and other Climacoceratidae (Text-fig. 7). This feature emphasises the separation of *Walangania* and by extension, the rest of the Climacoceratidae from forms such as *Andegameryx* and *Bugtimeryx* that possess primitive navicular-cuboid morphology (Ginsburg *et al.*, 2001).

***Walangania? whitworthi* (Hamilton 1973)**

Synonymy:

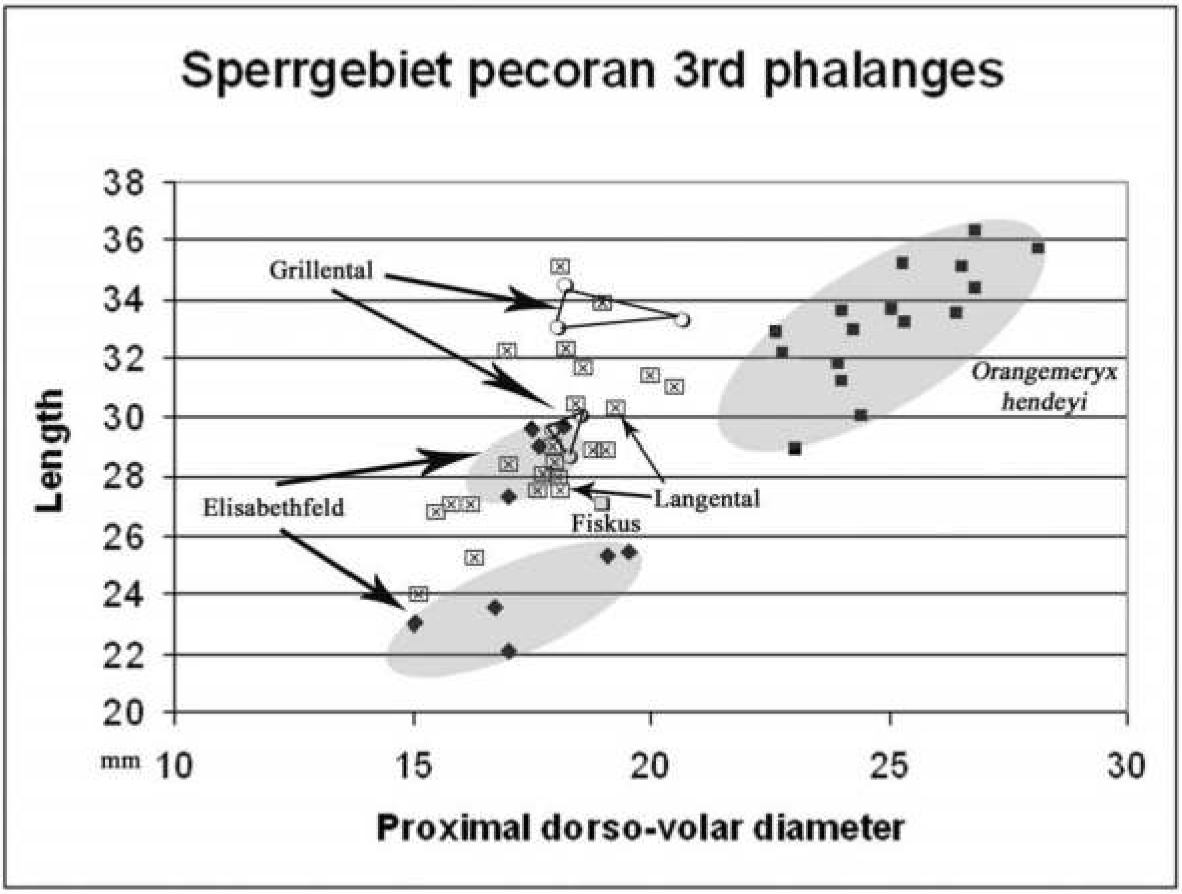
pv1958	*Palaeomeryx africanus*	Whitworth 1958.
v1958	*Gelocus whitworthi*	Hamilton 1973.

Holotype: K.Sgr.365.1949 left mandibular fragment figured and described by Hamilton (1973).

Original diagnosis: A medium sized species of *Gelocus* possessing a rounded metaconid on the lower molars; the median valley of the lower molars is very open lingually. Length of lower molar row about 33 mm.

Emended diagnosis: *Walangania* species slightly smaller than *W. africanus*, with lower molars endowed with a strong *palaeomeryx* fold. The median valley is very open lingually. Stylids of the inner wall strongly marked, bifurcate endoconid.

Discussion: Hamilton (1973) discussed at length the attribution of the mandible K.Sgr.365.1949 from Songhor, together with other mandible fragments from the same locality and an isolated m/3 from Rusinga, concluding that they belonged to a new species of *Gelocus*. For this author the separation of this material from *Walangania* is clear, especially by the rounded morphology of the metaconid, greatly different from more selenodont teeth of *Walangania*. Janis and Scott (1987) excluded the material from *Gelocus*. In addition, no known species of *Gelocus* possesses a degree of selenodonty comparable to that in mandible K.Sgr.365.1949. In contrast, species of *Gelocus*, including the most modern ones, conserve rounded, almost pyramidal, molar cusps, nothing to



Text figure 8: Length-breadth plot of IIIrd phalanges of *Propalaeoryx* from the Northern Sperrgebiet, showing two size groups at each locality, here interpreted as forelimb and hindlimb phalanges. This contrasts strongly with the sample of *Orangemeryx hendeyi* from Arrisdrift which shows a homogeneous variation suggesting that in this taxon the manual and pedal phalanges were the same overall size.

do with the more selenodont teeth of *G. whitworthi*.

This species, apart from the more bunodont lower molars than those of *Walangania africanus* and *Walangania gracilis*, possesses a major morphological complication of the lingual wall (bifurcate endoconid, strong metastylid, metaconid with a high cingulum and included with an anterior stylid) and a smaller m/3. We include the fossils with some hesitation in the genus *Walangania*, in the hope that additional material will be found, but we are convinced that it is manifestly far removed from *Gelocus*.

Genus *Propalaeoryx* Stromer 1923
Species *Propalaeoryx nyanzae* (Whitworth) 1958

Holotype: Fragment of mandible with left m/1-m/2 (Whitworth, 1958).

Type locality: Rusinga (Lower Hiwegi beds) Kenya.

Other localities: Muruorot, Kenya

Diagnosis: In Whitworth, 1958

Differential diagnosis: Whitworth (1958) included this species in *Propalaeoryx*, differentiating it from *Propalaeoryx austroafricanus* by its smaller dimensions, its less hypsodont teeth and the more columnar stylids on the lingual wall of the lower molars. Hamilton (1973) described additional fossils from the same strata on Rusinga Island and reached the conclusion that the closest affinities of the genus *Propalaeoryx* are with *Canthumeryx*.

African Early Miocene ruminants : The first aspect to emphasize concerning African Early Miocene ruminants regards the faunas prior to those of Arrisdrift (Namibia) and Maboko (Kenya) older than about 17 Ma. These Early Miocene ruminant faunas of Sub-Saharan Africa comprised three groups of hornless ruminants:

1.- Tragulids (still present in tropical Africa) are abundant and diverse in the Early Miocene of Kenya and Uganda, and much rarer and less diverse in the Sperrgebiet, although present at Langental and Elisabethfeld.

2.- Climacoceratidae, consists of *Walangania africanus* at Songhor and Napak, *Walangania gracilis* in the localities of Rusinga and Moruorot and *Walangania whitworthi* and *Propalaeoryx nyanzae* at Rusinga. In the Sperrgebiet the group is represented by abundant *Propalaeoryx austroafricanus* and *Propalaeoryx stromeri*. This group is now classified as a new subfamily Propalaeomerycinae.

3.- Bovoidea. The group in which the dentition is close to that of the family Bovidae is represented in Namibia by *Sperrgebietomeryx* and *Namibiomeryx*. In the East African fossil sites, only a single navicular-cuboid from Songhor (KNM SO 1647, 509'72) might be attributed to a form close to *Namibiomeryx*. Otherwise this group is absent from East African Early Miocene sites. The more modern faunas from Maboko (Kenya) and Arrisdrift (Namibia) in addition to tragulids, possess forms with cranial appendages belonging to the families Climacoceratidae and Bovidae, although they are represented by different genera in the two areas. There was probably geographic or ecological isolation between southern and equatorial Africa during the Early Miocene. The different representation of tragulids, which are abundant and diverse in Kenya and Uganda, and rare in Namibia, contrasts strongly with the greater abundance of bovids in Namibia and their almost total absence in East Africa prior to Maboko levels, and indicates that there were major differences between the areas during the Early Miocene which gradually began to weaken during the Middle Miocene.

These ruminant groups are also present at Gebel Zelten (Libya) which yielded *Canthumeryx sirtensis* (= *Zarafa zelteni* Hamilton 1973) which is considered to be the oldest known Giraffidae in Africa (Hamilton, 1973). This family could be represented in the Rusinga deposits by a specimen attributed by Whitworth (1958) to ?*Palaeomeryx* sp., a form the size of *Canthumeryx sirtensis*. However, the evidence is scarce, and it is only at the ypounger levels of Fort Ternan (Kenya) (Heintz, 1970, Hamilton, 1978 a, b; Churcher, 1978) that the family Giraffidae is securely identified in equatorial Africa. Thomas (1984) cited it at Nyakach (Kenya) but the material is not conclusive. We conclude that the first radiation of African pecorans show an originality and variety comparable to that known in other parts of the world. We can now endorse a relationship between Climacoceratidae and Giraffidae, even though their cranial appendages are quite different. The close relationship of *Namibiomeryx* and *Sperrgebietomeryx* on the one hand, to horned bovids (Hypsodontidae + Bovidae) on the other, appears clear, and a relationship to forms such as *Andegameryx* is possible on the basis of the structure of the lower molars, but without additional information it is difficult to affirm that all these genera comprise a strictly monophyletic group. The affinities of these Early Miocene African ruminants to those from Asia and Europe remain to be established with precision, but recognition of the diversity of African Early Miocene ruminants outlined above represents an advance in understanding the complex history of the ruminants.

Conclusions

Eight species of ruminants have been found in the Early Miocene deposits of the Northern Sperrgebiet (Table 1), belonging to three families - Climacoceratidae (*Propalaeoryx austroafricanus* and *Propalaeoryx stromeri* nov. sp.) Hypsodontidae

Table 1: Taxonomic representation of tragulids and pecorans by localities in the Northern Sperrgebiet, Namibia.

Taxon	Elisabethfeld	Grillental	Fiskus	Langental
Dorcatherium cf *moruorotensis*	-	x	-	-
Dorcatherium songhorensis	-	-	-	x
Dorcatherium cf *parvum*	-	-	-	x
Propalaeoryx africanus	x	-	-	-
Propalaeoryx stromeri nov.	-	x	x	x
Sperrgebietomeryx wardi	x	-	-	-
Namibiomeryx senuti	x	-	-	-
Namibiomeryx spaggiarii	-	cf	cf	x

(*Sperrgebietomeryx wardi*) and an uncertain family close to Bovidae (*Namibiomeryx senuti* and *Namibiomeryx spaggiarii* sp. nov.).

Tragulids are also present in the Namibian deposits but their remains are considerably more scarce than those of pecorans. In East African deposits spanning the same time range, tragulids are more diverse than pecorans, and are very common as fossils. These differences between the Early Miocene ruminant faunas of the Sperrgebiet and East Africa are probably due to differences in palaeoenvironment and palaeoclimatic conditions. It is evident that East Africa was covered in humid forest during the Early Miocene, whereas the Sperrgebiet was appreciably drier with more open vegetation types. The Namibian pecorans are not very hypsodont, but they do show a tendency towards this condition, as well as showing traces of cementum in the cheek teeth. It is thus likely that they included grass in their diets. As such, the Nambian Early Miocene pecorans reveal a greater propensity for including grazing in their behaviour than the East African ones. Palaeoenvironmental reconstructions of the Sperrgebiet reveal that it became more arid with a more open vegetation long before the equatorial parts of Africa began to dry up during the Middle Miocene. It is perhaps not surprising, under these circumstances, that the Early Miocene pecorans from Namibia show derived dental morphology in comparison with the East African lineages. For this reason, the Namibian pecorans appear to be more derived dentally than those from East Africa. Indeed, the Climacoceratidae and Bovidae from the Namib are among the earliest known in the world, and the other group, if it is related to the Bovidae, would also represent the earliest known record of the family.

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Appendix 1. Measurements (in mm) of the scapula of Sperrgebiet pecoran ruminants.
CC max; CCcg; Tcg; CC cuello; T cuello; CCcg/Ccmax; Tcg/CCcg; CCcg/Ccmx; Tcg/CCcg; Tcg/Ccmax; Tc/CCcg; Tc/CC max; Tc/Tcg; CCc/CCcg

Catalogue #	CC max	CCcg	Tcg	CC cuello	T cuello	CCcg/Ccmax	Tcg/CCcg
EF 22'00	>30.1	>26.8	>23	19.0	12.2	-	-
LT 45'00	36.1	31.0	25.4	-	12.8	86	82
LT 68'96	32.7	27.5	22.3	18.4	12.0	84	81
LT 102'04	34.0	27.4	21.9	-	-	81	80
SAM PQN 66	32.2	26.1	-	19.4	11.3	81	-

Catalogue #	CCcg/Ccmax	Tcg/CCcg	Tcg/Ccmax	Tc/CCcg	Tc/CC max	Tc/Tcg	CCc/CCcg
EF 22'00	-	-	-	-	-	-	-
LT 45'00	-	-	-	-	-	-	-
LT 68'96	84	81	68	44	37	54	67
LT 102'04	81	80	64	-	-	-	-
SAM PQN 66	-	-	-	-	-	-	-

Appendix 2. Measurements (in mm) of humeri of Sperrgebiet pecoran ruminants. Apd Antero-posterior diameter; Apdfc – Antero-posterior functional diameter; AP lat – antero-posterior lateral; Td max – maximal transverse diameter; Td fc – transverse functional diameter; PD med; PD lat; PDmd/Tdf; Apdf/PDmd.

Catalogue #	APd max	APd fc	AP lat	Td max	Td fc	PD med	PD lat	PDmd/Tdf	APdf/PDmd
EF 22'93	>30	17.1	24.2	34.4	31.3	-	-	-	-
EF 8'93	28.2	14.7	22.8	31.7	31.0	20.1	18.0	-	-
EF 37'94	30.3	-	-	-	-	-	-	-	-
EF 36'94	28.0	-	20.8	-	-	-	-	-	-
EF 22'94	29.8	-	20.5	-	-	-	-	-	-
EF 97'01	-	16.0	22.0	-	-	-	-	-	-
EF 239'03	31.0	17.0	25.2	34.0	30.5	-	-	-	-
EF 1a'04	27.0	14.0	-	33.5	>31	-	-	-	-
LT 2'96	ca 32	17.5	ca 20	34.5	33.1	ca 17	ca 17.5	-	-
LT 189'96	-	16.1	-	-	32.0	-	-	-	-
LT 83'98	-	16.0	-	33.8	33.6	23.5	20.3	70	79
LT 261a'99	-	16.7	-	-	>34	-	-	-	-
LT 57'01	32.7	-	-	-	-	-	-	-	-
LT 02'03	30.0	-	-	-	-	-	-	-	-
SAM PQN 48	-	17.1	-	-	-	-	-	-	-
SAM EF ss	-	16.8	-	30.6	29.4	-	-	-	-
SAM PQN 60	29.4	15.8	-	30.8	27.9	-	-	-	-
GT 51'96	31.2	16.8	-	-	-	-	-	-	-
GT 3'03	-	16.4	-	-	30.4	-	-	-	-
GT 40'03	-	14.6	-	-	-	-	-	-	-
GT 8'04	-	17.0	-	-	33.0	23.7	20.1	72	72
GT 7'04	32.7	-	-	-	-	-	-	-	-
GT 10'05	33.5	19.0	26.0	37.9	34.4	20.0	17.9	-	-

Appendix 3. Measurements (in mm) of the ulnae of Sperrgebiet pecoran ruminants.
H Olec; H olec1; Apt olec; Tt olec; Apm olec; Tm olec; AP pico; Hinc troc md; Tinc troc prx; T inc troc mx; AP df*; T df*; Tto/Hol; Tmol/Hol.

Catalogue #	H olec	H olec1	APt olec	Tt olec	APm olec	Tm olec	AP pico
EF 59'96	37.9	32.6	>24.4	10.8	24.1	8.0	28.5
EF 33'00	-	-	-	-	-	-	-
EF 1c '04	40.0	32.6	26.1	9.7	25.3	6.8	29.5
LT 70'96	37.8	-	>19.6	>9.1	-	-	-
LT 71'96	-	-	-	-	-	-	-
LT 43'00	38.8	-	-	11.0	-	8.4	30.0
LT 113'04	41.8	33.7	>26	11.9	26.3	8.7	32.0
SAM PQN 60	39.0	-	26.0	11.0	23.0	7.7	27.2
GT 107'04	38.2	34.0	-	9.7	24.0	7.3	27.4

Catalogue #	Hinc troc md	Tinc troc prx	Tinc troc mx	AP df*	T df*	Tto/Hol	Tmol/Hol
EF 59'96	-	9.9	-		-	28	21
EF 33'00	-	-	-	14.7	5.1	-	-
EF 1c '04	19.6	9.7	16.7	14.2	6.1	24	17
LT 70'96	-	-	-	-	-	-	-
LT 71'96	21.0	10.1	-	-	-	-	-
LT 43'00	-	-	-	-	-	28	22
LT 113'04	20.6	10.8	-	14.6	6.8	28	21
SAM PQN 60	-	-	-	-	-	28	20
GT 107'04	-	8.6	-	-	-	25	19

Appendix 4. Measurements (in mm) of radii of Sperrgebiet pecoran ruminants. L - length; App md; Tp mx; Tp fc; Apdfmu; Tdfmu; Apds; Tds; Apds fu; Tds fc"; AP/Tds fc

Catalogue #	L	APp md	APp lt	Tp mx	Tp fc	APd-fmu	Tdfmu	Apds	Tds	APds fc	Tds fc"	AP/Tds fc
EF 21'94	214	15.9	12.7	27.9	27.6	-	-	-	-	-	-	-
EF 23'94	-	-	-	-	-	-	-	-	25.6	-	23.9	-
EF 24'94	-	-	-	-	-	11.0	21.3	19.4	25.1	17	23.1	74
EF 41'94	-	17.7	13.5	31.5	30.2	-	-	-	-	-	-	-
EF 7'97	-	17.1	-	29.6	29.2	-	-	-	-	-	-	-
EF 10'01	-	16.2	13.0	29.6	28.9	-	-	-	-	-	-	-
EF 137'01	>216	16.8	13.2	30.0	30.0	10.6	21.0	-	-	-	-	-
Stromer	-	16.0	-	28.0	-	-	-	-	-	-	-	-
LT 77'96	-	-	-	30.0	28.0	-	-	-	-	-	-	-
LT 366'96	-	-	-	-	-	-	-	19.5	25.0	14.6	22.6	65
LT 15'97	-	17.8	-	31.3	30.2	-	-	-	-	-	-	-
LT 78'98	-	18.5	>13.4	>30.4	>30.4	-	-	-	-	-	-	-
LT 80'98	-	-	-	-	-	-	-	-	-	17.4	24.4	71
LT 147'99	-	-	-	-	-	-	-	19.8	27.2	18.7	24.6	76
LT 148'99	-	-	-	29.6	29.2	-	-	-	-	-	-	-
LT 261b'99	-	19.2	14.6	32.8	32.3	-	-	-	-	-	-	-
LT 38'00	245	17.5	-	30.6	30.6	11.9	21.0	-	30.4	20.0	26.0	77
LT 02'04	-	-	-	-	-	-	-	20.8	30.0	20.2	29.4	68
SAM PQN 48	-	18.9	-	31.6	-	-	-	-	-	-	-	-
SAM PQN 60	-	15.9	-	27.7	-	-	-	-	27.9	16.4	25.0	66
SAM PQN 68	-	18.2	-	32.0	-	-	-	-	-	-	-	-
SAM PQN 70	-	18.1	-	30.9	-	-	-	-	-	-	-	-
SAM PQN 71	-	-	-	-	-	-	-	-	30.2	17.2	27.3	63
GT 83'04	-	-	-	-	-	-	-	-	-	17.5	25.8	68
FS 9'04	-	17.7	-	-	-	-	-	-	-	-	-	-
BU 20154b	210	18.0	-	35.0	-	-	-	21.0	29.0	-	-	-

Appendix 5. Measurements (in mm) of the semilunar of Sperrgebiet pecoran ruminants.
AP; T max ant; H max ant.

Catalogue #	AP	T max ant	H max ant
EF 23'94	16.3	13.5	12.4
LT 82'96	18.6	14.0	14.8
LT 353'96	17.5	>10.8	13.3
LT 50'97	19.5	13.3	14.3
LT 48'00	19.1	12.4	13.8
LT 242c'03	18.6	13.0	14.5
LT 129'04	18.6	13.8	15.1
LT 05'04	17.0	12.8	13.6
FS 61'93	18.5	11.6	12.9
FS 20'01	-	12.2	11.9

Appendix 6. Measurements (in mm) of the magnum of Sperrgebiet pecoran ruminats. AP max – maximal antero-posterior diameter; T ant – anterior transverse diameter; T post – posterior transverse diameter; H ant; H post.

Catalogue #	AP max	T ant	T post	H ant	H post
LT 79'96	18.1	14.7	14.3	8.4	12.0
LT 532'96	16.9	13.9	12.0	7.7	-
LT 47'97	18.7	-	-	7.7	-
LT 184'99	>16.7	16.0	12.7	8.2	11.6
LT 50'00	-	12.4	-	8.4	-
LT 22'01	17.4	14.6	12.9	7.1	10.0
LT 23'01	17.2	13.8	12.9	6.9	10.3
LT 190'03	>15.1	14.4	12.9	7.8	10.5
LT 193'03	14.9	14.0	12.2	6.5	9.5

Appendix 7. Measurements (in mm) of unciforms of Sperrgebiet pecoran ruminants.
AP; T prox; T post; H max.

Catalogue #	AP	T prox	T post	H max
EF 23'94	-	-	-	11.2
LT 345'96	-	-	13.0	-
LT 354'96	17.0	11.1	12.2	11.5
LT 352'96	15.2	10.0	10.1	-
LT 56'97	17.8	12.2	13.0	12.1
LT 124'98	-	12.1	13.6	12.4
LT 261'99d	-	11.9	-	12.2
LT 276c'99	-	11.4	-	11.5
LT 51'00	14.3	9.9	11.3	10.4
LT 24'01	-	12.0	-	11.0
LT 62'03	16.5	10.5	11.0	10.9
LT 86'03	17.4	11.3	12.4	11.2
LT 195'03	-	-	-	11.0
LT 242d'03	18.0	10.9	13.2	10.7

Appendix 8. Measurements (in mm) of the maleolar of Sperrgebiet pecoran ruminants.
AP ; PD max; PD post; T max.

Catalogue #	AP	PD max	PD post	T max
LT 317'96	17.3	13.2	12.0	8.4
LT 313'96	17.5	14.2	11.0	8.5
LT 315'96	17.0	13.3	10.3	8.4
LT 89'96	17.4	11.3	11.0	8.5
LT 20'97	16.3	12.6	10.1	7.9
LT 93'96	15.8	14.0	-	8.5
LT 88'96	14.7	12.0	-	7.8
LT 309'96	15.0	12.1	-	8.3
LT 318'96	14.7	10.3	-	6.5
LT 115'98	17.6	15.0	11.5	8.8
LT 116'98	16.5	12.8	10.2	7.2
LT 117'98	16.7	12.9	9.1	8.4
LT 161'99	16.6	13.0	9.2	8.6
LT 162'99	15.5	12.7	9.9	8.5
LT 276e'99	16.0	15.2	10.4	9.0
FS 5'03	17.2	13.0	-	7.9

Appendix 9. Measurements (in mm) of metacarpals of Sperrgebiet pecoran ruminants. L - length; AP prox – proximal antero-posterior diameter; T prox – proximal transverse diameter; Tfac m; Tfac u; AP df; T df; AP ds pol; T ds pol; AP ds; T ds; AP/Tprox.

Catalogue #	L	AP prox	T prox	Tfac m	Tfac u	AP df	T df	AP ds pol	T ds pol	AP ds	T ds	AP/Tprox
EF 35'93	207	17.3	21.4	14.8	6.6	-	-	-	-	-	-	81
EF 24'94	205	17.8	-	-	-	-	-	-	-	-	-	-
EF 23'94	-	-	22.1	-	-	-	-	-	-	-	-	-
EF 66'01	-	16.5	22.8	13.7	9.0	-	-	-	-	-	-	72
EF 5'03	-	16.4	21.6	-	-	-	-	-	-	-	-	76
LT 1'96	-	16.7	22.8	14.8	7.8	16.3	15.0	-	-	-	-	73
LT 52'98	-	17.8	26.4	15.3	11.0	-	16.0	-	-	-	-	67
LT 51'98	-	-	-	-	-	14.0	16.0	18.2	27.8	17.6	28.0	-
LT 37'00	-	-	-	-	-	14.0	15.0	19.0	28.0	16.8	27.0	-
LT 04'03	-	-	-	-	-	-	-	16.0	27.1	-	-	-
LT 1a'97	-	-	-	-	-	-	-	20.3	30.0	-	-	-
SAM 48	-	20.5	26.8	15	10.9	16.9	16.0	-	-	-	-	76
SAM 60	-	-	-	-	-	-	-	17.0	24.9	-	-	-
SAM 72	-	18.7	23.8	13.1	10.1	-	-	-	-	-	-	79
SAM 73	-	18.6	25.1	13.8	11.2	-	-	-	-	-	-	74
SAM 106	-	19.1	25.6	16.0	10.0	-	-	-	-	-	-	75
AD 691'94	-	9.9	13.7	-	-	-	-	-	-	-	-	72

Appendix 10. Measurements (in mm) of pyramidals of Sperrgebiet pecoran ruminants.
AP prox – proximal antero-posterior diameter; AP dist – distal antero-posterior diameter; AP max maximal antero-posterior diameter; T prx – proximal transverse diameter; T ds fc ; T max – maximal transverse diameter; H ant; H max.

Catalogue #	AP prox	AP distal	AP max	T prx	T ds fc	T max	H ant	H max
EF 23'94	-	-	11.8	-	-	6.9	13.1	17.1
LT 343'96	10.2	13.8	14.8	9.5	-	-	13.9	20.0
LT 85'96	10.2	13.9	14.0	10.5	-	-	14.9	19.8
LT 347'96	11.9	14.2	14.9	9.1	6.5	-	15.1	-
LT 348'96	10.8	13.2	13.2	10.9	6.5	-	14.2	18.4
LT 349'96	11.9	13.9	14.8	8.8	-	-	13.9	17.6
LT 350'96	-	-	-	-	6.5	-	-	-
LT 91'96	11.4	12.7	12.8	9.8	6.6	-	13.5	17.5
LT 340'96	-	-	-	8.9	-	-	14.8	-
LT 51'97	10.1	13.7	14.1	9.2	-	-	14.4	18.6
LT 126'98	11.4	13.7	14.0	9.0	-	-	14.0	18.6
LT 122'98	10.8	-	-	9.0	6.3	-	14.1	-
LT 190'99	-	-	-	-	7.2	-	-	-
LT 200'99	12.3	13.8	15.0	10.5	-	-	16.0	20.0
LT 242f'03	12.6	12.6	15.6	10.0	-	-	15.0	18.8
LT 119'04	-	-	-	-	-	-	-	-
SAM PQN 60	9.6	-	12.6	8.2	-	-	12.0	15.6
SAM PQN 65 178	11.7	-	15.2	9.9	6.3	-	14.2	17.6
SAM PQN 65	11.9	-	15.0	10.8	6.2	-	14.3	18.7
SAM PQN 65 139	12.4	-	14.2	8.0	5.6	-	13.7	18.3
SAM PQN 65	11.2	-	16.2	9.4	-	-	14.7	18.8
SAM PQN 65 112	-	-	15.2	10.0	7.1	-	14.0	18.3
FS 81'93	-	-	-	-	-	-	12.9	-

Appendix 11. Measurements (in mm) of pisiforms of Sperrgebiet pecoran ruminants.
PD; AP prox; AP fac; T, T fac.

Catalogue #	PD	AP prox	AP fac	T	T fac
LT 339'96	15.9	10.2	10.3	6.7	5.2
LT 8'96	16.1	10.7	9.0	6.9	5.3
LT 531'96	-	11.3	-	6.6	-
LT 351'96	-	10.5	-	-	-
LT 46'97	17.2	10.9	10.7	8.4	5.0
LT 45'97	14.9	11.1	10.5	6.1	5.5
LT 276d'99	15.2	12.3	10.2	6.5	4.8
LT 49'00	14.6	10.7	-	6.6	-

Appendix 12. Measurements (in mm) of the scaphoids of Serrgebiet pecoran ruminants. AP ; T ant max ; H ant ; H pos ; Td.

Catalogue #	AP	T ant max	H ant	H pos	Td
EF 23'94	17.2	-	13.1	-	-
EF 197'01	-	-	12.6	-	-
LT 9'94	19.0	9.9	14.3	15.6	9.8
LT 83'96	18.4	10.0	13.1	14.0	11/0
LT 310'96	-	-	-	15.0	-
LT 312'96	-	9.3	15.1	15.3	-
LT 81'96	-	-	14.0	-	-
LT 314'96	18.1	9.2	-	-	-
LT 316'96	16.6	8.8	12.0	-	-
LT 97'96	16.6	9.1	11.4	11.5	-
LT 311'96	-	-	13.4	-	-
LT 87'96	-	8.9	12.0	-	-
LT 332'96	-	-	12.3	-	-
LT 48'97	19.9	10.3	16.1	16.6	11.0
LT 55'97	19.7	10.2	14.9	14.8	11.5
LT 110'98	18.6	-	13.4	13.4	-
LT 109'98	19.2	9.8	13.7	14.0	-
LT 111'98	17.0	8.9	13.1	13.3	-
LT 112'98	16.6	8.7	13.6	13.7	-
LT 108'98	-	9.5	13.7	13.7	-
LT 202'99	17.6	9.6	12.3	-	-
LT 46'00	19.5	9.9	14.4	13.5	9.4
LT 47'00	-	9.6	14.1	-	-
LT 20'01	-	-	12.2	-	-
LT 16'03	19.4	10.5	15.0	14.3	10.4
LT 136'03	19.0	9.7	14.3	13.5	10.7
LT 242'03	19.6	10.8	14.7	15.4	10.5
LT 67'04	18.6	-	14.3	14.7	-
SAM 60	17.9	9.4	13.0	14.7	9.6
SAM 63.1	19.7	-	14.4	14.5	-
SAM 63.2	20.3	11.2	13.3	14.7	10.7
SAM 63.3	17.7	8.8	13.5	13.4	9.7
SAM 63.4	18.2	10.2	14.7	14.9	10.0
SAM 63.5	17.3	9.4	14.5	14.6	10.7
GT 54'96	-	9.7	14.6	-	-
GT 4'01	19.3	10.4	14.8	16.0	9.4
GT 14'04	18.8	9.7	15.6	17.0	10.4
GT 15'04	18.9	>14.3	-	-	-
FS 56'93	18.4	9.2	13.2	-	-
FS 18'01	19.9	-	14.7	-	10.0

Appendix 13. Measurements (in mm) of tibiae of Sperrgebiet pecoran ruminants.
AP prox – proximal antero-posterior diameter; T prox – proximal transverse diameter; Apd max; Apd lat mx ; Apd med fc ; Aplat fc ; Td max ; Tfl ; Tf total ; AP df ; T df ; AP/Tmx ; Tfl/Apmx; Aplt/Tft.

Catalogue #	AP prox	T prox	APd max	APd lat mx	APd med fc	APlat fc	Td max
EF 37'93	-	-	-	17.8	-	14.9	29.0
EF 152'01	-	-	23.3	20.2	-	-	28.6
EF 208c'01	-	-	24.0	19.6	-	-	28.6
EF 9'01	-	-	-	19.3	-	18.8	-
EF46a'00	-	-	-	-	-	-	-
EF 10'06	-	-	22.2	-	-	-	28.3
EF'18f'07	-	-	23.8	-	-	-	29.4
LT 193a'96	-	-	24.4	18.6	23.4	-	29.2
LT 102'96	-	-	-	20.3	-	19.4	-
LT 78'99	>47.4	>49	-	-	-	-	-
LT 270'99	-	-	-	-	21.7	-	-
LT 2'01	-	-	22.3	-	21.4	-	-
LT 7'01	-	-	24.2	19.2	22.3	-	30.4
LT 51'04	-	-	-	-	-	-	-
LT 129'06	-	-	ca 21.5	-	-	-	ca 27
LT 132'06	-	-	23.5	-	-	-	32.6
SAM 77	-	-	24.4	-	22.1	-	-
SAM 83	-	-	-	14.2	-	-	-
SAM 76	-	-	-	17.6	-	-	-
GT 185'96	-	-	21.2	18.0	19.6	-	28.0
GT 28'00	-	-	ca 23.1	16.7	-	-	ca 30.5
GT 27'00	-	-	23.8	20.2	20.6	20.2	29.3
GT 31'03	-	-	-	-	-	-	-
GT 39'03	-	-	-	-	19.1	-	-
GT 47'04	-	-	-	21.9	-	21.5	-
GT 70'06	-	-	ca 19.5	-	-	-	ca 27
GT 65'07	-	-	ca 22	-	-	-	ca 26.4

Catalogue #	Tf1	Tf total	AP df	T df	AP/Tmx	Tf1/Apmx	APlt/Tft
EF 37'93	20.0	25.8	17.8	20.7	-	-	67
EF 152'01	21.0	27.0	-	-	81	90	75
EF 208c'01	22.0	27.0	-	-	84	92	73
EF 9'01	-	-	-	-	-	-	-
EF46a'00	-	-	-	-	-	-	-
EF 10'06	-	-	-	-	-	-	-
EF'18f'07	-	-	-	-	-	-	-
LT 193a'96	21.7	25.8	17.2	20.6	84	89	72
LT 102'96	22.0	28.1	-	-	-	-	72
LT 78'99	-	-	-	-	-	-	-
LT 270'99	22.3	-	-	-	-	-	-
LT 2'01	21.7	-	-	-	-	97	-
LT 7'01	22.6	28.2	-	-	80	93	68
LT 51'04	23.0	-	-	-	-	-	-
LT 129'06	-	-	-	-	-	-	-
LT 132'06	-	-	-	-	-	-	-
SAM 77	-	-	-	-	-	-	-
SAM 83	-	-	14.6	18.1	-	-	-
SAM 76	21.2	26.2	-	-	-	-	-
GT 185'96	20.8	26.2	-	-	76	98	69
GT 28'00	-	-	-	-	-	-	-
GT 27'00	23.3	27.8	-	-	81	98	73
GT 31'03	21.6	-	-	-	-	-	-
GT 39'03	22.3	-	-	-	-	-	-
GT 47'04	-	-	-	-	-	-	-
GT 70'06	-	-	-	-	-	-	-
GT 65'07	-	-	-	-	-	-	-

Appendix 14. Measurements (in mm) of the astragalus of Sperrgebiet pecorans. Ll - lateral length; Lm – Medial length; Apl Apm Tp Tp pol Td

Catalogue #	Ll	Lm	APl	APm	Tp	Tp pol	Td
EF 37'93	31.4	29.9	17.9	18.3	19.5	17.9	20.2
EF 46b'00	33.2	31.0	19.2	18.8	18.3	-	21.4
EF 54a'00	-	34.5	-	>20.2	-	-	-
EF 208d'01	32.9	31.6	18.0	-	18.8	-	21.2
LT 193b'96	35.1	33.2	20.4	20.0	20.8	-	21.8
LT 115'96	36.6	33.5	20.4	-	21.7	19.6	-
LT 214'96	-	32.5	-	19.4	21.1	19.4	-
LT 114'96	-	31.9	18.6	18.5	-	-	-
LT 211'96	-	-	-	-	21.6	-	-
LT 215'96	-	-	19.3	-	-	-	-
LT 57'98	34.7	-	18.7	>17.7	-	19.6	19.8
LT 58'98	36.1	-	20.0	-	-	-	20.8
LT 60'98	-	-	-	-	-	-	21.1
LT 139'99	-	33.6	-	20.3	-	-	22.0
LT 255'99	37.0	-	20.0	-	19.5	-	20.9
LT 259'99	-	32.1	-	18.4	-	-	20.7
LT 258'99	-	30.6	-	17.6	-	-	20.7
LT 98'03	-	33.0	-	-	19.3	-	-
LT 232'03	-	-	-	-	20.5	-	-
LT 9'06	35.3	33.6	19.9	19.9	23.5	20.5	19.5
LT 3a'06	37.4	34.5	20.0	19.5	22.5	19.5	22.4
LT 36'06	35.2	34.3	19.0	19.7	23.8	20.2	21.2
LT 29'07	34.4	32.8	19.7	20.6	20.6	-	21.3
SAM 76	37.0	35.2	20.4	20.8	20.6	-	22.0
GT 7'94	37.4	34.3	21.3	20.3	23.2	20.3	22.0
GT 5'03	-	32.0	-	18.7	-	-	21.2
GT 142'04	-	-	-	-	22.9	20.7	-
FS 37'93	36.8	35.5	19.5	21.2	22.5	20.5	21.9
FS 8’04	>35	33.8	19.2	>19.3	-	20.2	21.5

Appendix 15. Measurements (in mm) of the calcaneum of Sperrgebiet pecorans. L total – total length; L cc; AP cc; T cc; AP tc; T tc; AP s; T s; Apm; Apfc cc; TFc cb.

Catalogue #	L total	L cc	AP cc	T cc	AP tc	T tc	AP s	T s	Apm	APfc cb	Tfc cb
EF 37'93	70.9	49.1	18.9	8.6	18.4	17.8	-	-	25.9	-	-
EF 36'93	-	50.3	18.3	9.9	20.2	18.4	24.1	21.3	-	-	-
EF 26'94	-	-	17.3	10.0	-	-	21.7	-	27.5	-	-
EF 46c'00	-	-	-	-	-	-	22.5	20.2	27.3	-	-
EF 8b'01	-	50.2	17.6	>7.4	-	16.2	-	-	-	-	-
EF 208b'01	77.6	55.0	19.1	10.2	20.6	17.3	23.2	-	27.1	-	-
LT 118'96	-	52.2	20.0	9.8	21.3	16.4	23.9	20.6	-	-	-
LT 196'96	-	-	19.0	7.5	-	-	23.1	19.6	27.6	-	6.5
LT 200'96	-	50.0	-	-	18.0	16.6	-	21.0	-	-	-
LT 198'96	-	50.0	19.0	9.1	-	-	-	-	-	-	-
LT 195'96	-	50.5	-	>6.4	-	-	21.0	-	-	-	-
LT 203'96	-	-	-	-	-	-	-	-	-	19.3	6.9
LT 197'96	-	-	-	-	-	-	-	-	-	20.6	7.6
LT 204'96	-	-	-	-	-	-	-	-	-	-	8.4
LT 69'98	79.3	53.3	20.4	8.5	20.6	-	25.4	22.1	31.5	20.5	7.0
LT 71'98	-	-	-	-	21.9	17.1	-	-	-	-	-
LT 72'98	-	-	-	-	19.4	15.1	-	-	-	-	-
LT 137'99	-	48.0	18.2	9.3	-	-	-	-	-	-	-
LT 9'01	-	-	-	-	-	-	22.0	22.0	29.1	-	-
LT 01'03	78.5	52.6	21.2	10.0	21.0	17.3	24.3	23.2	27.7	20.4	7.0
LT 85b'04i	79.9	54.8	20.6	8.6	21.4	17.1	23.6	22.7	28.6	19.0	6.6
LT 85a'04d	77.7	53.2	20.9	8.5	21.4	17.0	-	21.2	27.8	-	6.8
LT 83'04	79.0	52.8	-	-	-	-	-	-	-	-	-
SAM PQN 76	79.7	54.1	20.0	8.5	-	-	25.5	22.4	29.0	18.9	7.0
SAM PQN 87	-	55.0	20.2	8.2	-	17.4	-	22.5	-	-	-
SAM PQN 88	-	-	-	9.1	-	-	-	-	-	-	-
SAM PQN 86	70.7	48.5	18.0	7.7	17.7	16.7	27.7	20.6	26.7	-	6.7
SAM PQN 109	-	52.8	17.8	9.0	20.4	-	-	-	-	-	-
GT 109'96	-	51.5	18.5	9.6	-	-	-	-	-	-	-
GT 11'03	-	53.2	18.9	9.0	19.2	15.7	-	-	-	-	-
GT 143'04	78.5	-	21.0	9.0	20.0	16.7	-	-	-	18.3	7.3
GT 50'04	80.0	55.7	-	-	>18.3	>16.3	-	22.7	-	17.4	6.3

Appendix 16. Measurements (in mm) of the navicular-cuboid of Sperrgebiet pecorans.
Apmx ds 1; AP cub; Tmx px; Tfc ast; Tds 2; Hmx ant 3; Hnav ant; Hcub ant 4; H post 5

Catalogue #	APmx ds 1	AP cub	Tmx px	Tfc ast	Tds 2	Hmx ant 3	Hnav ant	Hcub ant 4	H post 5
EF 29'94	-	-	>23	-	-	16.2	8.5	13.8	-
EF 47b'00	28.0	-	-	21.7	-	16.5	10.9	14.5	22.0
EF 32'01	28.3	22.1	26.0	21.4	23.5	18.4	10.8	15.6	20.0
EF 8c'01	-	21.5	26 .0	21.5	23.0	16.8	10.4	15.4	22.3
EF 208'01	26.3	22.7	25.3	-	-	17.8	-	15.0	-
LT 5'94	29.0	-	-	-	-	-	10.6	-	-
LT 208'96	-	-	-	-	-	-	-	16.0	-
LT 53'98	>25.4	24.0	28.8	23.0	27.7	19.0	10.4	16.3	23.2
LT 214'99	-	-	-	-	-	18.2	10.5	14.3	-
LT 256'99	-	-	-	-	-	19.4	12.1	16.8	-
LT 52'00	-	-	25.0	20.8	22.0	16.6	10.3	15.1	-
LT 50'01	28.7	23.6	28.3	22.6	24.8	19.8	12.4	17.8	21.1
LT 121'04	-	23.7	28.3	22.7	25.2	17.9	10.0	16.1	-
LT 85c'04	-	-	-	-	-	-	-	-	-
SAM PQN 83	31.7	24.9	28.5	22.5	-	-	11.7	18.9	-
SAM PQN 93	30.7	23.2	27.0	21.2	-	-	11.6	19.6	-
SAM PQN 104	26.2	21.3	25.7	-	-	-	11.6	17.9	-
GT 52'96	28.4	23.0	28.2	22.7	25.0	20.1	11.5	16.7	-
GT 84'96	-	23.8	29.0	23.7	26.0	18.6	12.3	16.7	24.6
GT 31'04	29.3	24.6	28.7	23.2	25.7	20.2	10.8	17.2	-

Appendix 17. Measurements (in mm) of the metatarsals of Sperrgebiet pecoran ruminants.
L frag; Ap prx – proximal antero-posterior diameter; T prx – proximal transverse diameter; AP df; AP ds pol; T ds pol ; Apds ; Tds.

Catalogue #	L frag	Ap prx	T prx	AP df	T df	AP ds pol	T ds pol	Apds	Tds
EF 25'94	71.0	-	-	-	-	18.5	28.6	15.8	17.0
EF 13'01	-	-	-	-	-	19.3	28.6	-	-
EF 208a'01	-	25.0	24.2	-	-	-	-	-	-
EF 4'03	-	24.2	26.2	-	-	-	-	-	-
EF 3'04	-	22.0	21.0	-	-	-	-	-	-
LT 192'96	-	26.5	23.8	-	-	-	-	-	-
LT 209'96	-	25.7	25.7	-	-	-	-	-	-
LT 381ab'96	123	26.1	-	-	-	21.0	31.5	-	-
LT 257'97	-	-	-	-	-	20.1	29.0	-	-
LT 261i'99	-	-	-	-	-	19.2	-	-	-
LT 64'04	104	-	-	16.3	14.9	20.3	29.4	18.0	28.4

Appendix 18. Measurements (in mm) of the Ist phalanges of Sperrgebiet pecoran ruminants.
Prox ap – proximal antero-posterior diameter; Prox ml – proximal medio-lateral diameter; Dist ap – distal antero-posterior diameter; Dist ml – distal medio-lateral diameter.

Catalogue #	Length	Prox ap	Prox ml	Dist ap	Dist ml
EF 00	37.4	14.6	12.5	9.0	9.8
EF 18c'07	42.5	17.2	14.8	10.3	11.3
EF 23a'96	43.5	15.5	15 .0	11.0	12.1
EF 27'94	40.1	15.7	14.5	9.7	12.1
EF 28'94	43.8	16.4	14.0	9.7	11.5
EF 33'01 16	9.6	12.9	40.0	10.9	-
EF 35'94	43.7	15.5	15.2	11.0	12.1
GT 13'05	ca 43.5	-	-	11.5	12.5
GT 62'07	45.0	17.0	14.9	12.3	-
GT 7'07	44.5	17.1	14.7	11.1	12.2
GT 9'04	43.5	ca 16.5	15.0	ca 10.5	11.5
LT 10'03	42.4	15.2	14.0	10.6	10.2
LT 158'06	44.5	17.0	15.3	11.0	11.1
LT 16'96	44.0	16.0	14.2	-	10.8
LT 20'96	43.5	17.0	14.5	10.6	11.2
LT 261'99	43.7	16.5	13.5	10.5	11.0
LT 276'96	42.8	16.5	14.2	10.7	11.8
LT 32'98	44.5	16.5	13.4	10.4	11.2
LT 33'98	42.9	16.3	12.7	10.0	10.8
LT 34'98	42.1	-	12.5	-	10.5
LT 37'98	E	16.9	13.5	-	-
LT 44'07	47.6	18.4	15.2	11.0	12.3
LT 52'04	ca 45.2	15.7	14.0	-	-
LT 79'99	42.5	-	13.5	10.3	11.5
LT 80'99	42.2	17.8	13.3	-	-
LT 82'99	41.7	17.2	15.1	10.9	11.1
LT 97b'97	47.1	17.6	15.1	11.0	11.9

Appendix 19. Measurements (in mm) of IInd phalanges of Sperrbegiet pecoran ruminants.
Prox ap – proximal antero-posterior diameter; Prox ml – proximal medio-lateral diameter; Dist ap – distal antero-posterior diameter; Dist ml – distal medio-lateral diameter.

Catalogue #	**Length**	**Prox ap**	**Prox ml**	**Dist ap**	**Dist ml**
EF 00	20.6	14.6	10.4	11.5	8.2
EF 151'01	23.6	ca 12.5	12.1	11.8	9.0
EF 208'01	25.1	15.9	12.7	13.2	9.2
EF 208f'01	25.2	16.2	11.9	13.2	9.5
EF 23b'96	23.5	14.1	12.5	12.0	9.6
EF 25b'98	23.0	15.9	11.7	13.5	10.0
EF 25c'98	24.0	15.5	11.5	14.3	10.0
EF 35'94	23.8	14.5	12.4	12.0	10.0
EF 4'04	22.2	15.0	11.1	13.4	9.4
GT 12'03	26.6	17.0	11.3	13.2	8.9
GT 16'04	21.2	14.5	10.2	11.0	7.8
GT 17'04	24.2	16.0	12.5	12.6	8.0
GT 2'07	21.9	13.2	11.0	11.6	9.6
GT 51'04	25.5	ca 14.3	12.0	13.0	9.0
GT 55'06	21.3	14.8	11.2	12.9	9.0
GT 7'07	22.9	14.9	9.9	11.7	9.2
LT 10'07	22.4	15.4	11.3	13.5	9.6
LT 107'00	25.8	17.0	12.1	13.9	10.0
LT 118'04	25.3	16.7	11.6	13.8	10.4
LT 11'98	25.3	16.4	12.0	14.4	10.2
LT 12'03	25.4	17.7	12.4	15.0	9.8
LT 129'03	24.8	16.2	11.9	12.7	10.6
LT 12'98	27.3	16.2	12.5	14.8	10.3
LT 13'03	26.7	16.0	12.8	13.4	10.7
LT 148'06	23.1	15.5	12.0	13.4	9.8
LT 148'06	22.7	15.1	10.2	13.4	10.0
LT 14'98	29.7	16.0	13.2	14.7	10.1
LT 155'06	23.2	15.5	11.0	13.0	9.2
LT 1c'97	26.6	18.2	12.7	14.6	8.3
LT 1d'97	26.4	16.0	12.6	14.2	8.9
LT 2'07	24.8	15.5	11.0	13.5	9.5
LT 232b'96	24.0	15.0	11.2	13.3	-
LT 242'03	25.8	16.5	13.4	14.4	10.6
LT 254'96	24.0	17.1	11.8	13.7	9.4
LT 260'96	26.9	17.0	12.2	14.1	8.5
LT 261'96	24.9	15.2	10.8	13.6	9.5
LT 263'96	24.8	15.1	11.1	12.0	9.2
LT 264'96	22.4	15.2	11.3	13.5	9.6
LT 32'97	28.2	17.8	13.1	13.4	9.9
LT 41'96	27.2	17.0	12.2	14.8	9.6
LT 45'07	24.1	15.0	12.6	13.4	9.6
LT 76'03	22.0	15.3	10.0	12.4	8.6
LT 76'04	22.8	14.5	10.0	12.5	8.3
LT 77'O3	21.4	13.1	10.1	11.4	8.0
LT 78'03	22.8	14.7	8.3	13.1	8.2
LT 88'99	22.7	16.1	11.4	12.9	9.3
LT 94'99	27.3	16.4	12.5	14.3	9.6

Appendix 20. Measurements (in mm) of IIIrd phalanges of Sperrbegiet pecoran ruminants.
Prox ap – proximal antero-posterior diameter; Prox ml – proximal medio-lateral diameter.

Catalogue #	Length	Prox ap	Prox ml
EF 208'04	29.6	18.1	10.4
EF 21'96	23.5	16.7	9.5
EF 25c'98	25.4	19.5	10.8
EF 25d'98	25.3	19.1	11.0
EF 26c'96	29.5	ca 17.5	10.5
EF 26d'96	30.5	-	10.2
EF 34'94	22.0	17.0	8.0
EF 35'94	23.0	15.0	9.2
EF 5'04	27.3	17.0	10.5
FS 42'93	27.0	19.0	9.5
GT 18'04	33.1	ca 18	11.2
GT 23'04	29.4	-	9.8
GT 24'04	33.4	20.6	11.5
GT 3'07	29.5	18.0	9.7
GT 42'05	ca 30	ca 18.5	10.5
GT 5'01	34.5	18.2	10.9
GT 5'94	25.7	-	-
GT 6'06	29.6	17.9	10.5
GT 95'06	28.8	18.2	10.3
LT 104'94	-	8.7	25.9
LT 105'99	-	19.7	10.8
LT 106'99	-	16.6	8.6
LT 108'99	31.6	18.6	10.0
LT 109'00	27.0	ca 16.2	8.9
LT 110'00	24.0	15.1	8.2
LT 122'04	>25	18.2	9.5
LT 125'04	30.2	19.2	10.1
LT 139'03	-	16.5	8.7
LT 14’04	>25	19.5	10.0
LT 147'06	30.4	18.4	9.8
LT 16'07	28.9	19.0	10.2
LT 161'06	28.4	17.0	9.6
LT 17'01	27.5	18.1	10.7
LT 1'98	35.1	18.1	10.1
LT 232a'96	29.0	17.9	9.6
LT 240'96	27.0	15.8	10.0
LT 242'03	ca 29	18.8	10.7
LT 247'96	29.0	17.7	9.5
LT 276'99	28.0	17.8	8.8
LT 2'94	28.0	18.0	9.7
LT 46'07	33.8	19.0	9.5
LT 48'96	27.5	17.6	10.6
LT 4'98	25.2	16.3	10.1
LT 49'96	28.5	18.0	10.0
LT 50'96	-	20.0	10.8
LT 53'96	27.1	16.2	9.8
LT 54'96	28.4	18.0	10.0
LT 55'96	32.2	ca 17	10.0
LT 56'01	>27	20.0	10.0
LT 57a'96	ca 31	ca 20.5	11.0
LT 7'98	32.3	18.2	9.6
LT 85'03	ca 26.8	ca 15.6	ca 8.5
LT 8'98	31.4	20.0	10.7