TAPHONOMIC EVIDENCE OF PREDATION AND SCAVENGING OF *TELEOCERAS* (MAMMALIA: RHINOCEROTIDAE), WITH A DESCRIPTION OF THE CAMELIDAE FROM THE MINIUM QUARRY LOCAL BIOTA OF NORTH-CENTRAL KANSAS

being

A Thesis Presented to the Graduate Faculty
of Fort Hays State University in
Partial Fulfillment of the Requirements for
the Degree of Master of Science

by

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PREFACE

This thesis is composed of two separate papers, and is presented herein in two parts. The individual manuscripts were prepared in the format required by the journal(s) to which they will eventually be submitted. The figures and tables for each paper are included following the text, and are numbered sequentially.

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THE CAMELIDAE FROM THE EARLY HEMPHILLIAN MINIUM QUARRY LOCAL BIOTA OF NORTH-CENTRAL KANSAS, WITH A DISCUSSION OF CAMEL METAPODIALS AS A SYSTEMATIC TOOL

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ABSTRACT

Three species of camels were recovered from the early Hemphillian (Miocene) Minium Quarry local biota (Ogallala Group) of north-central Kansas. A small and large camel, Hemiauchenia vera Matthew and Megatylopus cf. M. gigas Matthew and Cook respectively, were identified by comparison to known taxa. A medium-sized camel is assigned to Procamelus based on measurements and biometric analysis of referred metapodials, and may represent a new species. It is the largest Procamelus yet described, and suggests that a phylogenetic relationship exists between Procamelus and Megatylopus. Procamelus can be distinguished from Alforjas, a medium-sized Neogene camelid that consistently exhibits overlap of biometric parameters with Procamelus, by differences in the angularity and shape of metapodial proximal articular facets, and in the osteology of the plantar process.

INTRODUCTION

Many North American Hemphillian faunas contain camels of different sizes: small (Hemiauchenia); large (Megatylopus); and medium-sized (referable to either Procamelus or Alforjas) (Bennett, 1977, 1979; Harrison, 1979; Dalquest, 1980, 1985; Breyer, 1983; Leite, 1986, Thomasson et al., 1986; LaGarry, 1987). Because many of these faunas lack diagnostic cranial material it often is difficult to assign the medium-sized camel to an appropriate genus. Recently, the comparative use of post-cranial material has been demonstrated to be a reliable method of distinguishing most genera of North American Neogene camelids (Breyer, 1974, 1983; Webb, 1974). Neogene and extant camelids in which the post-cranial elements have been studied in detail include Alforjas (Harrison, 1979), Camelops (Webb, 1965; Breyer, 1974), "Tanupolama" [= Hemiauchenia], Titanotylopus, Camelus, and Lama (Breyer, 1974; Webb, 1974).

Two post-cranial elements that have been used with some success to make systematic assignments are the metacarpal and metatarsal (metapodials). Breyer (1983) demonstrated that most Neogene camelids can be assigned to genera based on bivariate plots of metapodial dimensions. Likewise, bivariate plots of metapodial dimensions have been used to distinguish between the lamine genera Hemiauchenia, Paleolama, and Lama (Webb,

1974). Dalquest (1980, 1985) recognized that, in the Coffee Ranch local fauna, the camelid genera "Pliauchenia" [= Alforjas] and Hemiauchenia could be distinguished readily by proportions of metapodial elements.

Three different-sized camels were recovered from the Minium Quarry local biota (l.b.) of north-central Kansas. The large and small specimens can be assigned readily to particular genera. The affinities of the medium-sized taxon are problematical, and I use a combination of limb osteology and Breyer's (1983) technique of biometric analysis to assign this camel to the genus Procamelus. Its large size suggests that it may represent a previously unrecognized species.

The Minium Quarry is located approximately 3.75 km northwest of Morland, Graham County, Kansas (Fig. 1). Excavated during the summers of 1985 and 1986 by field parties under the direction of J. R. Thomasson from Fort Hays State University, the Minium Quarry has yielded an abundant flora and vertebrate fauna (Thomasson and Zakrzewski, 1987). The mammalian taxa in the Minium Quarry l.b. indicate an Early Hemphillian age for the deposit (LaGarry, 1987; Thomasson and Zakrzewski, 1987). For a preliminary listing of the biota, see Thomasson et al. (1986). A systematic description of the mammals is in preparation (R. J. Zakrzewski, pers. comm.).

I (LaGarry, 1987) provided a preliminary account of the camelid genera from the Minium Quarry. However, since that report, more camel material has been recovered. The small species now can be assigned to Hemiauchenia vera Matthew. The large taxon is referable to Megatylopus gigas Matthew and Cook. The medium-sized species is assigned herein to Procamelus based on a biometric and osteologic analyses of the referred material.

Catalog numbers without an acronym are housed in the Fort Hays Sternberg Memorial Museum Vertebrate Paleontology collection (FHSM VP-). Other institutional acronyms are:

F:AM Frick American Mammals, American Museum of Natural History, New York

UF University of Florida State Museum, Gainesville

UNSM University of Nebraska State Museum, Lincoln

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linneus, 1758

Order ARTIODACTYLA Owen, 1848

Family CAMELIDAE Gray, 1821

Subfamily CAMELINAE Zittel, 1993

Tribe LAMINI Webb, 1965

Hemiauchenia Gervais and Ameghino, 1880

Hemiauchenia vera (Matthew, 1909) Webb, 1974

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Materials.-- 7812, partial right P4; 7813, partial right maxillary with M1; 8230, partial deciduous left P4; 8651, right m1; 8860, distal epiphysis of metapodial; 8863, left scaphoid; 8910, proximal end of right metatarsal; 8862, right navicular; 8771, left astragalus; 8820, partial left astragalus.

Description.-- Hemiauchenia vera is the least represented of the three camels in the Minium Quarry l.b., but is the only camel that can be assigned with certainty. Breyer (1977) stated that the three time-successive species of Hemiauchenia are nearly identical except for the c-p4 diastema and a progressive increase in hypsodonty. Therefore, the post-cranial elements of the Minium Quarry taxon can be assigned to genus by comparison to a related species. The post-cranial specimens of the Minium Quarry H. vera compare very well with, but are considerably smaller than, the Blancan specimens of H. blancoensis from the Broadwater A locality described by Breyer (1977).

The partial Rp4 (7812) lacks the lingual surface (Fig. 2a-b), is in a moderate state of wear, and the lophs are preserved in good detail. The RM1 (7813) is complete and has undergone very little or no wear (Fig. 2c-d), and lama butresses (Webb, 1965) are well

developed. Although these specimens are similar to Broadwater A H. blancoensis, they are smaller and less hypsodont, which suggests H. vera rather than H. blancoensis.

Tribe CAMELINI Webb, 1965

Procamelus sp. nov.

Figures 2g-h, 3

Materials.-- Minium Quarry 1.b.: 7816, right I3; 8700, axis; 8122, associated right forelimb, including the distal 4/5 of the humerus, radius-ulna, scaphoid, lunar, cuneiform, pisiform, trapezoid, magnum, unciform, metacarpal; 8938, 9367, 2 distal ends of humeri; 8995, proximal end of radius-ulna; 9043, radius-ulna; 8864, left scaphoid; 8910, proximal end of metacarpal; 8253, 8723, 2 distal ends of tibias; 8212, left metatarsal; 7958, first phalange; 8685, second phalange. Ogallala Beach locality (Kh-1), Keith Co., Nebraska: UNSM 88483, left metatarsal. Cambridge 1.f. (Ft-40) and associated localities (Ft-0, Ft-47), Frontier Co., Nebraska: UNSM 88479, 88482 right metatarsals; UNSM 88480, 88481, 2 proximal ends of left metatarsals.

Remarks.-- For the purpose of the paper I assign these specimens to Procamelus based on the osteology and ratios of the dimensions of the referred metapodials. The distinct osteological and size differences with the only contemporary species of Procamelus, P. grandis,

suggests that the Minium Quarry sample represents a previously unrecognized species. Comparisons were made with taxa in which the post-cranial osteology has been thoroughly described. I have not chosen a type specimen, per se, because materials of the type P. grandis were unavailable for comparison. Previous accounts of P. grandis generally have been based on teeth or crania, with little or no description of post-cranial osteology. Therefore, comparison to the post-cranial osteology of P. grandis is pending that description. However, metapodials of Procamelus from the Kepler (Morril Co., Nebraska) and Burge Quarries (Cherry Co., Nebraska), Procamelus cf. P. grandis from the Poison Ivy Quarry (Cherry Co., Nebraska), and P. occidentalis from the Railway Quarry (Cherry Co., Nebraska) were available and, if correctly identified, should provide a valid basis for the following discussion.

Description.--This species is well represented by post-cranial material, and is the largest component of the Minium Quarry camel sample. The only dental material referred to this taxon is an RI3 (Fig. 2g-h) that has an alveolar length of 9.2 mm, which is smaller than that of the paratype of P. grandis (12.8 mm) figured by Gregory (1949), and far smaller than those of A. taylori (14.2 mm) described by Harrison (1979).

Whether or not this difference signifies reduction of this tooth must remain speculative, pending the recovery of more teeth.

The axis is 203 mm long, with anterior and maximum widths of 80.0 mm and 86.4 mm, respectively. It is longer and narrower than in Camelops, and approaches Aepycamelus in overall proportion. The odontoid process is spout-like and robust as in Camelops, and the anterior articular surface of the body of the axis faces upward as in Aepycamelus, Camelops, Alforfas, and Camelus. The neural spine is low and undivided and is longer and thinner than in Camelops. The transverse process is thinner and terminates in tubercles that are less robust and narrower laterally than those of Camelops. The dorsal surfaces of the postzygopophyses are convex surfaces, rather than flat as in Camelops. The articular surfaces of the postzygopophyses are indistinct and slightly convex, merging with the centrum anteriorly. In Camelops they are concave, elongated transversely, and isolated (Webb, 1965).

The partial associated forelimb (8122) belongs to a medium-sized camel with stout legs (Fig. 3), similar in appearance to the specimen of P. grandis figured by Gregory (1949, p. 372). This camel is larger (Table 1) than the largest A. taylori reported by Harrison (1979) and the largest individual of P. grandis from Big Spring

Canyon, South Dakota (Gregory, 1949). It does, however, fall well within the range of measurements of a large Procamelus from the late Early Hemphillian Box T Quarry of the Texas Panhandle (Breyer, 1983 p. 303), and is 30-40% smaller than Aepycamelus and Hemphillian specimens of Megatylopus.

The proximal articular surface of the humerus is missing, as is approximately 2-3 cm of the shaft. The distal ends of the referred humeri range from 75.0-76.8 mm wide, with a mean of 76.1 mm. The deltoid crest is pronounced as in Camelops. The nutrient foramen is located posterolaterally equidistant from the the deltoid crest and the distal trochlear surface. The medial epicondyle is weak and proximal to the trochlear surface. The trochlear surface extends well into the olecranon fossa, as it does in Camelus. This is in contrast to the lamines Hemiauchenia, Alforjas, and Camelops (Webb, 1965; Harrison, 1979).

The radius-ulna has an articular length of 522.0 mm, a proximal width of 77.0 mm, and a distal width of 89.2 mm. This is longer and proportionately more slender than in Alforjas and Camelops, but less so than in Hemiauchenia. These proportions closely resemble those of Megatylopus, although smaller. The proximal part of the olecranon process is missing, whereas the distal part is preserved and merges with the radius

medially. The lateral tuberosity is either very weak, broken, or absent. The bicipital rugosity is small in comparison to later taxa (eg. Camelops; Webb, 1965). The anterior brachial rugosity is poorly defined and located more medially than in Camelops. The proximal interosseous foramen is elongate anteroposteriorly, not abbreviated as in Camelops. The proximal portion of the distal interosseous foramen is elongate anteroposteriorly, whereas the distal portion is weak or absent. In Camelops this feature is well-defined and wider (Webb, 1965). The scaphoid condyle is pronounced, broad, and conical, with the apex to the side. The channels on the anterior surface are shallow and broad.

The scaphoid is a very stout bone, averaging 34.2 mm in height by 49.0 mm in length, and is more thickly proportioned than in Alforjas and Hemiauchenia. On the proximal surface, the anterior convex facet is high, whereas the posterior convex facet is somewhat reduced. The concave facet is inclined laterally. The anterodorsal lunar facet is semicircular in shape. The anteroventral lunar facet is attenuated posterolaterally. The trapezoid facet is subequal with respect to the magnum facet, lying well above the distal extent of the magnum. These characters all differ slightly from those reported for Camelops and Lama by Webb (1965), except for the shape of the anterodorsal

facet, which is similar. The other characters resemble Webb's (1965) description of Camelus.

The lunar is 43.5 mm in height and 44.3 mm in length. The scaphoid facets of the lunar are mirror images of the facets on the scaphoid. The posteromedial branch of the bifid process is small and faces medially. On the median keel dividing the two facets, the magnum surface is larger than the unciform surface, and is inclined approximately fifty degrees from the horizontal. A groove separates the two facets.

The cuneiform is larger than the scaphoid, measuring 37.4 mm in height by 34.7 mm in length. The proximal convex facet is a narrow anteromedial strip. This is in contrast to the condition in Camelops, in which the cuneiform is smaller than the scaphoid, but similar to Camelops in the shape of the proximal convex facet (Webb, 1965). The convex pisiform facet is shortened. The anterodorsal lunar facet is simple, and corresponds well with its counterpart on the lunar bone. The anterior part of the ventral lunar facet faces medially and is at right angles to the posterior part, the vertex being somewhat rounded.

The free end of the pisiform is not as narrow and robust as in Camelops, and is rugose. The cuneiform and ulnoradial facets are nearly equal in size. The crest between these facets is long and curves ventrally.

The articular surfaces of the trapezoid are smaller than those of Camelops. The surface of the trapezoid articulating with the scaphoid is narrow. The dorsal anterolateral facet for the magnum joins the metacarpal facet distally, as it does in Camelops (Webb, 1965). The small ventral facet for the magnum joins the metacarpal facet distally.

On the magnum, the boundary between the lunar facets is weak but distinct. The posterolateral process is long, but not as robust as in Camelops. The posterolateral facet for the unciform is set sharply against the posterior convexity of the lunar facet. The posterolateral surface of the metacarpal facet is inclined laterally at the proximal end.

The unciform is 45.3 mm in height and 48.2 mm in length. The anterior distal surface of the unciform extends more distally than the distal surface of of the magnum, whereas in more advanced lamine genera their distal surfaces are adjacent (Webb, 1965; Harrison, 1979). The cuneiform facet is by far the largest facet on the proximal surface, changing from a faint concavity at the anteromedial end to a low convexity curving well down onto the posterolateral surface. The crest separating the lunar and cuneiform facets is shallow and weak, and is inclined slightly medially. The posteroventral process is large and well developed, but

not as blunt or heavy as in Camelops. The fossa between the two median facets for the magnum is shallow. The concave triangular ventral facet for the fourth metacarpal extends slightly onto the posterior posteroventral process.

The anterior face of the metacarpus (see Table 1 for measurements) is longitudinally concave as in Camelops and Camelus. The proximal articular surface of the third metacarpal is slightly higher than that of the fourth. These last characters are similar to those seen in Camelops and Camelus, and more pronounced than in Alforjas, Lama, and Hemiauchenia. The magnum and trapezoid facets are similar in size to those of Camelops, but form a posteriorly directed triangle as in Procamelus. The unciform facet is more square than in Camelops, but is of similar size. The metacarpus approaches that of Camelops in length, but is less robust distally.

The metatarsus (8212) is aproximately 10% smaller than the metacarpus (Table 1), and exceeds the metacarpus/ metatarsus size difference seen in Camelops (Webb, 1965), but is much less than in Procamelus (Gregory, 1949), Alforjas, and most other Neogene camelids (Harrison, 1979). The lateral and medial sides are slightly concave as in Camelus, rather than convex as in Alforjas, Camelops, and Lama (Webb, 1965;

Harrison, 1979). The anterior longitudinal groove is shallow, as is the anterior groove. The cuboid facet is separated from the ectomesocuneiform by a small trough as in Alforjas (Harrison, 1979) and Camelops (Webb, 1965). The plantar process extends 1/3 its length down the posterior of the proximal end. The cuboid facet is inclined medially. The vertical process is short and closed. The entocuneiform facet is small and separate from the ectomesocuneiform facet, but joined to the plantar process, as in Procamelus. In Alforjas, Camelops, and Camelus, this facet is isolated from the plantar process.

The proximal phalange (7958) is 119.6 mm long, has a proximal width of 49.2 mm, and is slender as in Lama and Alforjas, with a "w"-shaped suspensory ligament scar resembling those of Lama, Megatylopus, Titanotylopus, and Hemiauchenia (Breyer, 1974). It is quite worn, as is the second phalange (8685), which is slightly larger than that of Alforjas.

ANALYSIS OF METAPODIAL OSTEOLOGY

The distal limb elements of Pleistocene camelids have been studied in some detail (Breyer, 1974), and some of these observations have been applied in limited form to older taxa (Harrison, 1979; Voorhies and Corner, 1986). However, these studies have not described the articular surfaces of camelid metapodials. As a result,

many metapodials of medium-sized Neogene camels are misassigned. For example, the specimens assigned to Procamelus herein have been considered (Thomasson et al., 1986) to be Alforjas cf. A. taylori Harrison based solely on their Hemphillian age (Fig. 1). The scattered reports of Procamelus cf. P. grandis in Hemphillian faunas require that it too be distinguishable from contemporary taxa. The shape, size, and configuration of the proximal articular surfaces of the metapodials of P. grandis, Alforjas, and the new species of Procamelus from the Minium Quarry 1.b. are sufficiently different to allow them to be distinguished from one another, and in the following discussion specimens of each are examined and compared.

The most readily apparent difference between these species is size (Fig. 4). Metapodials of the Minium Quarry Procamelus are consistently larger (Table 1) than those of A. taylori described by Harrison (1979), and larger than most P. grandis, with the exception of the undescribed sample from the Box T Quarry reported by Breyer (1983).

Osteological differences between the three species are most readily apparent in the size, shape, and arrangement of the proximal articular facets, the degree of metapodial fusion, and several other characters. These differences are detailed below and in Figure 4.

Metacarpus

Unciform facet.- In Alforjas the unciform facet is triangular (Fig. 5) and lies below the level of the magnum facet. In Procamelus this facet is trapezoidal in outline and is most clearly defined in the Minium Quarry specimens. Alforjas has a small subsidiary facet articulating with the unciform on a postero-medial extension of the primary unciform facet. This feature is represented by a small process in P. grandis and the Minium Quarry Procamelus. In P. grandis and the Minium Quarry Procamelus, the unciform facet and shaft merge gradually rather than abruptly, as in Alforjas.

Magnum facet.- In Alforjas, the magnum and trapezoid facets form a posteriorly directed trapezoid. In P. grandis and the Minium Quarry Procamelus, these facets form a posteriorly directed triangle (Fig. 5). The inter-facet groove or notch flares posteriorly more so in Alforjas and P. grandis than in the Minium Quarry Procamelus.

Trapezoid facet.- The trapezoid facet in Alforjas is directed medio-laterally, rather than anteroposteriorly as in P. grandis and the Minium Quarry Procamelus. The ratios of anteroposterior to transverse lengths of this facet are approximately 1:2 in Alforjas, and 2:1 in both Procamelus.

Shaft.- The shaft of the metacarpus is square in

cross-section in Alforjas, whereas in P. grandis and the Minium Quarry Procamelus it is trapezoidal in cross-section. It is proportionately thicker in the Minium Quarry Procamelus than either Alforjas or P. grandis. The Minium Quarry Procamelus metacarpals III and IV are well fused as in Alforjas and more fused than in P. grandis.

Remarks.- P. grandis and the Minium Quarry Procamelus are similar in the shape and position of their articular facets, which differ from those of Alforjas. The Minium Quarry Procamelus and P. grandis are similar to Camelus in the shape and position of their articular facets, and the former is comparable to Camelus in overall size and increased thickness of the shaft. Alforjas shares most of these characters with Camelops, which suggests these characters may be consistant within the two tribes (Camelini and Lamini, respectively) of camelids.

Metatarsus

Plantar process.- In P. grandis and Alforjas, the plantar process extends further posteriorly than in the Minium Quarry Procamelus except in the specimen of Procamelus cf. P. grandis (UF 57486) figured by Webb and Perrigo (1984), in which the position of the plantar process is identical to that of the Minium Quarry Procamelus. Alforjas has a small subsidiary process on the anterior slope of the plantar process, which is

lacking in P. grandis and the Minium Quarry Procamelus. The Minium Quarry Procamelus differs from P. grandis in that the plantar process is proportionately smaller in P. grandis.

Ectomesocuneiform facet.- In Alforjas, this facet is narrower than in both samples of Procamelus but is proportionately larger in the Minium Quarry Procamelus than in P. grandis.

Entocuneiform facet.- In Alforjas, this facet is isolated from the medial plantar process. In the two species of Procamelus, this facet is joined to the medial plantar process. In P. grandis, it merges with it. This facet is proportionately larger in the Minium Quarry Procamelus than in Alforjas or P. grandis.

Cuboid facet.- In all three camels, the cuboid facet is similarly shaped and positioned, though narrower in Alforjas, and disproportionately larger in the Minium Quarry Procamelus.

Shaft.-The shaft of the metatarsus is square in cross-section in Alforjas and P. grandis, and trapezoidal and proportionately thicker in the Minium Quarry Procamelus. In the Minium Quarry Procamelus, metatarsals III and IV are fused as in Alforjas. Both taxa show more fusion than does P. grandis.

Remarks.- Metatarsals of Procamelus are distinct from those of Alforjas in the characters of the plantar

process, which are sufficient to distinguish the two genera in most cases. Alforjas metatarsals are most similar to those of Camelops, whereas Procamelus resembles Camelus, albeit only slightly. The Minium Quarry Procamelus is similar to ?Megatylopus cochrani (UNSM 89183) in the proportionately increased surface areas of the cuboid, ectomesocuneiform, and entocuneiform facets, and the reduction of the interfacet space, suggesting that these characters also may show consistancy at the tribe level.

Osteological contrasts between these genera occur irrespective of size, and are sufficiently distinct to be readily applied to unassigned material. Once able to distinguish between Alforjas and Procamelus, the biostratigraphic utility of these taxa equals that of other Neogene camelids (Breyer, 1983), and questionable assignments can be clarified. The osteological analysis of the Minium Quarry Procamelus suggests that it is a valid taxon related to other Procamelus.

BIOMETRIC ANALYSIS

Breyer (1983) summarized metapodial length and distal width measurements for the genera Aepycamelus, Hemiauchenia, Alforjas, Procamelus, Megatylopus, and Titanotylopus, which were the then known camel genera for the Barstovian through Blancan North American land mammal ages (see Harrison, 1985 for additions), and

included an Irvingtonian sample of Camelops for comparison. Bivariate plots of length vs. distal width and length vs. a ratio of length to distal width divide the genera into three morphotypes: attenuate, stocky, and intermediate, each with a separate "short"-and "long"-legged component (Table 2).

All of the generic fields are distinct except those for Alforjas and Procamelus, the two "short"-legged intermediate forms (Breyer, 1983). Dimensions of the Minium Quarry Procamelus plot outside the generic fields of both Alforjas and previously known Procamelus sp. (Figs. 6-9), overlapping only slightly with the latter in total metatarsal length vs. distal width (Fig. 6). I consider this result to be an extension of the Camelinae morphotype that consists of the "stocky" taxa Procamelus, Megatylopus, and Titanotylopus. Recent additions to the Camelinae (Harrison, 1985) are still poorly known, and unevaluated in this context. The differentiation of the Minium Quarry Procamelus is more apparent when its metapodial dimensions are plotted against those of other early Hemphillian (Fig. 10a) and late Hemphillian forms (Fig. 10b), which suggests that this taxon is distinct from other genera in both time periods. This analysis suggests that the Minium Quarry Procamelus represents a new species that may be closely related to Megatylopus.

Megatylopus cf. *M. gigas* Matthew and Cook, 1909

Figures 2e-f, 11

Materials.-- 7815, partial dentary and associated right dp3; 9008, partial left M1; 9338, partial left m3; 8410, left M3; 8978, distal end of tibia; 8106, distal trochlear surface of metapodial; 8211, distal end of metapodial; 8684, right astragalus; 8000, right cuboid; 8040, left calcaneum; 8041, right calcaneum; 8951, left navicular; 7843, first phalange.

Description.-- A very large camel, this taxon is distinguished from *Aepycamelus* in that it is more stout, and has a "w"-shaped suspensory ligament scar. It is distinguishable from the Minium Quarry *Procamelus* by its larger size. Positive assignment to a species awaits the recovery of a p3 to determine whether the roots are fused or unfused (Webb, 1965), although this character may be highly variable (Bennett, 1979; Leite, 1986). The LM1 (9008), LM3 (8410), and Lm3 (9338) are all moderately hypsodont, and lack any evidence of lama buttresses (Webb, 1965). However, the styles and ribs of the LM1 are well developed, which suggests the specimens can be referred to *M. gigas* rather than *M. matthewi* (Webb, 1965; Bennett, 1979; Leite, 1986). The Rdp3 (7815) is complete, well preserved, and in a moderate state of wear (Fig. 2e-f). The tooth is

simple, triangular, has a single fossetid, and is moderately hypsodont.

The first phalange (7843) is complete and well-preserved except for some chipping on the right side of the area to which the suspensory ligament attached (Fig. 11). The proximal articular surface is concave, with a pronounced ventral excavation. The roughened posterior surface for the insertion of the suspensory ligaments cover only the proximal third of the phalange and is "w" -shaped, resembling that of Camelus, Titanotylopus (Breyer, 1974), and the specimen of ?M. cochrani figured by Voorhies and Corner (1986). The distal articular surface advances equidistantly dorsally and ventrally. The distal trochlea is somewhat restricted dorsoventrally.

The left and right calcanea (8040, 8041) both measure 67 mm anteroposteriorly and 156 mm in length, and may represent the same individual. These calcanea are more slender, less robust, and longer than those of Alforjas or Camelops, and lack several Camelops-Alforjas synapomorphies (Webb, 1965; Harrison, 1979). The tuber calcis is capped by a smooth convex surface as in Camelops and Lama, but lacks the the curved transverse crest of the former, in which it closely resembles the condition in Camelus (Breyer, 1974). The cuboid facet is narrower than in Camelops.

The distal end of the metapodial (8211) includes both trochlear surfaces and approximately 20 cm of shaft. The distal width falls well within the range of measurements of Megatylopus reported by Breyer (1983).

Gen. et sp. indet.

Material.-- 7900, 7943, 8614, 3 partial proximal ends of first phalanges.

Description.-- The proximal articular surface is all that remains of these three first phalanges. The articular surface is slightly smaller than the maximum proximal width. As incomplete as these specimens are, it is difficult to infer much about their affinities except that the camel was of medium and slender build.

CONCLUSIONS

In addition to its biostratigraphic use, the biometric analysis of camel metapodials is a practical means of assigning Neogene camelids to the correct genera when cranial or dental materials are absent. When combined with the description of camelid metapodial osteology, biometric analysis becomes a valuable systematic tool, corroborating the validity of osteological differences. Its use can be expanded to other genera of camels, and similar applications should be attempted for other mammalian families.

The ability to differentiate between Alforjas and Procamelus in early Hemphillian faunas should allow a

better understanding of their individual biostratigraphic and paleobiogeographic ranges, as well as make their identification easier. The presence of a large Procamelus in the Early Hemphillian of north-central Kansas suggests that this taxon may have affinities to other large camelines such as Megatylopus, and a more prominent role in later Neogene faunas than has been previously suspected. Should more material of the Minium Quarry Procamelus be recovered, relationships within the late Neogene Camelinae may be clarified.

ACKNOWLEDGMENTS

I thank Pete and Doris Minium of Morland, Kansas, for their cooperation during the excavation of their property. I thank Charlotte Keith for bringing the site to the attention of M. E. Nelson, who then informed J. R. Thomasson and R. J. Zakrzewski of the site and its potential. I thank Frosty and Alice Paul of Morland, Kansas, for their support during the two field seasons of excavation, and the FHSU field crews for their help. I thank R. J. Zakrzewski and J. R. Thomasson for providing me with the opportunity to participate in the excavation of the quarry. I am especially grateful to R. J. Zakrzewski for his guidance and suggestions during the study. I thank M. E. Nelson and G. R. Corner for sharing their knowledge of camels. I thank R. J. Zakrzewski, R. H. Tedford, and M. R.

Voorhies for the opportunity to study specimens in their care. I thank R. M. Hunt and G. R. Corner for providing access to the University of Nebraska State Museum collections. R. J. Zakrzewski, J. R. Choate, M. E. Nelson, K. R. Neuhauser, and J. R. Thomasson critically read the manuscipt. The excavation of the Minium Quarry was supported by National Geographic Society Grants 3092-85 and 3315-86 to J. R. Thomasson.

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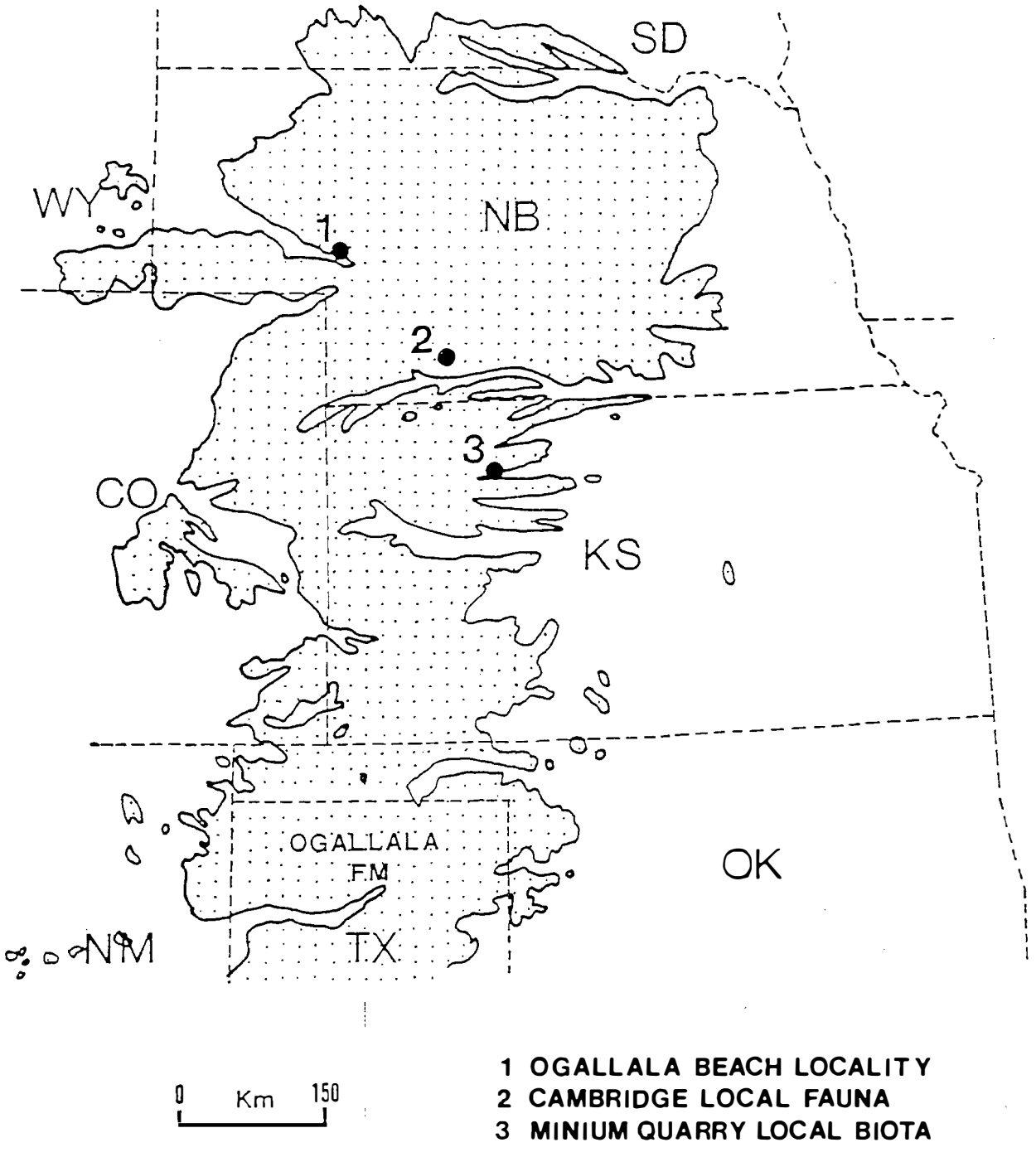
SD
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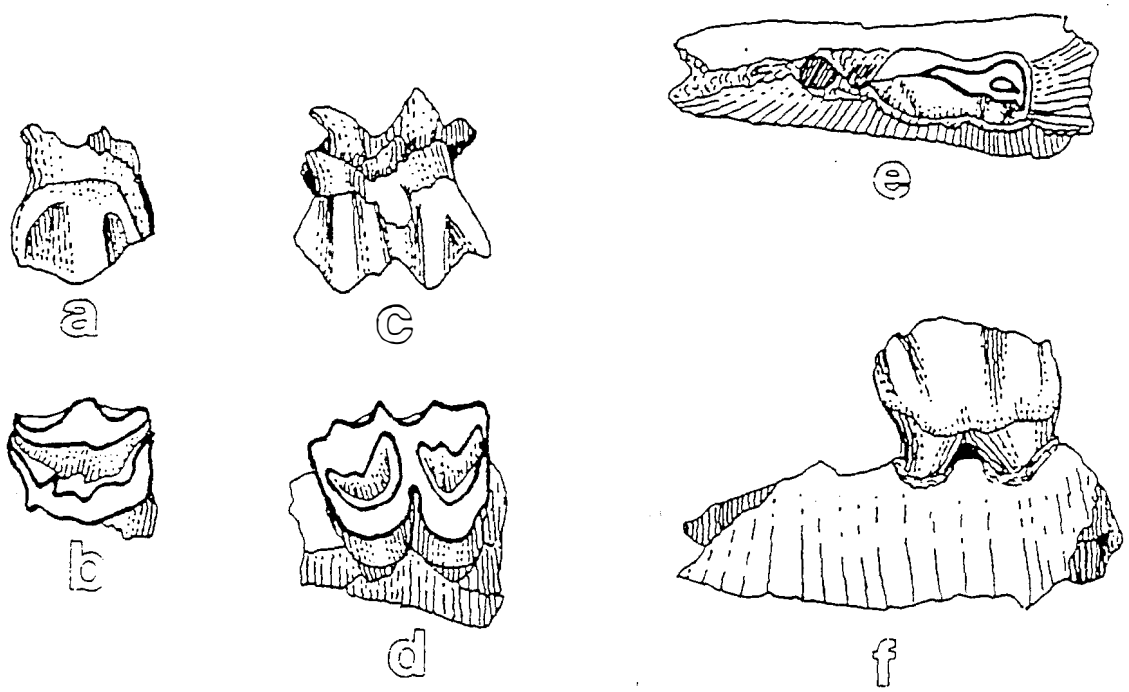
0 Km 150
1 OGALLALA BEACH LOCALITY
2 CAMBRIDGE LOCAL FAUNA
3 MINIUM QUARRY LOCAL BIOTA

Figure 1



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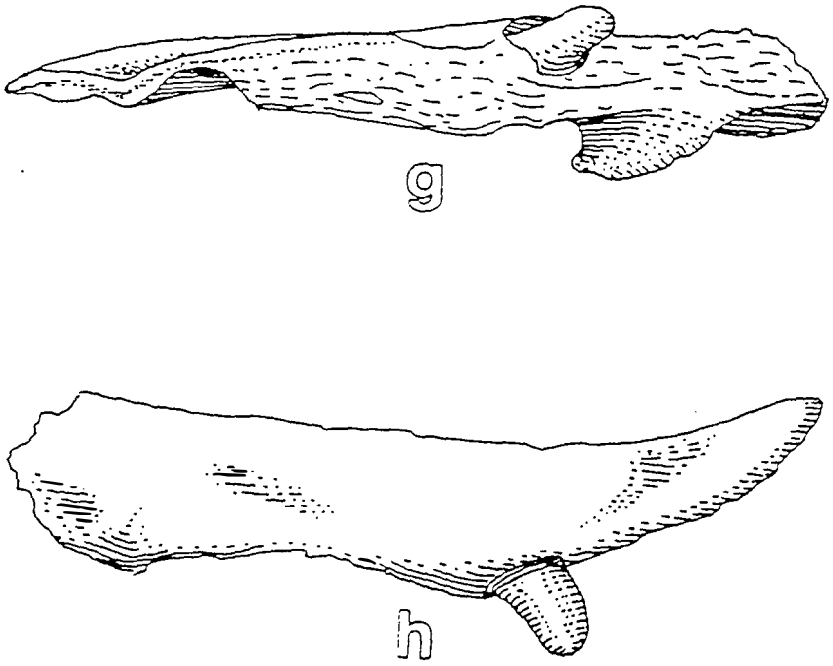


Figure 2

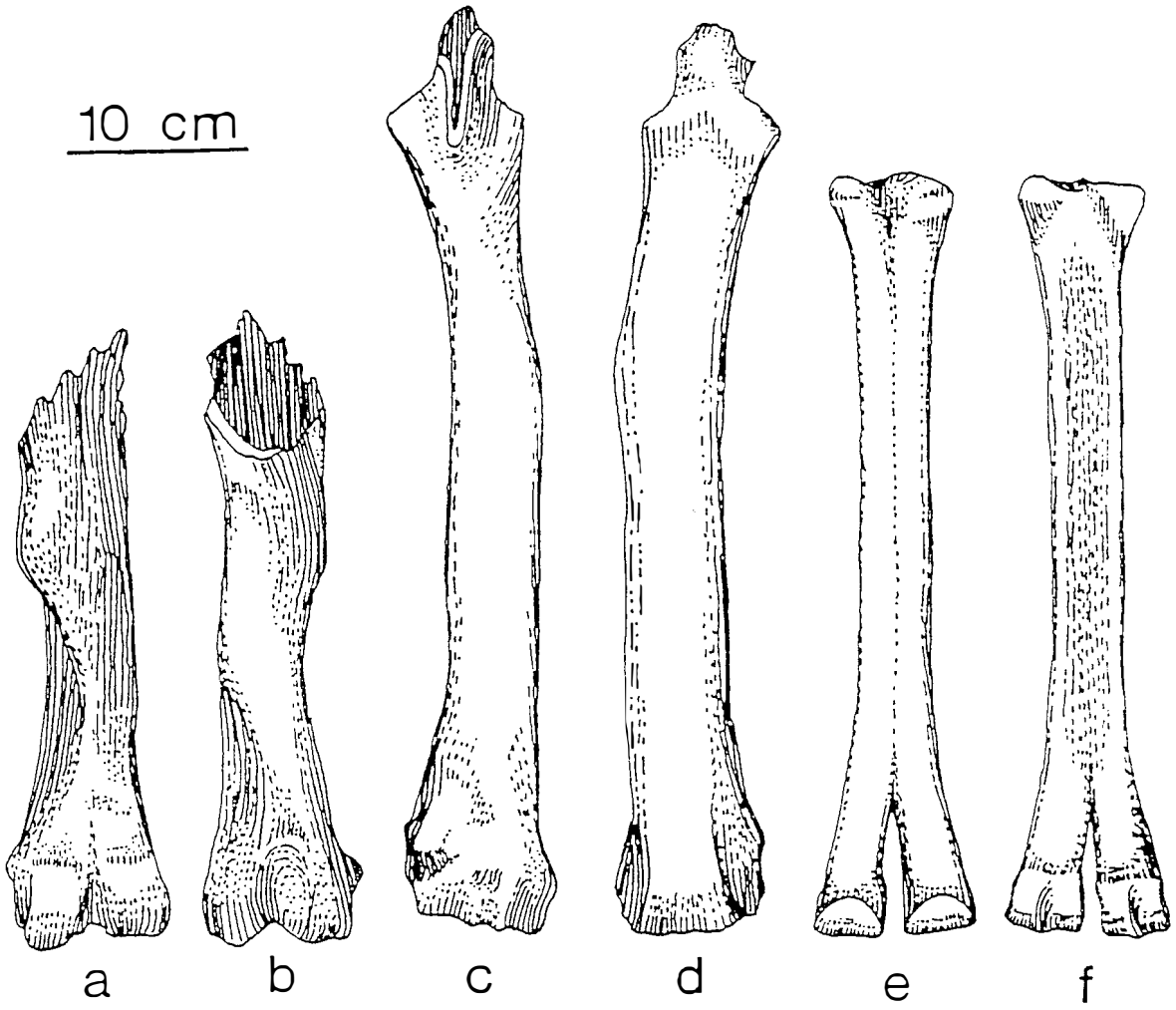
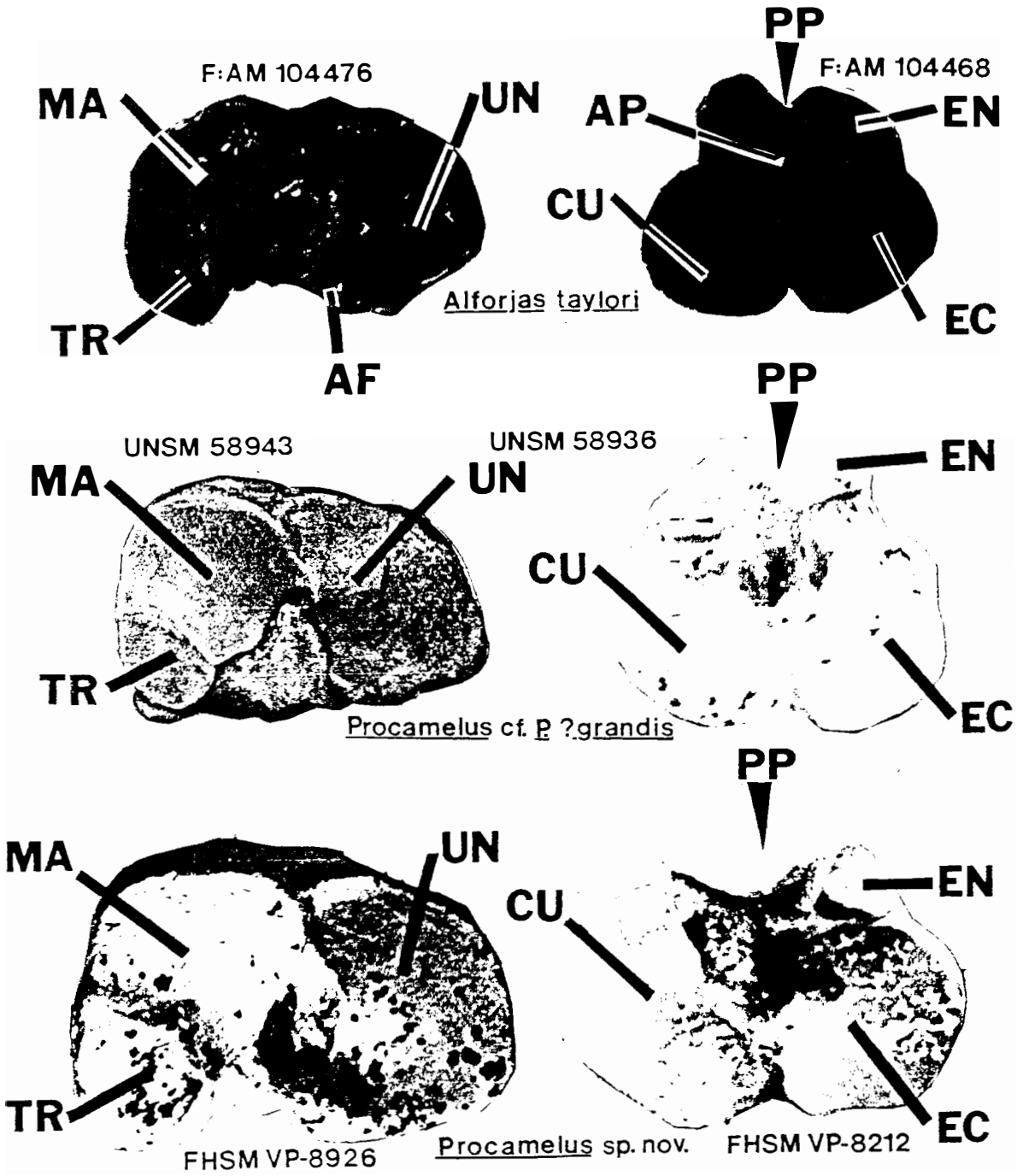
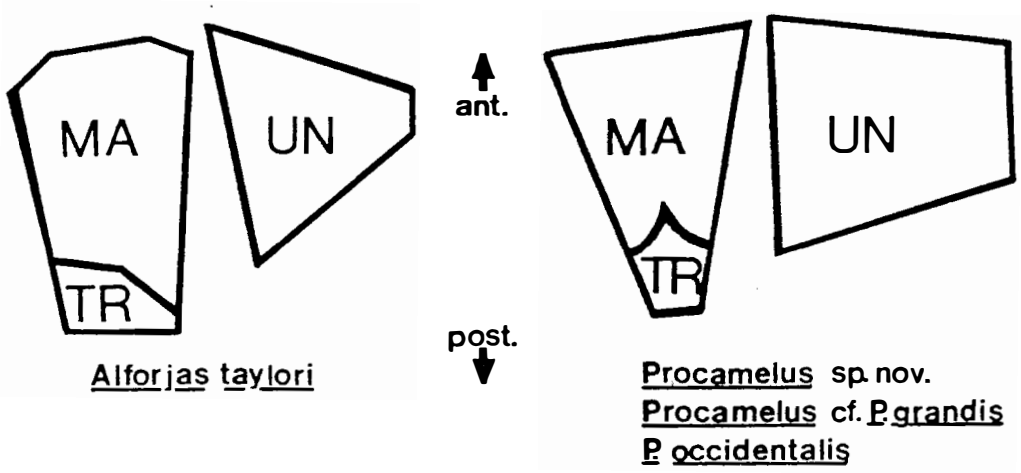


Figure 3



AF: ACCESSORY FACET
AP: ACCESS. PROCESS
CU: CUBOID FACET
EC: ECTOMESO. FACET
EN: ENTOCUN. FACET
MA: MAGNUM FACET
PP: PLANTAR PROCESS
TR: TRAPEZOID FACET
UN: UNCIFORM FACET

Figure 4



Alforjas taylori

Procamelus sp. nov.
Procamelus cf. P. grandis
P. occidentalis

Figure 5

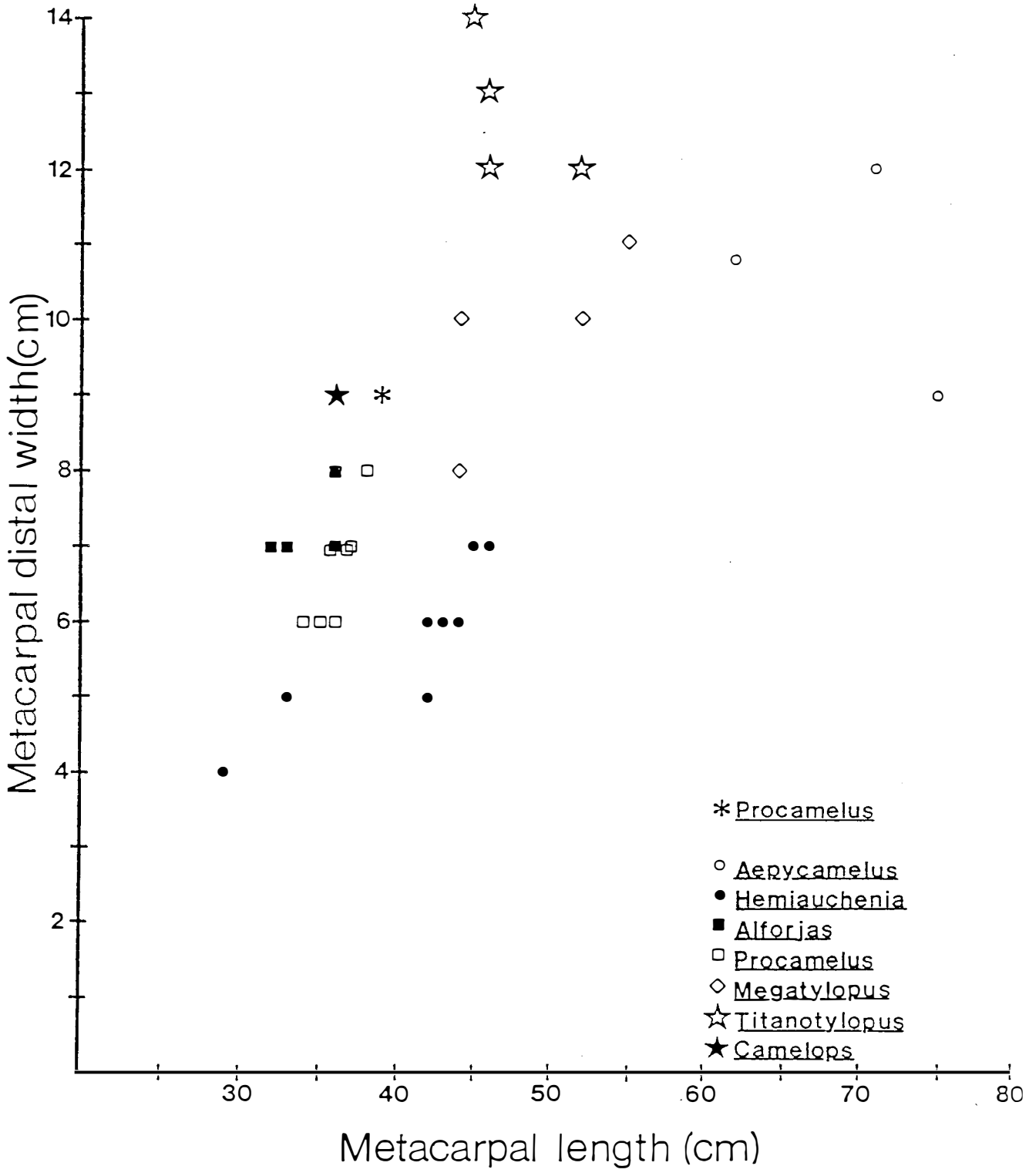

Metacarpal distal width(cm)
14
12
10
8
6
4
2
30
40
50
60
70
80
Metacarpal length (cm)
Procamelus
Aepycamelus
Hemiauchenia
Alforjas
Procamelus
Megatylopus
Titanotylopus
Camelops

Figure 6

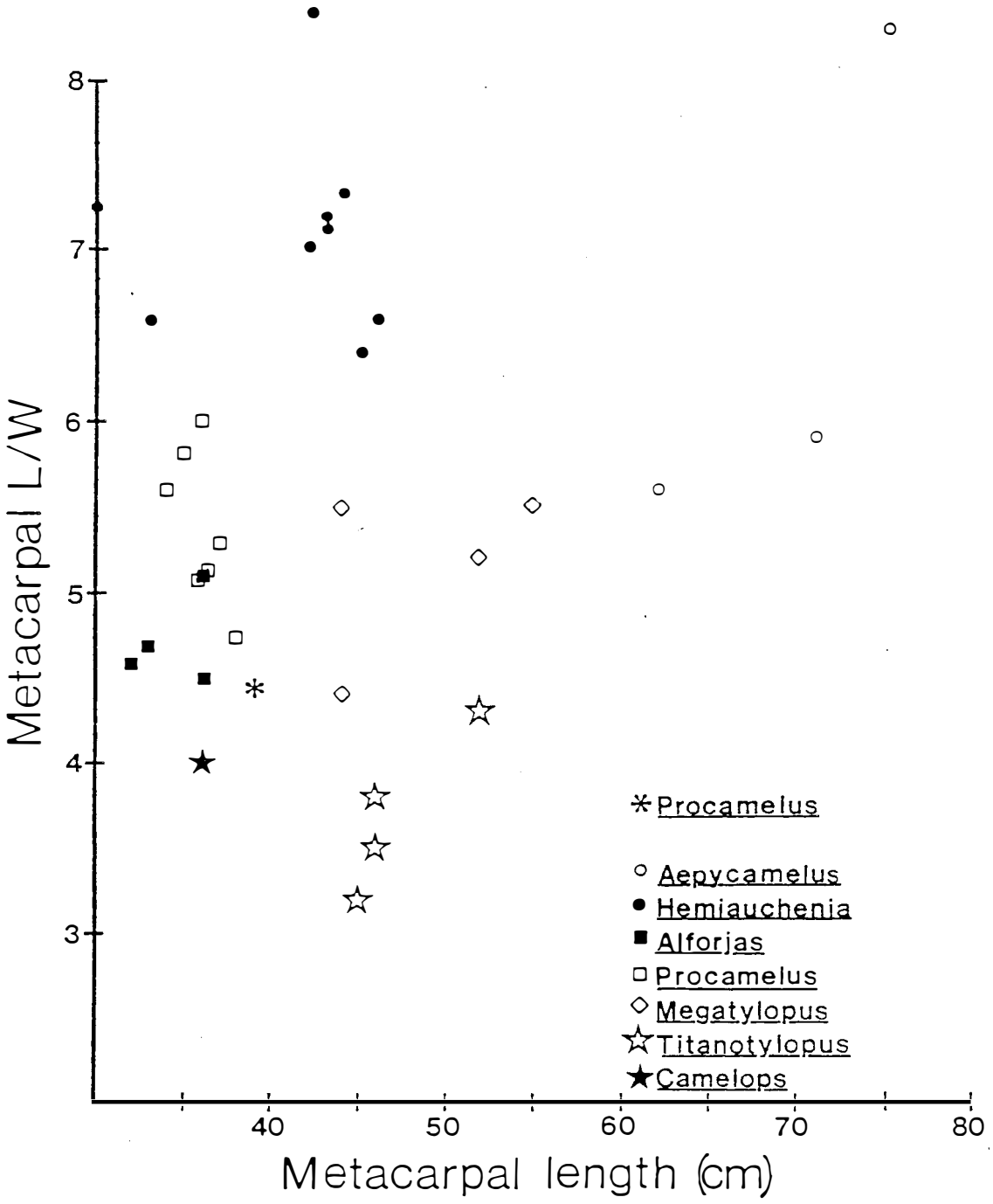

Metacarpal L/W
8
7
6
5
4
3
40
50
60
70
80
Metacarpal length (cm)
Procamelus
Aepycamelus
Hemiauchenia
Alforjas
Procamelus
Megatylopus
Titanotylopus
Camelops

Figure 7

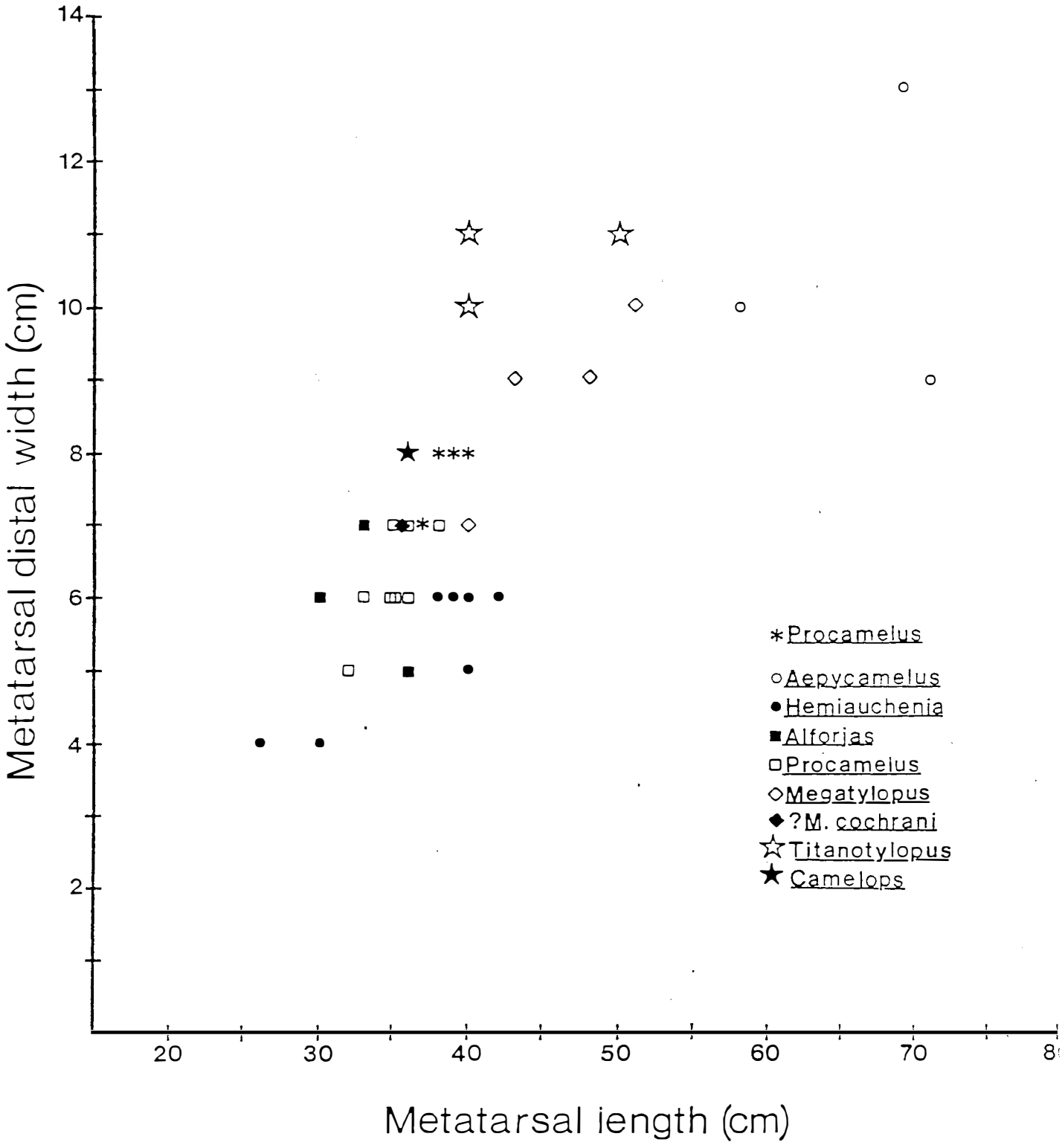

Metatarsal distal width (cm)
14
12
10
8
6
4
2
20
30
40
50
60
70
Metatarsal length (cm)
*Procamelus
○Aepycamelus
●Hemiauchenia
■Alforjas
□Procamelus
◇Megatylopus
◆?M. cochrani
☆Titanotylopus
★Camelops

Figure 8

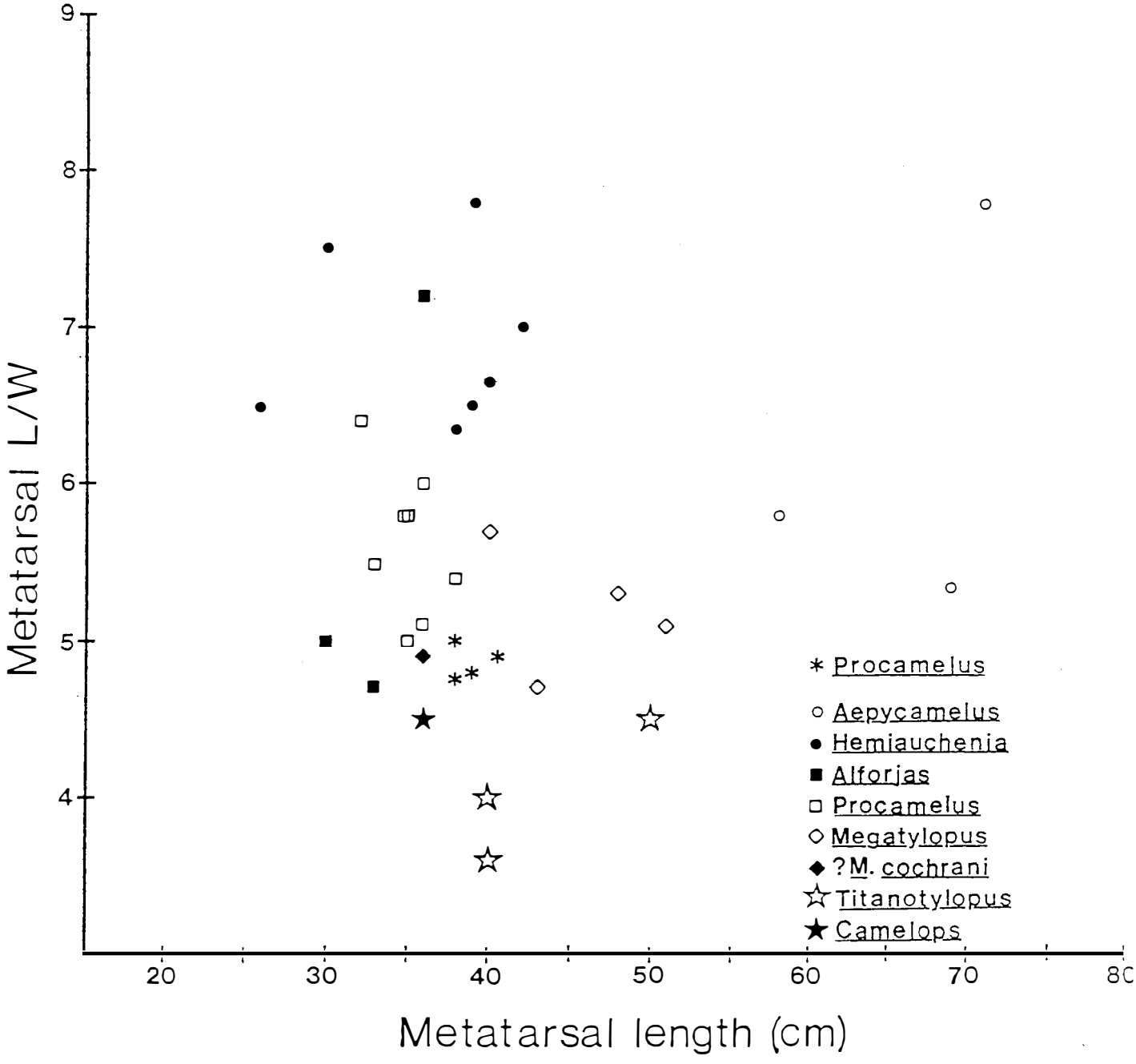

9
8
7
6
5
4
Metatarsal L/W
20
30
40
50
60
70
80
Metatarsal length (cm)
* Procamelus
○ Aepycamelus
● Hemiauchenia
■ Alforjas
□ Procamelus
◇ Megatylopus
◆ ?M. cochrani
☆ Titanotylopus
★ Camelops

Figure 9

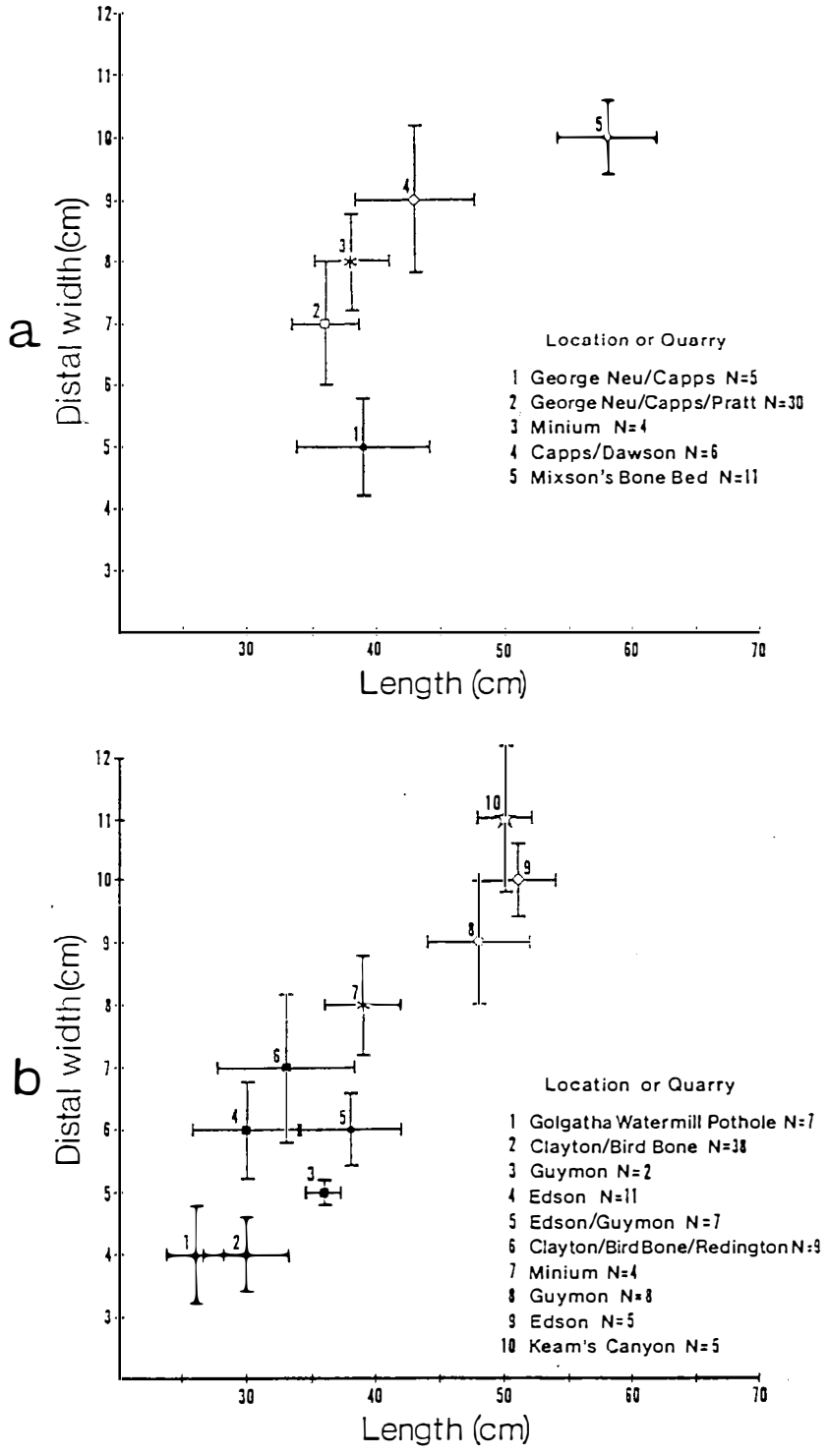

a
Distal width(cm)
Length (cm)
Location or Quarry
1 George Neu/Capps N=5
2 George Neu/Capps/Pratt N=30
3 Minium N=4
4 Capps/Dawson N=6
5 Mixson's Bone Bed N=11
b
Distal width(cm)
Length (cm)
Location or Quarry
1 Golgatha Watermill Pothole N=7
2 Clayton/Bird Bone N=38
3 Guymon N=2
4 Edson N=11
5 Edson/Guymon N=7
6 Clayton/Bird Bone/Redington N=9
7 Minium N=4
8 Guymon N=8
9 Edson N=5
10 Keam's Canyon N=5

Figure 10

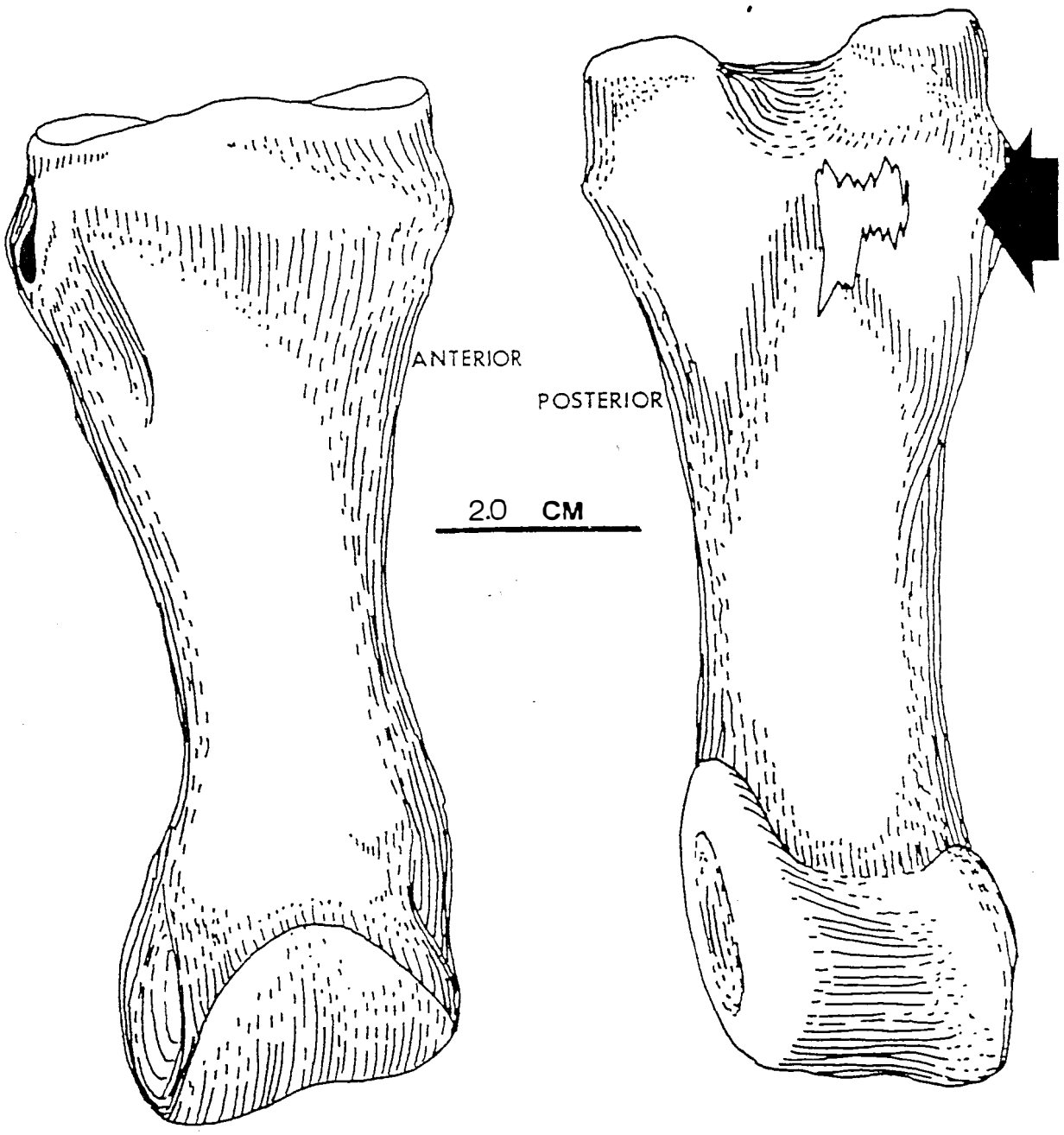


Figure 11

Table 1 - Measurements of metapodial dimensions of taxa represented in Text-figure 4.

	Alforjas taylori[1] (Harrison, 1979)			**Procamelus sp.nov.**			*Procamelus grandis*[3] (Gregory, 1949)		
	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD
Metacarpals									
length	10	313.4	17.8	1	385.0	---	3	381.0	9.6
prox. width	21	53.3	3.6	2	67.9	---	3	57.4	3.4
shaft width	2	30.2	---	1	41.6	---	2	33.3	---
dist. width	9	69.1	4.1	1	86.7	---	3	79.3	3.5
Metatarsals									
length	12	297.5	22.2	4	370.0	15.4	6	345.0	18.2
prox. width	15	47.9	3.6	6	63.5	3.1	6	47.9	2.9
shaft width	2	24.4	---	5	38.6	2.2	6	30.3	1.9
dist. width	12	63.9	3.7	4	79.6	4.0	4	61.3	6.9

1. from description of type material from Edson Quarry
2. includes specimens from Minium Quarry l.b., Cambridge l.f., and Ogallala Beach loc.
3. from description of type material from Big Spring Canyon

N = number of specimens; $\bar{X}$ = sample mean; SD = standard deviation

Table 2- Neogene camelid morphotypes, after Breyer (1983).

Genus	Age	Morphotype
Hemiauchenia	E. Clarendonian to Blancan	attenuate (short)
Aepycamelus	E. Clarendonian to E. Hemphillian	attenuate (long)
Alforjas	Late Hemphillian	intermediate (short)
Procamelus	E. Barstovian to E. Hemphillian	intermediate (short)
Megatylopus	L. Clarendonian to L. Hemphillian	intermediate (long)
Camelops	Irvingtonian	stocky (short)
Titanotylopus	L. Hemphillian to L. Blancan	stocky (long)

TAPHONOMIC EVIDENCE FOR THE PREDATION AND SCAVENGING OF *TELEOCERAS* (RHINOCEROTIDAE) FROM THE MINIUM QUARRY LOCAL BIOTA OF NORTH-CENTRAL KANSAS

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ABSTRACT

Fossil (non-dental) specimens of large herbivores (>100 kg) from the early Hemphillian (Late Miocene) Minium Quarry local biota were examined for taphonomic evidence of post-mortem influences on the bone deposit. The sample consists of genera representative of a savanna-like climate, and is dominated by the semi-aquatic rhinoceros *Teleoceras*. The weathering states of the untransported bone sample suggest that the bone deposit is an attritional accumulation that occurred in a swamp or marsh over a relatively long period of time (6-15 years minimum). Damage to bone material resulting from carnivore and scavenger activity is widespread throughout the sample, and suggests varying degrees of scavenging activity. The age profile of the *Teleoceras* population indicates highly selective mortality may be attributable to carnivory. The evidence for carnivore and scavenger activity suggests that *Osteoborus*, a morphologically, and possibly behaviorally hyaena-like

canid, preyed upon and scavenged Teleoceras, and may have been the primary bone accumulating agent at the site.

INTRODUCTION

Bone material, if not destroyed, often is subjected to subaerial exposure, post-mortem modification by other vertebrates, and other taphonomic processes before being buried and subsequently fossilized (Voorhies, 1969; Behrensmeyer, 1975; Hill, 1980). Once understood, the effects of these pre-burial processes on bone may provide a means of reconstructing many features of the local paleoenvironment. The effects of subaerial weathering on bone may be reflected in the nature of the enclosing sediments, and may support interpretations based on other taphonomic and sedimentologic phenomena. Pre-burial processes, such as the post-mortem modification of bone by predation and scavenging, can provide valuable clues to the paleoecology of organisms and habitats.

The effects of subaerial exposure on mammalian bone have been investigated in the recent East African savannah (Behrensmeyer, 1975, 1978; Hill, 1976, 1979, 1980; Behrensmeyer et al., 1979; Behrensmeyer and Dechant-Boaz, 1980), providing a model with which to evaluate paleoenvironments interpreted as savanna-like, such as the Miocene of North America (Shotwell, 1958; Webb, 1977). Studies of the post-mortem modification of vertebrate bone by the present-day biotic environment have focused primarily on the damage and disarticulation

caused by the predation and scavenging of large ungulates by carnivores, in various climates and habitats (Miller, 1969; Sutcliffe, 1970; Hill, 1976; Noe-Nygaard, 1977; Haynes, 1980, 1982, 1983). To date, these studies of recent pre-burial processes have been applied to fossil faunas of the North American Pleistocene (Haynes, 1980) and the Late Cenozoic of East Africa (Behrensmeyer, 1975; Noe-Nygaard, 1977).

Herein, I apply our knowledge of the effects of subaerial exposure in modern savannahs and the post-mortem modification of mammalian bone by predation and scavenging to the large ungulate community of the Minium Quarry local biota, a Miocene (early Hemphillian) savannah assemblage from the Ogallala Group of north-central Kansas (Thomasson et al., 1986; Thomasson and Zakrzewski, 1987; LaGarry, 1987, 1988). Evidence of weathering, predation, and scavenging are assessed to determine the habitat of accumulation, the time span over which accumulation may have occurred, the identity of the taxon responsible for the post-mortem modification of the bone sample, and the role of predation and scavenging behavior in contributing to the accumulation of the large ungulate material, of which the principle component is the semi-aquatic rhinoceros, Teleoceras. All vertebrate material from the Minium Quarry 1. b. is housed in the Fort Hays Sternberg Museum

Vertebrate Paleontology collections (FHSM VP-).

THE MINIUM QUARRY

The Minium Quarry is located 3.75 km northwest of Morland, Kansas (Fig.1) in the Ogallala Group, which is a complex and regionally varied system of fluvial sediments (Merriam, 1963) of Miocene age (Thomasson, 1979). The internal sedimentologic and stratigraphic relationships of the Ogallala Group have been worked and reworked several times (Frye et al., 1956; Frye and Leonard, 1959; Frye, 1971; Breyer, 1975; Skinner et al., 1977) with little lasting agreement about relationships (Thomasson, 1979; Diffendahl, 1980, 1982, 1984, 1985; Diffendahl et al., 1985). The diachronous nature of the Ogallala Group has necessitated the use of biostratigraphic zones of plants (Thomasson, 1979) and mammals (Tedford et al., 1987) for correlation of biotas and sediments. The abundant biota of the Minium Quarry is considered to be of Early Hemphillian age (LaGarry, 1987; Thomasson and Zakrzewski, 1987).

Detailed sedimentologic and stratigraphic analyses of the enclosing sediments at the Minium Quarry are in progress but incomplete (J. M. Churchill, 1987, pers. comm.). However, they are primarily of fluvial origin (Thomasson et al., 1986). The relationships of the enclosing sediments at the Minium Quarry are complex, but bone material is concentrated primarily in two units

(J. R. Thomasson, 1988, pers. comm.) and is present in several others (Fig. 2). Throughout the bone-bearing interval (approx. 1.5 m) are several lithologic breaks, and the abundance of weathered bone recovered suggests that some of these may represent surfaces of subaerial exposure and accumulation. Because the lithologic breaks may reflect prolonged (in ecologic time) periods of subaerial exposure and accumulation where pre-burial processes could be recorded on exposed bone, an analyses of weathering damage should provide a means of reconstructing those processes.

ANALYSIS OF WEATHERING

In order to evaluate the weathering of mammalian bone, the assessed sample must be composed of elements that: 1) have been sub-aerially exposed for sufficient ecologic time to record the effects of weathering processes; 2) have surface areas large enough to record weathering process characteristics; 3) survive weathering processes intact; 4) survive fossilization processes intact; and 5) represent the sample as a whole (Behrensmeyer, 1978). Criterion (1) is dependant on numerous paleoenvironmental factors, as well as serendipity, and each bone sample must be evaluated on its own merit. Criteria (2) through (5) can be satisfied by examining material assigned to the larger and more common components of the mammalian bone sample.

Behrensmeyer (1978) categorized the bones of known-age mammal carcasses observed in the East African savannah into weathering stages based on progressively increasing amounts of weathering damage (Table 1). The savannah sample is based on taxa >5 kg live body weight, and includes only non-dental elements. Dental material was excluded because no clear pattern of weathering was observed. Carcasses >5 kg body weight survived savannah weathering processes intact (criterion (2)), though many of the smaller bones may not survive fossilization processes intact (criterion (4)) (Hill, 1980). Therefore, samples of fossil faunas evaluated for the effects of weathering should contain material from larger taxa, the size of which will depend upon the degree of preservation within the sample.

The mammalian assemblage of the Minium Quarry is dominated by large ungulates >100 kg body weight (satisfying criteria (2) through (5) above), primarily the semi-aquatic (Kurten, 1972) rhinoceros Teleoceros (Table 2). In order to distinguish and isolate material representing localized conditions, only material not transported by fluvial processes was assessed for weathering damage (Fig. 3). Material interpreted to be untransported shows no evidence of wear produced by fluvial conditions, such as abrasion by fluvially- or eolian-transported sediment. It was observed that

fluvial transport partially destroys weathering characeristics, further requiring the separation of possibly transported material. The removal of transported material reduces the potential bias of influx of material from other habitats. Also, teeth have been excluded from the sample because their response to weathering processes is unclear (Behrensmeyer, 1978).

The untransported portion of the ungulate post-cranial material from the Minium Quarry is interpreted as having accumulated in a savanna-like environment (Thomasson and Zakrzewski, 1987; LaGarry, 1988). This material displays many of the weathering characters (Fig. 4) described by Behrensmeyer (1978) for the recent savannah assemblage (Table 1). In particular, LaGarry (1988) found that, when assigned to weathering stages, the Minium Quarry large ungulate sample (Fig. 5) closely resembles that which accumulated in a swamp on a recent savannah (Fig. 6). A Kolmogorov-Smirnov comparison yields a z value of 0.212, demonstrating an extremely close correlation between the two samples. This relationship supports the interpretations of Thomasson et al. (1986) and Thomasson and Zakrzewski (1987), who suggested the presence of standing water based on the abundance of aquatic plant taxa such as: sedges (3 species); Carex, Cyperocarpus, and Eleofimbris

(Cyperaceae); Limnocarpus (Potamogetonaceae); and Chenopodium (Chenopodiaceae). Behrensmeyer (1978) pointed out that the dense woodland savanna habitat produces a weathering profile similar to that of the savannah swamp (Fig. 6). However, comparison of the Minium Quarry sample to that of the savannah woodland yields a z value of 0.707, indicating less similarity between the two samples. Characteristic of both savannah habitats is relatively high humidity and shade, which Behrensmeyer (1978) suggests may be the factors controlling the rates of bone weathering and decay. If similar rates of weathering can be assumed, the presence of stage 4 and 5 material suggests that some of the bone recovered from the Minium Quarry was subaerially exposed for a minimum of 6 years (LaGarry, 1988).

Examined individually, the three families of large ungulates represented in the sample show markedly different weathering profiles (Fig. 7B-D) and, therefore, it is reasonable to assume different processes affected each taxon. The even distribution of weathering stages exhibited by the camel bones (Fig. 7C) was not observed in the recent savannah assemblage (Fig. 7A), and no explanatory model exists. This even distribution may simply be an artifact of small sample size (5 individuals), or a periodic mortality event that

contributed carcasses at intervals that matched weathering rates. The abundance of weathering stage 1 material (6 individuals) exhibited by the horses (Fig. 7D) may reflect a mass mortality event, such as a drowning, that produced a large number of carcasses of the same age (see Voorhies, 1969 for an example; Behrensmeyer, 1978). Neither the camel nor the horse weathering profiles resemble that of the attritional accumulation observed in the recent savannah (Fig. 7A). However, the weathering distribution of the dominant Teleoceras population (Fig. 7B) does ($z = 0.424$). This suggests that the rhinoceros sample is attritional and locally accumulated, whereas the camel and horse material may have accumulated by different processes. The rhinoceros population can therefore be further assessed as to local agents of post-mortem bone modification.

ANALYSIS OF BONE MODIFICATION

Pre-burial modification of bone material by non-weathering processes is common in the Minium Quarry large ungulate sample, and is present in several forms (Table 3). The most common form of post-mortem damage is that caused by the secretion of acid by plant roots (Fig. 8a). Behrensmeyer (1978) noted that damage of this type is common on carcasses exposed subaerially on the recent savannah, and its dominance is primarily a

factor of prevailing microhabitat conditions such as shade and moisture. To what degree these factors control damage of this type is presently unknown. The other types of damage present in the Minium Quarry sample include: gouging and pitting of compact bone; sets of parallel and non-parallel shallow scratches; spiral fracturing; nicks and scrapes attributable to trampling; and burrowing in bone by insect larvae. Post-mortem damage is most common in the largest segment of the ungulate sample, the Teleoceras population. This consideration, as well as the probability that the Teleoceras population accumulated locally by attritional processes, suggests that analysis of damage present in the Teleoceras segment of the sample may indicate conditions prevalent at the site of accumulation. Analyses of post-mortem damage induced by carnivory may indicate the identity and certain aspects of the behavior of the major predator or scavenger at the site of accumulation. The following discussion will attempt to resolve the identity of the bone modifying taxa or taxon, and determine to what extent the behavior of the carnivore contributed to the accumulation of the Minium Quarry large ungulate sample.

Two types of damage cannot be attributed to carnivory and scavenging. The first type is represented by two specimens that exhibit irregular, shallow grooves

in cancellous bone (Fig. 8b) similar to those produced by the larval form of the moth Tinea (Behrensmeyer, 1978). These grooves suggest that insects were an active part of pre-burial decay processes at the Minium Quarry and add a new organism to the faunal list. Also present is evidence of trampling. This damage is manifested as small, crescent-shaped sets of parallel scratches. Thomasson et al. (1986) attributed some sedimentary structures present at the Minium Quarry to trampling. Also present were several bones oriented in nearly vertical positions within the substrate. This suggests a soft substrate, such as would be encountered near standing or semi-permanent water. Clear evidence of trampling from bone damage is minimal, however.

Damage attributable to carnivores or scavengers is the most prevalent form of bone modification, and varies in form. Two forms, scratching and spiral fracturing, are difficult to assess for several reasons. Spiral fracturing results when opposing torques are applied to opposite ends of a bone (Fig. 9a). This type of fracture is the product of, and can be attributed to, many species of bone-utilizing scavengers and predators, including man (Sutcliffe, 1970; Hill, 1976; Noe-Nygaard, 1977; Haynes, 1980, 1983). As such, a particular taxon cannot be cited as the cause until these processes are

better understood. This is best illustrated by the frequent assignment of spirally fractured bone caches in East Africa to Pliocene and Pleistocene hominids, which were later found to have been accumulated by hyaenas (Hill, 1976). Scratching of bone by carnivores (Fig. 9b) is easily distinguishable from that caused by sedimentary processes (Sutcliffe, 1970; Haynes, 1980, 1983), but is also nondiagnostic, as this damage is known to be associated with wolves (Canis lupus), lions (Panthera leo), and hyaenas (Crocuta crocuta), and is frequenly the result of the manipulation of the bone during feeding (Haynes, 1980, 1983). The difficulty of assigning this damage to a particular taxon, and the difficulty of assigning a definite cause to this damage, precludes its use in this analysis.

Gouging and pitting of cancellous bone is the most common form of carnivore damage observed in the Teleoceras population of the Minium Quarry 1.b. and is usually associated with missing spalls of bone, exposed cancellous bone, and ground and bitten off ends of limb bones and epiphyses (Fig. 9c-e). This type of damage can be readily assessed, as many comparative models exist, based on the activities of extant carnivores (Miller, 1969; Sutcliffe, 1970; Hill, 1976, 1980; Haynes, 1980, 1982, 1983). Well-defined pits and gouges frequently preserve the contours of the damage-

inflicting teeth, and it is possible to evaluate these impressions by direct comparison with fossil carnivore dentitions. Many sets of pits replicate partial tooth rows, as well as the character of occluding teeth. From these pits and punctures it is evident that the bone modifier possessed a large, blunt carnassial pair with P4 and m1 averaging greater than 19 x 13 mm, a short, wide palate, and large, low-crowned teeth. Comparisons of tooth marks with dentitions of carnivores reported from the Minium Quarry (Thomasson et al., 1986; LaGarry, 1988) -- Nimravides, Osteoborus, and Vulpes -- suggests a close match with dentitions of Osteoborus.

Extant carnivore bone utilization behaviors vary, and it is also possible to determine the source of carnivore damage by comparison of utilization behaviors (Miller, 1969; Sutcliffe, 1970; Hill, 1976; Haynes, 1980, 1982, 1983). Mammalian bone utilized by extant hyaenas (Sutcliffe, 1970) exhibits damage very similar to that observed in the Minium Quarry Teleoceras sample. Comparison of the style of modification in the Minium Quarry Teleoceras sample with behaviors characteristic of several recent carnivores (Table 4) also suggests a hyaena-like style of bone modification, which has been attributed to osteoborine dogs (Dalquest, 1969). This also suggests that Osteoborus was responsible for the post-mortem bone damage attributable to carnivores.

Evidence from the Minium Quarry suggesting that Osteoborus was the primary bone modifier of the Teleoceras sample supports the long-standing supposition that Osteborus was a scavenger that utilized bone as a dietary resource (Matthew, 1930; Dalquest, 1969). Evidence supporting this taxon's appellation of "bone-crushing dog" includes its possession of heavy dentition and short jaws, and the presence of partly digested bone shards in its feces (Dalquest, 1969). These characters have been observed in Crocuta crocuta, the spotted hyaena (Sutcliffe, 1970; Behrensmeyer, 1978), which is a common component of the recent savannah carnivore fauna (Kingdon, 1977). The spotted hyaena is both a predator and a scavenger, having been observed actively hunting juvenile hippopotami (Kingdon, 1977), wildebeest, and zebra (Sutcliffe, 1970). However, Osteoborus has been considered as primarily a scavenger (Dalquest, 1969). This supposition has been based, in part, on its inferred relationships with other extinct carnivores. Extant hyaenas (Crocuta) are known to frequently scavenge carcasses abandoned by lions (Panthera), consuming most of what other carnivores reject, such as bone (Sutcliffe, 1970; Kingdon, 1977). Matthew (1930) suggested that Osteoborus maintained a similar relationship with sabre-toothed cats. The observation of extant hyena packs preying on hippopotami suggests

that Osteoborus, a hyaena equivalent, may have formed packs (Dalquest, 1969) and preyed upon Teleoceras, a hippopotamoid rhinoceros.

Studies of bone modification by carnivores (Miller, 1969; Sutcliffe, 1970; Haynes, 1980, 1982, 1983) do not distinguish between predation and scavenging. Sinclair (1974b) and Kingdon (1977) stated that in attritional carcass assemblages, the results of predation and scavenging are inseparable. A sample resulting exclusively from scavenging should contain material representing the available carcass supply (Noe-Nygaard, 1977; Haynes, 1982). The types and numbers of carcasses should indicate the dominant causes of mortality. Attritional mortality due to disease, starvation, and old age produces a sample that contains progressively fewer numbers of older individuals. Episodic events that can kill several individuals produces a sample that reflects the distribution of numbers and ages of individuals in the living population (Voorhies, 1969; Klein and Cruz-Uribe, 1984; Korth and Evander, 1986). Indiscriminate scavenging should reflect whichever of these processes provided the greatest percentage of the carcass supply. Predation, however, draws from the available standing crop, and favors particular age classes (Sutcliffe, 1970).

Analysis of the population dynamics and mortality profile of the Minium Quarry Teleoceras population, although possibly unable to differentiate the two behaviors, may indicate the degree to which carnivore behavior contributed to the bone deposit. The dentition of the Minium Quarry Teleoceras, although not useful in analyses of bone weathering and modification processes, provides a means of reconstructing the population structure of the sample.

Many extant and fossil species of migratory ungulates that seasonally occupy mesic habitats, give birth once yearly, undergo attritional mortality, and leave carcasses that vary in age by one year intervals (Caughly, 1966; Laws, 1968; Spinage, 1972a, 1972b; Leuthold and Leuthold, 1975; Hulbert, 1982; Miller and Zammutu, 1983). This step-wise distribution of ages allows accurate reconstruction of population age profiles by the use of Spinage's (1972a) formula:

$$Y = Yo\ [1 - (T/N)^{1/2}] \qquad [1]$$

where Y is the crown height, Yo is the unworn crown height, T is the age is the age at crown height Y, and N is the age at which Y becomes zero. This formula assumes a variable rate of wear, such that unworn teeth wear faster than worn teeth, and that the maximum age of

an individual is the age when the permanent cheek teeth are worn away (Spinage, 1972a). These assumptions have been supported by numerous observations (Klein and Cruz-Uribe, 1984).

Whether or not Teleoceras migrated and gave birth seasonally is unknown. However, Teleoceras may have formed herds (Voorhies, 1978), a behavioral pattern that is common to migratory species (Leuthold and Leuthold, 1975). Other large non-migratory species, such as the hippopotamus (Hippopotamus amphibius), also have birth patterns that permit teeth to be used to construct age profiles (Laws, 1968; Sayer and Rakha, 1974). Teleoceras is extremely similar to the extant hippopotamus in size, morphology (Osborn, 1898; Matthew, 1931, 1932; Voorhies, 1979; Voorhies and Thomasson, 1979), and habitat (Voorhies, 1979; Voorhies and Thomasson, 1979). If it can be assumed that body size and habitat controlled age at sexual maturity and rates of reproduction in extinct ungulates, as it does in extant ungulates (Leuthold and Leuthold, 1975; Wooten, 1987), it may be reasonable to assume that criteria applicable to the hippopotamus may also be applied to Teleoceras. In the following analysis of the Teleoceras dentition, the potential longevity of Teleoceras is assumed to approximate that of Hippopotamus, which averages 45 years in the wild (Laws, 1968). Other means

of determining this information, such as the sectioning of teeth, have not been attempted for Teleoceras.

Measurements of the lengths and breadths of alveoli in Teleoceras dentitions (Table 5) provide criteria for assigning positions to isolated teeth, and measurements of crown heights determine the approximate state of wear. The teeth chosen for analysis were the dp4 and m1 for reasons detailed by Van Valen (1964). The ages at which the Teleoceras dp4 is lost and m1 erupts are also assumed to approximate those of Hippopotamus, and are 7.5 and 5.0 years respectively (Laws, 1968; Sayer and Rakha, 1974). Unworn maximum crown heights of the Minium Quarry Teleoceras dp4 and m1 are 48 mm and 84 mm, respectively. The Teleoceras life table is divided into tenths of the total longevity for ease of computer analysis (see Klein and Cruz-Uribe, 1984). The results of the analysis (Table 6) show that the Teleoceras population is heavily biased towards very young and very old individuals, with no prime adults in the sample.

The mortality profile of the Teleocera population does not resemble either the catastrophic or the attritional accumulations discussed by Voorhies (1969) and Korth and Evander (1986). Though demonstrated to be an attritional assemblage on the basis of post-cranial material, the Teleoceras dentition sample appears highly selected, being biased towards specific age groups.

Sinclair (1974b) stated that in East African water buffalo, the effects of mortality caused by predation in attritional population profiles are absorbed by mortality caused by disease and starvation. This characteristic suggests that in most attritional assemblages, the effects of predation are present but unobserved. Prey selection by large carnivores, especially hyaenas, favors the very young, very old, and diseased (Sutcliffe, 1970; Sinclair, 1974a, 1974b; Kingdon, 1977; Haynes, 1982). Very young and very old animals often are the most susceptible to disease (Caughly, 1966; Sinclair, 1974a, 1974b), increasing the number of young and old individuals in a carnivore-induced mortality profile. Therefore, predation may bias a mortality profile towards young and old individuals, as seen in the Minium Quarry Teleoceras sample.

Extant scavengers, such as the hyaena, continue to use bone as a dietary resource long after the bone has been denuded of consumable flesh, often stockpiling the bone around their lair or den (Sutcliffe, 1970; Behrensmeyer, 1975; Hill, 1976; Behrensmeyer and Dechant-Boaz, 1980; Klein and Cruz-Uribe, 1984). The bone material in scavenger stockpiles, or caches, is subaeriallly exposed and subject to weathering processes, which is also true of non-cached, scavenged

bone (Behrensmeyer, 1978). The degree to which a bone deposit was scavenged can be determined by comparing the amount of damaged bone within a particular weathering stage (Behrensmeyer, 1978) relative to the total number of bones within that weathering stage. The Minium Quarry Teleoceras assemblage shows an increase in the relative amount of carnivore-induced bone damage as the amount of weathering damage increases (Fig. 10a). This correlation indicates that the Teleoceras bones continued to be gnawed for as long as 6 to years (stages 4 and 5) after being denuded of flesh; providing clear evidence that the bone sample was extensively scavenged. The amount of spiral fracturing and scratching also increases with weathering, suggesting that these types of damage were produced by related sources. The bimodal distibution of ages in the Teleoceras mortality profile corresponds with age-specific skeletal part representation (Fig. 11), and variations in carnivore-induced damage and scavenging. The ends of limb bones of very young individuals that lack epiphyses are often gnawed to a considerable degree, and exhibit more intensive damage overall. When compared to the scavenging of adult material (Fig. 10b), juvenile Teleoceras bone is consumed at a faster rate, surviving only to weathering stage 3. This reflects both the smaller size and the thinner compact bone of the

juvenile Teleoceras bone, and may suggest that this material was consumed preferentialy over adult bone.

WAS OSTEOBORUS A COLLECTOR OF BONE ?

The analysis of the Minium Quarry Teleoceras population suggests that the Teleoceras mortality was the result of predation, yet the possibility remains that Osteoborus scavenged carcasses killed by other carnivores that infrequently leave discernable marks on bone, such as felids (Haynes, 1983). Extant felids such as Panthera leo, as well as the hyena, Crocuta, typically hunt in the open savannah away from standing water (Sutcliffe, 1970; Kingdon, 1977). If the Teleoceras population did in fact accumulate in a moist habitat, it is reasonable to suspect that either the extinct taxa behaved in a different manner than their extant analogs, or that other agents contributed to the accumulation of material at the burial site. The hyaena is a well-known accumulator of bone, and will frequently carry carcass material considerable distances to its lair/bone cache (Sutcliffe, 1970; Behrensmeyer, 1975, 1978; Hill, 1976; Klein and Cruz-Uribe, 1984). Hyaena bone caches often contain several thousand identifiable skeletal elements (Klein and Cruz-Uribe, 1984). The excavated portion of the Minium Quarry bone has an area of less than 75 sq. meters, averaging 0.33 Teleoceras carcasses/sq. meter. Attritional mortality

in the East African savannah resulting from predation, starvation, and disease produces a lower bone density of only 0.0026 carcasses/sq. meter (Behrensmeyer, 1978). The high concentration of bone at the Minium Quarry may be the result of an agent of accumulation.

Statistical comparison (Kolmogorov-Smirnov Z) of skeletal parts represented at the Minium Quarry (Figs. 3, 11) and in extant hyaena caches reported by Klein and Cruz-Uribe (1984), suggest different modes of accumulation were responsible for the two deposits ($z = 3.10$). There are several major differences between the Minium Quarry assemblage and accumulations resulting from hyaena scavenging. The Minium Quarry assemblage has a lower percentage of carnivore material (< 5%) than a typical hyena cache (>20%). However, Klein and Cruz-Uribe (1984) noted that caches made by the spotted hyaena (Crocuta) contain less carnivore bone than those of the brown hyaena (Hyaena). The Minium Quarry assemblage is characterised by an increase in cranial material as ungulate size increases. The opposite is true of hyaena accumulations (Klein and Cruz-Uribe, 1984). Age profiles of hyaena accumulations tend to be attritional, rather than highly selected as is the Minium Quarry accumulation. Also, small, hard bones (carpals, tarsals) tend to be rare in hyena accumulations (they get eaten), but are a major

component of the Minium Quarry assemblage.

Thus, there is little similarity between The Minium Quarry bone assemblage and that typically produced by extant hyaenas. This does not mean that accumulatory behavior was not present in osteoborine dogs, but that if such behaviors existed it cannot be determined from the Minium Quarry sample, or that it was different from that of extant hyaenas and alternate models for comparison must be found.

CONCLUSIONS

This study supports Behrensmeyer's (1978) suggestion that weathering damage analysis techniques might be applicable to other fossil and extant bone deposits. Her method of analysis provides a means to determine many conditions of the paleoenvironment necessary to obtain an accurate estimate of paleoecologic conditions, and its use has yet to be fully explored in fossil faunas. Conditions such as vegetative cover, habitat, and climate can be reasonably concluded from weathering damage, with the potential for increased accuracy as the effects of weathering processes on bone become better understood. Although the Minium Quarry Teleoceras sample appears to be the result of predation, was extensively scavenged by Osteoborus, and represents a more dense accumulation than would be expected from such activity, clear

correlations between osteborine and hyaena collecting behaviors cannot yet be drawn. However, this study does show that the use of carnivore damage to reconstruct predator/prey relationships and the effects of scavenging is another useful tool that can reasonably be applied to fossil faunas. However, it will require additional studies to determine the degree of behavioral analogy between extant and fossil carnivora.

ACKNOWLEDGMENTS

I thank R. J. Zakrzewski for his guidance and suggestions during the study, and for permission to study specimens in his care. I thank J. M. Churchill, D. N. Wilcots, and R. S. Vandenberg for their helpful comments and discussions. I thank J. R. Thomasson, Director of the Minium Quarry excavations, for access to the Minium Quarry. R. J. Zakrzewski, J. R. Choate, M. E. Nelson, K. R. Neuhauser, and J. R. Thomasson critically read the manuscript. The excavation of the Minium Quarry was supported by National Geographic Society Grants 3092-85 and 3315-86 to J. R. Thomasson.

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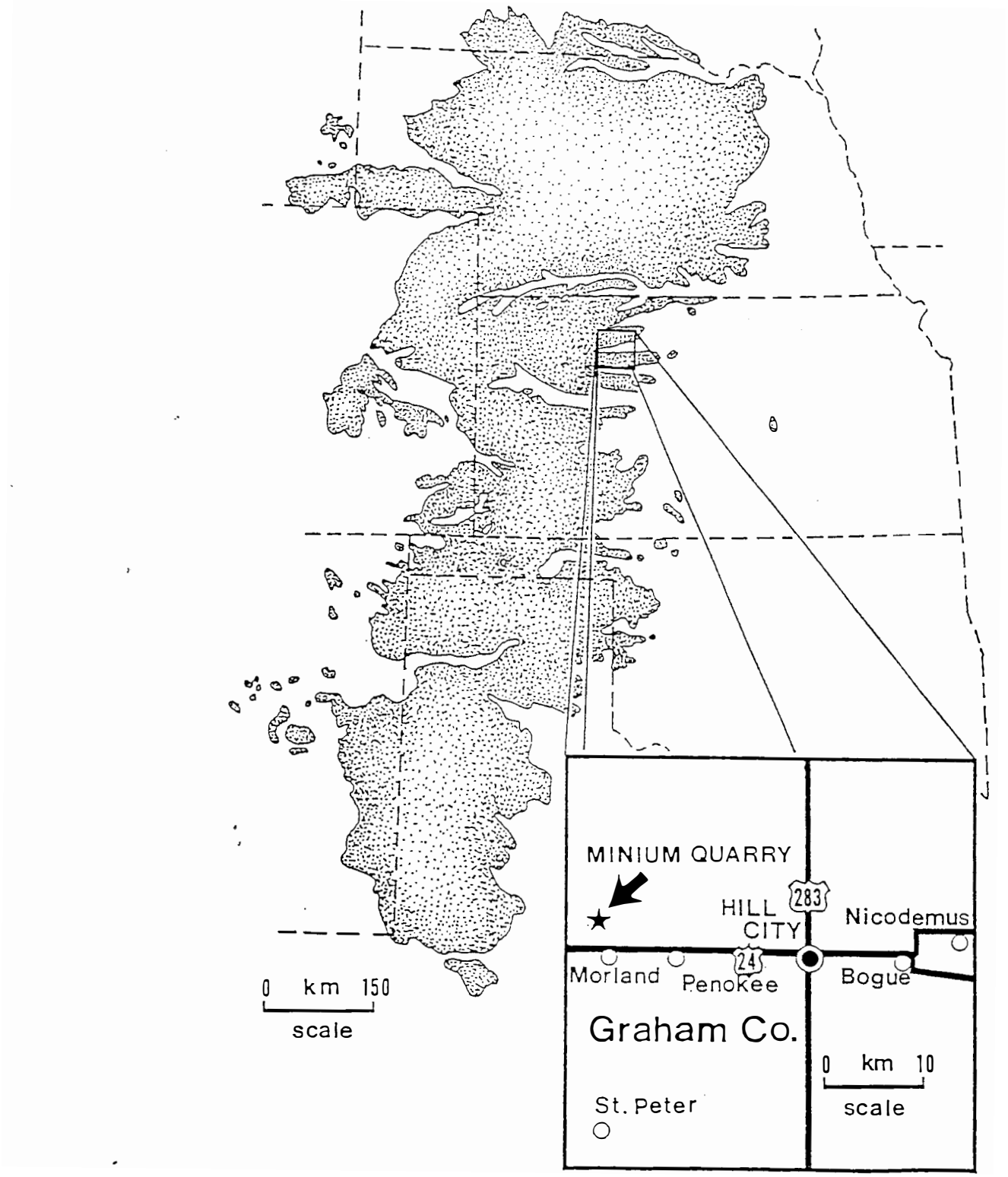
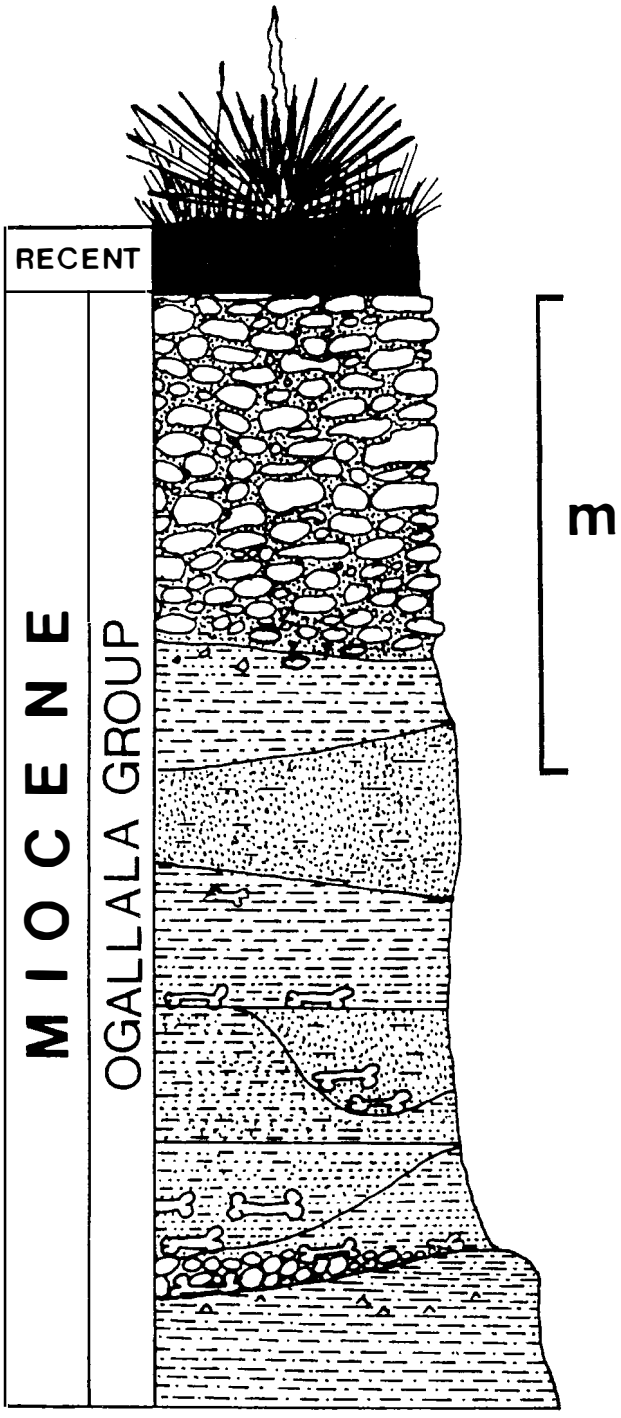

MINIUM QUARRY
HILL CITY
283
Nicodemus
24
Morland
Penokee
Bogue
Graham Co.
St. Peter
0 km 10
scale
0 km 150
scale

Figure 1



SOIL

CALICHE

SANDY SILTSTONE

SILTY SANDSTONE

SILTSTONE

?LAG DEPOSIT

BONE

MARL

Generalized Stratigraphy of the Minium Quarry

Figure 2

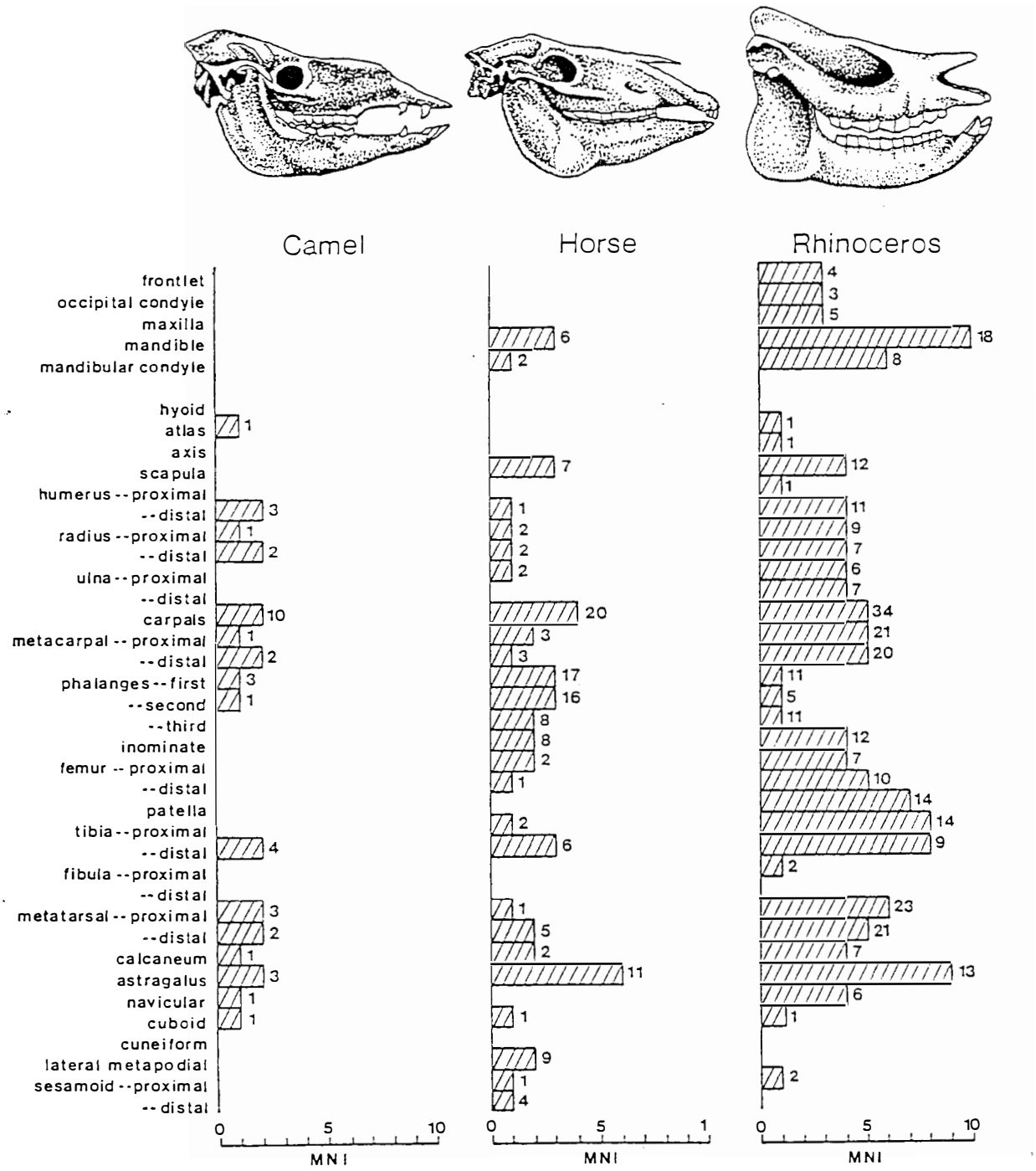

Camel
Horse
Rhinoceros
frontlet
occipital condyle
maxilla
mandible
mandibular condyle
hyoid
atlas
axis
scapula
humerus--proximal
--distal
radius--proximal
--distal
ulna--proximal
--distal
carpals
metacarpal--proximal
--distal
phalanges--first
--second
--third
inominate
femur--proximal
--distal
patella
tibia--proximal
--distal
fibula--proximal
--distal
metatarsal--proximal
--distal
calcaneum
astragalus
navicular
cuboid
cuneiform
lateral metapodial
sesamoid--proximal
--distal
0 5 10
MNI
0 5 1
MNI
0 5 10
MNI

Figure 3

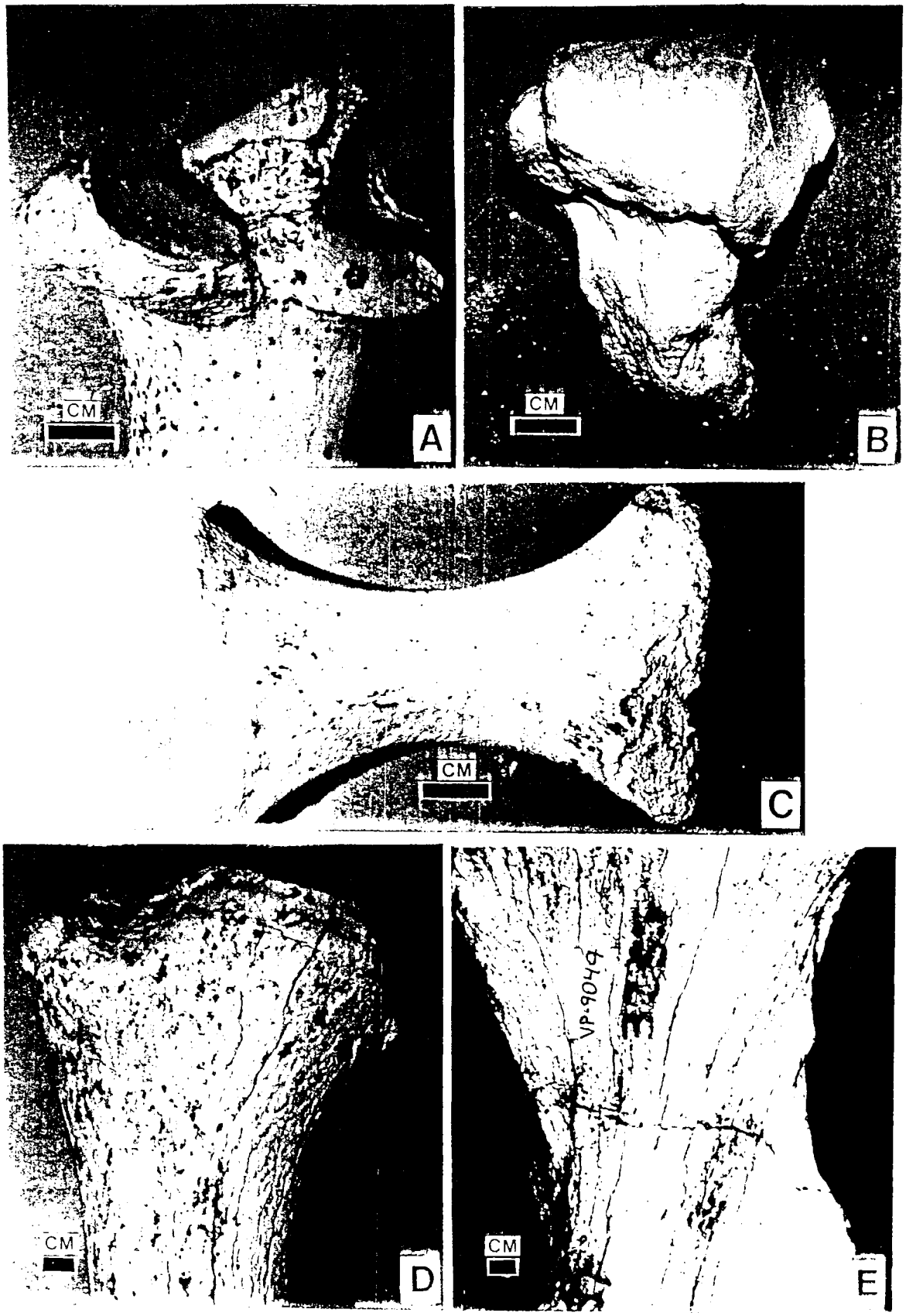


Figure 4

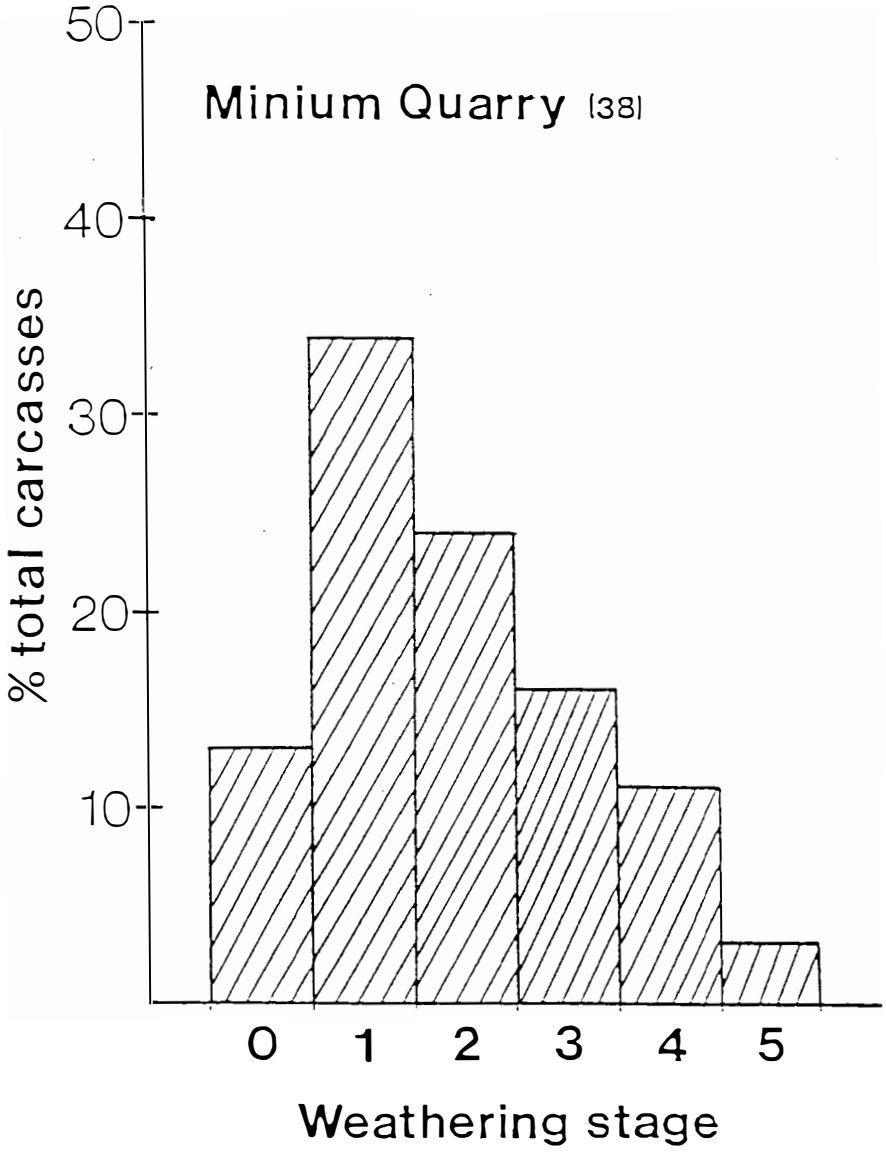

Minium Quarry (38)
% total carcasses
50
40
30
20
10
0
1
2
3
4
5
Weathering stage

Figure 5

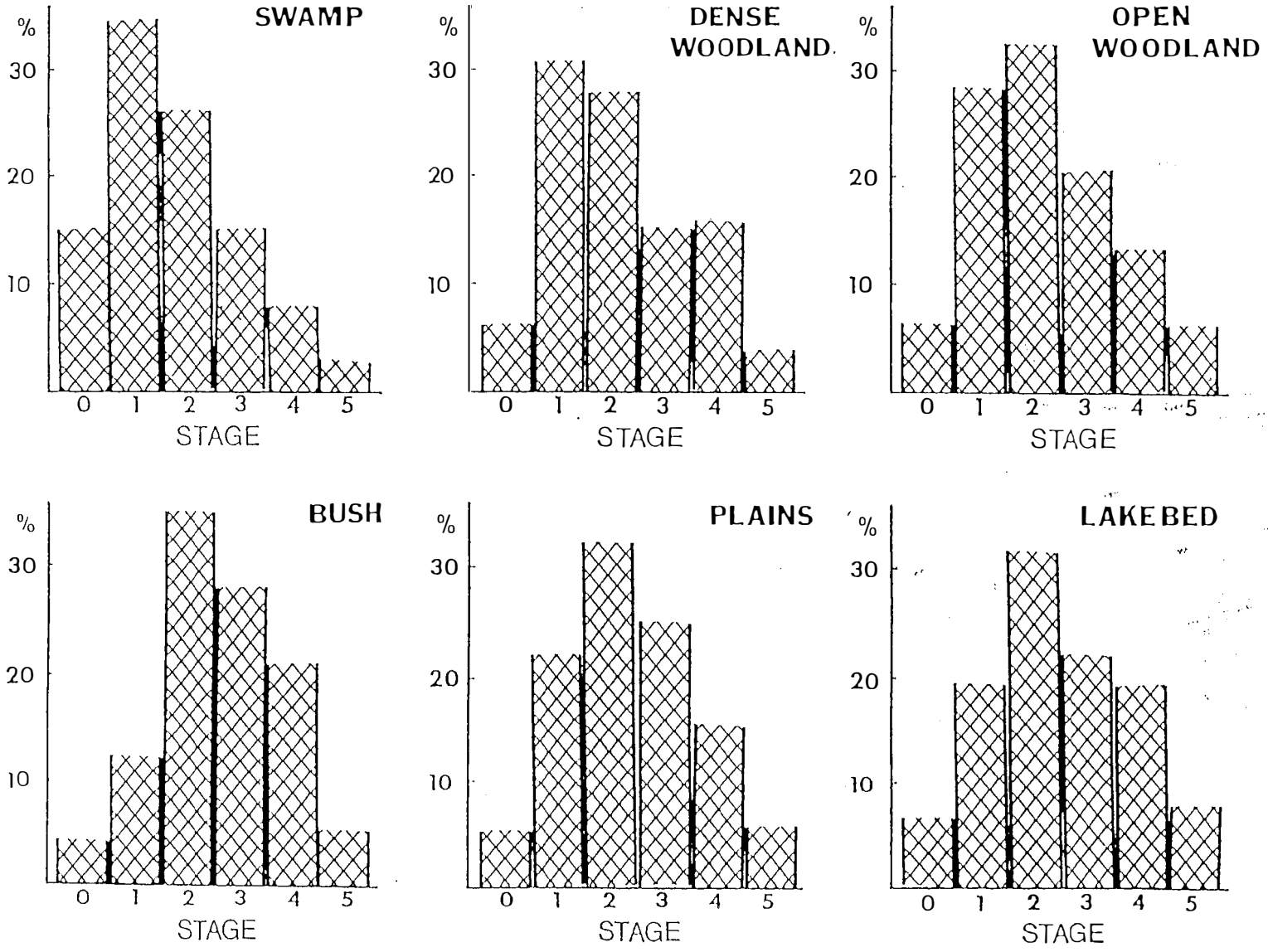

SWAMP
DENSE WOODLAND
OPEN WOODLAND
BUSH
PLAINS
LAKEBED
%
30
20
10
0 1 2 3 4 5
STAGE

Figure 6

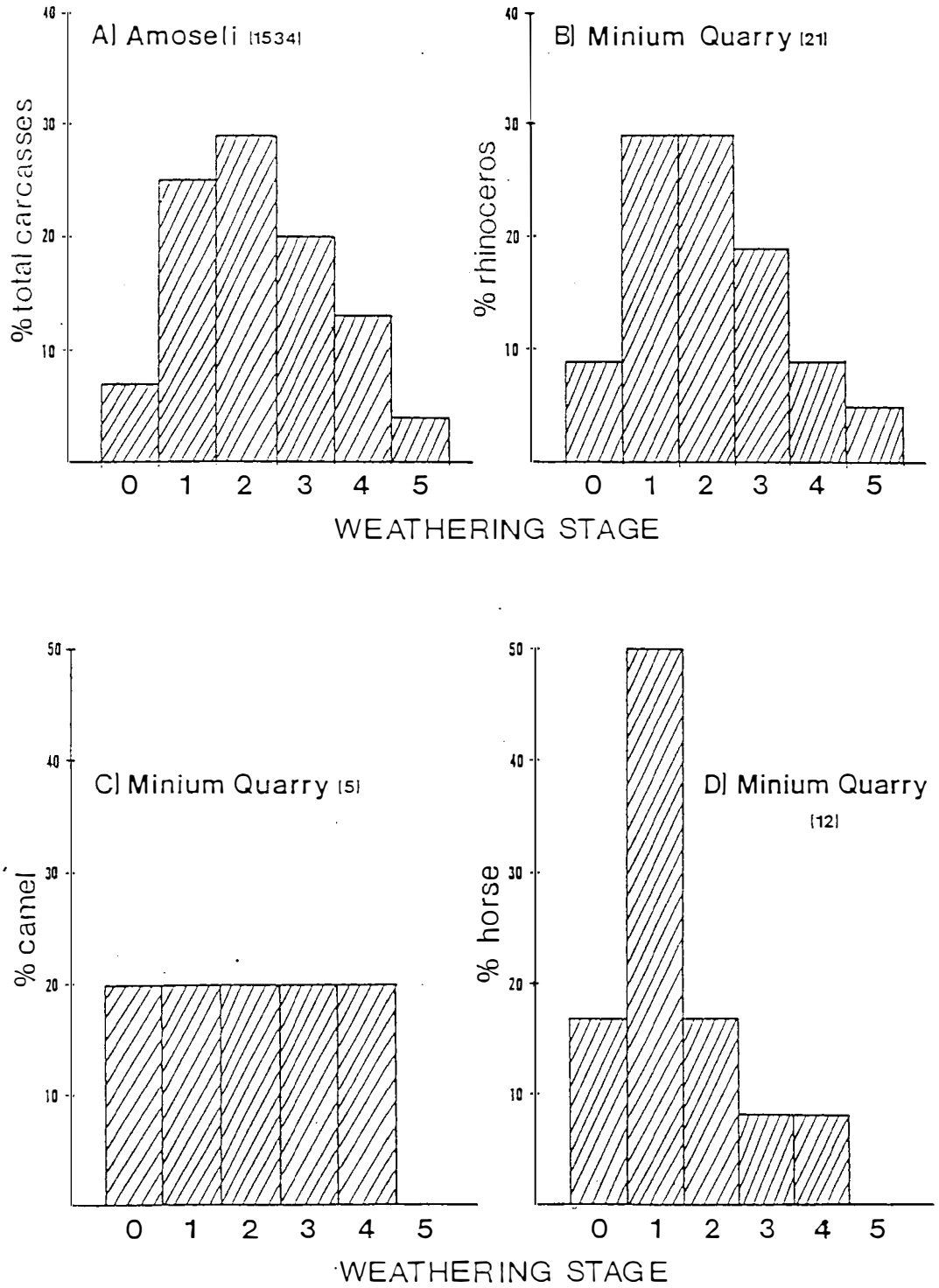

A] Amoseli [1534]
B] Minium Quarry [21]
% total carcasses
% rhinoceros
40
30
20
10
0 1 2 3 4 5
WEATHERING STAGE
C] Minium Quarry [5]
D] Minium Quarry
[12]
% camel
% horse
50
40
30
20
10
0 1 2 3 4 5
WEATHERING STAGE

Figure 7

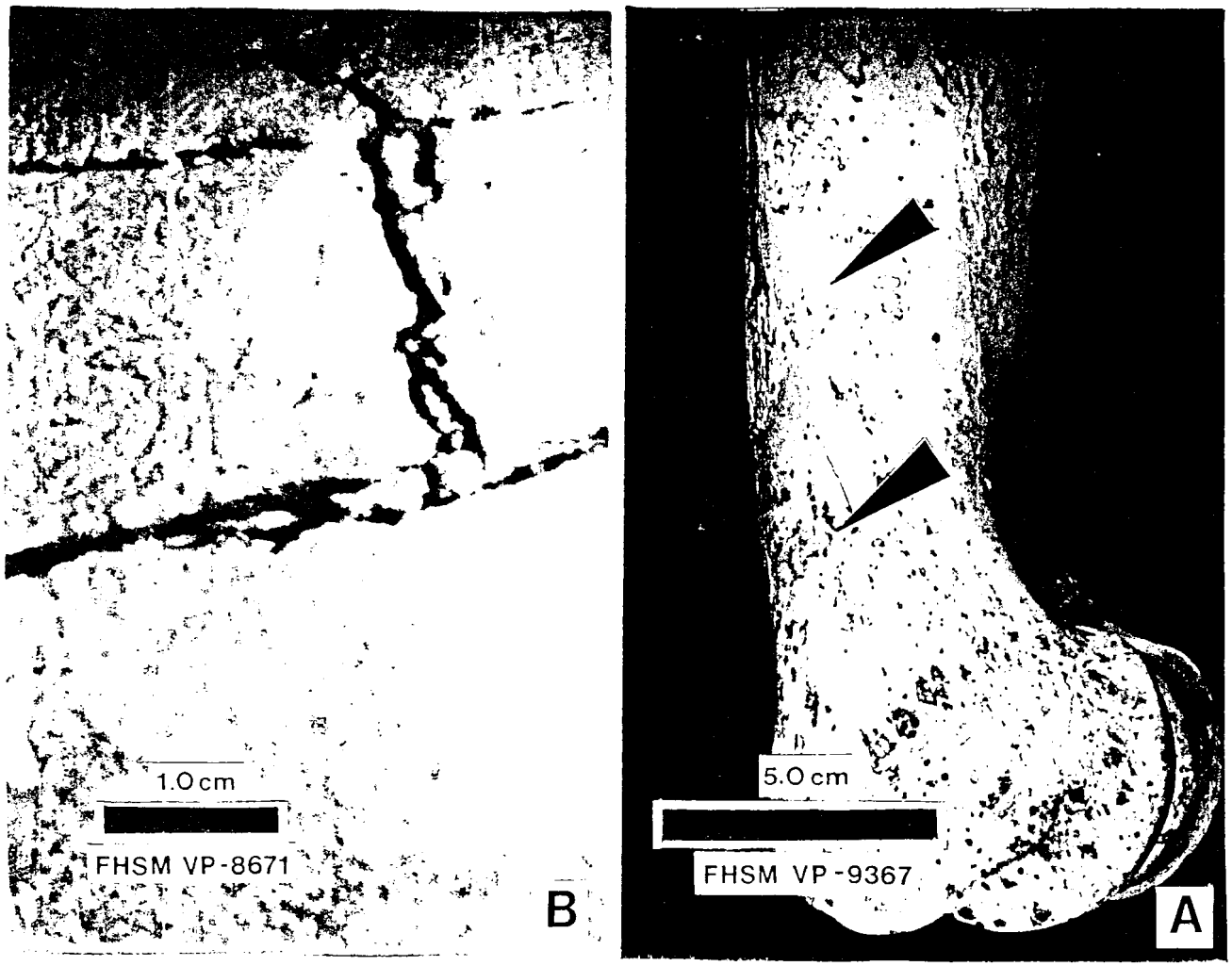


Figure 8

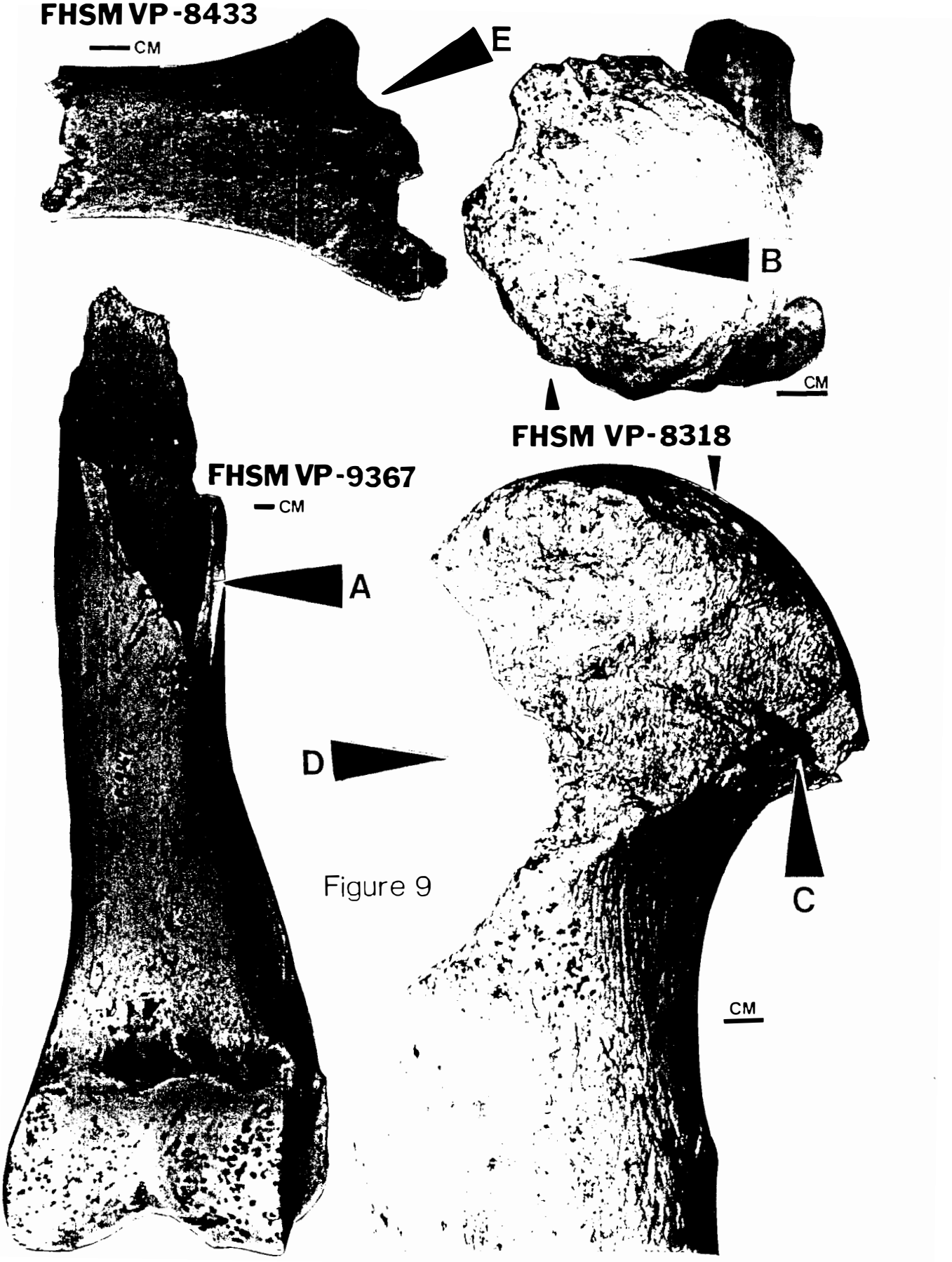


Figure 9

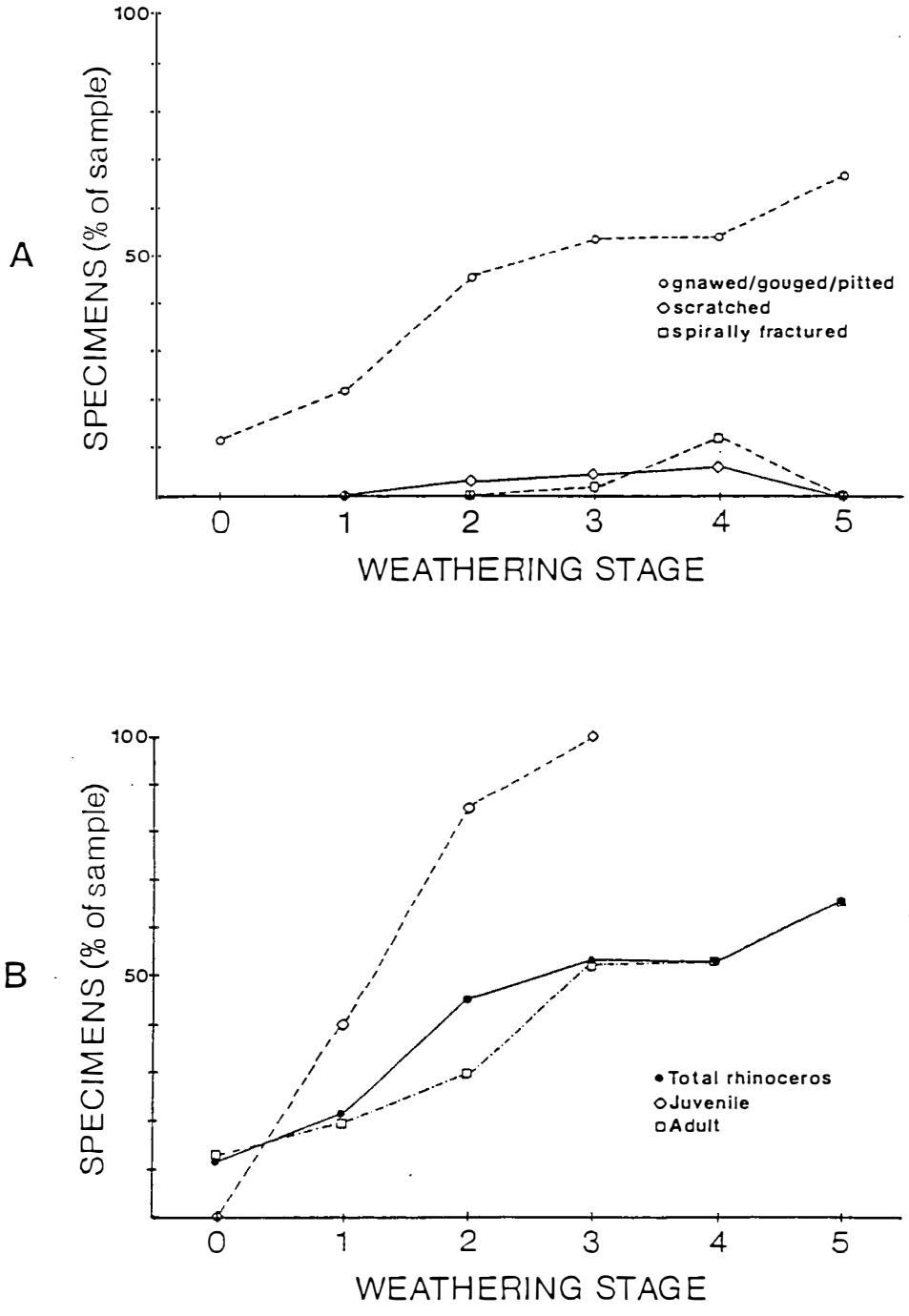
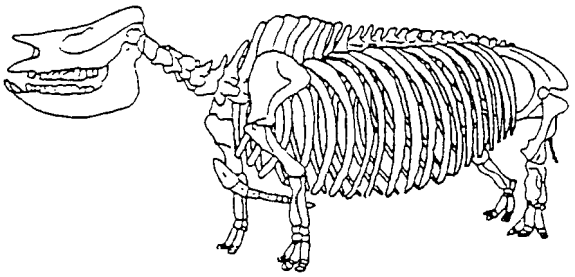

A
100
50
SPECIMENS (% of sample)
gnawed/gouged/pitted
scratched
spirally fractured
0
1
2
3
4
5
WEATHERING STAGE
B
100
50
SPECIMENS (% of sample)
Total rhinoceros
Juvenile
Adult
0
1
2
3
4
5
WEATHERING STAGE

Figure 10



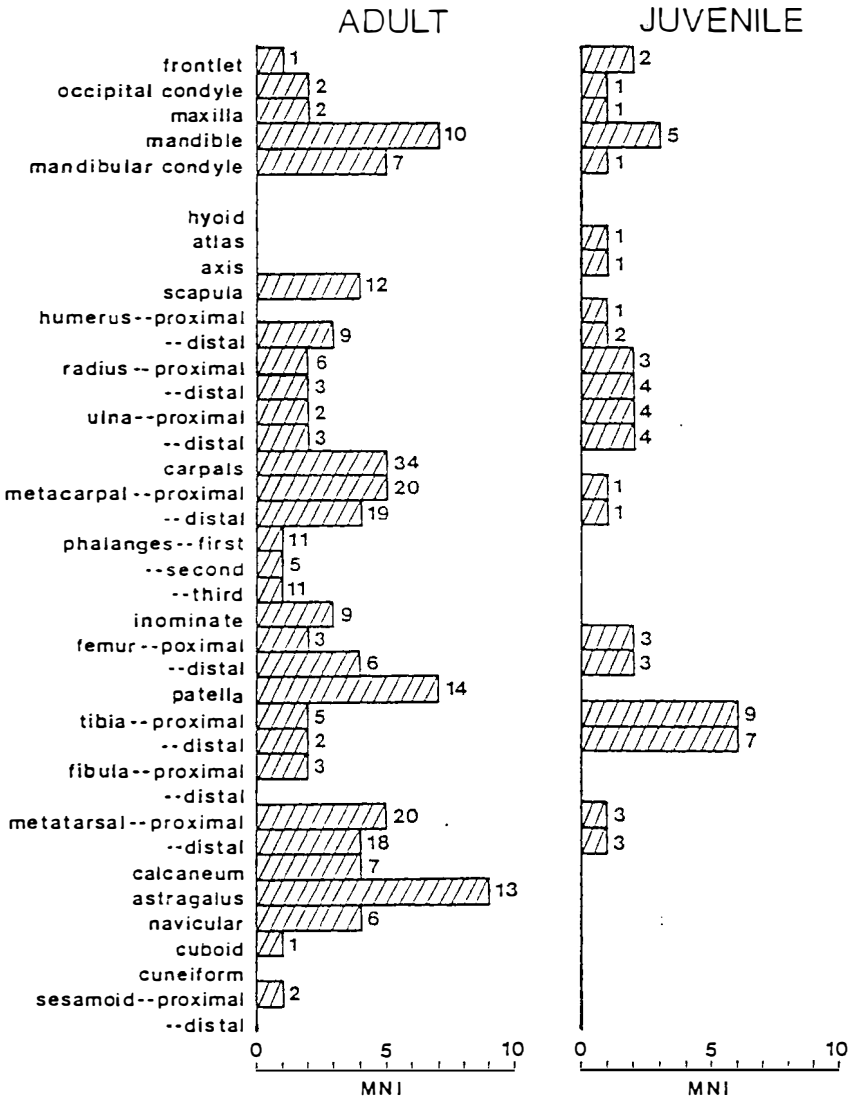

ADULT
JUVENILE
frontlet
occipital condyle
maxilla
mandible
mandibular condyle
hyoid
atlas
axis
scapula
humerus--proximal
--distal
radius--proximal
--distal
ulna--proximal
--distal
carpals
metacarpal--proximal
--distal
phalanges--first
--second
--third
inominate
femur--poximal
--distal
patella
tibia--proximal
--distal
fibula--proximal
--distal
metatarsal--proximal
--distal
calcaneum
astragalus
navicular
cuboid
cuneiform
sesamoid--proximal
--distal
1
2
2
10
7
12
9
6
3
2
3
34
20
19
11
5
11
9
3
6
14
5
2
3
20
18
7
13
6
1
2
2
1
1
5
1
1
1
1
2
3
4
4
4
1
1
3
3
9
7
3
3
0
5
10
MNI
0
5
10
MNI

Figure 11

Table 1- Summary of weathering stage characteristics (after Behrensmeyer, 1978).

Weathering Stage	Years since death	Characteristics
0	0-1	-surface of bone shows no evidence of cracking or flaking due to weathering
1	0-3	-bone cracked parallel to fiber structure, and articular surfaces show mosaic cracking
2	2-6	-outermost concentric thin layers of bone show flaking, especially near cracks. Long thin flakes attached at one end common, followed by loss of most outer bone.
3	4-15+	-surface has patches of rough, evenly weathered compact bone, resulting in fibrous texture, with loss of all external concentrically layered bone. Penetration of weathering less than 1.0-1.5 mm, crack edges rounded.
4	6-15+	-surface coarsely fibrous and rough, with loose large and small splinters. Weathering reaches inner cavities, and cracks are open and have rounded or splintered edges.
5	6-15+	-bone fallen apart in situ, mostly in splinters and very fragile. Difficult to tell original shape of bone. Cancellous bone exposed.

Table 2- Large ungulates >100 kg assessed for weathering damage, carnivory, and scavenging.

Taxon	Total Specimens	Untransported Sample		
		% of total[1]	% of individuals (MNI)	% of ungulates[2]
Hemiauchenia sp.[3]	10	100(10)	100(4)	2(6)
Procamelus sp.[3]	27	78(21)	100(5)	5(9)
Megatylopus sp.[3]	8	66(6)	66(2)	1(4)
Equidae (small)[4]	71	80(57)	63(8)	13(15)
Equidae (medium)[4]	99	78(77)	90(10)	17(19)
Equidae (large)[4]	4	75(3)	75(3)	1(5)
Teleoceros sp.[5]	267	95(253)	100(21)	60(40)
Aphelops sp.[5]	3	100(3)	100(1)	1(2)
TOTALS	489	84(410)	87(53)	100(100)

1. number in parentheses = untransported specimens
2. number in parentheses = percent of untransported individual ungulates
3. Family Camelidae (LaGarry, 1987)
4. post-cranial material not assigned to individual taxon
5. Family Rhinocerotidae

Table 3- Post-mortem bone modification observed in Minium Quarry ugulates >100 kg.[1]

Damage	% of total sample	% of camel	% of horse	% of rhinoceros
gouging, pits, and broken spalls	32	22	12	42
scratching	4	19	3	2
spiral fracturing	7	11	15	1
trampling	--	--	--	**
insect burrows	--	--	--	**
plant roots	55	16	26	73

1. untransported sample only
** this damage represented in less than 1% of sample

Table 4- Comparison of bone damage types: Extant carnivora

	CANIDS	HYENAS	BEARS	FELIDS
Tooth marks on compact bone ➧	LIKELY	MOST LIKELY	NOT LIKELY	UNLIKELY
Grinding of ends vs. biting through ➧	MOSTLY BITING	BITING & GRINDING	GRINDING ONLY	BITING ONLY
Shape of tooth impression in trabecular bone ➧	CONE	CONE	▭ OR ▭	"V"

(after Haynes,1983)

Table 5- Compiled measurements of Teleoceras lower cheek teeth (mm).[1]

Tooth	A-P Length				breadth			
	N	Range	$\bar{X}$	SD	N	Range	$\bar{X}$	SD
dP_2	2	30.2-35.1	32.65	3.46	2	17.0-19.0	18.00	1.41
dP_3	4	43.5-48.8	46.30	2.19	4	23.3-26.2	24.70	1.20
dP_4	2	52.9-53.1	53.00	0.14	2	29.1-29.9	29.50	0.57
P_2	2	20.5-21.0	20.75	0.35	2	16.0-16.4	16.20	0.28
P_3	2	44.2-54.4	49.30	7.21	2	29.7-45.6	37.65	11.24
P_4	3	49.8-56.3	52.59	3.35	3	36.9-41.9	39.33	2.50
M_1	4	54.3-64.2	59.88	3.86	4	37.0-40.0	39.10	1.43
M_2	6	60.3-75.0	66.62	5.25	6	36.7-42.6	39.87	1.93
M_3	3	65.3-76.5	69.77	5.93	3	37.9-40.6	39.50	1.42

1. socketed dentitions of known position only

Table 6- Age profile of Minium Quarry Teleoceras population, with no distinction between sexes.

Age Intervals (in years)		# Individuals
At least	But below	
0.0	4.5	0
4.5	9.0	10
9.0	13.5	0
13.5	18.0	0
18.0	22.5	0
22.5	27.0	0
27.0	31.5	0
31.5	36.0	0
36.0	40.5	7
40.5	45.0	7

Total number of individuals = 24

Number of dP_4 analyzed = 6

Number of M_1 analyzed = 19