

UPPER MIOCENE RHINOCEROSES FROM SANSAN (GERS), FRANCE: THE MANUS

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ABSTRACT—Articular facets and bone shapes and sizes distinguish carpal and metacarpal bones of three genera of upper Miocene rhinoceroses from Sansan (Gers), France. These same features suggest detailed functional patterns for the manuses of the 3-toed mediportal *Rhinoceros sansaniensis*, the 4-toed mediportal *Aceratherium tetradactylum*, and the 3-toed graviportal *Brachypotherium brachypus*. Comparisons with and inferences from living tapirs and rhinos suggest that neither the number of toes nor the medi- or graviportal condition of the body can adequately describe the patterns of movement and of support that are built into any given manus. Only three distinctive patterns of movement and support can be inferred for the Recent and Miocene ceratomorphs. One is the tapiroid pattern; another is that of *B. brachypus*; and the third belongs to the other three- and four-toed rhinoceroses.

INTRODUCTION

VIRET (1958, p. 424) introduced his descriptive summary of the Rhinocerotidae with this quotation:

Differentiations within this family are based primarily on the cranium which is seldom available, and on anterior dentition which is rarely found *in situ* with the molars. The bones of the limbs, which are often quite characteristic, have not yet been sufficiently utilized for classification.

Students of the perissodactyls have never denied the importance of foot structure. Like teeth, hooves "come directly and simply into relation with special food habits and environment" (Gregory, 1910, p. 111). However, attempts to correlate dentition and foot structure with habitat have resulted in a picture of converging adaptive radiations, like those Osborn (1929, p. 778) summarized, of little phylogenetic significance.

Dentition offered a promising lead for studying the Rhinocerotidae, and it has been followed by work on associated cranial systems. The number of nasal horns, slope of the occiput, height of the nasal boss, height of the

ascending ramus, dolichocephaly or brachycephaly of the brain case and degree of hypsodonty are some of the criteria used to define subfamilies, genera and species. In many major studies, definitions of rhinoceros groups are established in the spirit of Colbert's (1942, p. 4) work on two *Rhinoceros* species, "not by virtue of a few isolated characters but in all features throughout the structure of the skull, jaws and dentition."

Post-cranial regions are not always available for study. Whether they are or not, manus and pes are often interpreted or assumed to be in conformity with the generalized skull pattern (see, for example, Colbert, 1942, p. 4). The long-headed (dolichocephalic) rhinoceros—typically *Atelodus simus*—has an elongate (dolichopodial) manus, and the short-headed (brachycephalic) rhinoceros—like *Teleoceras fossiger*—has a short and stocky (brachypodial) manus (Osborn, 1900). When bones of the manus are available, and even when they are examined in detail as in Scott et al. (1941), systematic position is ultimately determined by the corresponding skull. One notable exception

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EXPLANATION OF PLATE I

Abbreviations: Mag. = Magnum; Pyr. = Pyramidal; Scap. = Scaphoid; Trap. = Trapezoid; Unc. = Unciform.

FIGS. 1,4,7—*A. tetradactylum*. 1, left scaphoid, lunar (ectal) surface, $\times \frac{5}{8}$; 4, left lunar, scaphoid (entol) surface, $\times \frac{3}{2}$; 7, left lunar, pyramidal (ectal) surface, $\times \frac{3}{2}$.
2,5,8—*R. sansaniensis*. 2, right scaphoid, lunar (ectal) surface, $\times \frac{5}{8}$; 5, left lunar, scaphoid (entol) surface, $\times \frac{3}{2}$; 8, left lunar, pyramidal (ectal) surface, $\times \frac{3}{2}$.
3,6,9—*B. brachypus*. 3, left scaphoid, lunar (ectal) surface, $\times \frac{5}{8}$; 6, left lunar, scaphoid (entol) surface, $\times \frac{3}{2}$; 9, left lunar, pyramidal (ectal) surface, $\times \frac{3}{2}$.

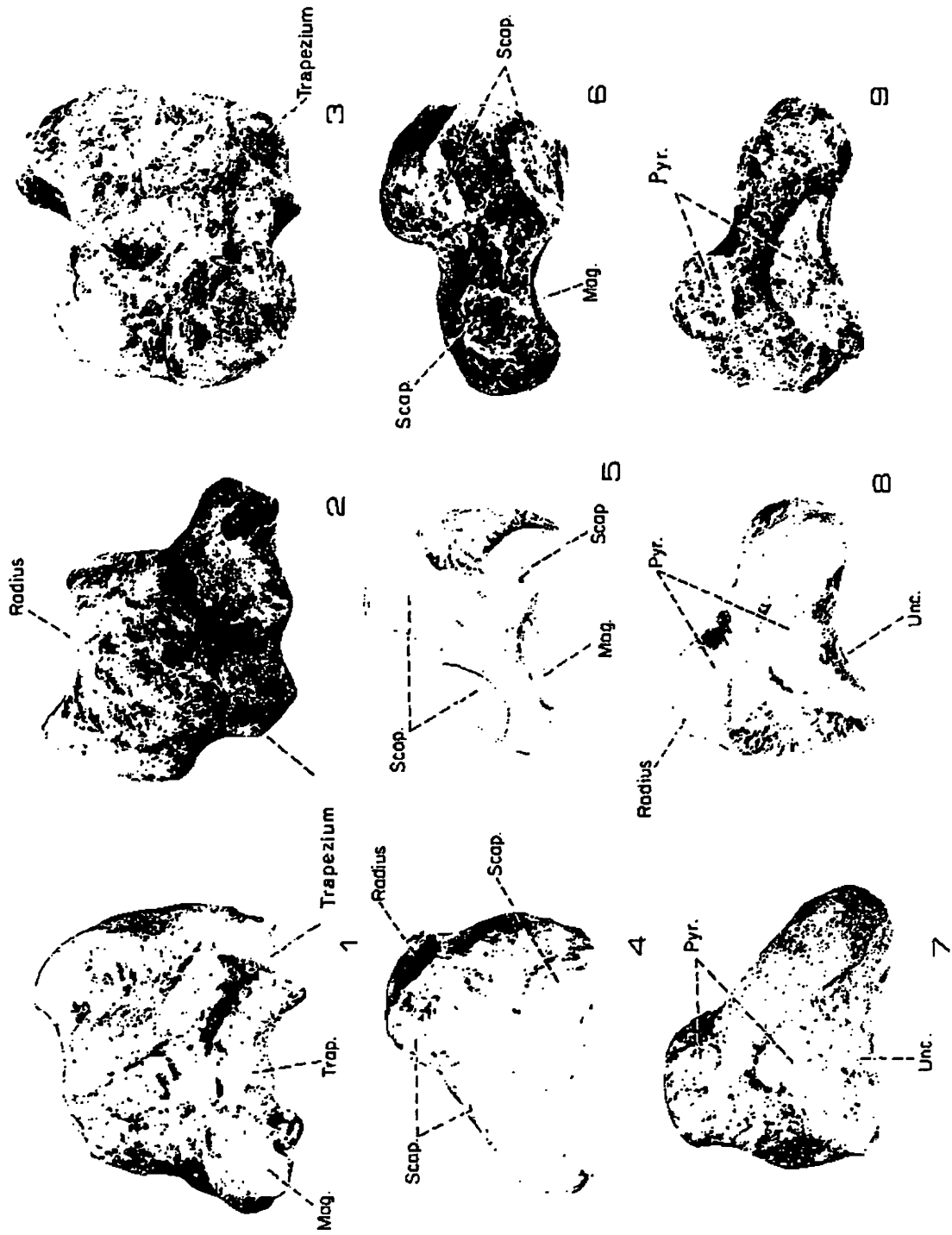


TABLE 1—Carpal characteristics reflecting weight-gait types, according to Osborn (1929, p. 774-775).

Cursorial Type	Mediportal Type	Graviportal Type
1. All the elements are high and narrow.	1. The lunar broadens and gains a facet on the broadening magnum.	1. The carpus is very broad.
2. The lunar rests mainly on the unciform with small lateral contact on the magnum.	2. The mediportal tapir and the long-footed rhinoceroses have magna with deep hooks.	2. The lunar rests broadly on the magnum.
3. The magnum has a deep hook forming the arm of a lever in flexing the carpus.		3. The magnum hook is reduced; the magnum is flattened and supports half the weight of the lunar.

is *Aceratherium tetradactylum*, which Filhol (1891) originally described as *A. incisivum* (Kaup). Cope (1887, p. 1001) recognized the importance of Lartet's (1851) and Filhol's discovery of a four-toed *Aceratherium manus*.

The Rhinocerotidae [*sic*] came into existence in the Miocene of Europe, in a genus nearer to the Caenopidae than any other of the family. This approximation is shown in the persistence of the external or fifth digit of the anterior foot in the genus *Aceratherium* (Kaup). In this form all the superior premolars have the structure of true molars; so it enters the present family.

Even here the manus is subordinated to the cranium.

The head does not lead the foot for lack of specimens of bones of the manus; to the contrary, these are far more abundant than complete skulls. The problem lies in interpretation of carpal and metacarpal features. A given bone may vary widely from one individual to the next with respect to relative lengths of several dimensions, and to shapes and even the presence of certain articular facets. Characteristics that one would expect to be constant are actually variable, appearing in unpredictable combinations in distantly related forms. Osborn (1929, p. 739) explained such "convergent, parallel or homoplastic forms, proportions, ratios and indices" as typical ungulate adaptations to mediportal, graviportal or cursorial locomotion (see Table 1). Extreme caution must be used, Osborn implied, in assigning systematic significance to such features.

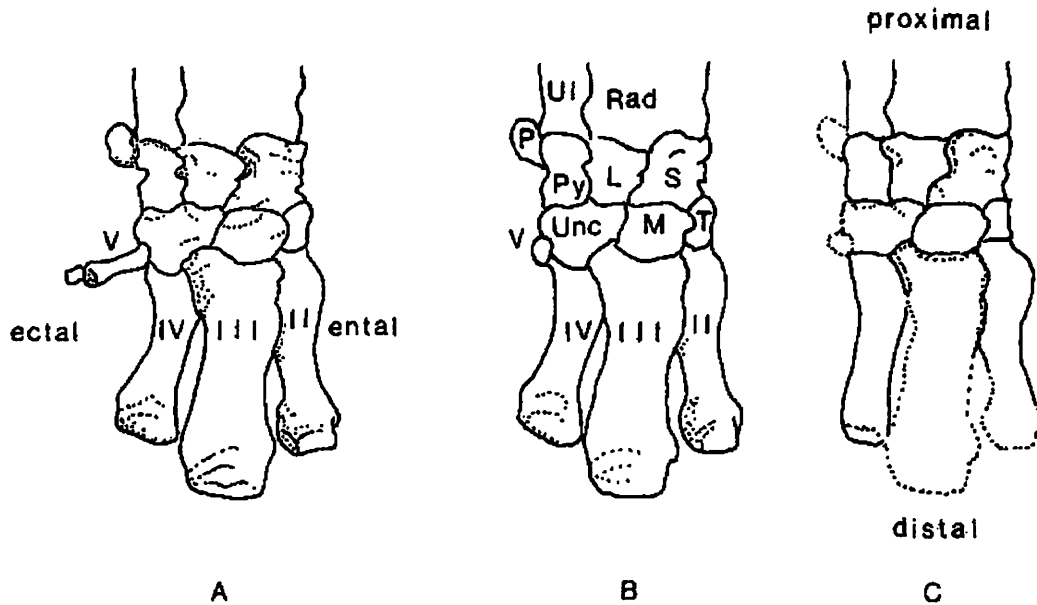
The cranium does not offer hard and fast rules for determining rhinoceros lineages. Adaptive radiations have produced converging and parallel developments of the cranium just as they have for the manus. Romer (1966, p. 272) summarized the combined efforts of many students of skull and dentition in these words:

Rhinoceros evolution . . . may be pictured as a branching bush. There is no main evolutionary stem, but a complex of sprouts, the components of which are difficult to disentangle.

However, despite parallel evolution which, according to Osborn (1929, p. 739), "masks, dominates, or completely conceals the . . . ancestral characters, there still remain two causes of distinction or separation between members of different phyla." The first is that certain features of original resemblance survive. Following this principle, Radinsky (1966a, p. 740) proposed a redefinition of the Rhinocerotidae to include only a monophyletic line defined by characteristics of anterior dentition and by the M³. For the limb, Osborn suggested a second clue for establishing valid phyletic lines. "The adaptation of structure is rarely exactly analogous, because the functions or movements of the limbs in two unrelated forms are rarely, if ever, exactly analogous." Osborn described two kinds of structural adaptations. One is reduction of lateral digits, and the other consists of modifications of bone shape in conformity with cursorial, mediportal or graviportal body proportions. But no matter what its position in any evolutionary sequence, the manus of any given ungulate is an internally harmoniously functioning unit.

Matthew (1909), Gregory (1912), Osborn (1929) and Smith & Savage (1956) contributed to the definition of the terms cursorial, mediportal and graviportal. In its entirety, the definition includes various osteological proportions and numerical translations of these measurements into certain styles of movements. Despite the precision of such measurements, ungulates have locomotor capabilities that are not summarized adequately by these terms. If the functional capabilities of each manus were thoroughly understood, it might be possible to determine which are the analogous and which the original or ancestral structural features of the manuses of the several ungulate groups. Lineage may come to be discussed in terms of evolution of the features that fix certain patterns of movement.

Hildebrand's (1966) analyses of gait through



TEXT-FIG. 1.—Dorsal views of articulated manuses. Note positions of metacarpals V. A, *A. tetradactylum*; B, *R. sansaniensis* and living rhinoceroses; C, *B. brachypus*. Bones are Ul = ulna, Rad = radius, P = pisiform, Py = pisiform, L = lunar, S = scaphoid, T = trapezoid, M = Magnum, Unc = unciform, numerals II-V indicate metacarpals.

films is one direction to be followed in this quest. Another is represented by Yalden's (1971) study of the potential displacements within the carpus. My approach harkens back to Osborn's. I accept axiomatically the idea that each manus has a set of internal balances to support and to move a particular animal. Bone shapes and articular facets endow each manus with both rigidity and flexibility in characteristic patterns. In living animals, patterns of rigidity-flexibility are reflected exactly and predictably in observable movements of the forelimb. For tapirs and rhinoceroses, bone shapes, facet structures and their reflections, observable movements, suggest greater divergence between these ceratomorphs than Osborn derived from phenomena related to digital reduction and than Yalden saw on the surfaces of carpal rows. Differences among carpal and metacarpal bones reflect differences of individual, generic and subordinal magnitude. On the other hand, similarities within each sub-order stress the ultimate stability of form and function.

An examination of *Aceratherium tetradactylum* (Lartet) and *Rhinoceros sansaniensis* (Lartet) shows that these upper Miocene rhinoceroses from Sansan (see Crouzel, 1956, and Ginsburg, 1961) had carpal bones resembling, even to details of individual variation, those of

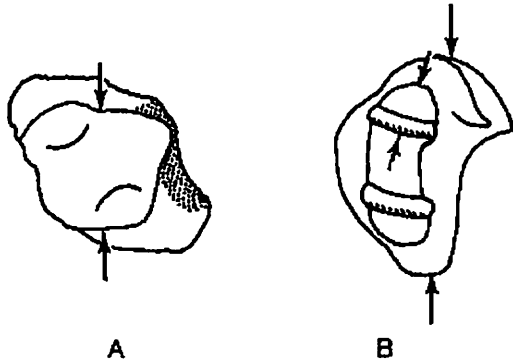
living rhinoceroses (Text-fig. 1). Functional similarity, of course, cannot be verified. But the possibility of continuity should not be discounted. A third rhinoceros from the same upper Miocene formation is *Brachypotherium brachypus* (Lartet). Internal forms of this manus suggest functional patterns that differ radically from living tapirs or rhinos as well as from the other two rhinoceros genera from Sansan.

These three rhinos are particularly interesting because each one represents one of Osborn's adaptive phases. *A. tetradactylum* was a four-toed mediportal rhinoceros; *R. sansaniensis* was three-toed and mediportal; while *B. brachypus* had three toes and was graviportal. What follows is a description of features of each carpal and metacarpal bone useful in differentiating the genera. In conclusion, I shall attempt, however imprudently, to tread the turbulent waters of adaptive radiation to describe some of the problems of adaptive phase and function.

SYSTEMATIC DISCUSSIONS

Scaphoid.—This description is based on examination of 26 specimens of *A. tetradactylum*, 10 specimens of *R. sansaniensis*, and two specimens of *B. brachypus*.

The palmo-dorsal widths (see Text-fig. 2) of



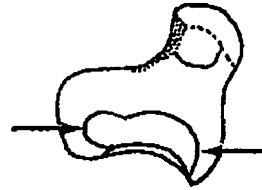
TEXT-FIG. 2—Scaphoid. *A*, Proximal head, indicating points of measurement of palmo-dorsal width. *B*, Distal head, indicating palmo-dorsal width of distal head and palmo-dorsal width of trapezium facet.

the proximal heads of the two *B. brachypus* specimens are 6.0 and 6.2 cm, respectively. The largest specimen of either of the other two genera measure 5.6 cm in this dimension; the smallest, 4.1 cm. The modal value is 5.3 cm.

The palmo-dorsal widths of the most palmar of the distal trochlea range from 0.6 to 0.9 cm in *R. sansaniensis*. In *A. tetradactylum* these trochlea are 1.0 to 1.7 cm wide. The palmo-dorsal widths of the distal surfaces of *A. tetradactylum* specimens cluster at 6.2 cm, while for the same dimension in *R. sansaniensis*, measurements have a modal value of 5.8 cm.

In *A. tetradactylum*, the outline of the palmar facet for the lunar is shaped like a teardrop; the long axis is directed palmo-distally (Pl. 1, fig. 1). In *R. sansaniensis* and in *B. brachypus* the facet outline is more nearly rectangular (Pl. 1, figs. 2, 3). In the latter two genera, a rugose bulge may be seen from the proximal head and from the palmar faces of the bones.

In *A. tetradactylum* and in *B. brachypus*, the profile of the palmar edge of the bone is gently convex from its proximal to its distal borders (see right edges of figs. 1, 3 on Pl. 1). In *R. sansaniensis*, the profile is roughly S-shaped. It is convex from the proximal terminus to



TEXT-FIG. 3—Lunar; palmo-dorsal width of distal facet for the pyramidal.

about $\frac{2}{3}$ of the distance to the distal terminus (see left edge of Pl. 1, fig. 2). There it becomes sharply concave before plunging along a vertical path to its intersection with the distal surface of the bone.

Lunar.—This description is based on examination of 22 specimens of *R. sansaniensis*, and one specimen of *B. brachypus*.

In *A. tetradactylum* the palmo-dorsal widths of the distal facets (see Text-fig. 3) for the pyramidal vary from 2.0 to 2.8 cm. In *R. sansaniensis*, the range of measurements is from 3.0 to 3.6 cm. In *A. tetradactylum*, *B. brachypus* (Pl. 1, figs. 7, 9) and in the living genus *Rhinoceros*, this distal facet is equal in palmo-dorsal width to the palmo-dorsal width of the unciform facet, which marks its distal border. It is weakly convex palmo-dorsally. In *R. sansaniensis* and in the living genus *Dicerorhinus* the same facet is concave palmo-dorsally. Further, it continues palmarly beyond the contact with the unciform facet as a lobe that is circular in outline.

The proximal palmar facet for the scaphoid has a circular outline in *B. brachypus* and an elliptical outline in *R. sansaniensis* and in *A. tetradactylum*. In all specimens it is a flat surface. Its position on the bone, however, varies characteristically. In *B. brachypus* (Pl. 1, fig. 6) the facet, which covers most of the ental face of the palmar tubercle, is directed laterally. In the other two genera, and in all living rhinoceroses, the facet is directed obliquely to laterally. Each genus has a distinctive position for this facet. In *R. sansaniensis* (Pl. 1, fig. 5)

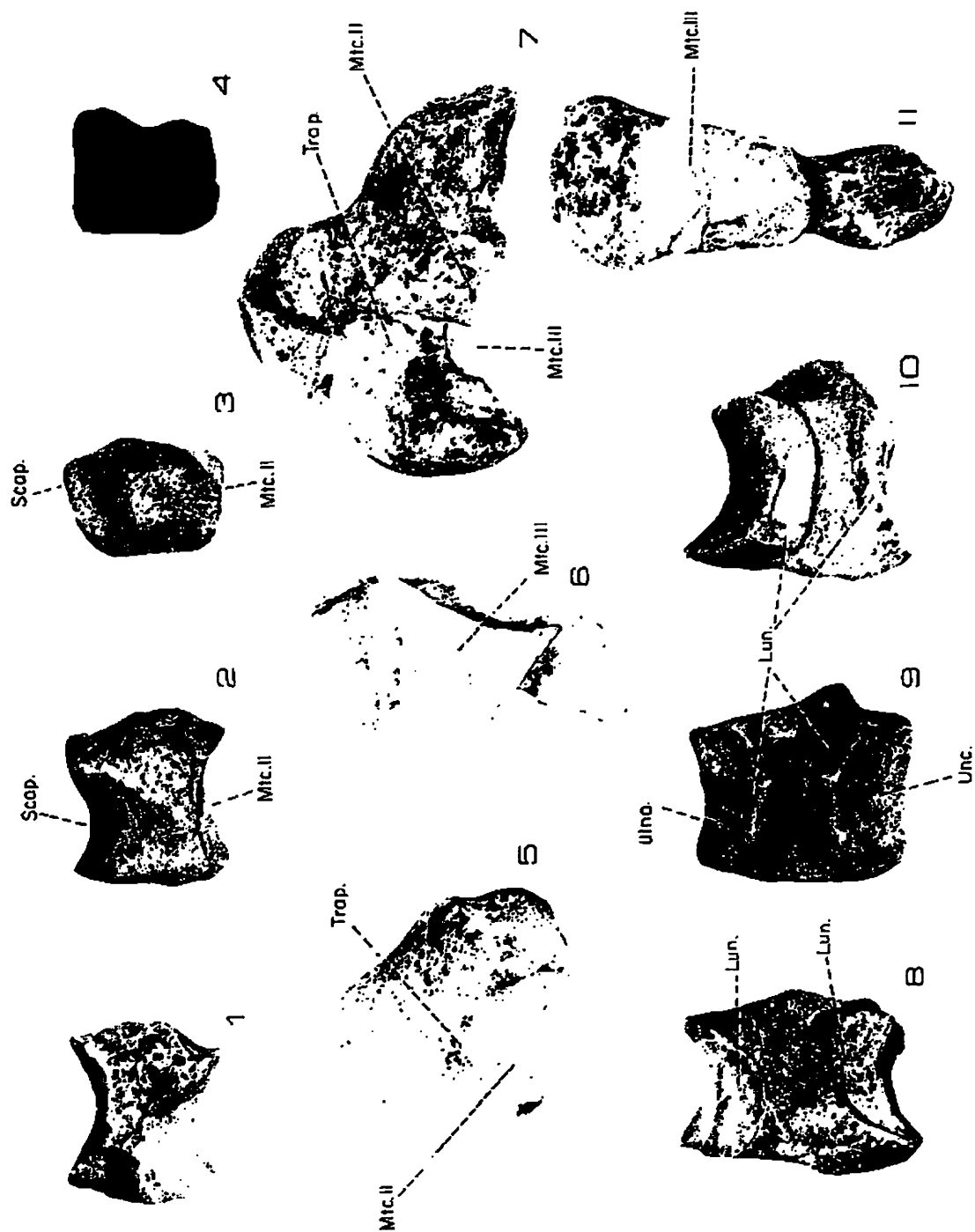
EXPLANATION OF PLATE 2

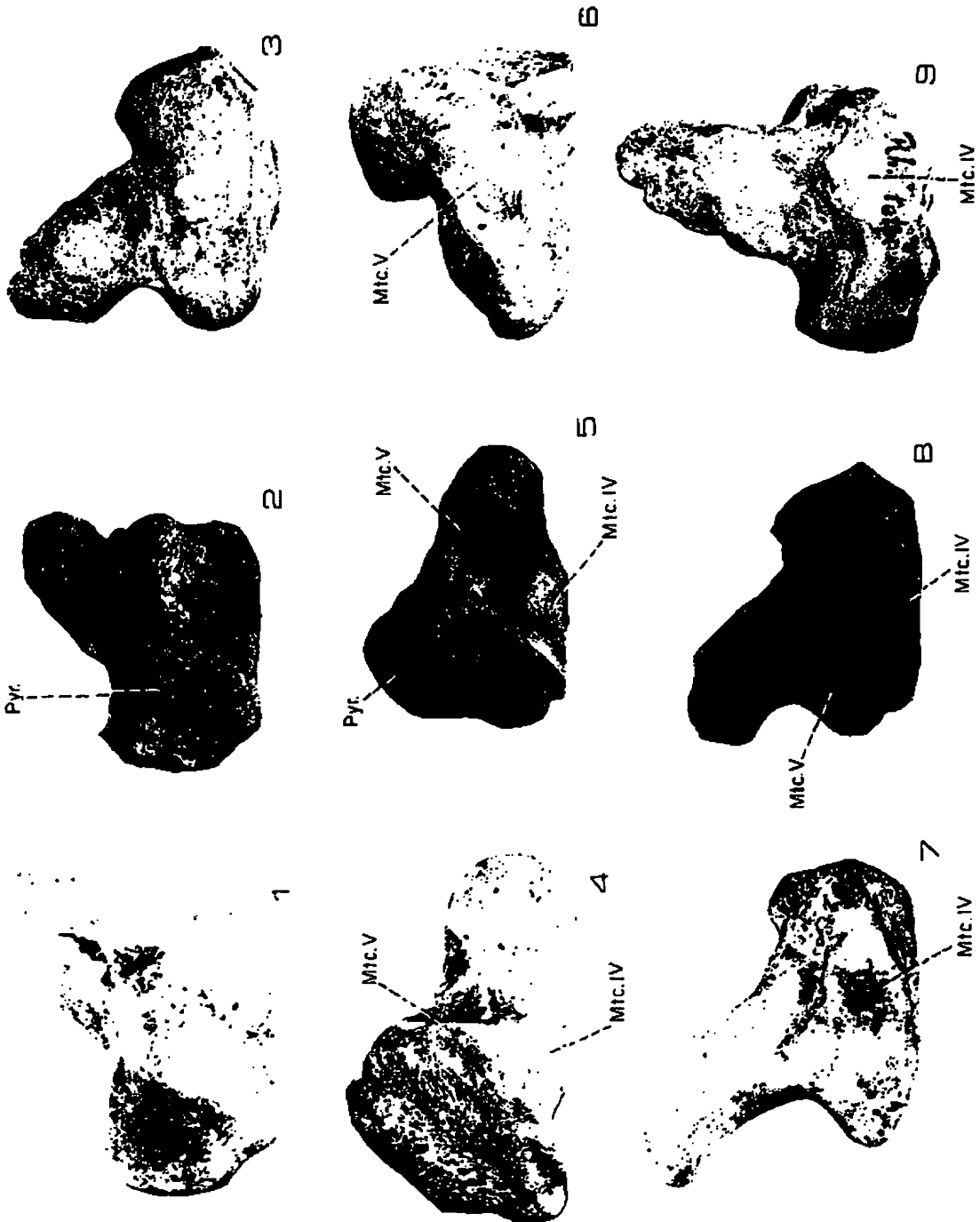
All figures are $\times \frac{2}{3}$; abbreviations: Lun. = Lunar; Scap. = Scaphoid; Trap. = Trapezoid.

FIGS. 1,3,5,6,8—*A. tetradactylum*. 1, right trapezoid, trapezium (ental) surface; 3, left trapezoid, dorsal face; 5, left magnum, ental surface; 6, left magnum, Mtc. III (distal) surface; 8, left pyramidal, lunar (ental) surface.

2,4,7,9,11—*R. sansaniensis*. 2, left trapezoid, trapezium (ental) surface; 4, left trapezoid, dorsal face; 7, right magnum, ental surface; 9, right pyramidal, lunar (ental) surface; 11, right magnum, Mtc. III (distal) surface.

10—*B. brachypus*. Right pyramidal, lunar (ental) surface.





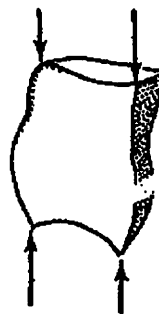
it occupies most of the upper half of the ental face of the palmar tubercle, and it faces slightly proximally as well as entally. In *A. tetradactylum* (Pl. 1, fig. 4) it is visible in its entirety only from the proximal face of the palmar tubercle. The *A. tetradactylum* facet, which is situated closer to the radius facet than it is in either of the other genera, is directed slightly entally but predominantly proximally.

In all rhinoceroses, the distal surface of the lunar is divided for facets for the unciform and the magnum. With the exception of *B. brachypus*, the division is oblique so that the unciform facet is broadest near the dorsal margin of the bone, tapering palmarly along the ectal side; while the magnum facet is broadest palmarly, tapering dorsally as it trends along the ental side of the bone. In *B. brachypus* the division is more nearly transverse than palmo-dorsally diagonal. The unciform facet is situated dorsally of the magnum facet, rather than laterally of it. In no other rhinoceros under consideration does the unciform facet extend so far entally as to meet the distal scaphoid facet. This appears in profile in Plate 1, figure 6, as the double arch of the distal border of the bone. By contrast, in *A. tetradactylum* and in *R. sansaniensis* (Pl. 1, figs. 4, 5) the distal profile is a single arch.

Pyramidal.—This description is based on examination of 34 specimens of *A. tetradactylum*, six specimens of *R. sansaniensis*, and two specimens of *B. brachypus*.

In *A. tetradactylum* and in *R. sansaniensis* the proximo-distal lengths of the palmar faces (see Text-fig. 4) exceed those of the dorsal faces by no more than 0.4 cm. In *B. brachypus* the relationship is reversed; the palmar face is shorter proximo-distally than the dorsal face. The difference is 0.8 and 0.9 cm, respectively, for the two specimens.

In *A. tetradactylum* and in *R. sansaniensis*, the two articular facets for the lunar are subequal in area. In *B. brachypus* (Pl. 2, fig. 10) the proximal facet has approximately twice the area of the distal facet. In *A. tetradactylum* (Pl. 2, fig. 8) the distal facet is a single plane



TEXT-FIG. 4—Ectal face of a pyramidal. Proximo-distal length of dorsal face (left) and proximo-distal length of palmar face (right).

surface. In *R. sansaniensis*, this facet is divided by a foldline into two plane surfaces; the palmar flange is smaller in area than the dorsal zone, and it is directed palmarly of laterally, while the dorsal zone looks laterally. In these features, the pyramidal of *R. sansaniensis* resembles that of the genus *Dicerorhinus*, and that of *A. tetradactylum* looks like the pyramidal of genus *Rhinoceros*.

The profiles of the palmar surfaces of the pyramidals may be viewed from the ental sides of the bones in Plate 2, figures 8–10. In all genera the profile has a convex aspect. In *A. tetradactylum* (see the left edge of fig. 8, Pl. 2) a broad, shallow arch extends from the proximo-distal midpoint to the distal contact of the face with the unciform facet. In *R. sansaniensis* (see the right edge of fig. 9, Pl. 2) a sharp, asymmetrical bulge is initiated just distally of the proximo-distal midpoint; its baseline is equal to only about $\frac{1}{4}$ of the proximo-distal length of this face of the bone. In *B. brachypus* (see the right edge of fig. 10, Pl. 2) the entire palmar face of the bone arches roundly from its proximal to its distal terminae.

In *A. tetradactylum* and *R. sansaniensis*, as in living rhinoceroses, the pisiform facet is developed on the corner between the palmar and ectal faces of the bone. In *B. brachypus*, it is developed entirely on the palmar face.

Pisiform.—Of the six pisiforms observed,

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EXPLANATION OF PLATE 3

All figures are $\times \frac{5}{8}$; abbreviation: Pyr. = Pyramidal.

- FIGS. 1,4,7—*A. tetradactylum*. 1, left unciform, pyramidal (proximal) head; 4, left unciform, ectal surface; 7, left unciform, Mtc. IV (distal) surface.
 2,5,8—*R. sansaniensis*. 2, left unciform, pyramidal (proximal) head; 5, left unciform, ectal surface; 8, left unciform, Mtc. IV (distal) surface.
 3,6,9—*B. brachypus*. 3, right unciform, pyramidal (proximal) head; 6, right unciform, ectal surface; 9, right unciform, Mtc. IV (distal) surface.



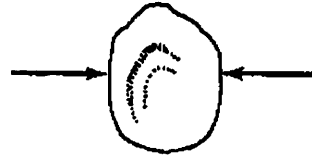
TEXT-FIG. 5—Pisiform, palmo-dorsal width.

five belong to *A. tetradactylum* and one to *R. sansaniensis*. The *A. tetradactylum* pisiforms are 5.6 to 5.9 cm wide palmo-dorsally (see Text-fig. 5). There is one specimen for each measure from 5.6 to 5.8 cm and two specimens measuring 5.9 cm. The *R. sansaniensis* pisiform measures 6.9 cm in this dimension. In *A. tetradactylum*, the transverse face of the bone—the face opposite the articular facets—arches from its ectal to its ental terminae. In *R. sansaniensis* this facet is nearly flat transversely.

Trapezoid.—This description is based on examinations of nine specimens of *A. tetradactylum*, 12 specimens of *R. sansaniensis* and three specimens of *B. brachypus*.

The shapes of the dorsal faces (see Text-fig. 6) of the trapezoids characterize *A. tetradactylum* and *R. sansaniensis*. The proximal and distal margins are approximately parallel in *R. sansaniensis* (Pl. 2, fig. 4); both are transversely trending straight edges. In *A. tetradactylum* (Pl. 2, fig. 3) the proximal margin of the face slopes along a straight edge from an ectal peak to its more distal terminus at the ental side of the bone. The distal margin of the face has a shallow convex outline. For specimens of both of these genera the transverse widths of the faces range from 1.8 to 2.3 cm. In *B. brachypus*, the transverse widths of the three specimens measure 2.4, 2.8, and 2.9 cm, respectively.

In *R. sansaniensis* and *A. tetradactylum* the distal surfaces are strongly concave palmo-dorsally (see Pl. 2, figs. 1,2). In *B. brachypus* the surface is only weakly convex transversely; palmo-dorsally it is nearly flat.



TEXT-FIG. 6—Trapezoid, transverse width of dorsal face.

Magnum.—This description is based on examination of 17 specimens of *A. tetradactylum* and eight specimens of *R. sansaniensis*.

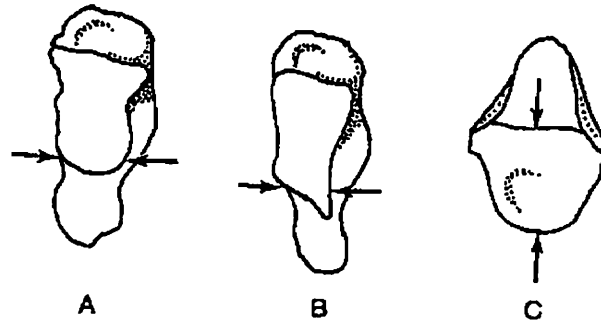
In *A. tetradactylum* the transverse widths of the distal facets (see Text-fig. 7) range from 1.4 to 2.2 cm. For this same dimension the *R. sansaniensis* specimens measure between 2.2 and 2.5 cm. In the range of possible overlap, between 2.0 and 2.2 cm, the proximo-distal lengths of the dorsal faces of the magna determine the genus. In *A. tetradactylum*, specimens having these larger transverse measurements have dorsal faces of 3.3 and 3.4 cm, while the proximo-distal lengths of the *R. sansaniensis* dorsal faces never exceed 3.1 cm.

The palmar margin of the facet for the third metacarpal is a short, transversely symmetrical crescent in *R. sansaniensis* (Pl. 2, fig. 11). In *A. tetradactylum* this margin is straight and it trends palmarly from an ectal corner to a point at its ental extremity (Pl. 2, fig. 6).

In *A. tetradactylum* the facet for the second metacarpal is a plane surface (Pl. 2, fig. 5). In *R. sansaniensis* it is weakly concave palmo-dorsally.

Unciform.—This description is based on examination of 17 specimens of *A. tetradactylum*, 13 specimens of *R. sansaniensis*, and two specimens of *B. brachypus*.

In *R. sansaniensis* and in *B. brachypus* the proximo-ental shoulder of the dorsal face bulges between its contacts with the pyramidal facet and the facet for the fifth metacarpal. In *R.*

TEXT-FIG. 7—Magnum. A, *A. tetradactylum*, transverse width of distal facet; B, *R. sansaniensis*, transverse width of distal facet; C, proximo-distal length of dorsal face.

sansaniensis (see the upper right margin of Pl. 3, fig. 2) the protuberance is rounded proximo-distally as well as transversely; thus it is visible in profile, as we see at the left margin of Plate 3, figure 5. In *B. brachypus* (see the left portion of the dorsal face, Pl. 3, fig. 3) the bulge extends the transverse dimension of the bone, but it is not rounded proximo-distally and so it is not visible in profile. The living genus *Dicerorhinus* also have tuberosities at the proximo-ectal shoulder of the unciform. In *A. tetradactylum* and in the genus *Rhinoceros* the bone slopes continuously along a short, straight path between the pyramidal and metacarpal IV facets (see the upper right edge of the dorsal face in Pl. 3, fig. 1).

In *R. sansaniensis* there is a depression in the articular material between facets for the fourth and fifth metacarpals. This puncture in the surface has an oval outline; it is located at the palmo-dorsal midline of the articular material just distal to the Mtc. V facet.

In all rhinoceroses the facet for the fifth metacarpal is developed principally behind the dorsal face of the bone. In *B. brachypus*, *R. sansaniensis* and genus *Dicerorhinus* a narrow band of articular material extends the facet well across the neck of the palmar tubercle. In *A. tetradactylum* and genus *Rhinoceros* the articular material has an amorphous and faint outline at the neck of the palmar tubercle.

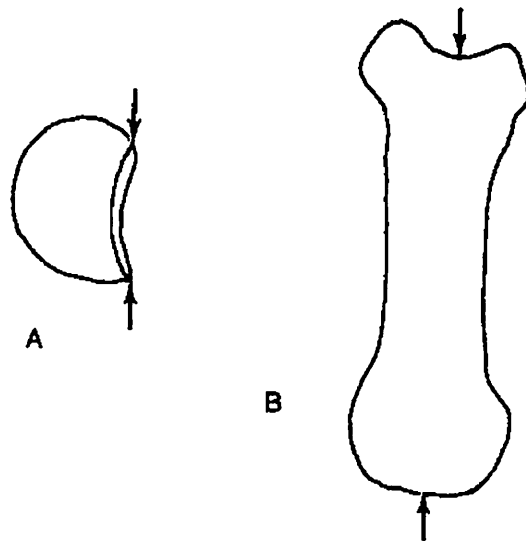
In *B. brachypus* the facet for the fourth metacarpal is narrow palmo-dorsally, and it is flat. In all other rhinoceroses, this facet is broad palmo-dorsally, and the surface form is complex: concavo-convex palmo-dorsally and concave transversely (compare figs. 7-9 on Pl. 3).

In *B. brachypus* facets for the fourth and fifth metacarpals are independent surfaces, one parallel to the transverse plane of the bone, and the other parallel to the palmo-dorsal plane. A narrow perpendicular band connects them. In all other rhinoceroses, articular material blends the facets for the fourth and fifth metacarpals, obscuring the perpendicular orientations of the facets and the ectal limit of the Mtc. IV facet.

Metacarpal II.—This description is based on examination of 18 specimens of *A. tetradactylum*, four specimens of *B. sansaniensis* and one specimen of *B. brachypus*.

Proximo-distal lengths of the second metacarpal (see Text-fig. 8) range from 14.0 to 15.3 cm for the *A. tetradactylum* specimens. Only two of the *R. sansaniensis* second metacarpals are complete; both are 16.0 cm long.

The palmo-dorsal widths of the proximal



TEXT-FIG. 8—Mtc. I. *A*, palmo-dorsal width of the proximal head; *B*, proximo-distal length of a metacarpal.

heads of *A. tetradactylum* specimens range from 2.9 to 3.4 cm; the mode is 3.2 cm. Two of the four *R. sansaniensis* specimens measure 3.5 cm and the others are 3.6 and 3.9 cm wide, respectively. The lone *B. brachypus* specimen has a palmo-dorsal width of 5.0 cm at the proximal head.

The articular surface for the third metacarpal consists of a single, weakly concave facet in *A. tetradactylum* (see Pl. 4, fig. 3). In *R. sansaniensis* (Pl. 4, fig. 4), in *B. brachypus* and in all living rhinoceroses there are two facets for the third metacarpal. The dorsal facet has a larger area than the palmar. Both are plane surfaces, but their positions on the bone render the unit weakly concave. The gap between the two surfaces receives the proximal terminus of a hollow in the ectal side of the bone. In all specimens, the third metacarpal lies distally of the second at their contact.

There is a facet for the trapezium in *R. sansaniensis*, *B. brachypus* and in genus *Dicerorhinus*. In *A. tetradactylum* (Pl. 4, fig. 6) and in the living genus *Rhinoceros* there is no such facet. In *R. sansaniensis* (see Pl. 4, fig. 5) the facet is visible from the ental side of the bone; it is rounded proximally as it blends into the proximal head. In *B. brachypus* the facet is a plane surface that forms a tangent to the corner between the ental and palmar faces of the bone. The facet is folded along a straight line from the proximal head.

Distinctive profiles of the proximal heads may be viewed in figures 3 and 4 of Plate 4. In *A*,

tetradactylum (Pl. 4, fig. 3) the line that represents the junction of the magnum facet with the proximal head slopes distally from its dorsal (left) terminus along a convex path to its palmar terminus. In *R. sansaniensis* and in *B. brachypus* the margin is nearly horizontal dorsally (right half). Near the dorso-palmar midline, the profile becomes elevated and then gently convex as it slopes to the palmar terminus.

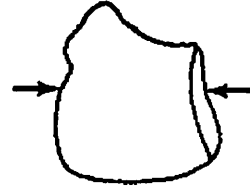
Metacarpal III.—This description is based on examination of 17 specimens of *A. tetradactylum* and six specimens of *R. sansaniensis*.

The proximo-distal lengths of the bones range from 15.5 to 16.0 cm for the five complete *R. sansaniensis* specimens. In *A. tetradactylum* 12 specimens are intact. Of these, nine are 16.3 to 16.5 cm long; three measure from 17.3 to 17.5 cm in this dimension. In *A. tetradactylum* there is a greater difference between the proximo-distal lengths of metacarpals II and III than there is in *R. sansaniensis*.

A. tetradactylum resembles the genus *Dicerorhinus* and *R. sansaniensis* looks like the genus *Rhinoceros* with respect to shapes of their palmar facets for the fourth metacarpal. In *A. tetradactylum* (see Pl. 4, fig. 1) the proximal edge of that facet is a straight line that is palmo-dorsally broad. In *R. sansaniensis* (see Pl. 4, fig. 2) the facet is nearly oval in outline; its proximal margin is rounded, and it is palmo-dorsally short.

Metacarpal IV.—This description is based on examination of 19 specimens of *A. tetradactylum*, seven specimens of *R. sansaniensis* and two specimens of *B. brachypus*.

With the exceptions of two specimens, the proximo-distal lengths of these bones range from 14.0 to 14.5 cm for *A. tetradactylum*. *R. sansaniensis* specimens are 13.4 to 13.9 cm long. The two *B. brachypus* specimens differ from each other by a full centimeter; one is 13.0 cm long and the other 14.0 cm long. The exceptional *A. tetradactylum* specimens measure within the *R. sansaniensis* range. The transverse widths of the proximal heads (see Text-fig. 9) are greatest for the two *B. brachypus* specimens, at 3.8 and 4.0 cm. *A. tetradactylum*



TEXT-FIG. 9—Mtc. IV; Transverse width of the proximal head.

and *R. sansaniensis* specimens range from 2.5 to 3.5 cm.

The palmar facets for the third metacarpals have elliptical outlines in *A. tetradactylum* and in *R. sansaniensis*. In *B. brachypus* (Pl. 5, fig. 3) the facet is rectangular. Proximally, the long axis of the palmar facet in *A. tetradactylum* (Pl. 5, fig. 1, left) is directed toward the dorsal facet. In *R. sansaniensis* (Pl. 5, fig. 2, left) the long axis of the palmar facet is directed away from the dorsal facet at its proximal terminus. Consequently, the gap between the two facets appears to be broader in *R. sansaniensis* than in *A. tetradactylum*.

There is no visible facet for the fifth metacarpal in either *B. brachypus* specimen. In *R. sansaniensis* (Pl. 5, fig. 5) a sharp crest parallel to the ectal margin of the proximal head separates facets for the unciform and the fifth metacarpal. The metacarpal V facet is a flat surface, directed more laterally than proximally. In *A. tetradactylum* (Pl. 5, fig. 4) a rounded foldline separates the two facets on the proximal head. The metacarpal V facet is a weakly concave surface, directed only slightly laterally of proximally.

The unciform facet is a plane surface in *B. brachypus* (Pl. 5, fig. 6), while in *A. tetradactylum*, *R. sansaniensis*, and in living rhinoceroses it is convex palmo-dorsally and concave transversely.

Metacarpal V.—This description is based on examination of one specimen of *R. sansaniensis* and five specimens of *A. tetradactylum*.

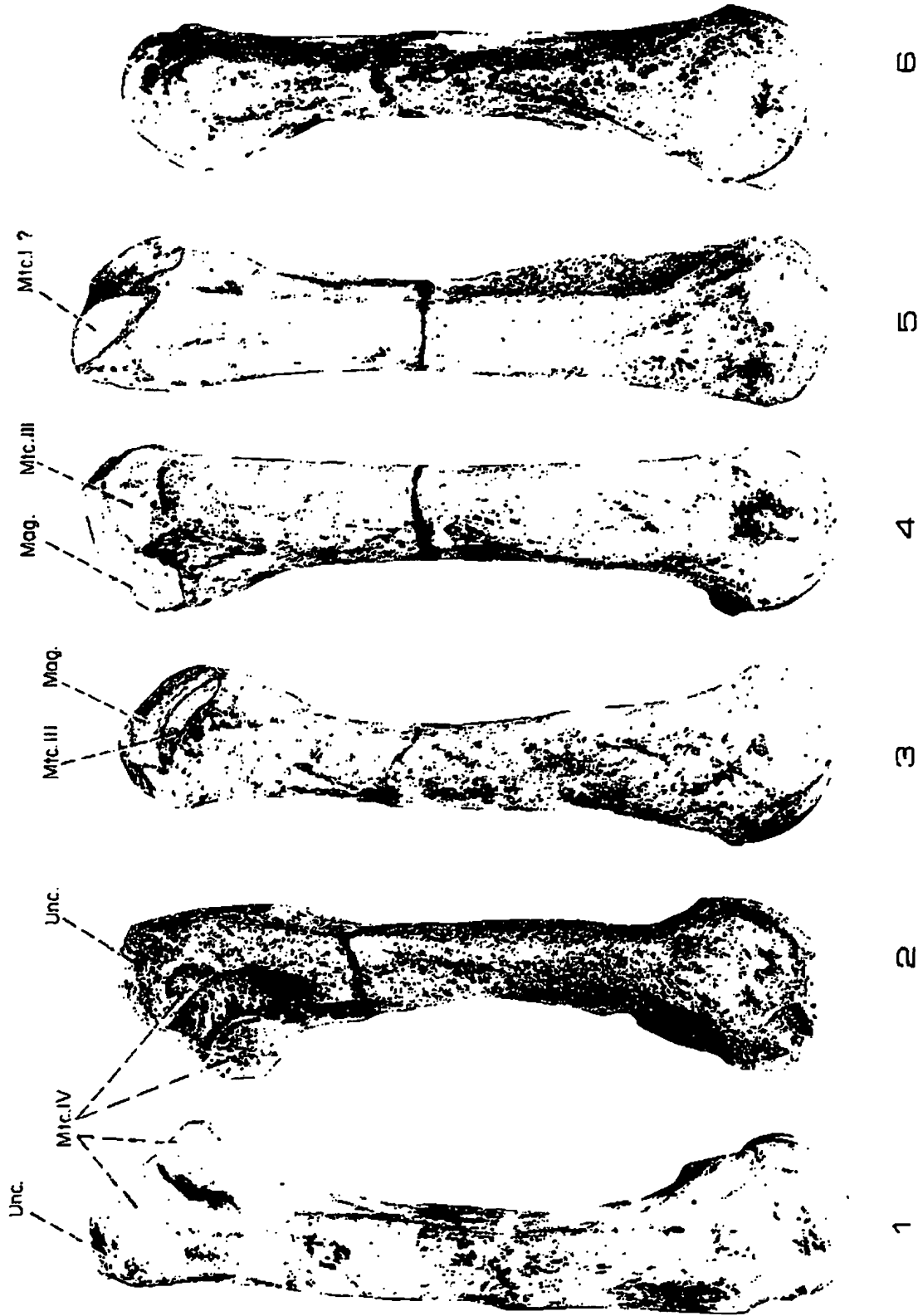
The fifth metacarpal of *A. tetradactylum* is 7.0 to 7.8 cm long; no two specimens have the same proximo-distal lengths. The distal head

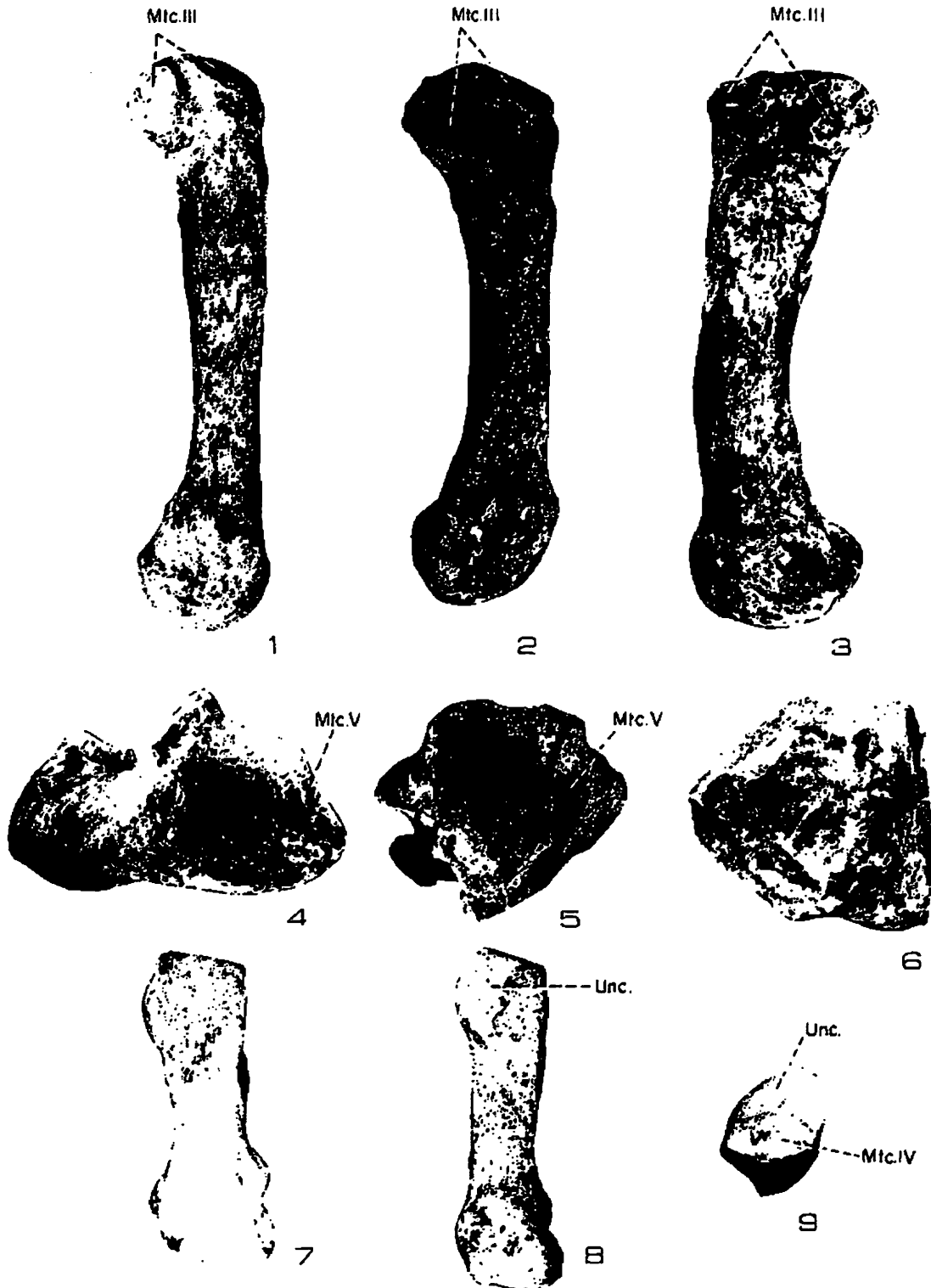
EXPLANATION OF PLATE 4

All figures are $\times 9/8$; abbreviations: Mag. = Magnum; Unc. = Unciform.

FIGS. 1,3,6—*A. tetradactylum*. 1, left Mtc. III, ectal surface; 3, left Mtc. II, ectal surface; 6, left Mtc. II, ental surface.

2,4,5—*R. sansaniensis*. 2, right Mtc. III, ectal surface; 4, right Mtc. II, ectal surface; 5, right Mtc. II, ental surface.





has well-formed trochlea for the first phalanx. The proximal head is capped by a facet for the unciform; there is no facet for the fourth metacarpal. In *R. sansaniensis*, as in living rhinoceroses, the fifth metacarpal consists of facets for the unciform and the fourth metacarpal buttressed by a rounded chunk of bone.

In *R. sansaniensis* the unciform facet is divided by folds into three parts. The dorsal half of the facet is divided for two of these flat surfaces and the palmar half is unbroken. In *A. tetradactylum* (see Pl. 5, fig. 8) the unciform facet is continuously but asymmetrically convex; the arch levels out palmarly. In the living genus *Rhinoceros* the unciform facet is a flat surface occupying a position analogous to the dorsal half of the *R. sansaniensis* unciform facet. In genus *Dicerorhinus* the unciform facet is predominantly a flat surface in a position like that of genus *Rhinoceros*, but a narrow band of articular material branches off palmarly to fit within the neck of the unciform. If an evolutionary trend is represented by these specimens, it would consist of reduction of the unciform facet to a dorsal zone on the fifth metacarpal.

The *R. sansaniensis* facet for the fourth metacarpal is a palmo-dorsally elongate trough. Both living rhinoceros genera have facets similar to that of *R. sansaniensis* in outline, but the surfaces are flat and not depressed.

Functionally, the *A. tetradactylum* fifth metacarpal seems to have resembled fifth digits of the other rhinoceroses. Its proximo-distal length relative to that of the fourth metacarpal, muscle scars, and positions of articular facets on the unciform and on the fourth metacarpal all point to this conclusion. Discrepancies in proximo-distal lengths between two adjacent bones do not necessarily prove that the shorter one is not a functional metapodial; in the four-toed tapir, for example, the fifth metacarpal is only 4/5 as long as the fourth. But, the *A. tetradactylum* fifth metacarpal is only half as long as the fourth; it is hard to visualize that fifth toe reaching the ground.

The bulge near the proximal head on the dorsal face of the *A. tetradactylum* fifth metacarpal (see Pl. 5, fig. 7) is rugose in texture. No other zone on that bone suggests so clearly an area for muscular insertion. The outline and form of that bulge closely resemble the entire dorsal faces of the other rhinoceros fifth metacarpals. Muscle scars cover those faces in modern specimens. If muscles had, in fact, gathered in that restricted area of the *A. tetradactylum* fifth metacarpal, we can expect the bone to have been ill-equipped for the operations of flexion, extension, abduction and adduction as is the fifth metacarpal of the tapir (see Klaitz, 1972).

The *A. tetradactylum* fifth metacarpal fit together with the unciform and the fourth metacarpal in the same ways that the fifth metacarpals of other rhinoceroses fit together with their respective unciforms and fourth metacarpals. The unciform offers a concave facet that looks palmo-ectally, and the fourth metacarpal provides a narrow shelf that is directed as much proximally as laterally (see Pl. 5, figs. 4,5). Within these narrow boundaries, the fifth metacarpal is fixed at the level of the distal carpal row.

CONCLUSION

For Osborn (1929, P. 775), "each carpal . . . mirrors the primitive cursorial, mediportal or graviportal locomotor stage of the limb." To illustrate, Osborn chose the two medial, pivotal, bones of the carpus, the lunar and magnum, for perissodactyls of differing sizes and geologic ages. Looking at the front and at the rear of each articulated carpus, Osborn derived the descriptions shown in Table 1.

By contrast with the mediportal *Tapirus* and *Rhinoceros*, *B. brachypus* seems to fit the graviportal model. Palmo-dorsal widths of *B. brachypus* carpal bones tend to exceed their proximo-distal lengths by a greater margin than similar relative measurements observed for the other rhinoceroses. In this way the elements are higher and narrower in the other rhinoceroses

←

EXPLANATION OF PLATE 5

Abbreviation: Unc. = Unciform

- FIGS. 1,4,7,8—*A. tetradactylum*. 1, left Mtc. IV, ental surface, $\times \frac{5}{8}$; 4, left Mtc. IV, unciform facet (proximal), $\times \frac{2}{3}$; 7, right Mtc. V, dorsal surface, $\times \frac{5}{8}$; 8, left Mtc. V, palmar surface, $\times \frac{5}{8}$.
2,5,9—*R. sansaniensis*. 2, left Mtc. IV, ental surface, $\times \frac{5}{8}$; 5, left Mtc. IV, unciform facet (proximal), $\times \frac{2}{3}$; 9, right Mtc. V, articular face, $\times \frac{5}{8}$.
3,6—*B. brachypus*. 3, right Mtc. IV, ental surface, $\times \frac{5}{8}$; 6, right Mtc. IV, unciform facet (proximal), $\times \frac{2}{3}$.

than they are in *B. brachypus*. However, while some bones are broader palmo-dorsally in *B. brachypus* than in other rhinos, the *B. brachypus* carpus is not broader transversely.

If the lunar-magnum-unciform contact is examined internally, rather than from the front or back, we have a hint of what may be a profound difference between *B. brachypus* and the other rhinoceroses. First, in all the rhinos studied and in the tapir, the lunar rests equally on the magnum and unciform. What is significant is the disposition of facets for the magnum and unciform upon the distal surface of the lunar. In *Tapirus* and in *B. brachypus*, magnum and unciform facets are separated by an approximately transversely-trending fold-line. In all other rhinoceroses, the foldline trends palmo-dorsally diagonally. For all rhinos but *B. brachypus*, internal forms of the facets suggest that during normal operations of flexion and extension, magnum and unciform might have been displaced with respect to the lunar along curved paths cutting all three perpendicular planes of the manus. In *B. brachypus* and in *Tapirus*, magnum and unciform can only have see-sawed with respect to the lunar, cutting neatly proximo-distal and palmo-dorsal paths as the magnum was flexed and extended. No specimen of a *B. brachypus* magnum was available for comparison with Osborn's contentions as to the magnum hook, but the distal surface of the lunar reveals that the magnum certainly was not flattened proximally.

The palmar contact between scaphoid and lunar is parallel to the proximo-distal plane of the manus in *Tapirus* and in *B. brachypus*, while in all other rhinos studied, the plane of this contact marks diagonals to proximo-distal and transverse planes. For all rhinoceroses but *B. brachypus*, the lunar can only rotate within a scaphoid socket. But in *Tapirus* and in *B. brachypus*, there are no impediments to displacement along proximo-distally trending paths. Modifications at the dorsal halves of the scaphoid and lunar exclude any but a proximo-distal displacement path for the tapir; *B. brachypus* has no such specialization. Proximo-distally trending paths for displacement are seen again in *Tapirus* and in *B. brachypus* between unciform and magnum. In the other rhinos, magnum and unciform have curved contacts trending across all three planes of the manus.

The unciform-Mtc. IV contact is a nearly horizontal surface in *B. brachypus* (Pl. 3, fig. 9). For no other studied species is this contact so lacking in relief. The distal surface of the *B. brachypus* trapezoid is flat palmo-dorsally, whereas trapezoids of other rhinoceroses and

tapirs are deeply concave. One likely interpretation of these phenomena is that the *B. brachypus* metacarpals were functional continuations of the immediately proximal carpal bones. In this event, intra-carpal displacements associated with flexion could not have been translated into digital adduction. Neither could the opposite interplay occur; extension would not be accompanied automatically by digital abduction, as it is in living tapirs and rhinoceroses.

In this interpretation, the *B. brachypus* manus was, despite its thick block-like bones, mechanically weaker than the manuses of either the tapir or other rhinoceroses. Uplift of the foot at the beginning of a step would not be initiated by digital adduction but by simple, forceful flexion. The impact of landing would not be distributed across the carpus by adducted digits, but absorbed by the very massiveness of the bones. The magnum and Mtc. III, bones that might add weight to or disprove this hypothesis, are unavailable for study, but the proximo-distally trending and flat facet for the Mtc. III on the unciform tends to support this interpretation.

The concepts of medi- and graviportalities do not even suggest the degree and quality of functional diversity among *Tapirus*, *B. brachypus* and the other rhinos. Certainly these terms obscure the phyletic diversity represented here.

Viret (1958), following Roger, recognized the "primitive" quality of the *B. brachypus* carpus, and he suggested that the type might originate with undifferentiated Aceratheriinae stock. If functional simplicity is primitive, then the *B. brachypus* carpus was primitive. The idea that simplicity equals primitivity must be applied particularly cautiously here, since this idea has contributed so much to the stultification of investigations into carpal functions. In the theoretically primitive, simple carpus bones are aligned serially; one proximal bone meets one distal bone. The theoretically advanced, complex condition is the alternating carpus, where two proximal bones and two distal bones each meet more than one element of the other row. But in fact, *Tetraclaenodon* had an alternating carpus while large species of its descendant *Phenacodus* (especially *P. primaevus*, according to Radinsky, 1966b) had a serial carpus. After Matthew (1897) had made a similar observation, Osborn formally abandoned his previous work on ungulate carpal functions (1929, p. 774). Without reference to fossils, the choice of Aceratheriinae stock for ancestry of *B. brachypus* seems arbitrary. In addition, this choice is contradictory to another standard measure of primitivity: the fifth metacarpal.

No specimen of a *B. brachypus* Mtc. V appears in the collections. To judge from the shapes and positions of facets on the unciform and to deduce from the lack of facets or modifications of the shaft of the fourth metacarpal, Mtc. V was much reduced from a functional digit. The *A. tetradactylum* Mtc. V, by contrast, had the shape of a functional digit, even if, as described in the text, it probably functioned much like Mtc. V in living rhinoceroses and in *R. sansaniensis*. Osborn (1929) explained this shape as a persistent relic of a rhinocerotoid transition to a mediportal (isotridactyl) condition. Osborn associated the fully functional Mtc. V with "weight-bearing types" of titanotheres and with the "graviportal amynodonts." One way to account for a weight-bearing type (*B. brachypus*) with a reduced Mtc. V and a mediportal type (*A. tetradactylum*) with an elongate fifth metacarpal, is to question the proximity of phyletic relationship between the forms. Another way is to question the validity of Osborn's theory. After all, living perissodactyls confront us with an exception to the implied rule; the hound-sized tapir has four toes and the rhinoceros has three.

A possible source of difficulty is an assumption underlying the concept of digital reduction; the idea that the metacarpal is lost functionally when its digital shape is lost. For living rhinoceroses, bone shapes and positions as well as observable movements of the forelimb strongly suggest the contrary. For the tapir, each step of a walk, trot or gallop is initiated by adduction of digit V. In the rhinoceros, digit IV is adducted before the wrist is flexed to leave the ground. At the conclusion of a step, digits are abducted for both animals, and the most ectal digit appears to lead the operation in both animals. In the tapir, the only digital abductor muscle (*M. abductor digiti quinti manus*) links the fifth metacarpal with the pisiform. Myology of the rhinoceros digits is incompletely known. But muscle scars and bone shapes and positions suggest that (1) pisiform and Mtc. V may have been linked by a muscle analogous to the *M. abductor quinti digiti*, and (2) Mtc. V and the ectally deflected distal head of Mtc. IV may have been connected by muscle or tendon. In the tapir, the pisiform represents the arm of a primary lever useful in abducting digit V. The rhinoceros would be endowed with a lever of the second degree, for Mtc. V would serve as a fulcrum between pisiform and Mtc. IV. Whether or not this apparatus exists for the rhinoceros, *R. sansaniensis* and *A. tetradactylum* had pisiforms, and

Mtcs. IV and V of the same functional position as seen in living Rhinocerotidae.

Since it is unlikely that the *B. brachypus* manus initiated a step with an adductive operation, or concluded it with an abductive one, the fifth metacarpal probably had a role neither like that of *Tapirus* nor like that of *Rhinoceros*. Yet, if that bone existed at all, it probably had a role in the uniquely *Brachypotherium* system of flexion and extension.

Internal forms of all available bones of the *B. brachypus* carpus show that this manus was highly specialized to flexor, extensor, orthal-pathed operations. Forms of all bones of living rhinos and probably the other two rhinoceros genera from Sansan are specialized to adductive-flexor, abductor-extensor, rotational-pathed operations. And forms of *Tapirus* bones are specialized to adductive-flexor, abductor-extensor, orthal-pathed operations. No evidence from these specimens indicates that any form might have preceded any other, although fossils of ancestral forms might show common lineages. Neither gross size nor any other criterion that would summarily describe these animals as medi- or graviportal can explain these distinctive solutions to the problems of lifting the foot from the ground and of absorbing the impact of landing.

If the elongate Mtc. V of *A. tetradactylum* represents a transitional phase, no other feature of the carpus suggests that this manus was not functionally specialized in the same way as *R. unicornis*. Perhaps the elongate shaft with the first phalanx of a digit are aberrations meriting specific denomination. Perhaps they merit no more note than sub-specific variation. This was Filhol's explanation of cranial differences he observed between specimens from Sansan and *Aceratherium incisivum* Kaup from Eppelsheim.

Among the rhinoceroses studied—excluding *B. brachypus*—no other differences would deserve either specific or sub-specific notation. Characteristics I used in the text to differentiate among genera are of the same order, scale and functional insignificance as characteristics that are individually variable. When genera and species are defined by the cranium, the distinctions I have indicated are useful to the system. However, the foot characters themselves do not in any way support the validity of these groupings. For many criteria, *A. tetradactylum* resembles the living Rhinocerotinae and *R. sansaniensis* looks like a member of the living Dicerorhinae. But for other features *A. tetradactylum* and the living Dicerorhinae are

identical and *R. sansaniensis* and the living Rhinocerotinae look alike. One possible explanation for these cross-overs is that *R. sansaniensis* and *A. tetradactylum* represent an early stage in the divergence between the Rhinocerotinae and Dicerorhinae lines, when subfamilial characteristics were not rigidly fixed. If the Rhinocerotinae and Dicerorhinae had exhibited widely divergent or distinctive structural-functional forms, this would be a satisfactory explanation. But in fact, they do not. Here again only minor, functionally insignificant characteristics distinguish the taxa. Only *B. brachypus* offers substantive contrasts to this stable rhinocerotoid form. The taxonomic significance of this observation may emerge in context of studies of cranial and locomotor systems, beyond the scope of this paper.

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