THE MOVING MESAXONIC MANUS : A COMPARISON OF TAPIRS AND RHINOCEROSES

by

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L'étude comparée des os du carpe et du métacarpe et des mouvements de la main, chez les tapirs et les rhinocéros, permet une nouvelle interprétation de l'idée d'une symétrie mésaxonique.

Ce sont les structures caractéristiques du carpe et du métacarpe qui déterminent le type de flexibilité ou de rigidité de la main. Les types de flexibilité ou de rigidité se traduisent eux-mêmes par des types de mouvements caractéristiques.

Chez les rhinocéros la réduction du métacarpien V peut être considérée comme une modification de la fonction digitale plutôt que comme une suppression de celle-ci.

La signification systématique de ces types de structure et de mouvement est envisagée à la lumière d'observations faites sur le rhinocéros tétradactyle miocène, *Aceratherium tetradactylum*.

INTRODUCTION

In 1884 Marsh established organizational symmetry of the limb as a principle for classifying ungulates. The system calls attention to the longest and most persistent elements of both manus and pes. If the axis of the limb passes through digits three and four, paraxonic symmetry is exhibited; while the term « mesaxonic » describes the condition wherein the axis of the limb passes through the third digit.

At about that same time several other students — notably Rütimeyer (1865), Gaudry (1878), Baur (1885) and Schlosser (1886) — were also considering bone structures, the symmetry of their dispositions, the relationship of carpal and tarsal bones to a functioning manus or pes, and the evolutionary significance of these features. Cope (1883) contributed the term « taxeopod » to describe carpal and tarsal systems in which bones are aligned serially in straight rows, and the term « diplarthrous » to describe carpal and tarsal systems exhibiting overlap or alternation between proximal and distal rows. In addition, Cope (1887) speculated upon the evolution of the ungulate manus or pes in context of their functions :

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Mammals (excepting the horse and plantigrade animals such as bears) turn the toes out in walking... As the foot is descending toward the ground, it is, with the distal part of the leg rotated from within outwards. The rotation of the foot is promptly arrested at the moment of its contact with the ground, and the effect of this arrest is to produce a torsion of the leg, and a pressure from within outwards of the proximal or moving element of each articulation against the distal or fixed element. Thus a constant torsion or strain from within outwards has been exerted by the first row of carpal and tarsal bones, on the second row, and thus has arisen the gradual transition from the linear arrangement in condylarthra to Diplarthra. The advance of diplarthrism is in direct ratio to the advance of digitigradism, for the greater the length of the foot, the greater the elasticity of the leg and the greater is the torsion. (p. 988).

Kowalevsky, Ryder and Osborn subsequently considered this topic. Osborn (1890) concurred with Cope's thesis that the unguligrade manus and pes evolved from plantigrade analogues; in fact, Osborn outlined six evolutionary phases featuring, simultaneously, elevation, progressive digital reduction and diplarthrism. Unlike Cope, Osborn believed that any functioning manus or pes is itself equipped to brake displacements as well as to facilitate them. The limb would not need a moving row and a fixed row of bones to achieve these capacities, only an accommodation *within* the manus to the kinds of strains sustained by the given elevation and degree of digital reduction. Unequal growth of carpal and tarsal bones, and bone displacements within the manus or pes effect this accommodation.

Growth is more directly brought about by vertical pressure, as seen in the magnum of the Equidae ; and displacement, by lateral strain, as seen in the shifting of the metapodials to the ectal side of the carpus. (p. 560).

Osborn stressed the interactions among the several developments.

...the reduction of the lateral digits in the ungulate foot is largely the direct result of elevation to the unguligrade position which rendered useless the shorter lateral digits of the plantigrade foot. Yet, every step in reduction of toes influenced the growth and displacement of the more proximal elements. (p. 560).

Osborn chose the following illustrative example.

In the perissodactyla, the reduction of McV, as can be observed in rhinoceroses... is accompanied step by step by displacement of the lunar from the magnum. Lateral compression of the carpus has nothing to do with this displacement, because the tapir, which even now is in the transition stage between Types IV and V, has a narrower carpus than *Aphelops*. The tapir manus is now in the stage of evolution which was passed by the rhinoceros in the Miocene period. (p. 567).

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Students of locomotion mechanics subsequently fastened upon adaptations to cursorial (fleet) mediportal (heavy) and graviportal (ponderous) gaits. Matthews (1909) described ratios of limb segments and accordingly classified ungulates into one of these and other, gradational, modes of locomotion. Gregory (1912) continued these studies, adding to the definition of each mode the angular dispositions of limb segments. These Gregory tied to the « acceleration increment of stride », a translation of structural ratios into observable movements of the limb. Osborn (1929) described an evolutionary trend for the perissodactyls beginning with a cursorial mode and progressing to a graviportal one. Bone shapes were particularly important in this analysis. As for the manus, Osborn indicated hooks on the magnum and widths of the distal surface of the magnum and so inserted carpal bones into the evolutionary theory (p. 774-776). Some of the inadequacies in this theory become apparent when one considers more recent detailed analyses of the gait (Hildebrand, 1966) and of the roles of axial and vertebral muscular systems (Camp and Smith, 1942 and Slijper, 1946). In 1968, Sondaar went back to study the Equidae carpal system for functional capacities and evolutionary tendencies in light of more recent findings. And in 1971 Yalden, who was dissatisified with what he termed Osborn's external approach to the carpus, offered an elaborate analysis of the potential displacements along the facets of each horizontal level of the ungulate manus. By imposing grids upon the proximal surfaces of each row of carpal bones and by locating structural impediments, Yalden determined the angles at which bones may be displaced within the manus. As for the ceratomorphs, Yalden believed that « ... living rhinoceroses, tapirs, *Aceratherium* and *Paleotherium* conform morphologically to the same displacement pattern. » (p. 475).

The present study is limited to the manuses of living rhinoceroses and tapirs. But since both of these animals exhibit mesaxonic symmetry and since they represent two successive evolutionary phases in Osborn's scheme, a detailed study of their structures and functions may hopefully contribute to a more thorough understanding of the ungulate manus.

We will consider here the interactions among eight carpal and four metacarpal bones. The fused radius and ulna meet, entally-to-ectally, the scaphoid, lunar, pyramidal and pisiform. The pyramidal has a palmo-ectal articulation with the pisiform. Distally, the scaphoid meets the trapezium, trapezoid and magnum; the lunar articulates with the magnum and unciform; and the pyramidal meets the unciform. The distal carpal bones meet the meta-

carpals : trapezoid and magnum — Mtc. II, magnum and unciform
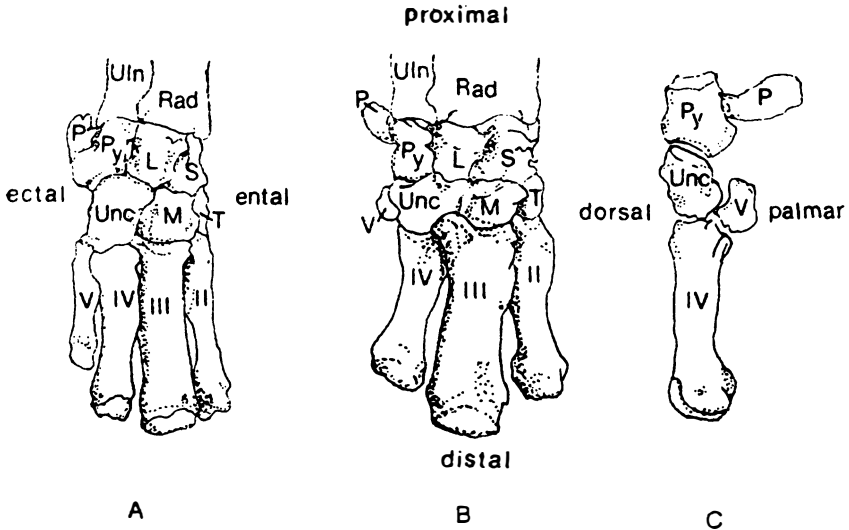—. Mtc. III, and unciform — Mtcs. III, IV and V.

Fig. 1. — A : Dorsal view of tapir manus. B : Dorsal view of rhinoceros manus. C : Ectal view of rhinoceros manus. (Figs. A and B adapted from Lessertisseur and Saban).

Proximal, distal, lateral and oblique contacts within these diplarthrous manuses offer extensive surface areas for displacements. Yet, as Osborn has shown, carpal and metacarpal bones must endow the manus with rigidity as well as flexibility. Shapes and sizes of the bones, and as Yalden emphasized, characteristics of their articular facets reveal both how adjacent bones support one another and the paths along which these same bones might be displaced with respect to one another.

Since synovial fluid, cartilage and ligaments modify in immeasurable ways the theoretical displacements as determined from dry bones, I approached the problem negatively : in which directions are displacements not impossible ? The question is put to each of a series of adjacent pairs of carpal and metacarpal bones. For each pair, one can determine the directions of « not impossible » displacements between the two bones as well as between the unit and tangential bones. In combination, answers to this negative question form positive and detailed pictures of feasible movements. for the manus. These pictures compare well with observable motions of the forefeet.

Both pictures show that over the course of a step, the rhinoceros

manus rotates while the tapir manus describes an orthal path. For the tapir and rhinoceros, subtle differences in the shapes, positions and orientations of articular facets within the carpus account for the contrasting motions. Bone alignments within the carpus account for part of the difference, but shapes and sizes of metacarpal bones, and particularly of the fifth metacarpal play important supporting roles. The rhinoceros fifth metacarpal is a vestige of the kind of functional digit observed in the tapir ; even so, it is part of the rhinoceros suspension system.

Because of their elongate and robust digits III, tapirs and rhinoceroses exhibit mesaxonic symmetry. However, other features of the third digits — such as articular facets and bone shapes at the proximal head — suggest that the third metacarpal does not represent a plane of bi-lateral symmetry. Within the carpus, though, there are similar bone shapes and facet structures disposed as mirror images at diagonally opposite sides of the manus. Since these structures are the same ones that endow the manus with both flexibility and rigidity, these planes of symmetry of form are also planes of symmetry of function. The two planes intersect at the lunar-magnum contact, vertically above the third digit. The third digit is, then, a fulcrum for the two shifting balances within the carpus. In the tapir and in the rhinoceros the balances move along different paths. Determination of these paths is the subject of this paper.

MATERIALS AND METHODS

While I was privileged to study many specimens in the large collection of the Laboratoire d'Anatomie Comparée of the Muséum National d'Histoire Naturelle, Paris, the following descriptions are based primarily on these individuals :

    T. americanus (1931-528),
    T. indicus (1937.1),
    R. unicornis (1967.101),
    R. sondaicus (A.7075),
    D. bicornis (1944-278),
    D. sumatrensis (A.7965).

I am indebted to the Institut für den Wissenschaftlichen Film, Göttingen, for loan of P. Leyhausen's films, « *Rhinoceros unicornis* — Schritt » and « *Rhinoceros unicornis* — Galopp. » The moving forefoot was studied for both gaits, from anterior and posterior views. Excerpts from the former film were chosen to show the walking forefoot rising and returning to the ground. M. Rinjard, director of the Vincennes zoo, Paris, kindly permitted filming of a woolly South American mountain tapir (*T. terrestris*) and of a young *T. americanus*. M. Gordon of the Laboratoire d'Anatomie Comparée photographed these animals walking and running. While studying the Miocene rhinoceroses of Sansan (Gers) at the Institut de Paléontologie, Paris, for another paper, I

became acquainted with the rich collection of *Aceratherium tetradactylum* carpal and metacarpal bones to which I refer in the conclusion of this study.

Specific differences in patterns of bone fit are so unimportant to observable movements of the manus, that I have compared the generalized tapir with the generalized rhinoceros for this presentation. Structures endowing the manus with rigidity and with flexibility are identified for each of five adjacent pairs of carpal and metacarpal bones. The directions of such rigidities and flexibilities are compared for the tapir and the rhinoceros. Wherever possible, theoretical displacements derived from bone shapes are compared with pictures of the moving forefeet of the animals.

DESCRIPTIONS

SCAPHOID - LUNAR

In both the tapir and the rhinoceros, the proximo-ental pair of bones meet each other along three articular zones. But the positions of these facets on the bones and the shapes of their internal forms show that the bones fit together differently in the two animals. In the tapir, the palmar facet on the lunar is projected entally to meet the scaphoid; the facet is a flat surface, trending parallel to the proximo-distal plane of the manus. In the rhinoceros, the palmar facet on the scaphoid is projected ectally to meet the lunar; and the contact zone is inclined to the proximo-distal plane of the manus so that the lunar lies distally of the scaphoid. The proximo-dorsal facet on the scaphoid is a flat surface inclined to the proximo-distal plane of the manus in the same direction as the palmar facet. The distal contact is a smooth, vertical surface in the tapir, while in the rhinoceros it is inclined in the opposite direction to the other two contact surfaces. The lunar sits above the scaphoid here (fig. 1. A). In the rhinoceros, the scaphoid contains the lunar; but in the tapir, the two bones embrace each other. The scaphoid extends an arm proximo-dorsally while the lunar offers a disto-palmar limb. Within these structures, it is possible for the rhinoceros lunar to rotate within the scaphoid « socket », and for the tapir lunar to be displaced vertically with respect to its scaphoid.

The scaphoid-lunar present a dorsally convex and palmarly concave surface at their proximal heads for the radius. In the tapir (fig. 1. D), the lunar provides the convex zone and the scaphoid, the concave. For the rhinoceros (fig. 1. C) the convex form of the lunar continues upon the dorso-ectal corner of the scaphoid, and the palmo-ectally trending depression in the scaphoid continues upon the back of the lunar. The trends of these forms are

diagonal to the transverse plane of the manus. In the tapir, the division between forms is marked by the transversely trending border between the scaphoid and lunar. Consequently, when the tapir radius moves fore-and-aft across this surface, its path will parallel the palmo-dorsal plane of the manus ; but in the rhinoceros, the path will be palmo-ental to dorso-ectal.

The magnum articulates distally with the scaphoid and lunar. In the tapir, facets are separated by a palmo-entally trending gap; while in the rhinoceros, facets have an extensive contact near the dorsal faces of the bones (figs. 1. E and 1. F). In the tapir, both facets are palmo-dorsally concave with respect to transverse mid-lines that are inclined toward each other. In the rhinoceros, the

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EXPLANATION OF THE PLATES I TO IV

Fig. 1. — Bone pairs of the left manus, elements indicated left to right.
A. *R. unicornis* (1967. 101), scaphoid-lunar, dorsal view.
B. *T. indicus* (1937.1), scaphoid-lunar, dorsal view.
C. *R. unicornis*, scaphoid-lunar, proximal (radius head) view.
D. *T. indicus*, scaphoid-lunar, proximal (radius head) view.
E. *R. unicornis*, lunar-scaphoid, distal (magnum head) view.
F. *T. indicus*, lunar-scaphoid, distal (magnum head) view.
G. *R. unicornis*, lunar-pyramidal, dorsal and proximal (radius and ulna head) view.
H. *T. indicus*, lunar-pyramidal, dorsal and proximal (radius and ulna head) view.
I. *R. unicornis*, pyramidal-lunar, distal (unciform head) view.
J. *T. indicus*, pyramidal-lunar, distal (unciform head) view.
K. *R. unicornis*, magnum-unciform, proximal (lunar head) view.
L. *T. indicus*, magnum-unciform, proximal (lunar head) view.

Fig. 2. — Bone pairs of the left manus, elements indicated left to right.
A. *R. unicornis*, magnum-scaphoid, distal view.
B. *T. indicus*, magnum-scaphoid, distal view.
C. *T. americanus* (1931-528), unciform-magnum-trapezoid, distal view.
D. *D. bicornis* (308-1941), unciform-magnum-trapezoid, distal view.
E. *T. indicus*, unciform-Mtc. IV- Mtc. V, ectal view.
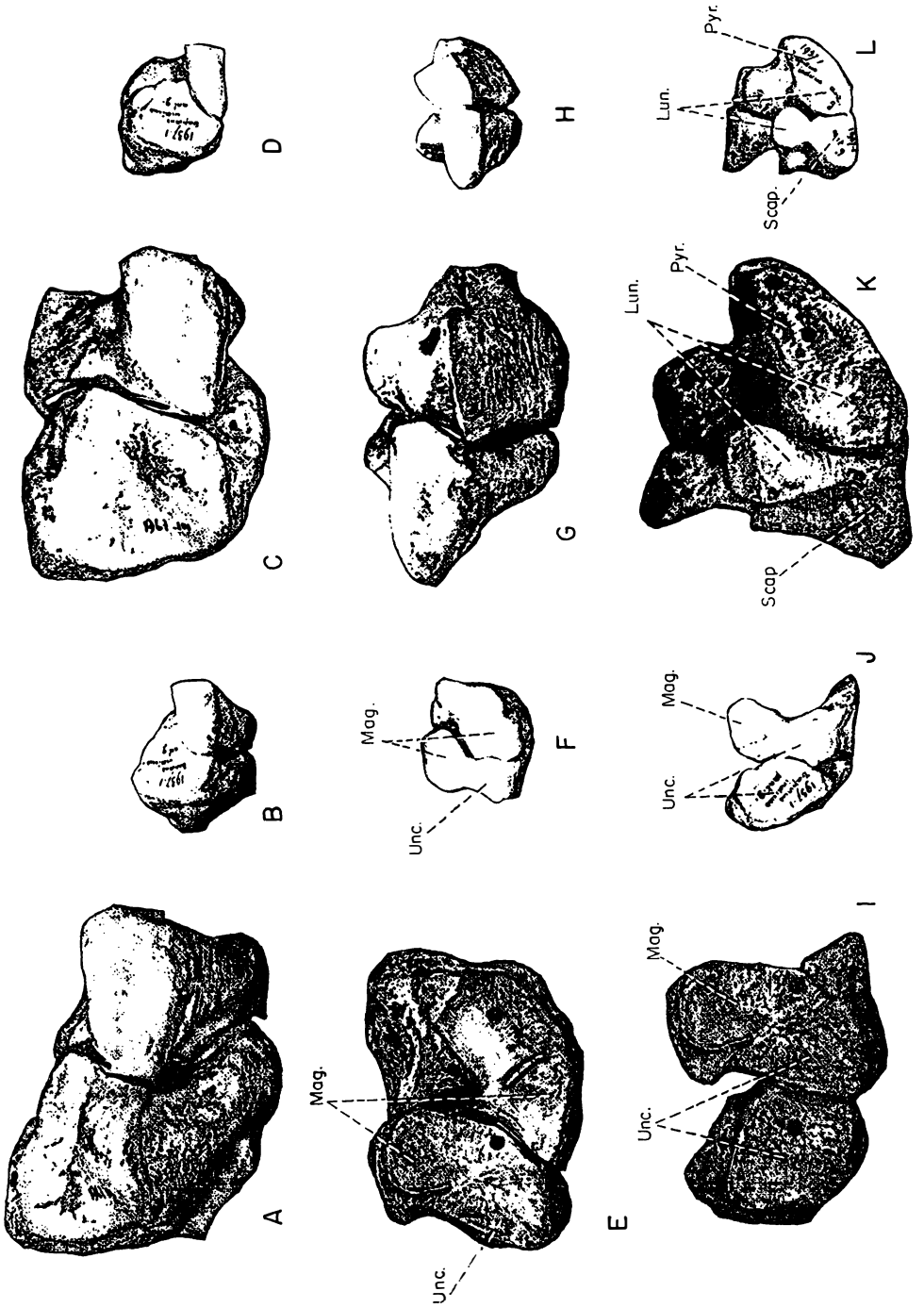F. *R. unicornis*, Mtc. IV-Mtc. V, surface for unciform.
G. *R. sondaicus* (A-7075), unciform-Mtc. IV-Mtc. V, ectal view.
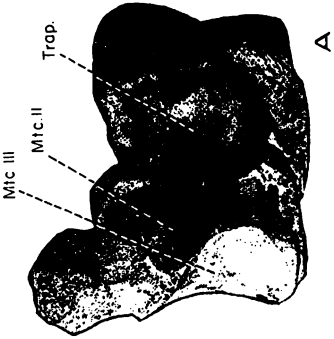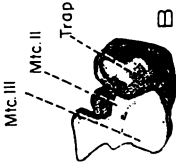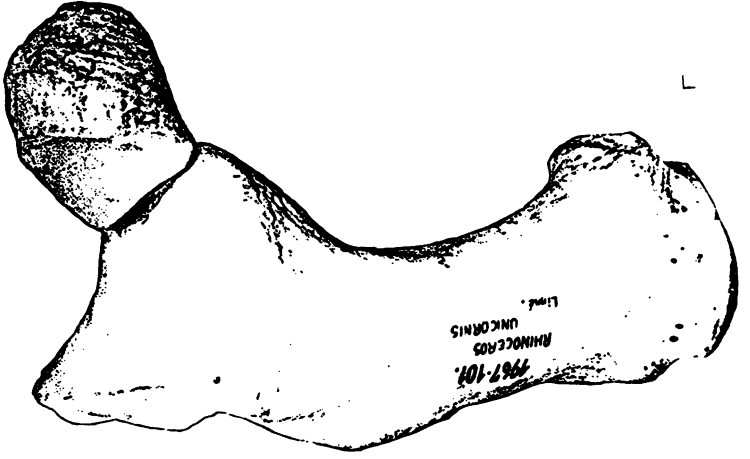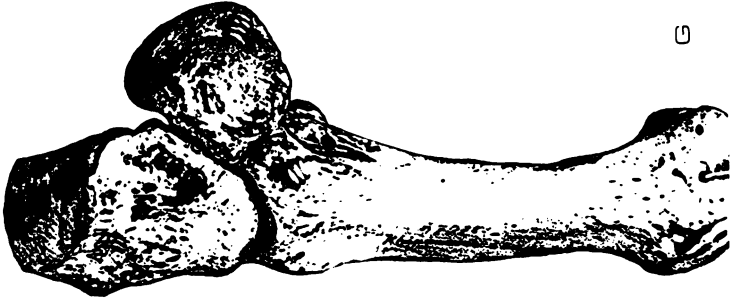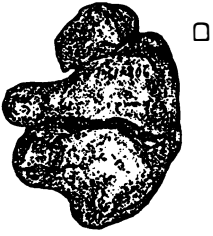
Fig. 3. — Uplift of the forefoot, walking.
A.1 — A.4. *R. unicornis*, posterior view.
B.1 — B.4. *T. terrestris*, posterior view.
C.1 — C.2 *T. americanus* (young), posterior view.
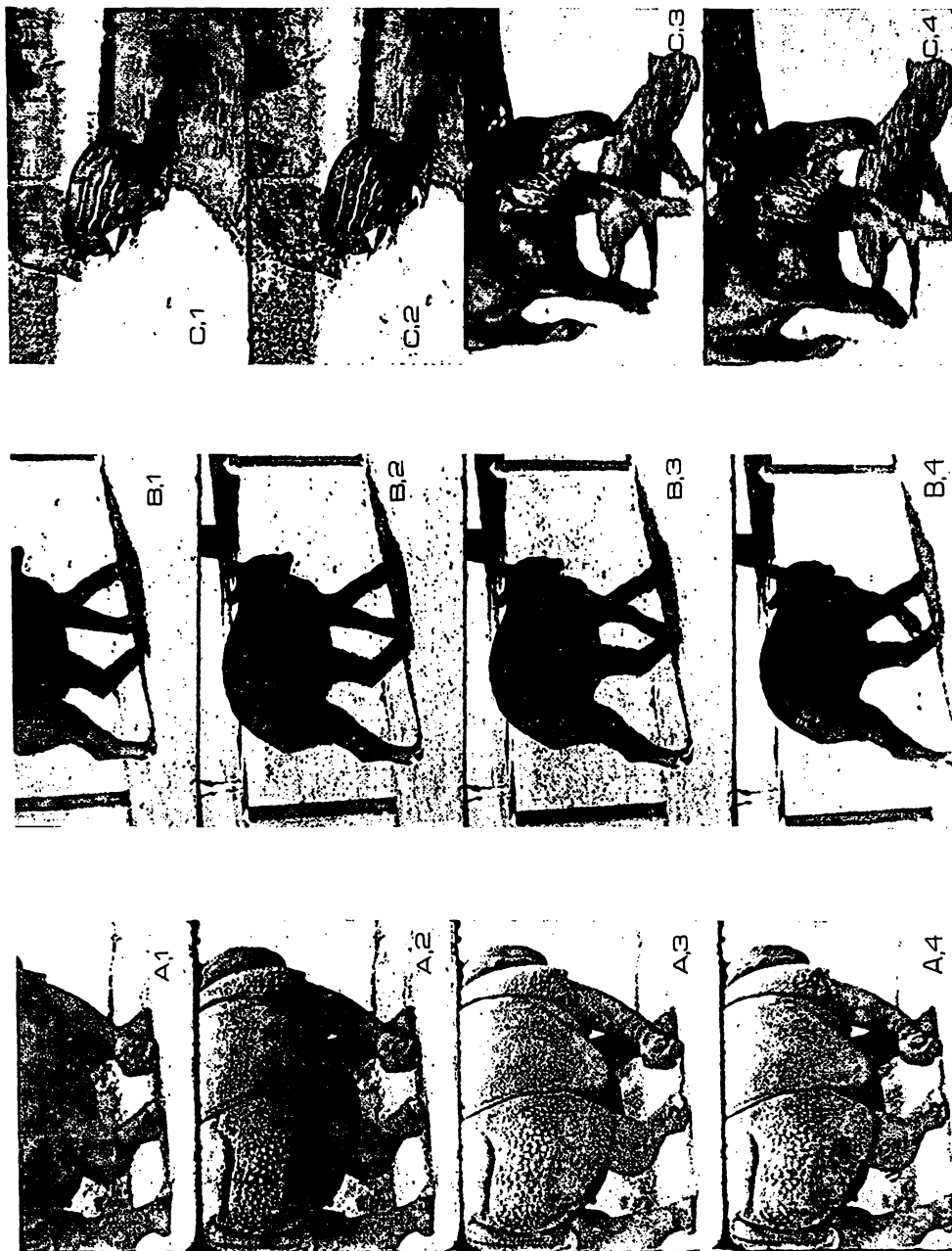C.3 — C.4. *T. terrestris*, anterior view.

Fig. 4. — Descent and landing of the forefoot.
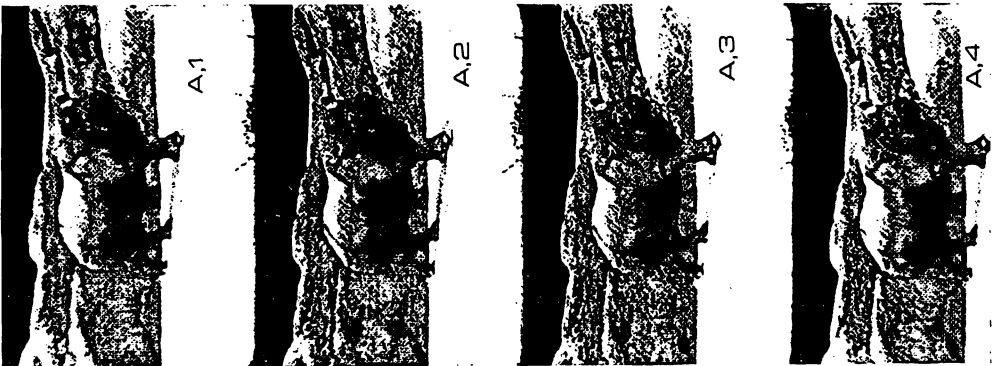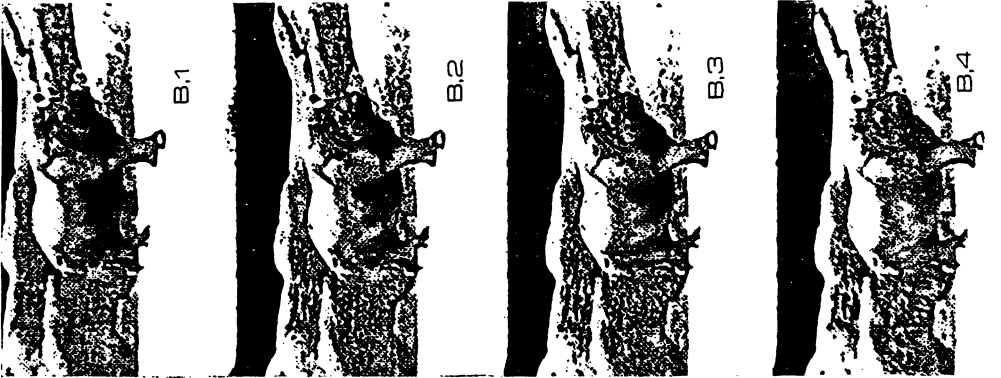A.1-4, B.1-4. *R. unicornis*, walking, anterior view.
C.1 — C.2 *T. terrestris*, walking, posterior view.
C.3 — C.4. *T. terrestris*, running, lateral-anterior view.

For Figs. 1 and 2, broken lines indicate facets for bones tangential to the unit.

D

G

C

L

Trap
Mtc. II
Mtc. III

B

Mtc III
Mtc. II
Trap.

A

79.67-101.
RHINOCEROS
UNICORNIS
Linné.

1931

E

magnum facet on the unciform is flat to weakly convex, but never concave. The form blends with that of the adjacent part of the magnum facet on the lunar. The latter grows increasingly concave and transversely broad as it develops palmarly.

When flexion occurs between carpal rows, scaphoid and lunar roll palmarly with respect to the magnum along these rounded articular surfaces. However, since the magnum meets the lunar palmarly with a tall tubercle, and the scaphoid, dorsally, with a less inflected surface, lunar and scaphoid are affected differentially by the magnum. When the carpus is flexed, the magnum's vertical tubercle is elevated well above its scaphoid facet. Thus, to achieve flexion, the lunar must be uplifted and the scaphoid relatively depressed. In the tapir, bone shapes and facet forms direct displacements between scaphoid and lunar along a vertical path. But in the rhinoceros, the lunar must wind its way around and up the scaphoid. These displacements between scaphoid and lunar bring the radius into the flexion operation. The rising lunar head abuts against the dorsal (or dorso-ectal) half of the radius's distal head, while the depressed scaphoid leaves a hiatus to be closed only when the radius rolls palmarly (or palmo-entally) to resume contact with the scaphoid. This rolling action is flexion between radius and proximal carpal bones. The differences between the tapir and rhinoceros with respect to the shapes of scaphoid-lunar-radius contacts, and with respect to patterns of scaphoid-lunar articulation are reflected in different patterns of movement. In figs. 3. C, 1-2 and 3. A, 1-4, we see that the tapir forefoot is flexed and rises parallel to the sagittal plane of the body ; while the rhinoceros forefoot winds around as it is flexed and uplifted. When there is extension between carpal rows and between radius and proximal carpal bones, the directions of displacements are reversed, but the paths are the same.

PYRAMIDAL — LUNAR

In both the tapir and the rhinoceros, the most proximo-ectal pair of bones lacks the kind of integration of form observed for the scaphoid and lunar. Internally, pyramidal and lunar meet along two parallel, flat or weakly concavo-convex surfaces, one near the proximal and the other near the distal heads of the two bones. Nothing about these forms and positions prevents displacements between the bones parallel to proximo-distal or palmo-dorsal planes of the manus.

Proximally, the pyramidal-lunar meets the fused radius-ulna

along a discontinuous surface. The lunar head is subcylindrical and the pyramidal head is concavo-convex. The borderline between the bones hardly exists in the rhinoceros (fig. 1. G) and in the tapir, while the contact is along a straight edge, the pyramidal exceeds the lunar in palmo-dorsal width (fig. 1. H).

In both animals, the pyramidal and lunar provide palmo-dorsally concave surfaces at their distal heads for articulation with the unciform. The two facets are inclined toward each other, an arrangement permitting the articulated unciform to secure these bones to one another. The unciform facet covers the entire distal surface of the pyramidal, but only half of the corresponding head of the lunar. The tapir lunar offers the dorsal half of its distal surface to the unciform, while the rhinoceros provides the diagonal-ectal half of its distal head for its unciform. The rhinoceros facet is most broad transversely, its ental border tapering as the facet trends along the ectal side of the bone (fig. 1. I).

The pyramidals of the tapir and rhinoceros are similar to each other not only with respect to shapes and positions of articular facets, but in their massiveness. In figs. 1. G and 1. H, we see that the pyramidal proximal head is rectangular or rhombohedral in outline and that the dorsal face of the bone would form another face of a block were it not for the broadly-based expansion of the bone near its distal head. The distal head (figs. 1. I and 1. J), which bears only a facet for the unciform, sustains the simple regular form. This form alone suggests that the pyramidal is a strong buttress to a mobile lunar.

TRAPEZOID - MAGNUM

The disto-ental pair of bones, like the pyramidal and lunar, lack the integration of form observed for the scaphoid and lunar. Internally, the trapezoid and magnum meet along a flat surface equal in area to that of the ectal flank of the trapezoid. Nothing about this form prevents displacements between the bones parallel to proximo-distal and plamo-dorsal planes of the manus. Proximally, each bone meets the scaphoid separately in trochlea divided by a rounded ridge (figs. 2. A and 2. B). The trapezoid proximal head is palmo-dorsally concave, while the scaphoid facet on the magnum is convex.

In the rhinoceros, the scaphoid facet covers the dorso-ental half of the proximal head of the magnum; while in the tapir, the corresponding facet covers the dorsal half of the proximal head. The tapir facet is symmetrically convex with respect to the trans-

verse plane of the manus, while that of the rhinoceros is asymmetrically convex with respect to a dorso-ental to palmo-ectally trending plane. In the tapir, the scaphoid has a palmo-dorsal path for displacement with respect to the magnum (fig. 1. L); but in the rhinoceros, the scaphoid must move along a path that is oblique to palmo-dorsal and transverse planes of the manus (fig. 1. K).

Fore-and-aft displacements between the carpal rows can take place along these smooth and rounded surfaces. When the manus is flexed, the scaphoid is shifted palmarly across the scaphoid and trapezoid. But in addition, it is depressed relatively to its adjacent lunar. The trapezoid, situated slightly palmarly of the magnum, is in position to receive much of this vertical pressure from the scaphoid. Some of these pressures are absorbed, and some transferred distally to the second metacarpal. The distal head of the trapezoid is not only palmo-dorsally concave, but transversely convex. The transverse path may be taken to distribute vertical pressures. A displacement of this sort might explain the phenomenon of digital adduction that always accompanies flexion of the manus (fig. 3. C, 1). Near the conclusion of a step, the manus is extended and pressure from the scaphoid is withdrawn from the trapezoid. The trapezoid then rolls in the opposite direction across the proximal head of the second metacarpal. The digit would be deflected by this rolling motion into the abducted position. The trapezoid has extensive lateral support from the magnum for all of these movements ; yet, lacking a series of rigid articular structures, the magnum and trapezoid are free to respond independently to the scaphoid and to the several bones meeting each but not both of them.

MAGNUM - UNCIFORM

The disto-ectal pair of carpal bones meets laterally in the tapir, while in the rhinoceros, the unciform is perched on the proximo-ectal shoulder of the magnum. The unciform facet on the tapir magnum is a palmo-dorsally narrow, flat band that is contiguous with the dorsal face of the bone and that trends parallel to the proximo-distal plane of the manus. The rhinoceros magnum has a proximo-distally concave and palmo-dorsally flat facet for the unciform. The vertical tubercle on the tapir magnum is situated palmarly of the unciform-magnum contact (fig. 1. L). But in the rhinoceros, the vertical tubercle on the magnum meets the dorsal face of the bone and then, without interrupting its concave profile, expands palmarly upon the ectal flank of the bone (fig. 1. K). The

unciform fits within the hollow of the tubercle and upon the broad surface that is its continuation and base. In the tapir, the unciform may be displaced along a short, vertical path with respect to the magnum. But in the rhinoceros, the unciform moves proximally, entally and palmarly or disto-ecto-dorsally with respect to the magnum.

The unciform and magnum each bear facets for the lunar. In the tapir, facets are separated by a palmo-ectally trending gap; while in the rhinoceros, facets have an extensive contact near the dorsal faces of the bones (fig. 1. K and 1. L). In the tapir, both facets are palmo-dorsally convex with respect to transverse midlines that are inclined toward each other. In the rhinoceros, the lunar facet on the unciform is weakly convex. The form blends with that of the adjacent part of the lunar facet on the magnum. The latter grows increasingly convex and transversely broad as it develops palmarly. The rhinoceros lunar has here a surface sufficient in area and in inflection to support the rotational path of displacement posited for that bone with respect to the scaphoid. And the tapir lunar has on the magnum and unciform two perches upon which to see-saw up and down during flexion and extension operations.

The scaphoid meets the magnum, as we have described; and the pyramidal meets the unciform. The smooth and extensive concavo-convex articulating surfaces permit fore-and-aft displacements between carpal rows when the manus is flexed and extended. But for the pyramidal and unciform another dimension is involved when displacements occur between carpal rows. During flexion, the pyramidal, like the scaphoid, is displaced distally with respect to a rising lunar. The unciform, pressed from above, slides toward the uplifted lunar. There are two components to this displacement : transverse, along the fourth metacarpal ; and proximal, along the magnum. In the tapir, the unciform slips vertically up the magnum ; but the rhinoceros unciform winds around and up. When the manus is extended, the lunar is depressed upon the unciform. The unciform reverses direction as it moves along the magnum and the fourth metacarpal.

These operations are reminiscent of the displacements described for the trapezoid with respect to scaphoid and magnum. But on the ectal side of the manus, two bones — the lunar and the pyramidal — press in turn upon the distal bone. The unciform responds to these pressures as does the trapezoid, by rolling transversely across the proximal heads of adjacent metacarpals. Unlike the trapezoid, the unciform meets two metacarpal bones. When the

manus is flexed digits four and five (the latter being questionable for the rhinoceros) are adducted ; and when the manus is extended, digits four and five are abducted.

DISTAL CARPALS - METACARPALS

Like the distal surfaces of the scaphoid, lunar and pyramidal, the distal surfaces of the trapezoid, magnum and unciform are palmo-dorsally concave. The concavities tend to be deeper for the distal carpal bones, and in both tapir and rhinoceros, the inflections are distributed nearly symmetrically with respect to the transverse midline of each bone (figs. 2. C and 2. D). Fore-and-aft displacements between distal carpal and metacarpal bones are feasible along such surface forms. The distal carpal-metacarpal bones acquire rigidity in the same ways that adjacent pairs of carpal bones acquire rigidity : through over-lapping support structures.

With the exception of the fifth, each metacarpal has on its ectal flank an elevated facet for the carpal bone ectally adjacent to its principal support. The second metacarpal meets the trapezoid proximally, and the magnum proximo-ectally (figs. 2. A and 2. B). The third metacarpal meets the magnum proximally and the unciform proximo-ectally (figs. 2. C and 2. D, the concavities at the right edges of the left bones). In the tapir, the fourth metacarpal meets the unciform proximally and the fifth metacarpal ectally. The fifth metacarpal is developed proximally from that contact within a niche in the unciform. In the rhinoceros, the fourth metacarpal also meets the unciform proximally; but the fifth metacarpal is perched on the proximo-ectal shoulder of the fourth (fig. 2. G).

Since for all these bones, only the ectal flanks are reinforced, it would appear that the forefoot does not bear stresses symmetrically with respect to the third metacarpal. In fact, the foot sustains greatest stress when it returns to the ground at the conclusion of a step. And in both animals, the ectal side of the manus bears more pressure than the ectal flank at this time. For the rhinoceros manus, we observe in fig. 4. A, 1-4 and 4. B, 1-4 that the ectal side of the forefoot is first to sustain the impact of landing. In the tapir (fig. 4. C, 1-4) we see that the digits are headed for more extensive contact at their ectal flanks than at their ental sides.

However, over the course of a step, ental and ectal flanks are both involved in lifting and supporting the forefoot. Digital adduction and abduction are the observable expressions of this invol-

vement. In both animals, flexion is always associated with adduction and extension is always accompanied by digital abduction. In the tapir, digit V is adducted even before the carpus is flexed to begin a step (fig. 3. B, 2-3). In the following frame (fig. 3. B, 4) the carpus is flexing and digits II and IV are adducted. In figs. 3. C, 3-4, we see that digit III remains on the ground as the carpus is flexed and lateral digits adducted. Muscular structure is partly responsible for the simultaneity of adduction of digits II and IV. This may be inferred from Campbell's (1936) description of the Mm. contrahentes digitorum manus (adductores).

Three of the muscles are present, one each for the second, fourth and fifth digits. Those for the second and fourth are complementary and mirror images of each other. In their origins, they both show a peculiarity in the deep branch of the ulnar nerve... That nerve, which in mammals usually passes dorsal to these muscles, pierces them near their origins. As the part lying superficial to the nerve have the usual origin from the volar process of the capitate and the portions dorsal to the nerve arise with the flexores breves profundi, it is probable that this unnusual relationship has been brought about by annexation of deeper muscle elements by the contrahentes of these two toes. The slips are weak and compressed vertically instead of horizontally as in other animals. Insertion is upon the axial side of the basal phalanges of toes II and IV. (p. 238).

Campbell's description of the third muscle offers a structural explanation for the independent adduction of the fifth digit.

The contrahens digiti quinti differs widely from the two just described. It lies entirely superficial (volar) to the nerve and is flattened horizontally, thus resembling the corresponding muscles of the artiodactyls. Origin is from the volar process of the capitate. Insertion is upon the axial side of the basal phalanx of the fifth digit. (p. 238).

A separate system of flexor muscles has insertions upon the basal surfaces of the metacarpal bones and upon the phalanges. Bone alignments within the manus bind the operations of flexion and adduction to each other. Adduction requires the proximal head of the fifth metacarpal to be displaced transversely ectally across the unciform. The unciform is displaced in the opposite direction to the fifth metacarpal : transversely axially. During flexion, the pyramidal — which is depressed relatively to the uplifted lunar — presses the unciform along in this same direction. The unciform slides transversely toward the magnum and proximally toward the lunar. The scaphoid, too, is depressed with respect to the lunar during flexion. As the scaphoid moves plamarly across and distally upon the trapezoid, the distal head of the trapezoid slides toward the magnum. The proximal head of the second metacarpal is correspondingly displaced entally transversely and its distal head is

directed axially. The second digit, too, is thus adducted (fig. 3. C, 1-2).

In the tapir, the scaphoid-lunar, lunar-pyramidal, magnum-unciform and trapezoid-magnum meet along surfaces permitting displacements parallel to proximo-distal planes of the manus. The short and similarly uncomplicated paths permit the ental and ectal sides of the manus to be adducted simultaneously.

In the rhinoceros, too, the lunar and pyramidal and the trapezoid and magnum meet along surfaces permitting displacements parallel to proximo-distal planes of the manus. But, the scaphoid and lunar and the magnum and unciform meet along curving paths; paths that are oblique to all three perpendicular planes of the manus. In addition, the fifth metacarpal is only a rounded nubbin of bone (fig. 2. G) wedged into a palmo-ectal shelf formed by the unciform and the fourth metacarpal. Plainly, it is incapable of the kind of adductive operation by which the fifth metacarpal gives impetus to uplift in the tapir manus. But the rhinoceros fifth metacarpal is in position to support the fourth metacarpal as that digit initiates each step. A twist in the shaft of the fourth metacarpal places its distal head vertically distally of the fifth (fig. 2. F). Muscle scars on the fifth metacarpal and on the distal aponeurosis of the fourth metacarpal point intriguingly to a suspension system between the two bones. An insertion of the contrahens digiti quinti on the fifth metacarpal and a tendinous or muscular (adductor) link between the two bones might account for the observation that the ectal flank of the manus has greater powers of adduction than does the ental flank. At the beginning of each step, before flexion is initiated, the fourth digit is raised high in the air, while the manus is supported by digits II and III (fig. 3. A, 1). When flexion begins (fig. 3. A, 2-3), digit II rises from the ground. As the adductive forces between ental and ectal sides of the manus are equalized, the manus rotates across the medial digit (fig. 3.A, 3-4). Torsion can be observed at the wrist as the forefoot turns along the tip of digit III. This torsion is explained by the curving paths for bone displacement within the carpus. The lunar is winding entally-proximally along the scaphoid; and the radius is being flexed along a path marking a palmo-ental diagonal to the palmo-dorsal plane of the manus. Further, the unciform is impelled by the rising fourth metacarpal and sustained by the pyramidal, in moving not only axially transversely across the fourth metacarpal, but proximo-palmo-entally up the long vertical tubercle of the magnum. Curving paths for bone displacements at the proximo-ental and at the disto-ectal extremities represent structural balances for the

carpus; but they prevent the kind of simultaneous operation between ental and ectal flanks observed for the tapir.

When the manus is extended, the rhinoceros wrist again undergoes torsion (figs. 4. A, 1-4). This time, the radius must roll dorso-ectally across the scaphoid-lunar while the lunar winds ectally-distally with respect to the scaphoid. The unciform is pushed by the descending lunar disto-dorso-ectally with respect to the magnum. The unciform, rebounding proximally beneath the pyramidal, also slides transversely ectally across the fourth metacarpal. The fourth metacarpal is abducted as the unciform slides across it, as when the forefoot approaches landing (fig. 4. A, 4 and 4. B, 1-4). Another muscular bridge may be imagined to support this operation. The proximal surface of the fifth metacarpal has several muscle scars (fig. 2. F), one of which may possibly represent an insertion for the abductor digiti quinti manus. In the tapir, that muscle originates on the pisiform; and in this scheme the pisiform would fill the same role for the rhinoceros. Another abductor muscle not yet identified might extend from the fifth to the fourth metacarpal, parallel to the hypothetical adductor bridge described above.

In the tapir, the manus is extended parallel to the sagittal plane of the body (fig. 4. C, 1-4). Ental and ectal digits are abducted at the same time (fig. 4. C, 1-2) and simultaneously with carpal extension. Campbell (pp. 222-226) described an elaborate system of extensor muscles. The insertions of Mm. extensor digitorum communis, the largest extensor, and extensor carpi radialis partly explain the more extensive involvement of the ectal than the ental sides of the digits as observed in figs. 4. C, 3-4. The former muscle inserts « nearly entirely on the third metacarpal, only a few fibers going to the fourth » ; and the medial tendon of the latter muscle « inserts on the dorsal surface of the basal phalanx of the fourth digit and contributes many fibers to the dorsal aponeurosis of the fifth toe. » Surprisingly, Campbell described only one abductor muscle. Originating on the pisiform, the M. abductor digiti quinti manus empowers only the fifth digit. Abduction of other digits, then, must be explained as a component of the extension operation. Certainly, the bone alignments we have described indicate that digits are necessarily abducted when there is extension between carpal rows.

In both tapir and rhinoceros, adduction of the most ectal digit initiates each step. In both animals flexion within the carpus is associated with digital adduction, and digital abduction is bound to occur when the manus is extended. Structures within the manus

involve both ental and ectal flanks in uplifting and supporting the forefoot over the course of a step. In the tapir, ental and ectal flanks operate simultaneously; while in the rhinoceros operations are slowly shifted from one flank to the other as bones are displaced along curved paths. The slow shifting is observed as torsion of the carpus as the forefoot is uplifted and as it returns to the ground.

DISCUSSION

For both tapir and rhinoceros, digit III marks a plane of functional symmetry for the manus. In the rhinoceros, digits II and III share the burden of support as the forefoot is prepared to be elevated from the ground (fig. 3. A, 1) and digits III and IV share the burden of impact as the manus lands (figs. 4. A, 1-4 and 4. B, 1-4). Even as the rhinoceros stands, the burden of support is primarily shared by two digits on each forefoot, the medial and one lateral digit. In the tapir, digits II and IV move toward the third digit as the manus rises from the ground (fig. 3. B, 3-4) ; and the lateral digits move away from the medial one as the foot is prepared to land (fig. 4. C, 4). When standing, lateral digits serve as struts to the medial one. Structures associated directly with the metacarpal-distal carpal bones do not suggest this balance of function. They only reveal that the ectal flank of the manus must withstand greater pressures than the ental flank.

Within the carpus, however, there are structural balances between ental and ectal flanks. These include 1) similar structures located at diagonally opposite sides of the manus and, 2) symmetrically opposite bone shapes and facet structures located at the other diagonally opposite sides of the manus. The first is represented by the pyramidal and trapezium. Both bones are simple block-like shapes bearing concave facets for articulation with proximal and distal bones, and flat facets for lateral bones. With respect to the pyramidal and the trapezium, the tapir and the rhinoceros differ from each other only in absolute sizes. The second set of balanced elements consists of two pairs of bones, the scaphoid-lunar and the unciform-magnum. We have seen how tapir and rhinoceros differ from each other with respect to bone shapes and facet structures here. But, in both animals, scaphoid-lunar and magnum-unciform are mirror images of each other, particularly at the contact between carpal rows where any displacement affects the entire carpus (figs. 1. E, F, K, and L). Each of the medial bones (lunar and magnum) meets both of the elements of the opposite

pair; the lunar articulates with the magnum and unciform while the magnum makes contact with the scaphoid and lunar. Thus, it is through the lunar and magnum that displacements on one side of the manus are reflected to the other side. As the lunar moves up the magnum during flexion, the scaphoid is relatively depressed and its diagonal opposite, the unciform, is elevated. When the manus is extended and the lunar lowered upon the magnum, the unciform is shifted distally while its diagonal opposite, the scaphoid, is elevated. Since ental and ectal flanks of the carpus move in opposite directions, lateral digits move in opposite directions to each other under the same stimulus, be it flexion or extension. Simultaneity of adduction and abduction operations between ental and ectal sides of the manus in the tapir is facilitated by the perpendicular alignments between carpal bones. The lack of simultaneity between ental and ectal sides of the forefoot in the rhinoceros is explained by the curving paths for displacements which slow down the process of translating movements from one flank of the manus to the other. These differences in form and operation point to adaptations of the mesaxonic system to different over-all proportions of the bodies to be carried. The tapir manus is equipped to rise quickly from the ground and to return there nimbly; while the rhinoceros manus has the strength of a screw lever, a development suitable for supporting and carrying its characteristic weight and proportions.

Modifications of the fifth metacarpal also represent adaptations of the mesaxonic system to characteristic body sizes. In the tapir, the fifth metacarpal acts independently of the other digits to initiate a step. And in the rhinoceros, the fifth metacarpal is in position to increase the power of the fourth metacarpal to initiate each step and to share the principal burden of landing.

CONCLUSION

Similarities observed for tapir and rhinoceros manuses are predictable from their common perissodactyl lineage. But the differences between them suggest that their relationship is more complicated than generally assumed.

The screw-lever carpus is clearly an adaptation for lifting and carrying the 1.5 to 3-ton rhinoceros body; the elephant manus, too rotates upon a medial axis over the course of a step. But not all graviportal animals have this characteristic. The bison manus, for example, moves along the same essentially orthal path as does that of the muntjac and other cursorial artiodactyls. What is

there about perissodactyl architecture that requires major modifications in the style of movement to accommodate bodies of different sizes and proportions ?

Tendency to digital reduction may be part of the answer. While the bison and the smallest deer have the same number of digits, each of the three living perissodactyls has a different number. If the method employed in this paper has any value other than to confirm readily observable movements of living animals, it is to derive patterns of motion for extinct animals from their fossils. I attempted this for the four-toed Miocene rhinoceros, *Aceratherium tetradactylum,* the animal Osborn had taken to represent the rhinocerotoid equivalent of the living tapir. Except for the fifth metacarpal, positions, sizes, shapes and outlines of articular facets and of the bones themselves are similar, even in detail, to those of living rhinoceroses. The fifth metacarpal resembles that of the living tapir in shape and in being shorter and less robust than the adjacent fourth metacarpal. However, articular facets on the unciform and on Mtcs. IV and V reveal that in *A. tetradactylum,* these three bones fit and worked together in the same ways as they do in living rhinoceroses, and not at all like tapirs. Since the Miocene, at the latest, the rhinoceros line has been characterized by a fifth metacarpal that functions as a buttress to the fourth metacarpal. The tapir manus requires a Mtc. V to work like any other digit in the processes of lifting, landing and supporting the animal. Surely, there is no internal evidence to connect these perissodactyls in a general « tendency to digital reduction ». Our question remains unanswered; if anything it is now more complicated : Why are major structural modifications, including restyling of a digit, required to accommodate perissodactyls of differing sizes ?

Foot structures, especially features of the astragalus, legitimatize the common membership of tapirs and rhinoceroses in the order Perissodactyla. For the manus, an external criterion, namely, mesaxonic symmetry as defined by a single robust medial digit, links the two. But internally and functionally those systems are so disparate as to raise doubts as to the syngenetic relationship between these families. If the external form of the carpus would appear to be inadequate for building a system of classification, so does the isolated moving manus. All parts of the skeleton determine systematic positions; and all parts are involved in lifting, landing and supporting each animal. The structures that permit these varied and apparently contradictory capacities throughout the body may prove to be as constant and definitive as the articular facets within the carpus. Perhaps perissodactyl architecture is to

be defined, and our question answered, over the course of a search for all structures endowing the body with both flexibility and rigidity.

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SUMMARY

The idea of mesaxonic symmetry is explored for the tapir and the rhinoceros through comparative studies of their carpal and metacarpal bones and their moving manuses. The manus of each animal acquires flexibility and rigidity through characteristic carpal-metacarpal structures. Patterns of flexibility-rigidity are reflected in predictable ways in characteristic patterns of motion. Reduction of the fifth metacarpal in the rhinoceros is viewed as a change rather than a loss of digital function. The systematic significance of these patterns of structure and motion is considered in light of observations of the four-toed Miocene rhinoceros, *Aceratherium tetradactylum*.

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