EXTREME CARPAL VARIABILITY IN *TELEOCERAS*
(RHINOCEROTIDAE, MAMMALIA)

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ABSTRACT—A large population of the common American Miocene rhinoceros, *Teleoceras,* shows extreme variability in the shape of the magnum and unciform. A small number of the specimens show a de novo posterior (volar) articulation between these two carpals. The new articulation may have been formed as an early stage in the fusion of the two bones. It is suggested that in order to evolve a complex new structure, a population will sometimes produce more variation in the affected elements than is actually necessary to form the structure.

INTRODUCTION

One of the most extensive samples of fossil rhinoceros remains was recovered from the Mixson Bone Bed of Levy County, Florida. Most of this late Miocene fauna is housed in the Frick Collection of the American Museum of Natural History (F:AM). While curating the Mixson rhinos, the junior author noticed some aberrant foot bones which appeared to be rhinocerotid in general morphology, but which did not seem to represent either of the known rhinos from the fauna, *Aphelops longipes* and *Teleoceras fossiger.* Subsequent study of the articular facets indicates that these elements represent unusual magna. The magnum (synonymous with the capitate in human anatomy and Carpale III in the European literature) is the central carpal in the distal series of carpals in the manus (Fig. 1) and is situated directly proximal to metacarpal III.

We have referred these magna to *Teleoceras* because they exhibit the proximodistal flattening characteristic of this taxon's podials, a derived condition that Osborn (1929) suggested is related to a graviportal body type. A survey of the entire sample of unbroken magna (N = 111) of adult *Teleoceras* from Mixson reveals an extremely wide but morphologically continuous range of variation. The aberrant magna (Fig. 2D–F) represent one extreme of this range. Such a degree of carpal variability in rhinoceroses has not been documented previously in the literature. The purpose of this study is to analyze the extent and function of this unusual variability and to speculate upon its significance to evolutionary morphologic change.

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DESCRIPTION

The sample of late Miocene (earlyHemphillian) *Teleoceras fossiger* from Mixson is one of the largest known from a single locality. It is comparable to, and possibly larger than, that from the contemporaneous Long Island Rhino Quarry of Kansas. Leidy (1890) quotes W. H. Dall's description of the sample from Mixson: "The fossils consist of isolated bones, fragments of others, and teeth, mostly of the larger and firmer kind, well preserved and neither water-rolled nor weather-worn." As in the Long Island sample, there is a dearth of articulated material; however, almost every element is represented. Moreover, the Mixson sample is unusually rich in the bones of both manus and pes.

The geology of Mixson has been discussed by many workers including Leidy (1884, 1885, 1887), Leidy and Lucas (1896), Matson and Clapp (1909), Sellards (1916), Simpson (1930), and Patton and Webb (1970). The fossils were contained in a clay deposited in a shallow sinkhole resulting from karstification of the underlying Eocene Ocala Limestone. The sinkhole, about 30 × 15 × 2 m, evidently experienced active deposition for a relatively brief interval; hence, the Mixson locality was sharply restricted stratigraphically as well as geographically.

The distinctive morphology of the carpals and tarsals of *Teleoceras* facilitate their separation from those of *Aphelops* or any other taxon in the fauna. *Aphelops* podials are generally of a primitive ceratomorph type, somewhat like enlarged tapir foot bones. They do not display the striking proximodistal compression present in the podials of *Teleoceras.* Thus, despite the lack of
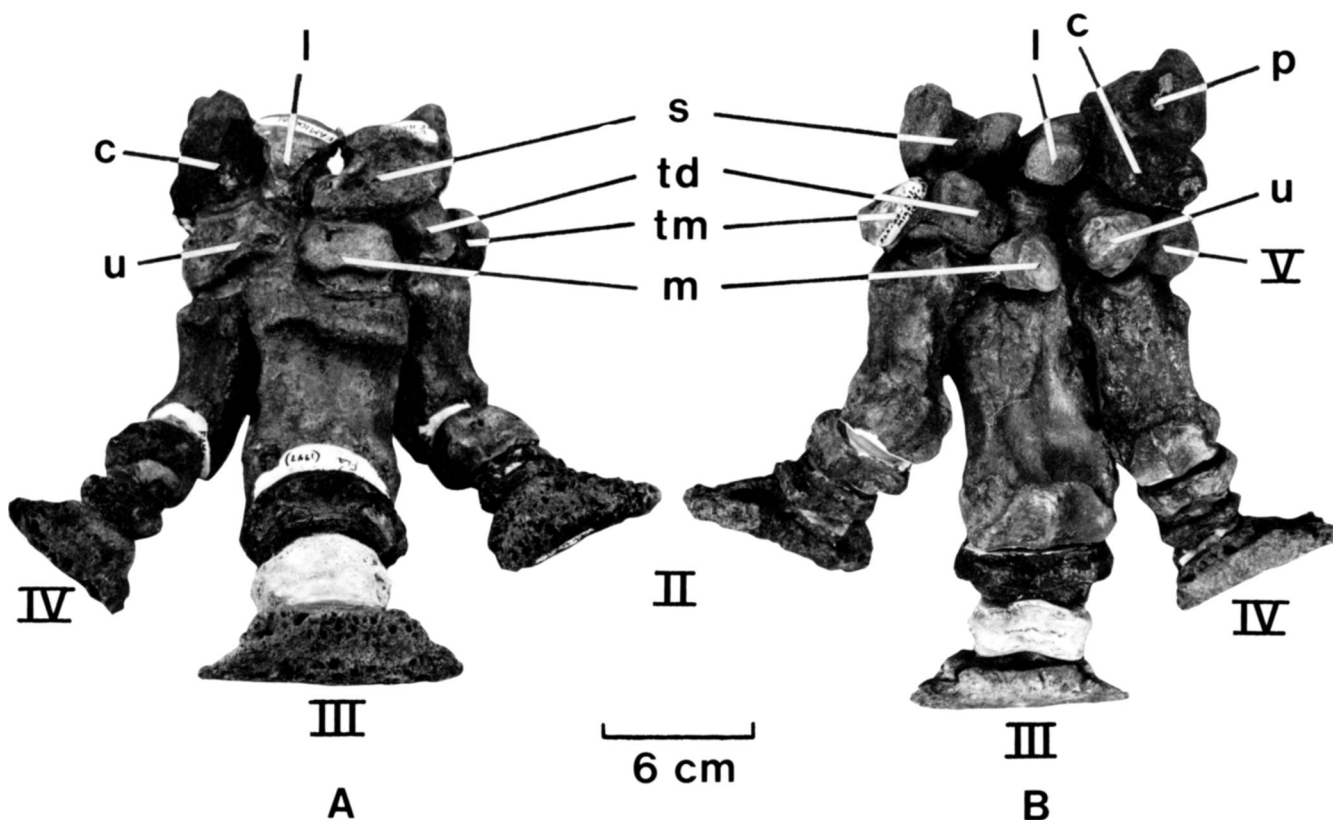
FIGURE 1. Composite right manus (F:AM 104161) of *Teleoceras* from Mixson, Levy County, Florida (late Miocene). (A) anterior and (B) posterior views. The proximal series of carpals contains the scaphoid (s), lunar (l), cuneiform (c), and pisiform (p); the distal series contains the trapezium (tm), trapezoid (td), magnum (m), and unciform (u). Metacarpals and phalanges of digits II, III, and IV are much larger than the remnant of metacarpal V (V).

articulated material, it is possible to identify accurately the skeletal elements of the two rhinoceros genera.

Magnum

In *Teleoceras,* as in many mammals, the more loosely articulated bones on the medial and lateral sides of the feet are more variable in shape than are the other carpals and tarsals. This is probably because their shape is not as tightly controlled by the articular surfaces of the surrounding bones. Unlike these relatively unrestricted foot bones, the magnum is in the center of the manus, completely surrounded by other bones, which probably accounts for the low variability in the anterior portion of the *Teleoceras* magna.

The single most variable feature in the magnum of *Teleoceras* is the posterior (volar) process, sometimes referred to as a "hook." The two magna in Figure 2 illustrate the extremes of development observed in this process, while those in Figure 3 show the full range of intermediary forms. The distribution of morphotypes in the Mixson magna is strongly biased towards the primitive, well-developed posterior process. Magna with such a derived, reduced process (a character un-

known in any other rhinocerotid and, indeed, any ceratomorph) comprise only about 35% of the sample. This distribution confirms that the variation in the posterior process is not a gender-dependent character because the ratio of male to female *Teleoceras* in the Mixson fauna is approximately 1:1, as indicated by the sexually distinctive lower tusks (Osborn, 1898). Moreover, the variation in the posterior process is not correlated with overall size of the magnum. When the anterior portion of the magnum (width plus depth from the anterior surface to the base of the posterior process) is plotted against the length of the posterior process in the scatter diagram in Figure 4, a random rather than a linear pattern emerges. A third potential source of the variation, ontogenetic age, has been eliminated because juvenile magna (Fig. 5), which are easily distinguished from those of adults by their porous texture and rounded edges, were not included in the illustrated sample (Fig. 3). The posterior process is invariably small in juvenile magna. The mature magna bearing a small posterior process may represent various retained paedomorphic stages. It appears, therefore, that the
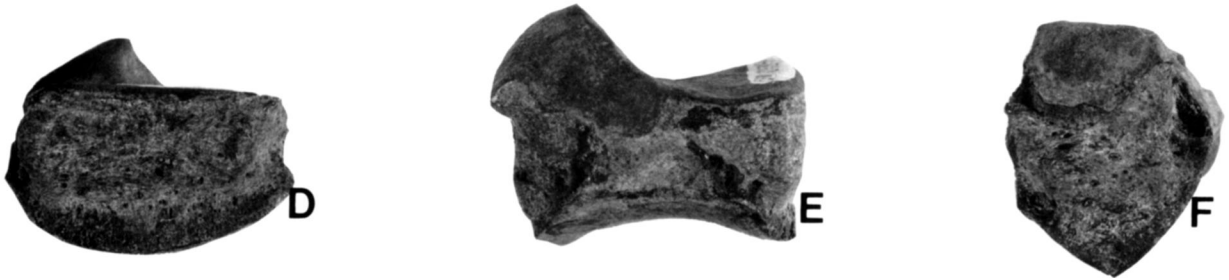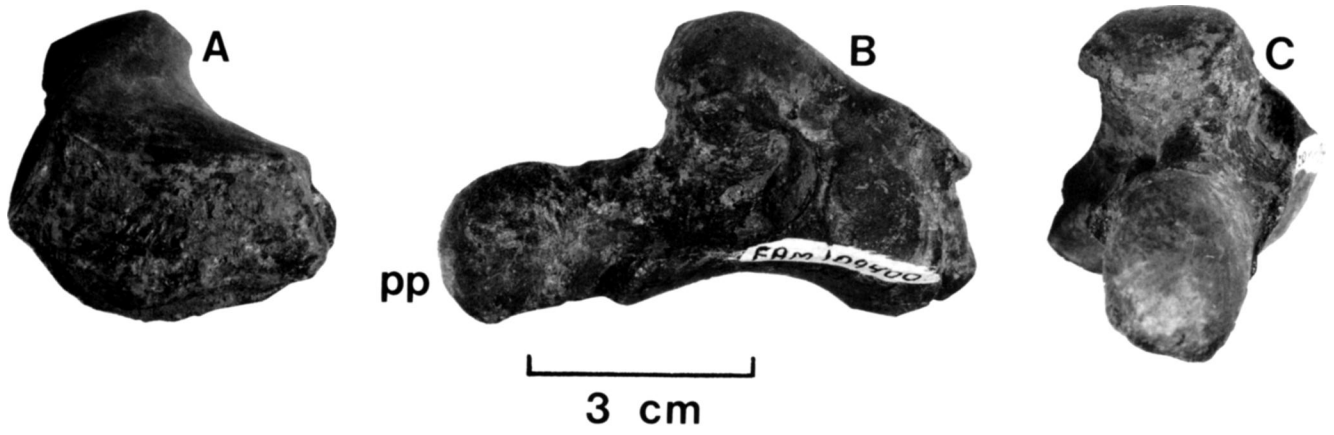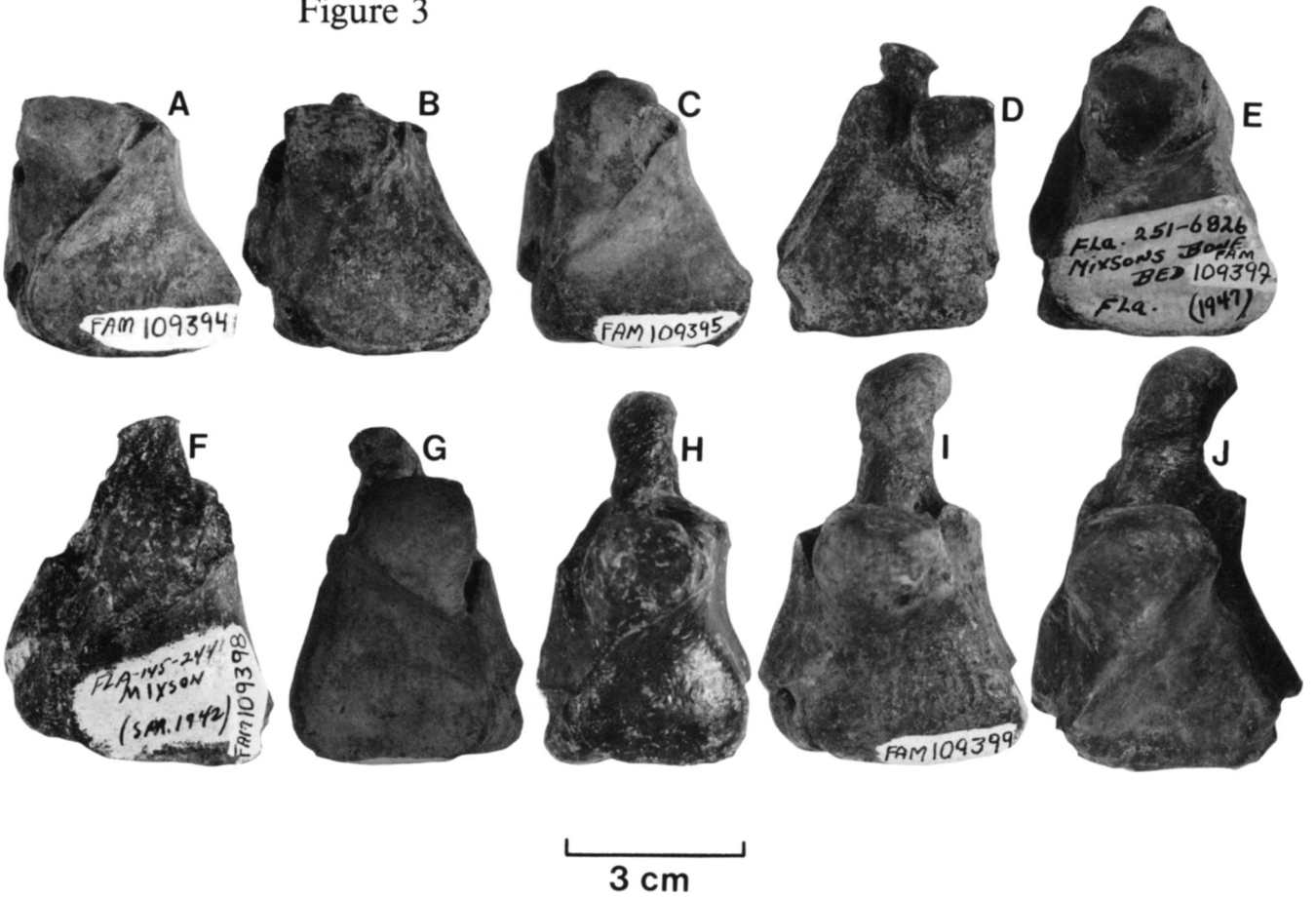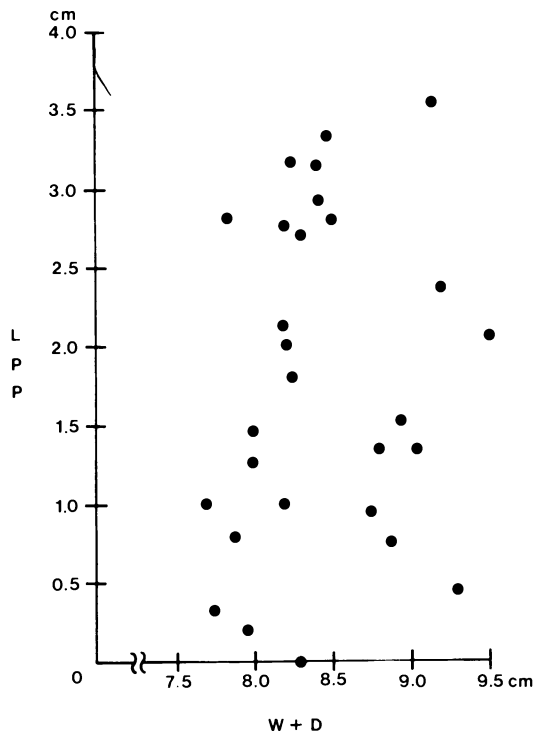
Figure 3

cm
4.0

L
P
P

W + D

FIGURE 4. Scatter diagram of the length of the posterior process (**LPP**) of the magnum plotted against the sum of the width (**W**) of the magnum plus the depth (**D**) from the anterior surface to the base of the posterior process for a random sample of adult *Teleoceras* from Mixson. The random pattern indicates that there is no linear relationship between the length of the posterior process and the overall size of the magnum.

FIGURE 5. Right magnum of juvenile *Teleoceras*, F:AM 109391. (**A**) proximal view with anterior face down; (**B**) lateral view with anterior face to the right.

derived magna simply occur as a variation in a third of the adult *Teleoceras* population at Mixson.

Unciform

The extreme variability of the magnum in the Mixson *Teleoceras* is mirrored in the unciform (synonymous with the hamate in human anatomy and Carpale IV in the European literature), the carpal lateral to the magnum (Figs. 1, 6). In about 25% of the total sample of unbroken adult unciforms (N = 149), an unusual process occurs on the medial surface of the posterior
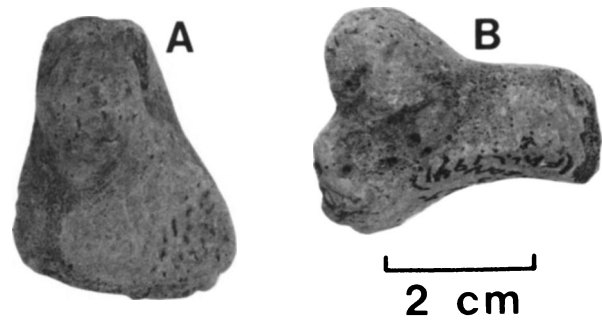
process (Fig. 6E–I). Unlike the reduction of the posterior process of the magnum, this process is clearly not paedomorphic in development. Of particular interest is the presence of a circular articular facet on the anterior surface of this medial process (about 6% of the total sample). Intriguingly, a few of the aberrant magna (about 13% of the total sample) bear a complementary facet on the posterior tip of the rudimentary posterior process. The facet occurs only on magna with greatly reduced posterior processes (Fig. 3F–H), though not on the most derived variants which retain only a small nubbin or no process at all (Fig. 3A–C). The articulation of an unassociated unciform and magnum bearing these facets (Fig. 7) clearly shows that some individuals had formed a de novo posterior articulation, by abutting the reduced posterior process of the magnum against the new medial process of the unciform. This condition is unknown in any other rhinoceros.

DISCUSSION

Function of the Processes

The function of the posterior processes of the magnum and unciform is not entirely clear. In humans, a structure homologous to the posterior process of the unciform, the "hook of the hamate," serves as a point of origin of two small muscles for flexing the fifth metacarpal and digit (Gray, 1901). *Teleoceras*, like living rhinos, has a vestigial fifth metacarpal, which buttress-

←   →

FIGURE 2. Right magna of adult *Teleoceras* from Mixson representing the extremes of development of the posterior process (**pp**). (**A–C**) F:AM 109400, maximum development; and (**D–F**), F:AM 109394, minimum development. (**A & D**) anterior views, (**B & E**) lateral views, (**C & F**) posterior views; proximal face at the top.

FIGURE 3. Magna of adult *Teleoceras* from Mixson illustrating the range of variation present in the sample; compare the relatively constant size of the body of the magnum to the much more variable posterior process. (**A**) F:AM 109394, (**B**) F:AM 109396, (**C**) F:AM 109395, (**D**) F:AM 104177, (**E**) F:AM 109397, (**F**) F:AM 109398, (**G**) F:AM 109393, (**H**) F:AM 104186, (**I**) F:AM 109399, (**J**) F:AM 109400. All but (**D**) are right magna; all are in proximal view with the anterior face down.
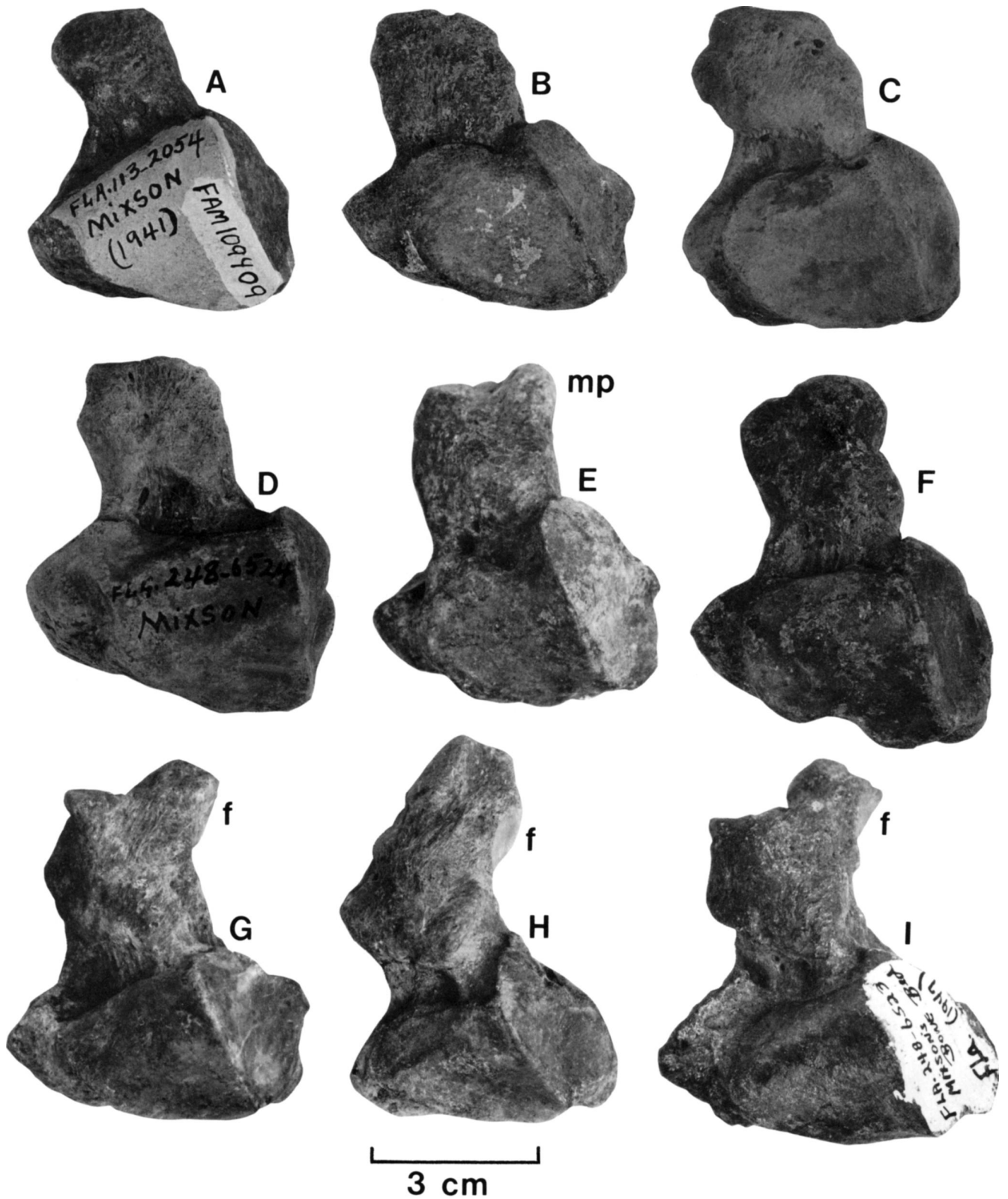
FIGURE 6.   Right unciforms of adult *Teleoceras* from Mixson illustrating the range of variation in the medial projection (**mp**) of the posterior process. (**G–I**) exhibit well developed circular facets (**f**) for articulation with the posterior process of the magnum. (**A**) F:AM 109409, (**B**) F:AM 109408, (**C**) F:AM 109406, (**D**) F:AM 109407, (**E**) F:AM 109404, (**F**) F:AM 109405, (**G**) F:AM 109403, (**H**) F:AM 109402, (**I**) F:AM 109401. All are in proximal view with anterior face down.

es the fourth metacarpal (Klaits, 1972), and no fifth digit at all (see V in Fig. 1B), making the same function impossible.

Posterior processes are usually not well-developed in higher ungulates. As pointed out by Yalden (1971), similar processes are found in living hippos and tapirs, as well as rhinos. They are absent or poorly developed in sheep, pigs, horses, and elephants. These processes serve as "points of origin for some of the flexor ligaments and some of the short muscles to the toes," but not as points of insertion for any major flexor muscles of the wrist (Yalden, 1971). Because of this, Yalden suggested that, contrary to earlier notions (Osborn, 1929), these processes are not primarily involved with the flexion of the manus in ungulates. He hypothesized that they may be involved with the hyperextension of the forefoot, either to secure ligaments for preventing hyperextension or to utilize the elastic contraction of those ligaments (stretched in hyperextension) for propulsive purposes. Such hyperextension would be significant when the forefoot is at the most posterior point of its backward power stroke.

It may be that the processes are necessary in short-footed ungulates with rather extensile wrists, but are lost when the wrist loses extension ability and gains in flexion (as Yalden demonstrated in several cursorial forms). The ligament-attachment function of the posterior processes is not lost even in those individuals of *Teleoceras* which have formed the de novo magnouniform articulation. The enlarged posteromedial surface of the posterior process of the unciform compensates for the reduction of the posterior process of the magnum, with the potential for a single, large ligament to substitute for two small ones. It would seem, then, that the modification of these carpal processes in the Mixson *Teleoceras* population was to serve an additional function, not to lose the original one.

The new articulation would tend to restrict proximodistal movement between magnum and unciform. Normally, such movement is possible between these two carpals, as between most other carpals. Restriction of this intercarpal movement would in turn hinder the relative movement of manus digits III and IV which articulate beneath the magnum and unciform, respectively. We speculate that such restriction of movement could represent an early stage in the fusion of these two carpals. A fused magnouniform, unknown in any rhino, would permit simultaneous motion of manus digits III and IV, and thus provide a more rigid foot.

Evolution of the Structure

Magna and unciforms of the sort described herein are found only in later-appearing, Hemphillian *Teleoceras*. They are not known from Barstovian (middle Miocene) or Clarendonian (early late Miocene) faunas, not even in such large samples as those from the early Barstovian Olcott Formation or the early Clarendonian Poison Ivy Quarry of Nebraska, or the late Clarendonian Love Quarry of Florida (only slightly older than Mixson). Such carpal modification is only found
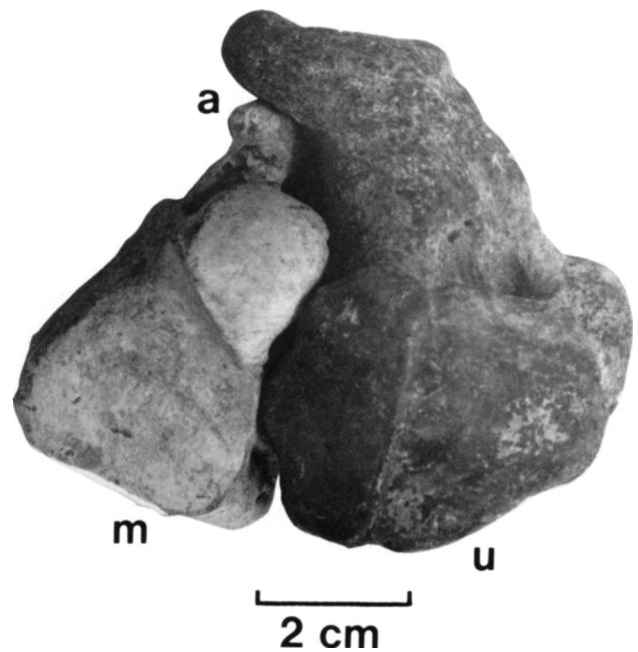

FIGURE 7. Left magnum (**m**), F:AM 109393, and unciform (**u**), F:AM 109392, exhibiting a de novo posterior articulation (**a**); proximal view with anterior face down. Note that this magnum has a reduced posterior process but is not at the extreme end of process reduction (see Fig. 3G).

in early Hemphillian localities such as Mixson, Long Island Rhino Quarry, and Higgins, Texas. The seemingly abrupt appearance of these structures suggests a non-random increase in variation in the early Hemphillian.

Teleoceras is very rare in the late Hemphillian; however, carpals are known from Edson Quarry, Kansas, and Optima, Oklahoma. In both of the two magna present in the Optima fauna, the posterior process has been lost; the unciform is not represented. The two unciforms present in the Edson Quarry fauna both have a long, robust posteromedial process; the magnum is not represented. Therefore, it would appear that the incidence of derived magna and unciforms increases throughout the Hemphillian.

The most puzzling aspect of the carpal variability discussed herein is the complete loss of the posterior process of the magnum in a few individuals (Fig. 2D–F). If the functional significance of the reduction in size of the posterior process is the development of a posterior articulation with the unciform, then what is the value of a complete loss of the process? We believe that the explanation has to do with the development of new features in evolution, for example a fused magnouniform. We postulate that in evolving a complex new structure, a population will sometimes produce more variation in the affected elements than is actually necessary to form this structure. Many other such examples of "functionless" variation probably exist, and

should be sought as such. The extreme variability of shape in the Mixson magna could represent a glimpse of evolutionary change at the population level.

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