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A NEW GENUS OF RHINOCEROTOID FROM THE EOCENE OF UTAH AND THE STATUS OF NORTH AMERICAN "*FORSTERCOOPERIA*"

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ABSTRACT—A skeleton of a primitive rhinocerotoid from the Uintan (middle Eocene) of Utah provides the basis for a new genus and species, *Uintaceras radinskyi*; *Hyrachyus grande* Peterson, 1919 is a nomen dubium. The anterior dentition of this specimen is unlike that of any other known rhinocerotoid, although it most resembles the anterior teeth of some primitive rhinocerotids. The cheek teeth are primitive in morphology and similar to those of specimens referred to "*Forstercooperia*" *grandis*. North American specimens referred previously to *Forstercooperia* are here referred to this new genus. This taxonomic change implies that the evolution of indricotheriine hyracodontids was restricted to Eurasia. The postcranial skeleton of *Uintaceras* is robust and shows many primitive characters, including a tetradactyl manus. *Uintaceras* is the sister taxon of the Rhinocerotidae and demonstrates that rhinocerotids, at their origin, retained the primitive condition for many characters, including some that have been used to unite rhinocerotids with other rhinocerotoids, such as indricotheriine hyracodontids.

INTRODUCTION

Our knowledge of the phylogeny of rhinocerotoids, like that for other mammalian taxa with fossil representatives, has been somewhat limited by the incompleteness of available specimens. Indeed, one result of Radinsky's (1966) work on the anterior dentitions of rhinocerotoids was that relationships were then based on a part of rhinocerotoid anatomy that is often poorly preserved. The premaxillae of rhinocerotids are easily broken off the skull, and the anterior ends of the skull and jaws are unknown for many other ceratomorph taxa. More recent research (e.g., Lucas et al., 1981; Prothero et al., 1986) has shown that postcranial characters may be useful in determining rhinocerotoid phylogeny, but, again, the postcrania of many taxa are not well known. Thus, cheek teeth, the most commonly preserved elements, have served as the major source of information for characterizing rhinocerotoid taxa and their interrelationships. Morphologically primitive cheek teeth, however, may not be diagnostic in themselves, and taxa based upon them are often at best tenuous. New discoveries of rhinocerotoid anterior dentitions and postcrania are therefore likely to lead to significant taxonomic changes. Such is the case with CM 12004.

In 1987, a Carnegie Museum expedition working at Myton Pocket, Utah, collected the skeleton of a primitive rhinocerotoid from beds of Uintan age. This specimen, CM 12004, was found mostly articulated and, hence, represents a single individual. CM 12004 consists of a badly crushed skull and most of the postcranial skeleton. All of the cheek teeth are present, and 13 associated teeth represent the anterior dentition. This skeleton documents a new genus of rhinocerotoid, described below. Moreover, several specimens previously referred to *Forstercooperia* Wood, 1938 are herein referred to this new genus. The results of this study demonstrate that this new genus represents the sister-taxon of the Rhinocerotidae. A number of characters of this genus have important implications for hypotheses of rhinocerotoid relationships. The taxonomic changes resulting from this study have implications for the biogeography of rhinocerotoids, particularly the indricotheriines.

Abbreviations—**AMNH**, American Museum of Natural History, New York; **CM**, Carnegie Museum of Natural History, Pittsburgh; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge; **UCMP**, University of California Museum of Paleontology, Berkeley; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington; **UW**, University of Wyoming Geology Museum, Laramie.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order PERISSODACTYLA Owen, 1848
Suborder CERATOMORPHA Wood, 1937
Superfamily RHINOCEROTOIDEA Owen 1845
Family uncertain
UINTACERAS, gen. nov.

Forstercooperia?: Radinsky, 1967:25, figs. 11–12, table 6.
Forstercooperia (in part): Lucas et al., 1981:827, figs. 1–2, tables 1–2.
Forstercooperia (in part): Lucas and Sobus, 1989:362.

Type Species—*Uintaceras radinskyi*, sp. nov.

Included Species—Known only from the type species.

Known Distribution—Late Eocene (Uintan) of western United States (Fig. 1).

Generic Diagnosis—Medium-sized rhinocerotoid (LM1–3 = 81–93 mm), distinguished from hyracodontids by tetradactyl manus and non-cursorial limb structure; synapomorphies of amynodontids, including enlarged and labially deflected M3 metastyle, elongated upper molar metalophs, reduced premolars, elongated lower molar talonids and preorbital fossa lacking; distinguished from rhinocerotids by distinct M3 metastyle; most resembling the indricotheriine hyracodontid *Forstercooperia*, but distinguished by isolated p3–4 entoconids, relatively tall maxillaries contributing to short, high rostrum, nasal incision above P1, orbits above M1–2, high braincase, and large sagittal crest; differing from all other rhinocerotoids in possessing buccolingually compressed upper incisors with triangular profile.

UINTACERAS RADINSKYI, sp. nov.

Forstercooperia? *grandis*: Radinsky, 1967:25, figs. 11–12, table 6.

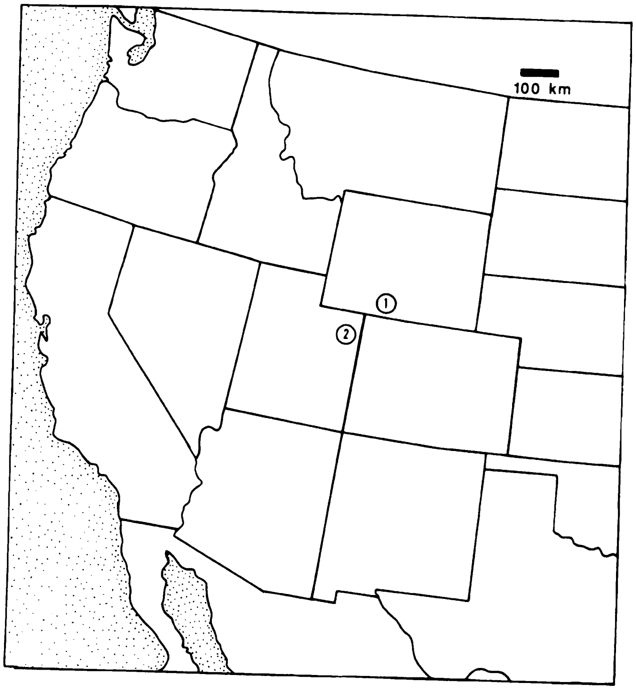

FIGURE 1. Map of the western United States showing *Uintaceras* localities. 1—Washakie Formation, Washakie Basin, Wyoming; 2—Uinta Formation, Uinta Basin, Utah.

Forstercooperia grandis (in part): Lucas et al., 1981:827, text-figs. 1–2, tables 1–2.

Forstercooperia grandis (in part): Lucas and Sobus, 1989:362.

Holotype—CM 12004, fragmentary skull and dentition, most of postcranial skeleton, from Myton Pocket, Uinta Basin, Utah.

Referred Specimens—From the Uinta Basin of Utah: CM 2908, mandible with c1–m3 (Fig. 5B). From the Uintan interval of the Washakie Formation in Sweetwater County, Wyoming: UCMP 69369, right maxillary fragment with damaged M1–3 (Fig. 3H) from UCMP locality V78102; UCMP 69370, left dentary fragment with M1–3 (Fig. 5D) from UCMP locality 78102; UCMP 69722, skull with left C, P1–M3 and badly damaged right P2–M3, and lower jaw with left p1–m3, right c, p2–m3 (Radinsky, 1967:figs. 11–12; Figs. 2A–B, 3G, 5C) from UCMP locality 5426; UW 2410, incomplete skull with left P1–M3 and right P4–M3 (Figs. 2C–D, 3I).

Distribution—As for genus.

Diagnosis—As for genus.

Etymology—Named for the late Leonard Radinsky to honor his many contributions to our knowledge of the evolution of the ceratomorph perissodactyls.

Description

Skull and Dentition—The skull of *Uintaceras* is known from two specimens, UCMP 69722 (Fig. 2A–B; Radinsky, 1967:fig. 12) and UW 2410 (Fig. 2C–D). The UCMP skull is more nearly complete than the UW skull, but it is badly crushed in the lateral plane. Sutures are mostly impossible to discern on both skulls, and their basicrania are so poorly preserved that almost no anatomical observations can be presented.

The skull of *Uintaceras* is about the same size as that of *Forstercooperia confluens* described by Wood (1963). Based on UCMP 69722, skull length (measured from the foramen magnum to the anterior edge of the maxillary) is about 360 mm. Only fragments of the premaxillaries are preserved, but a relatively small, conical, slightly recurved upper canine appears to follow immediately (no diastema) a much smaller I3. The nasal incision is retracted to above P1, further than Radinsky (1967:fig. 12) indicated.

The rostrum is high, convex laterally, and slightly shorter than the postorbital portion of the skull. The large infraorbital foramen is dorsal to P3 and opens to face nearly anteriorly. The anterior edge of the orbit is dorsal to the M1/M2 border. The zygomatic arches are stout anteriorly, thin posteriorly (across the jugal-squamosal contact), and flex slightly dorsally.

The braincase is high and rises to the occiput. It has a sharp and prominent sagittal crest confluent with the supraorbital crests. The occiput is tall, narrow, and rugose. A large foramen opens dorsolaterally near the posterior end of the braincase. The postglenoid process is blunt, oblique, and much larger than the joined mastoid and paroccipital processes. These processes bound a deep external auditory meatus that is notched ventrally. The basicranium is crushed.

The lower jaw of *Uintaceras* is similar to that of *Forstercooperia confluens,* as illustrated by Wood (1963:fig. 1). It has a long and shallow horizontal ramus. The symphysis extends to beneath the p1/p2 border. A relatively small, conical, slightly recurved canine is immediately preceded by a smaller i3 root. The roots suggest that i2 is only slightly smaller than i3 and that i1 is smaller than i2. There are five foramina on the lateral aspect of the horizontal ramus—a small foramen under i3, somewhat larger foramina under the anterior end of the postcanine diastema and under p1, and two larger foramina, one under p2 and the other under the m1 talonid. The ascending ramus is tall and thin, with thickened anterior and posterior borders.

The skull of CM 12004 is extensively crushed and little can be said about its morphology. One fragment from the dorsal skull roof shows evidence of a sagittal crest. The teeth are either isolated or held in fragments of the skull and mandibles.

The anterior dentition is represented in CM 12004 by 13 isolated teeth, but which are incisors and which might be canines is uncertain. Two general morphologies are present: six large, robust, bladelike teeth (Figs. 3A–B, 4A–B), which have a triangular profile, and five smaller conical teeth (Fig. 3C). One tooth shows an intermediate morphology (Fig. 3D), and another is too distorted to determine its original shape.

At least some of the bladelike teeth are incisors. One of the 13 teeth is represented only by a root, oval in cross section and held in a fragment of the premaxilla. This root is very similar in size and shape to that of a complete bladelike tooth (Fig. 3B), which is also held in a fragment of what appears to be the premaxilla. These teeth are smaller than the other bladelike teeth. Since the premaxilla is mediolaterally narrow posterior to the teeth, these teeth probably represent I3.

Five other teeth are bladelike. Four appear to be associated with the lower jaw, but, because of extensive crushing, it is difficult to be certain. The fifth tooth (Figs. 3A, 4A–B) is the largest of the anterior teeth and is isolated. The root of this tooth is bilobate, giving it the appearance of having two roots. The root curves slightly in what may be the posterior direction. The bladelike teeth show only minor wear at their apices.

One isolated tooth (Fig. 3D) shows an intermediate morphology. It is heavily worn on one side, and it may have been a large conical tooth originally. It differs from other conical teeth in having a slight curve to its single large root.

Four isolated teeth and one associated with the symphysis have conical crowns. Two of these teeth (Fig. 3C) are heavily worn on one side, while two others show wear facets on either side that are continuous at the apex. The extent of wear cannot be determined for the tooth associated with the symphysis.

The four upper premolars (Fig. 3E) of both sides are in place in the crushed maxillae of CM 12004. All are worn, some are

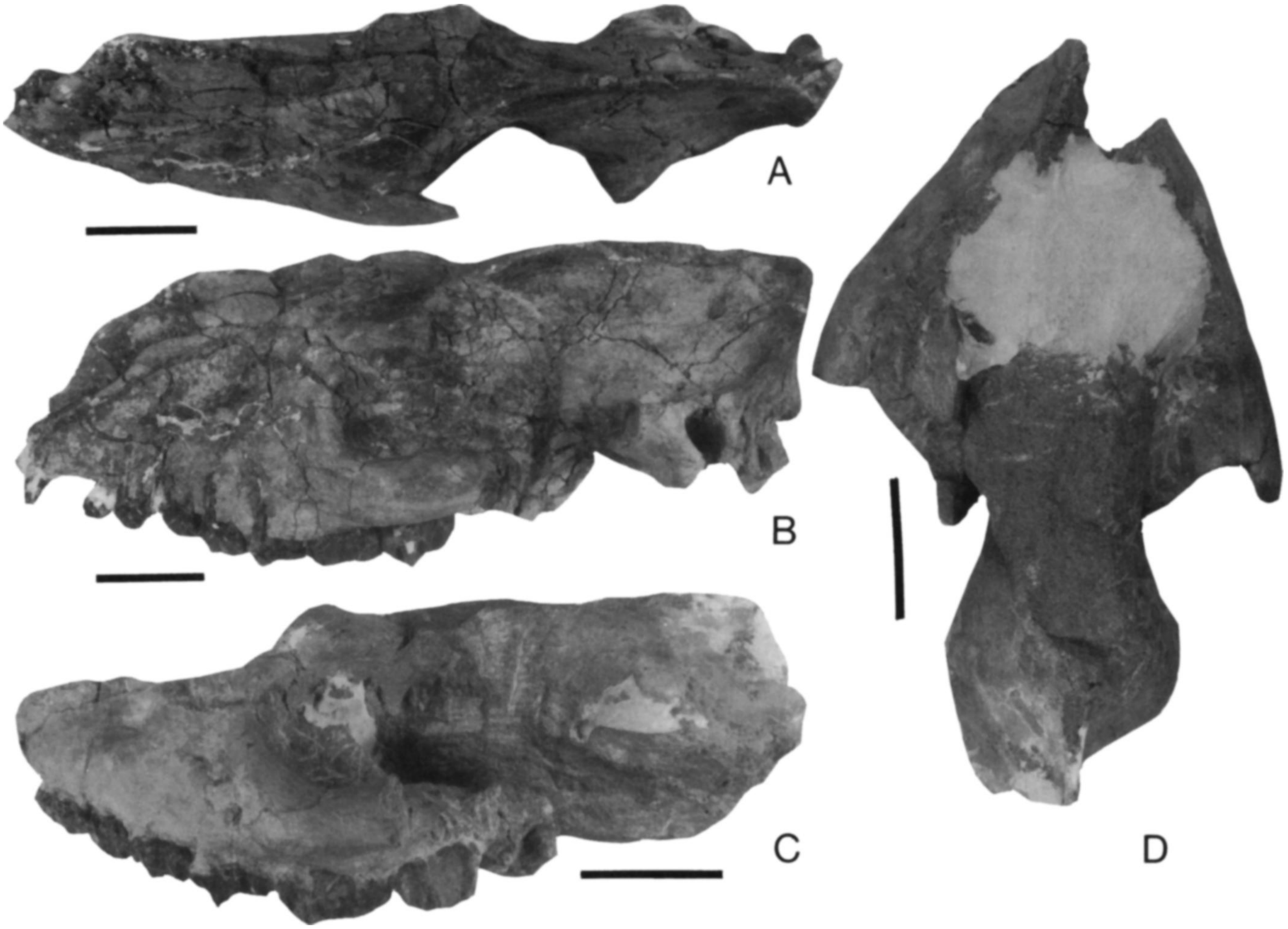

FIGURE 2. Skulls of *Uintaceras*. UCMP 69722 in **A**, dorsal and **B**, left lateral views. UW 2410 in **C**, left lateral and **D**, dorsal views. Scale bar = 5 cm.

damaged, and little can be said of their morphology beyond that they appear not to be molariform. The upper premolars are better preserved on UCMP 69722 and UW 2410 (Fig. 3G and 3I), and these specimens show more clearly the nonmolariform condition of the upper premolars.

The upper molars (Fig. 3F) have come free of the maxillae, but all six are present. M1 is the most worn on both sides, and the left M1 is damaged. They are generally similar to those of *Hyrachyus*, the main differences being the smaller size, presence of a lingual cingulum, and relatively large parastyles of *Hyrachyus*. Much as in *Hyrachyus*, the metacone on M3 of CM 12004 is larger and placed more labially than in *Hyracodon*; it is not as lingually deflected as in *Hyracodon*. The upper molars of UCMP 69722, UCMP 69369, and UW 2410 (Fig. 3G–I) are similar to those of CM 12004.

The lower cheek teeth of CM 12004 (Fig. 5A), like the upper series, are similar to those of *Hyrachyus* except for their larger size. All four premolars are present on both sides; no molarization is evident, and they are similar to those of CM 2908 and UCMP 69722 (Fig. 5B, C). Radinsky (1967; see fig. 11) noted the presence of an isolated entoconid on p3 and p4 in UCMP 69722, a characteristic absent in species of *Forstercooperia*. On CM 12004, p3 and p4 are too worn to determine if the entoconid is present and isolated. The lower molars of CM 12004 (Fig. 5A) are essentially indistinguishable from those of CM 2908, UCMP 69722, and UCMP 69370.

Vertebrae—An indeterminate number of vertebrae are present in CM 12004, but all are either heavily distorted and damaged, or are still embedded in matrix. The remains of several cervical vertebrae are embedded in the matrix, close to the various skull fragments. The atlas and axis are identifiable, but little can be said of the morphology of either. The odontoid process of the axis is cylindrical.

The first 12 thoracic vertebrae are present (Fig. 6). Distortion

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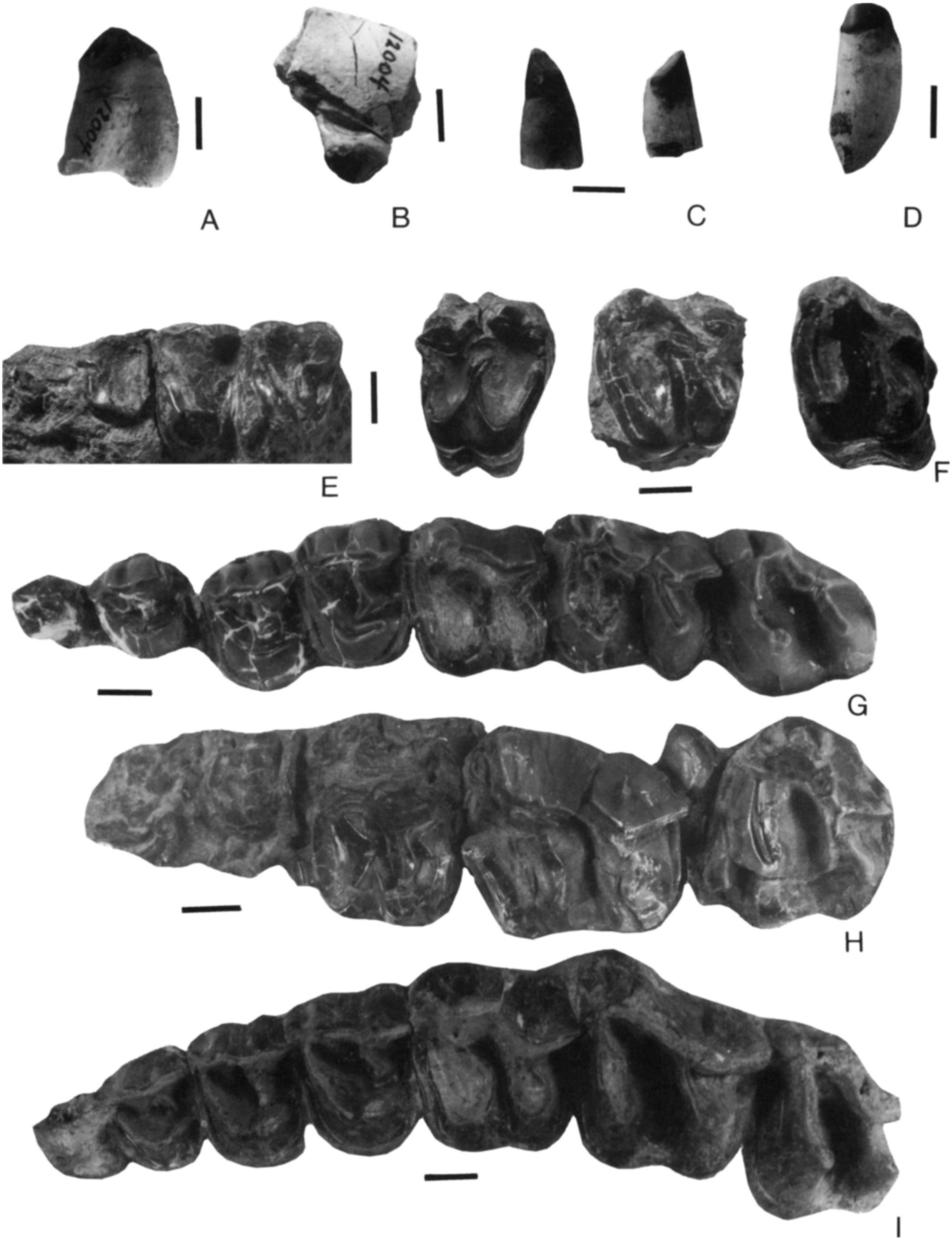
FIGURE 3. Anterior and upper dentitions of *Uintaceras*. **A**, CM 12004, undetermined bladelike anterior tooth, here pictured as an upper incisor, labial(?) view. **B**, CM 12004, left I3, labial view. **C**, CM 12004, undetermined conical anterior teeth. **D**, CM 12004, undetermined intermediate anterior tooth, labial(?) view. **E**, CM 12004, P2–4, occlusal view. **F**, CM 12004, right M1, left M2 and M3, occlusal view. **G**, UCMP 69722, left P1–M3, occlusal view. **H**, UCMP 69369, right M1–3 (negative reversed), occlusal view. **I**, UW 2410, left P1–M3, occlusal view. Scale bar = 1 cm.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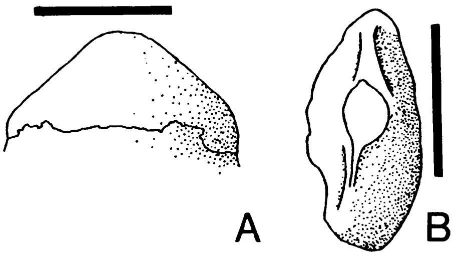

FIGURE 4. **A** and **B**, CM 12004, *Uintaceras*, bladelike anterior tooth, labial (**A**) and occlusal (**B**) views. Scale bar = 1 cm.

makes it impossible to determine the orientation of the zygapophyses. The centra are slightly opisthocoelous. Neither lumbar, sacral, nor caudal vertebrae are preserved in CM 12004.

Pectoral Limb—All of the elements of the pectoral limb are represented on one side or the other. In the interests of space, only those features relevant to rhinocerotoid phylogeny are emphasized here.

The left scapula (Fig. 7A) is fairly complete, lacking only parts of the dorsal and anterior borders, whereas only the distal end of the right scapula is preserved. The supraspinous fossa is expanded anteriorly, forming a shallow notch in the anterior border at the neck. The spine extends distally to the proximal end of the neck. The tuber spinae is relatively prominent. There is no evidence of an acromion process. The glenoid fossa is round, and the tuber scapulae and coracoid process are relatively low and not pronounced.

The left humerus has been distorted by crushing, but the right humerus (Fig. 7B–D) is relatively undistorted. The greater and lesser tuberosities extend only slightly beyond the head proximally. The greater tuberosity has a prominent anterior "hook," which is separated from the rest of the tuberosity by a shallow groove. The hook forms the anteromedial border of a deep bicipital groove. The lesser tuberosity is not distinctly separated from the head. On the anterior side, a prominent deltopectoral crest extends along the proximal end of the shaft, for about one-half of its length. The proximal portion of the crest hooks posterolaterally and has a strong deltoid tuberosity. The distal third of the humerus has a relatively broad brachialis flange (supinator crest) on the lateral side. The coronoid and olecranon fossae appear to be separated by a thin sheet of bone; the perforation seen in Fig. 7B is probably artificial. Overall, the humerus is very robust.

The radius and ulna (Fig. 7E–F) are unfused. The radius (Fig. 7E) is about 80% of the total length of the humerus. The two proximal humeral facets are shallow concavities, the rectangular medial facet being larger than the more triangular lateral facet. A fairly prominent tuberosity extends from the lateral side of the lateral facet.

The ulna (Fig. 7F) has a relatively large olecranon process that hooks medially. The medial and lateral humeral facets are about equal in surface area. The proximal radial facets do not appear to be confluent, and the medial radial facet appears to be quite small. The distal facet for the cuneiform is rectangular, while that for the pisiform is triangular.

The manus (Fig. 7G) is nearly complete on both sides. The only major elements missing are the right pisiform, the trapezia, and the left trapezoid. The manus is tetradactyl, with a completely functional digit V.

The scaphoid has a prominent posterior process. The radial facet (Fig. 8A) is somewhat rhomboidal in shape. It has a saddlelike contour—anteroposteriorly convex and mediolaterally concave. The lateral border, which adjoins the medial side of the lunar radial facet, extends posterolaterally. The two lunar facets do not wrap around the lunar posteriorly, as in *Tapirus*. On its distal end, the scaphoid has three adjacent facets for the magnum, trapezoid, and trapezium, respectively.

The lunar (Fig. 7G) is mediolaterally wide. The radial facet is convex anteroposteriorly and extends onto the proximal surface of the posterior process. Distally, the lunar has a broad anterior articulation with the unciform and a small one with the magnum. Extensive contact is made more posteriorly with the magnum "hump." The distal facets for the unciform and magnum are about equal and have a relatively extensive, anterolaterally trending contact. The posterior process of the lunar is moderately developed but does not extend posteriorly beyond the distal facets.

The cuneiform is roughly triangular in anterior view (Fig. 8C). Its ulnar facet is rectangular. The pisiform facet is posteriorly inclined. The unciform facet is roughly triangular in outline.

The pisiform has a prominent posterior process that hooks slightly medially. On the medial side, a tubercle, possibly for the attachment of ligaments (Radinsky, 1965), is present just posterior to these facets.

The trapezium does not appear to be represented in CM 12004, although it is possible that one or two of the apparent sesamoids may in fact be a trapezium that has been damaged beyond recognition. In any case, facets on the scaphoid, trapezoid, and second metacarpal testify to its presence.

The anterior face of the magnum (Fig. 7G) is roughly pentagonal, with the proximal apex lining up with the "hump." The sides of the pentagon correspond to facets for the scaphoid, trapezoid, second metacarpal, third metacarpal, lunar, and unciform. The trapezoid facet is distally confluent with the facet for the second metacarpal, and these two facets form the mediodistal side of the pentagon. Proximolaterally, there is a large facet, mostly for the unciform but shared by a small part of the lunar. This facet extends posteriorly over a large area of the "hump," reaching almost to the medial side. This marks the posterior contact of the lunar, which is much more extensive and less vertically inclined than that of the scaphoid. The distal facet for the third metacarpal is a large, anteroposteriorly concave facet. The posterior process of the magnum is prominent.

The proximal end of the unciform (Fig. 7G) is covered by facets for the lunar and cuneiform. The medial side of the unciform curves distally and laterally. This curve is made up of a series of essentially confluent facets for the magnum and third, fourth, and fifth metacarpals. The lateral end of this series of facets covers the distal aspect of the otherwise fairly prominent posterior process.

All four metacarpals (Fig. 7G) have saddle-shaped facets for their main proximal articulations. The proximal ends of the second and third metacarpals also have narrow lateral facets for the magnum and unciform, respectively. The metacarpals are robust. Metacarpal V is well developed and appears to have been part of a functional digit.

The phalanges are short, especially the middle elements. The flattened distal phalanges are asymmetrical on the second, fourth, and fifth digits, whereas the distal phalanx of the third digit is symmetrical.

Pelvic Limb—The pelvis is missing, although some fragments may be from this area. All other elements of the pelvic limb are represented in CM 12004. Again, the following description emphasizes features relevant to phylogeny.

Both femora are distorted and broken in several places, but much of their morphology can still be discerned (Fig. 9A). The head is large and hemispherical, the fovea interrupting its medial margin. The head is connected to a short but distinct neck. The greater trochanter extends proximally above the head, although not to the extent seen in many cursorial taxa. The lesser trochanter is represented by a ridge located medially about one-

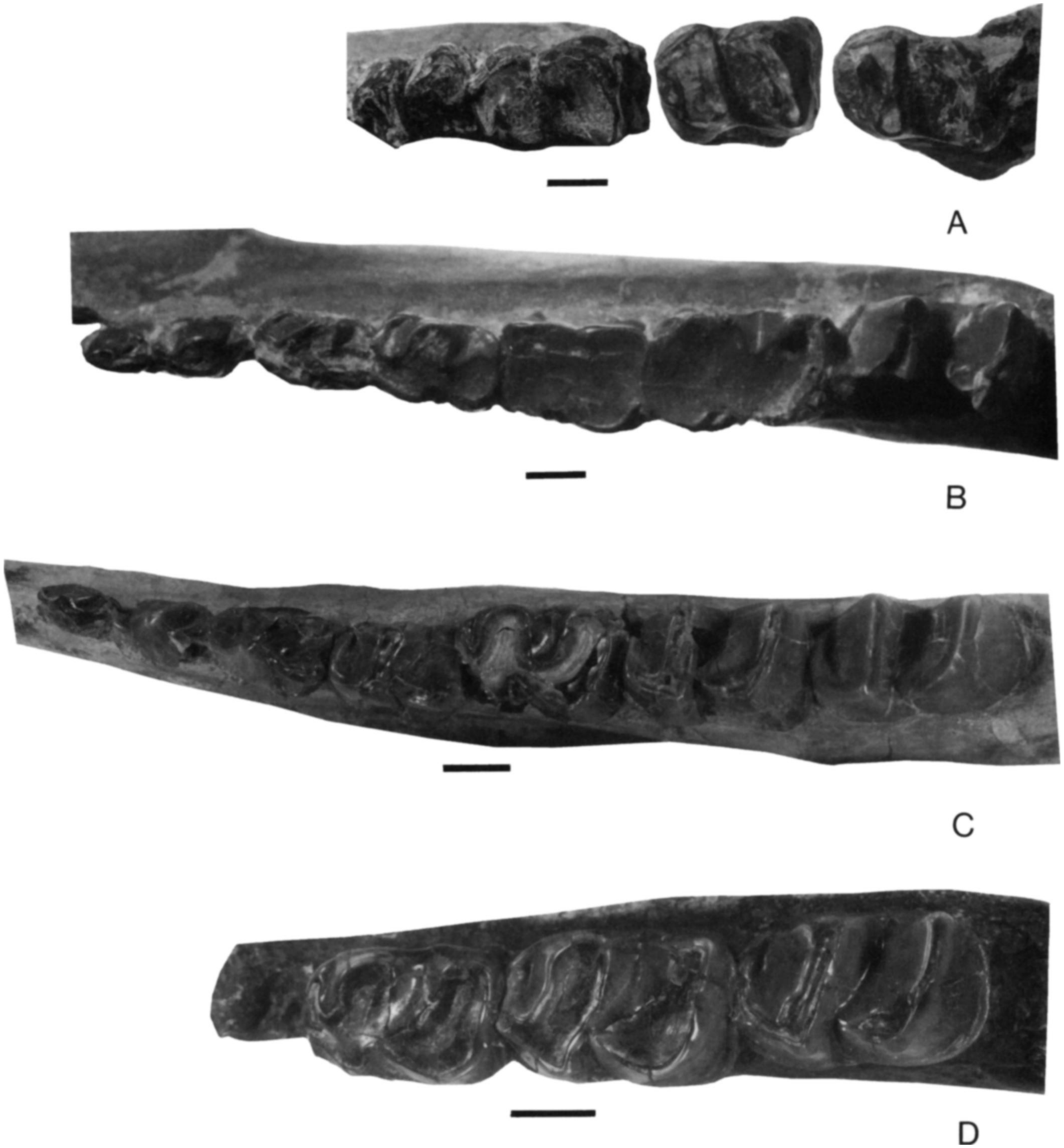

FIGURE 5. Occlusal views of lower dentitions of *Uintaceras*. **A**, CM 12004, right p4–m3. **B**, CM 2908, left p1–m3. **C**, UCMP 69722, left p1–m3. **D**, UCMP 69370, left m1–3. Scale bar = 1 cm.

quarter the length of the shaft from the proximal end. The prominent third trochanter lies in a slightly more distal position on the lateral side.

The tibia (Fig. 9B) and fibula are unfused. The lateral femoral facet of the tibia and its intercondyloid eminence lie slightly above their medial counterparts. The cnemial crest is weakly developed, with little or no tuberosity. The proximal end of the cnemial crest has a relatively deep fossa for the middle patellar ligament. At the distal end, the medial astragalar facet is deep and mediolaterally narrow, whereas the lateral facet is broad, shallow, and sweeps proximolaterally to the distal fibular facet.

The patella (Fig. 9C–D) is robust but otherwise similar to those of other primitive ceratomorphs: oval in posterior outline, with two subequal posterior facets, the medial facet extending more distally. The patella of CM 12004 is anteroposteriorly thick, not flattened as in rhinocerotids and indricotheriines.

FIGURE 6. First (**A**) and second (**B**) thoracic vertebrae of CM 12004, *Uintaceras*, left lateral view. Scale bar = 5 cm.

The tarsus and foot (Fig. 9E) are nearly complete on both sides. The astragalus (Fig. 9G–H) has a very short neck. The trochlea is offset laterally relative to the neck; this is accentuated by a tubercle on the distal end of the medial side. The trochlear groove is shallow, so that it grades into the medial aspect of the lateral condyle. The lateral trochlear condyle is larger than the medial, and there is a moderately developed lateral tuberosity. On the posterior side, the proximal facet for the calcaneum is deeply concave proximodistally. This facet is separated on its distomedial side from the broad, oval, and flat sustentacular facet. The sustentacular facet is confluent with the distal calcaneal facet. On the distal end of the astragalus, the cuboid facet occupies the lateral side as a narrow band and lies adjacent to the distal calcaneal facet. The remainder of the distal aspect is covered by the saddle-shaped navicular facet.

The calcaneum (Fig. 9F) has a mediolaterally compressed shaft, which is moderately expanded posteriorly as the tuber calcis. The lateral astragalar facet and the facet of the sustentaculum are expanded such that they are nearly in contact. The distal astragalar facet is a narrow strip that is confluent at its medial end with the facet of the sustentaculum. The pit that accomodated the distal fibula during extreme flexion of the ankle is small and shallow, and located behind the lateral astragalar facet. On the lateral side, at a position just distal to this pit, there is a larger depression for the short lateral ligament (see Radinsky, 1965). The peroneal tubercle is prominent at the distal end of the lateral aspect of the calcaneum. The distal end is covered by the crescent-shaped cuboid facet. There is no facet for the navicular.

The cuboid is relatively short. The posterior process is fairly prominent. The proximal surface is covered by a nearly flat, saddle-shaped facet. This facet is divided into medial and lateral parts by a ridge. The lateral part of the facet, which articulates with the calcaneum, is about twice as large as the medial part for the astragalus. On the distal end, there is a large, round, flat facet for the fourth metatarsal.

The navicular is proximodistally compressed. On its proximal surface, there is a saddle-shaped facet for the astragalus. The distal surface is covered by a gently convex facet, which articulates with the ectocuneiform and mesocuneiform. A facet for the cuboid extends along the lateral side.

The navicular facet of the ectocuneiform is gently concave. There are a pair of facets on the lateral side for the cuboid, and a pair of facets are present on the medial side for the second metatarsal. The distal facet for metatarsal III is essentially flat, with the exception of the most posterior part, which extends slightly distally. This distal extension appears to be caused by a distal expansion of the posterior portion of the ectocuneiform, which accommodates the posterodistal facet for metatarsal II.

The mesocuneiform is relatively simple, with an anteroposteriorly concave facet for the navicular and a slightly saddle-shaped facet for metatarsal II. The entocuneiform is anteroposteriorly compressed and roughly oval in outline. This bone possesses anteromedial facets for the navicular and mesocuneiform. These small facets extend onto the anterior face to a greater extent than those of *Heptodon* illustrated by Radinsky (1965:fig. 21). There is a narrow facet anterodistally for metatarsal II. The existence of a facet for metatarsal I cannot be ascertained.

The proximal facets of the metatarsals are flatter than those of the metacarpals. A posterior projection on the proximal end of the left second metatarsal appears to articulate with the entocuneiform. It is possible that this process is a fused hallux (Fig. 9I; see Radinsky, 1963). It is unclear whether or not the posterior process of metatarsal III bears a posterior facet that would articulate with the vestigial hallux. No separate hallux has been identified in CM 12004

The phalanges are longer in the pes than in the manus. The lateral digits have asymmetrical distal phalanges, whereas the median distal phalanx is symmetrical and bears a median notch at the tip.

DISCUSSION

The dentition of CM 12004 combines unique anterior teeth with primitive cheek teeth. The cheek teeth are similar to those of *Hyrachyus,* although larger. The reduced upper molar parastyles confirm that the specimen is a rhinocerotoid (Prothero et al., 1986).

Peterson (1919) described a dentary fragment from the middle Eocene of the Uinta Basin, Utah (Uinta A), for which he erected the species *Hyrachyus grande* (which Wood [1934] emended to *H. grandis*). Radinsky (1967) referred this species to *Forstercooperia* Wood 1938, based on additional material, including a skull and several upper and lower cheek teeth, collected from the Washakie B beds of the Washakie Basin, Wyoming. These specimens are included here in *Uintaceras.*

In assessing the taxonomy of *Uintaceras,* the assignment of Peterson's type specimen of *Hyrachyus grandis* (CM 2908) would normally establish *Uintaceras grandis* as the type spe-

FIGURE 7. Forelimb elements of CM 12004, *Uintaceras*. **A**, left scapula, lateral view. Right humerus in **B**, anterior, **C**, medial, and **D**, lateral views. **E**, right radius, anterior view. **F**, right ulna, medial view. **G**, right manus, anterior view. Scale bar = 5 cm.

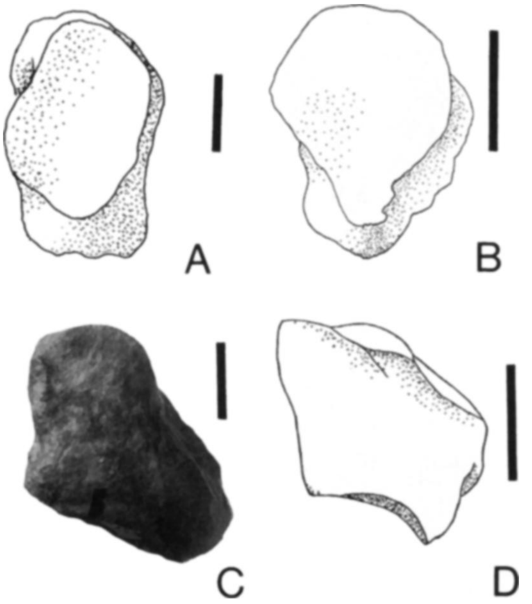

FIGURE 8. Scaphoid and cuneiform of selected ceratomorphs. **A**, right scaphoid of *Uintaceras* (CM 12004), proximal view. **B**, left scaphoid (reversed) of *Hyrachyus* (AMNH 17436), proximal view. **C**, left cuneiform of *Uintaceras* (CM 12004), anterolateral view. **D**, right cuneiform of *Heptodon* (redrawn from Radinsky, 1965:fig. 21), anterolateral view. Scale bar = 1 cm.

cies, and the fate of the name *Uintaceras* would be determined by the taxonomic status of CM 2908. CM 2908, however, bears none of the diagnostic characteristics of any of the genera to which it has been referred. Our arguments for establishing *Uintaceras* are tied far more closely to other specimens, particularly CM 12004 and UCMP 69722, than they are to CM 2908. We, therefore, consider Peterson's species to be a nomen dubium, and on that basis we do not make it the type species of *Uintaceras.* Instead, we have designated CM 12004 the holotype of a new species, *Uintaceras radinskyi,* the type species of the genus. What makes CM 12004 a more desireable choice for the holotype than other specimens is that it preserves diagnostic characters of both the anterior dentition and the postcranial skeleton.

The anterior dentition of CM 12004 is unique among rhinocerotoids. The anterior teeth of CM 12004 include a bladelike 13 (and other bladelike teeth), and at least some of the conical teeth are associated with the lower jaw. The clear differences between the anterior dentition of CM 12004 and AMNH 20116, the holotype of *Forstercooperia,* discussed below, suggest that these represent different genera. No other known rhinocerotoid possesses the anterior dental morphology of CM 12004, but the posterior incisors of primitive rhinocerotids appear to be most comparable.

A few rhinocerotid taxa, including *Teletaceras, Trigonias, Subhyracodon,* and *Diceratherium,* retain canines or posterior incisors. However, the upper "chisel" of rhinocerotids is buccolingually compressed and bladelike, although its characteristic shape is unlike that of the bladelike teeth of CM 12004. In *Trigonias,* 12–3 are reduced but buccolingually compressed. Small canines range from conical to bladelike. In *Subhyracodon,* 12 is consistently caniniform. One juvenile specimen of *Subhyracodon,* AMNH 534, possesses tiny but distinctly bladelike deciduous upper and lower incisors. *Diceratherium* consistently shows a bladelike 12.

Compared to other early ceratomorphs, the postcrania of CM 12004 show some interesting derived and primitive traits. Table 1 lists some of the features relevant to rhinocerotoid phylogeny and the condition observed in *Uintaceras.* A brief discussion of these characters is given below and is based on comparisons of CM 12004 with other ceratomorph specimens, as well as published descriptions of tapiroid skeletons (e.g., Radinsky [1965] for *Heptodon*).

Primitively, as in *Hyrachyus,* the spine of the scapula is relatively high at its distal end and may still bear a small but distinct acromion process (as in *Helaletes* [USNM 22481]). The coracoid process of *Hyrachyus* and *Helaletes* (but not *Heptodon*) is prominent and projects anteromedially. The reduction of the spine on CM 12004 is also seen in other rhinocerotoids, as well as in *Tapirus.*

The prominent deltopectoral and supinator crests of CM 12004 are derived, and this condition is shared with primitive rhinocerotids, such as *Subhyracodon.*

The radial facet of the ceratomorph scaphoid is primitively somewhat rounded. This is seen in most "tapiroids," including *Heptodon, Helaletes,* and *Tapirus,* as well as *Hyrachyus* (Fig. 8B). A rhomboidal radial facet, due to elongation of the lateral edge that articulates with the lunar, is found in amynodonts and rhinocerotids, including *Trigonias* and *Subhyracodon.* This elaboration of the articulation between the scaphoid and lunar is related to functional differences in the locomotion of rhinoceroses and tapirs, as noted by Klaits (1972, 1973).

The presence of a fourth digit on the manus is a primitive character for rhinocerotoids. A tridactyl manus is thought to be a synapomorphy of the family Hyracodontidae *sensu* Radinsky (1967; i.e., including indricotheres) (Lucas et al., 1981; Lucas and Sobus, 1989). Most rhinocerotids are tridactyl, but one of the most primitive, *Trigonias,* is tetradactyl. Hanson (1989) argued that the primitive rhinocerotid *Teletaceras* had a tridactyl manus, based on the shape of metacarpal IV, and that this may represent the primitive condition for rhinocerotids. The tetradactyl manus of *Trigonias* would, therefore, be secondarily derived. If CM 12004 represents the sister taxon to rhinocerotids, then the opposite scenario is more likely, i.e., the tridactyl manus of *Teletaceras* was evolved independently from that in other rhinocerotids.

Heissig (1989) claimed that a flattened patella was a synapomorphy uniting indricotheriines and rhinocerotids. Rhinocerotids and *Paraceratherium* both possess flattened, asymmetrical patellae with a medial projection. In *Paraceratherium,* the medial facet for the distal femur extends onto this projection, whereas in rhinocerotids, the medial and lateral facets are more nearly symmetrical and the medial facet does not extend onto the projection. The patella of CM 12004 is primitively unflattened and symmetrical. If CM 12004 is closely related to rhinocerotids, the shape of the patella of indricotheriines and rhinocerotids is probably convergent.

Some of the tarsal characters observed in CM 12004 show interesting distributions among rhinocerotoids. The "offset" position of the trochlea of the astragalus may be a synapomorphy of rhinocerotoids, including *Hyrachyus.* The distal process on the posterior ectocuneiform of CM 12004 is also found in amynodonts and rhinocerotids.

The limb proportions of CM 12004 suggest a very robust, non-cursorial animal. The radiohumeral index (Table 2) is the only index of long bone proportions available for this specimen, but its value is lower than that of any other ceratomorph studied. *Hyrachyus,* amynodonts, and rhinocerotids show the most similarity to CM 12004, indicating that an index of less than one is primitive for rhinocerotoids. The femora are broken and their original length cannot be determined, but it is clear that the tibia was much shorter than the femur (compare Figs. 9A, B). The metapodial proportions of CM 12004 are most similar to those of amynodonts and rhinocerotids (Table 3); it is diffi-

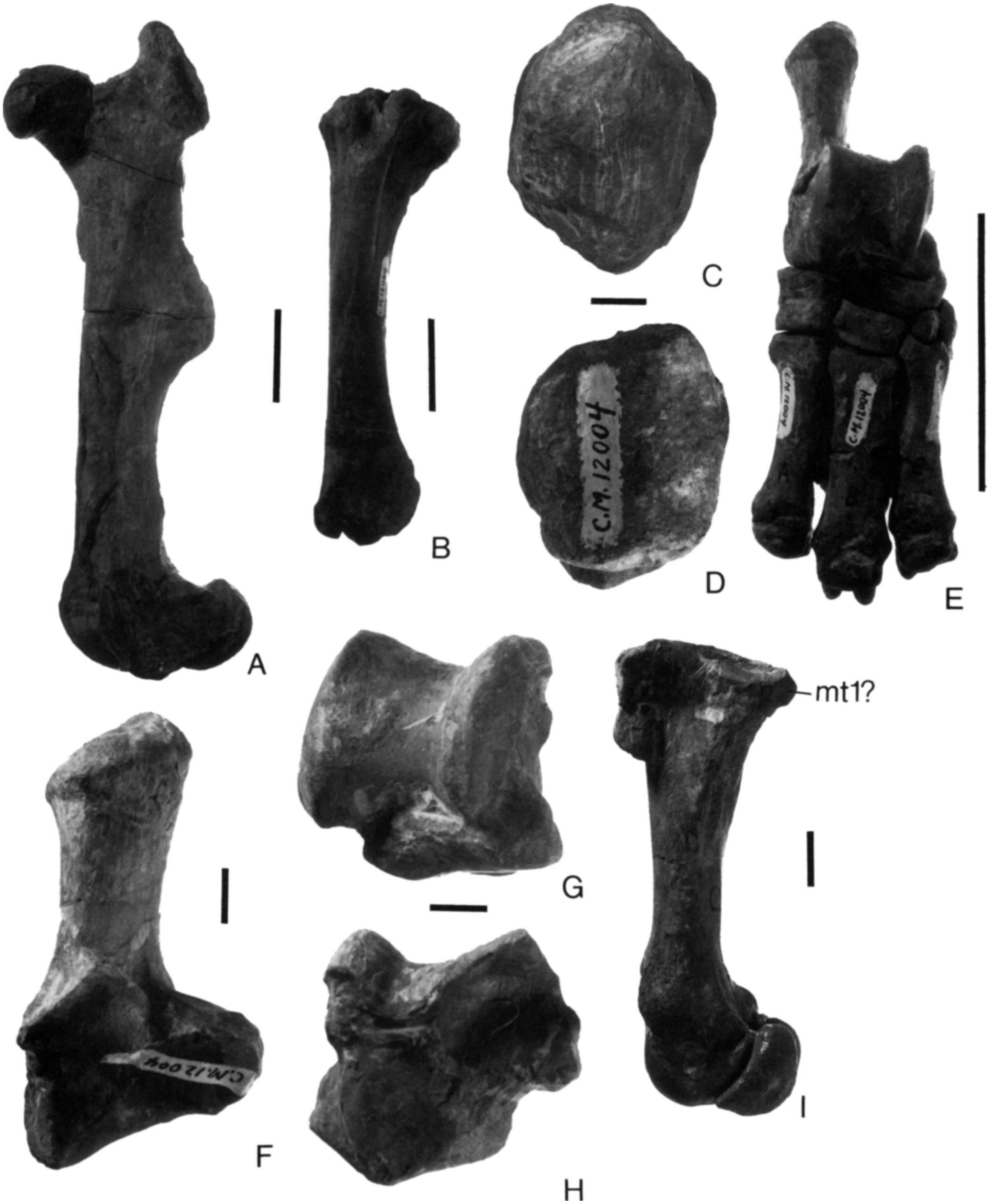

FIGURE 9. Hind limb elements of CM 12004, *Uintaceras*. **A**, left femur, anterior view. **B**, left tibia, anterior view. Patella in **C**, anterior and **D**, posterior views. **E**, right pes, anterior view. **F**, right calcaneum, anterior view. Right astragalus in **G**, anterior and **H**, posterior views. **I**, right second metatarsal, medial view. Abbreviations: mt1? = possible fused vestigial first metatarsal. Scale bar = 5 cm.

TABLE 1. Selected postcranial characters, their primitive and derived conditions as seen in rhinocerotoids, and the condition observed in *Uintaceras*.

Character	Primitive	Derived	*Uintaceras*
Scapular spine	high, extends distally	low, distally reduced	Derived
Acromion process	present	absent	Derived
Coracoid process	prominent	weak	Derived
Deltopectoral crest	weak	prominent	Derived
Supinator crest	weak	prominent, extends proximally	Derived
Radial facet of scaphoid	rounded	rhomboidal	Derived
Cuneiform	trapezoidal	triangular	Derived
Manus	tetradactyl	tridactyl	Primitive
Patella	unflattered	flattened	Primitive
Trochlea of astragalus	not offset from neck	offset laterally	Derived

cult to say whether this is the result of scaling or a derived trait uniting these taxa.

Phylogenetic Relationships of *Uintaceras*

Figure 10 summarizes the phylogenetic position of *Uintaceras* as interpreted in this study.

Uintaceras is a very primitive rhinocerotoid, but characters of the anterior dentition and postcranium suggest that this genus is most closely allied with rhinocerotids. The postcranial bones of *Uintaceras* also show some resemblance to those of amynodonts, but these similarities may be due to scaling. *Uintaceras* lacks the synapomorphies attributed to amynodonts (Wall, 1981), but shares one unequivocal synapomorphy with rhinocerotids: buccolingually compressed upper incisors. Because *Uintaceras* does not appear to possess the diagnostic "chisel/tusk" arrangement of the incisors of rhinocerotids, inclusion of this genus in the family Rhinocerotidae would require a new diagnosis for this family. Instead, we suggest that *Uintaceras* be tentatively referred to this family without emendation of the diagnosis or considered to be the sister-taxon of the Rhinocerotidae as currently defined, until we have a better understanding of the anterior dentition of this genus.

TABLE 2. Radiohumeral indices for selected ceratomorph genera.

Genus	Radius length/humerus length
Tapiridae	
Tapirus (n = 15)	0.899
Helaletidae	
Helaletes (n = 3)	0.957
Hyrachyidae	
Hyrachyus (n = 5)	0.924
Amynodontidae	
Amynodon (n = 1)	0.947
Hyracodontinae	
Triplopus (n = 1)	1.335
Hyracodon (n = 1)	1.047
Indricotheriinae	
Paraceratherium (n = 1)	1.05*
Rhinocerotidae	
Subhyracodon (n = 1)	0.948
Dicerorhinus (n = 1)	0.902
Rhinoceros (n = 2)	0.945
CM 12004	0.807

*Taken from Osborn (1923).

TABLE 3. Metapodial proportions of selected ceratomorphs.

Genus	Metapodial robustic index Metacarpal III L/W	 Metatarsal III L/W
Hyrachyidae		
Hyrachyus	4.64 (n = 5)	4.46 (n = 7)
Amynodontidae		
Amynodon	4.91 (n = 1)	2.80 (n = 1)
Hyracodontinae		
Triplopus	6.98 (n = 2)	5.39 (n = 2)
Hyracodon	5.33 (n = 2)	4.83 (n = 1)
Indricotheriinae		
Juxia	5.02 (n = 2)	4.57(n = 4)
Paraceratherium	3.52 (n = 3)	3.40 (n = 3)
Rhinocerotidae		
Subhyracodon	3.11 (n = 2)	3.75 (n = 2)
Dicerorhinus	3.00 (n = 1)	2.83 (n = 1)
Rhinoceros	2.99 (n = 2)	2.89 (n = 2)
CM 12004	3.42	3.14

Status of North American *Forstercooperia*

Radinsky (1967) first referred the North American Uintan specimens of *Uintaceras* to *Forstercooperia*. This made North American *Forstercooperia grandis* (Peterson, 1919) a senior subjective synonym of Asian *Forstercooperia confluens* (Wood, 1963) and thus gave the genus a trans-Pacific distribution. Subsequent workers (e.g., Lucas et al., 1981; Prothero et al., 1986; Lucas and Sobus, 1989) accepted this assignment. Indeed, given the previous lack of knowledge of the anterior dentition of *Uintaceras* and the overall similarity of the cheek teeth of *Uintaceras* and *Forstercooperia*, assigning the North American specimens to *Forstercooperia* was a reasonable decision. However, the cranial structure of the North American specimens excludes them from *Forstercooperia* and the Indricotheriinae.

Lucas and Sobus (1989) identified a unique association of

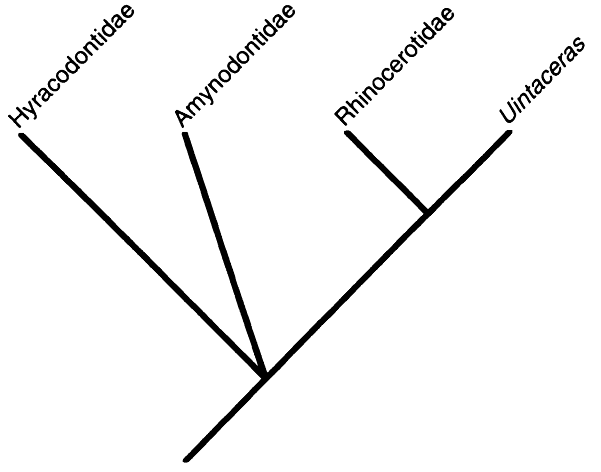

FIGURE 10. Cladogram depicting the phylogenetic relationship of *Uintaceras* to other rhinocerotoids. Eurasian indricotheriines are included in the family Hyracodontidae. (See text under "Status of North American *Forstercooperia*.") Synapomorphies uniting *Uintaceras* and rhinocerotids include: buccolingually compressed upper incisors; prominent deltopectoral crest of humerus; prominent supinator crest of humerus.

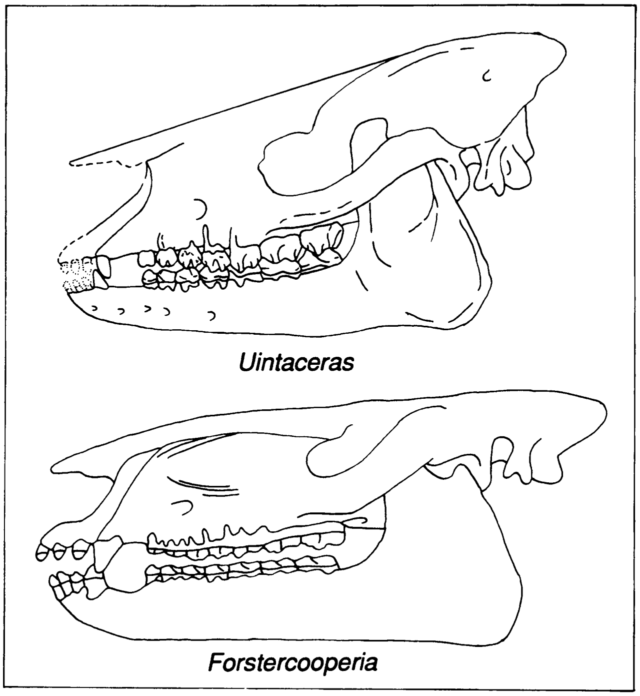

FIGURE 11. Lateral views of skulls of **A**, *Uintaceras* (after Radinsky, 1967), and **B**, *Forstercooperia* (after Wood [1963] and Lucas and Sobus [1989]), drawn to same scale to show contrasting cranial morphologies of the two genera.

characters in the anterior facial skeleton that distinguishes all indricotheriines, including *Forstercooperia,* from other rhinocerotoids. These features constitute a functional complex in which the nasal and maxillary bones are modified for the support of an elaborated muscular snout, which probably supported a short proboscis in the largest and most advanced indricotheriines. These modifications are well seen in their most incipient stage in *Forstercooperia,* where the nasal bones form a robust shelf that begins above the upper canine and a high flattened eminence that terminates above the orbits (Fig. 11B). This eminence is set at a distinct angle to the rest of the skull. A preorbital fossa on the maxillary bones runs parallel to most of the posterior tooth row. The rostrum is relatively long (much longer than the braincase) and the orbits are placed relatively posteriorly, above the M3. The nasal incision in *Forstercooperia* is little retracted and is above the canine. The braincase is low, the sagittal crest is relatively small, and the occiput is strongly inclined posteriorly. These modifications of the rostrum of *Forstercooperia* probably provided a wide site of attachment for muscles supporting the snout, notably the dilator naris, and a well-developed levator rostri, which would have manipulated a muscular rhinarium.

In contrast, the skull of *Uintaceras* (Fig. 11A) has relatively tall maxillaries that contribute to a short, high rostrum, the nasal incision is retracted to above P1, the orbits lie above M1–2, the braincase is high, and the sagittal crest is large. The glenoid fossa does not so nearly approach the plane of the anterior dentition as in *Forstercooperia.*

The holotype of *Forstercooperia,* AMNH 20116, described by Wood (1938), is the anterior part of a skull, including the upper incisors, canines, and premolars, and comes from the Eocene of Inner Mongolia, China. The holotype is larger than any North American specimen referred to *Forstercooperia.* The anterior dentition consists of large, robust canines and distinctly conical incisors. The buccolingually compressed incisors of CM 12004 are not found in AMNH 20116.

Cranial features allow easy distinction of *Uintaceras* from *Forstercooperia.* No skull having *Forstercooperia* morphology has ever been found in North America. Therefore, it is reasonable to infer that cheek teeth having *Uintaceras* morphology from North America not associated with cranial material do not belong to *Forstercooperia,* even though the two genera cannot be distinguished from cheek teeth alone.

Elimination of the North American occurrences of *Forstercooperia* recognized by previous workers has the following implications for indricotheriine taxonomy, phylogeny, and paleobiogeography:

1. *Forstercooperia grandis* (Peterson, 1919) is not the valid name for the medium-sized species of *Forstercooperia* from the middle Eocene (Irdinmanhan and Sharamurunian) of China and Mongolia. *F. confluens* (Wood, 1963) is the valid name of that species.
2. Lucas et al.'s (1981; also see Lucas, 1982) argument that F:AM 99662, a juvenile left dentary fragment with dp2–3 from the Duchesnean interval of the Galisteo Formation in New Mexico, is a specimen of *Forstercooperia minuta* seems improbable. This specimen is a primitive rhinocerotoid, but we consider it generically indeterminate.
3. Absence of *Forstercooperia* in North America eliminates a trans-Pacific original distribution (generalized track) of the earliest indricotheriines followed by vicariance, extinction in North America, and subsequent evolution (*Juxia* to *Paraceratherium*) in Eurasia. The entire evolution of the indricotheriines took place in Eurasia.

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APPENDIX 1. Tooth dimensions (in mm) for specimens of *Uintaceras radinskyi*.

	UCMP 69370	UCMP 69722	CM 12004		UCMP 69369	UCMP 69722	UW 2410	CM 12004
p1 length		13.1		P1 length		15.1	14.9	
p1 width		8.2		P1 width			16.1	
p2 length		15.9		P2 length		16.4	16.4	
p2 width		10.5		P2 width		22.7	21.6	
p3 length		20.4	18.8	P3 length		19.0	17.8	
p3 width		14.5	12.6	P3 width		27.4	26.2	
p4 length		21.5	19.2	P4 length		21.5	21.5	
p4 width		16.4	14.4	P4 width		29.1	28.6	
m1 length	25.7	27.8	24.5	M1 length	27.3	28.7	28.9	26.1
m1 width	18.9	19.6	18.3	M1 width	32.7	32.5	33.2	31.4
m2 length	29.5	30.7	29.0	M2 length	37.2	33.2	35.1	29.7
m2 width	21.2	19.5	19.5	M2 width	36.0	32.2	37.7	34.0
m3 length	32.5	33.5	31.2	M3 length	28.8	29.5	27.1	25.1
m3 width	20.2	19.3	20.2	M3 width	35.9	33.9	34.3	32.1

Note added in Proof

After the article went to press, new data on the distribution of *Uintaceras* appeared in five articles. Prothero (1996) and Walsh (1996) noted that specimens of *Uintaceras* (they refer to them as *Forstercooperia grandis*) previously reported from the "Uinta A" interval in the Uinta basin are actually from the "Uinta B1" interval. McCarroll et al. (1996a, b) reported (but did not illustrate) a left M3 they identified as "cf. *Forstercooperia minuta*" from the Adobe Town Member of the Washakie Formation in the Washakie basin, Wyoming; this specimen may pertain to *Uintaceras*. Stucky et al. (1996) reported *Forstercooperia grandis*, which we take to be *Uintaceras*, from the Washakie Formation in the Sand Wash basin of northwestern Colorado.

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