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Anatomy and Phylogenetic Relationships of the Theropod Dinosaur *Microvenator celer* from the Lower Cretaceous of Montana

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ABSTRACT

The holotype of *Microvenator celer* Ostrom, 1970 (AMNH 3041) is a partial skeleton of a small maniraptoran theropod from the Lower Cretaceous Cloverly Formation of Montana. We present a detailed redescription of this specimen, emphasizing those features that are of interest for discovering the phylogenetic relationships of *Microvenator*. Based on several postcranial features, especially the lack of fusion of the neurocentral sutures, we consider AMNH 3041 a juvenile individual. Reexamination of the holotype revealed the presence of several autapomorphies that provide the basis for a revised diagnosis of *Microvenator celer*. Diagnostic characters include pos-

terior dorsal and caudal vertebrae that are wider than high, the presence of a deep depression on the proximomedial part of the pubis, and an accessory trochanteric ridge below the lesser femoral trochanter. Phylogenetic analysis places *Microvenator* either among Oviraptorosauria, or as the sister group to the Oviraptorosauria. Among the characters diagnostic for the Oviraptorosauria, anteriorly concave pubes, a proximodorsal tubercle on the manual unguals, and possibly an edentulous dentary with a pronounced symphysis are present in *Microvenator*. *M. celer* is the earliest known oviraptorosaurian or oviraptorosaur-like theropod represented by diagnostic skeletal remains.

INTRODUCTION

In his monograph on the stratigraphy and fossil vertebrates of the Lower Cretaceous Cloverly Formation of Montana and Wyo-

ming, Ostrom (1970) briefly described the partial skeleton of a small theropod and designated it as the holotype of a new genus and

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species, *Microvenator celer*. This specimen was collected in south-central Montana by a field party from the American Museum of Natural History under the leadership of Barnum Brown in 1933 and is now housed in the collections of the American Museum of Natural History (AMNH 3041). Brown informally named the fossil "*Megadontosaurus*" because he had associated several large teeth (subsequently referred to the dromaeosaurid *Deinonychus antirrhopus* by Ostrom [1970]) with the gracile postcranial bones. He never published a formal description of this material although an extensive set of illustrations had been prepared for this purpose. We reproduce some of these drawings in this paper because they show the limb bones prior to extensive restoration.

Based primarily on its small size, Ostrom (1970) referred *Microvenator celer* to the family Coeluridae, but that taxon is now considered paraphyletic (Gauthier, 1986). Gauthier (1986) treated *M. celer* as a metataxon devoid of diagnostic characters and placed it within Maniraptora. Currie and Russell (1988) speculated that it might be a basal caenagnathid and cited several similarities in the postcranial skeleton shared with *Oviraptor*. In view of the rarity of associated skeletal remains of small nonavian theropod dinosaurs and the phylogenetic importance of these animals as the closest relatives of birds, we have restudied the holotype and only known specimen of *M. celer*. Our study assesses its phylogenetic position using explicitly cladistic approaches and taking into account recent studies on other theropod taxa.

ABBREVIATIONS

AMNH	Department of Vertebrate Paleontology, American Museum of Natural History
GI	Geological Institute, Mongolian Academy of Sciences, Ulaan Bataar
HMN	Museum für Naturkunde, Humboldt-Universität, Berlin
IVPP	Institute for Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing
ROM	Royal Ontario Museum, Toronto
RTMP	Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta
YPM	Peabody Museum of Natural History, Yale University, New Haven

SYSTEMATIC PALEONTOLOGY

Microvenator celer Ostrom, 1970

HOLOTYPE: AMNH 3041, partial skeleton including several cranial bones, parts of at least 23 vertebrae from all regions of the column, four ribs, left coracoid, left humerus, radius and ulna, four manual bones, fragments of both ilia, both pubes, both femora and tibiae, partial left fibula, left astragalus, two pedal bones, and several indeterminate bones or bone fragments. (Measurements for individual bones are listed in table 1.) Collected by an AMNH field party led by Barnum Brown in 1933.

TYPE LOCALITY, HORIZON, AGE: AMNH locality 33-1, SW 1/4 Sec. 26, T.7N, R.16E, Wheatland County, Montana. Cloverly Formation, Unit VII, about 60 ft (18.25 m) below Unit VIII. Age: Early Cretaceous (Albian-Albian; Ostrom, 1970).

REFERRED MATERIAL: Ostrom (1970: pl. 11, fig. K) tentatively referred a small theropod tooth (YPM 5366) to *Microvenator celer*, but this identification cannot be confirmed because the holotype does not include any unambiguously associated teeth.

DIAGNOSIS: *Microvenator celer* is distinguished from other nonavian coelurosaurs by dorsal and caudal centra that are distinctly wider than high and an accessory crest (for insertion of *M. iliotrochantericus* anterior) at the base of the lesser trochanter of the femur.

DESCRIPTION

SKULL: The holotype of *Microvenator celer* includes only a few poorly preserved cranial elements. Ostrom (1970) tentatively identified a palatine, both quadrates, and both postorbitals. Since Ostrom (1970) did not illustrate or label these elements, we were unable to match his identifications to the material at hand.

A tall, thin bone may represent a right lacrimal. The ventral end is expanded antero-posteriorly to form a small semicircular plate, which is gently convex laterally and concave medially where it would have contacted the lacrimal process of the jugal. It strongly resembles the ventral process of the lacrimal in other theropods. The ascending branch of the lacrimal becomes thin above

TABLE 1

Selected Measurements (in mm) of Bones of the Holotype of *Microvenator celer* (AMNH 3041)

A plus sign following measurement indicates that the bone is broken or distorted. Because of the incompleteness of the vertebral column, vertebrae with the exception of the axis are not numbered. Instead, tentative relative positions are designated in alphabetical sequence.

Skull elements		Pectoral girdle and forelimb	
?Dentary length (along ?dorsal edge)	37+	Coracoid height	26.2
?Dentary height of symphysis	13	Coracoid length	31.2
?Lacrimal length	31.2+	Humerus length	81.5
Centrum length of vertebra		Radius length	75.7+
Axis	13.9	Ulna length	78.0
Cervical A	15.1	Metacarpal I length	12.5
Cervical B	15.4	Manual phalanx I-1	34.0
Cervical C	15.0+	Larger manual ungual (dorsal edge curve)	21.9+
Dorsal A	13.5	Smaller manual ungual (dorsal edge curve)	17.8
Dorsal B	13.8	Pelvic girdle and hindlimb	
Dorsal C	14.2+	Ilium length	96.1+
Dorsal D	13.8	Ilium height (preacetabular)	36.2+
Dorsal E	13.9	Pubis length	108.6+
Dorsal F	14.1	Femur length	124.0
Dorsal G	13.7	Width of condyles	24.2
Dorsal H	13.1	Tibia length	150.0+
Sacral	15.1	Fibula length	53.8+
Caudal indet.	11.5	Astragalus height	29.4+
Caudal indet.	9.6+	Astragalus width	22.5
Caudal A	8.7	Metatarsal I length	11.8+
Caudal B	6.1+	Pedal digit I ungual length	11.9
Caudal C	9.9+		
Caudal D	9.8		
Caudal E	9.7		
Caudal F	9.5		
Caudal G	10.1		

the presumed facet for the jugal, but expands dorsally. The diameter of the shaft is smallest just ventral to the midlength of the preserved section. The dorsal half becomes slightly wider beneath the missing broken end. Breakage reveals that the interior of the bone was hollow. The preserved section does not show any trace of a lacrimal canal, although one may have been present in the now missing portion of the element. A small ridge extends along the dorsal half of the posterior edge. If this bone is correctly identified as a lacrimal, it differs in a number of features from the homologous element in other theropods. It is proportionately more slender than the lacrimal in other coelurosaurs and appears to lack any depression that could be interpreted as the posteroventral corner of the antorbital fossa. An alternative interpretation of this element may be as the suborbital part

of the jugal. The orbital portion of the jugal is slender and rodlike in ornithomimids and oviraptorids, and has a slight expansion where it is confluent with the lacrimal ramus of the jugal. No characters are coded based on this element, because of the tentative nature of the identifications.

The bone apparently identified as a palatine by Ostrom (1970) is more likely a right dentary. However, Barnum Brown identified the element as a surangular in a skeletal restoration that was published only recently (Norell et al., 1995). The bone in question (fig. 1) is subtriangular in outline, and its probable posterior end is divided into two rami. Both rami are broken near their anterior ends, but they appear to have been relatively slender mediolaterally and widely divergent at an angle of 31° (as measured from the symphysis through the midheight of each

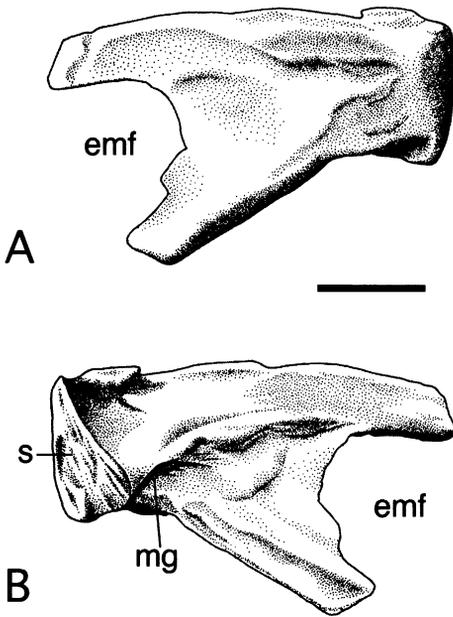


Fig. 1. Possible right dentary of *Microvenator celer* (AMNH 3041) in (A) lateral and (B) medial views. Abbreviations: emf, external mandibular fenestra; mg, terminus of Meckelian groove; s, symphysis. Scale bar equals 1 cm.

ramus). This angle is much wider than that between the posterior rami of the dentary in Dromaeosauridae, Ornithomimidae, and most other coelurosaurs, but approaches that in Oviraptoridae. The presumed dentary was flattened mediolaterally by postmortem crushing. It shows no traces of teeth or alveoli.

The symphyseal region (fig. 1B, s) is triangular in medial view, and in dorsal view is only weakly curved medially, although crushing may have obscured this feature to some degree. The symphyseal facet itself is rugose, and the dentary was not fused to its counterpart. A robust lateral ridge extends posteriorly from the lingual margin of the symphysis along the dorsal ramus of the dentary, as in Caenagnathidae (Currie et al., 1994). It gradually levels out and terminates above the external mandibular fenestra. The dorsal surface of the ridge forms a lateral groove in the symphyseal region, a feature also seen in Oviraptoridae and Caenagnathidae (Currie et al., 1994). The rostral end of the presumed dentary forms a thin, sharp

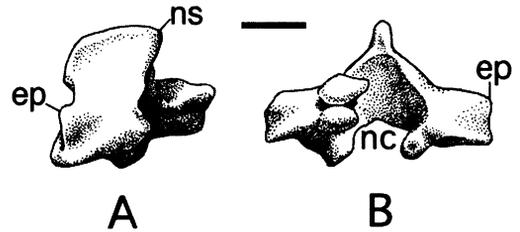


Fig. 2. Partial neural arch of axis of *Microvenator celer* (AMNH 3041) in (A) lateral and (B) anterior views. Abbreviations: ep, epiphysis; nc, neural canal; ns, neural spine. Scale bar equals 5 mm.

ridge, which is lingually concave. A pronounced depression located near the ventral terminus of the symphysis below the lateral ridge is the anterior terminus of the Meckelian groove (fig. 1B, mg). It is deep as in Oviraptoridae. The ventral end of the symphyseal facet is pointed, much as in Oviraptoridae but unlike the condition in Caenagnathidae where the ventral border of the symphysis bears a shallow depression (Currie et al., 1994). The ventral edge of the dentary bears a shallow groove in the symphyseal region. A comparable feature is not present in either Caenagnathidae or Oviraptoridae. It may be an artifact related to the mediolateral crushing of the bone.

VERTEBRAL COLUMN: Both the centrum of the axis and the posterior part of the axial neural arch (contra Ostrom, 1970) are preserved. The centrum is partially obscured by the reconstructed axial intercentrum and arch. Its sides are concave as the dorsal face is expanded to form the floor of the neural canal. A small pneumatic opening is situated close to the anterior intercentral face. Anteroventral to the opening, the corner of the centrum forms a low mound that probably constitutes the parapophysis. Only the posterior third of the axial neural arch is preserved (fig. 2), bearing the postzygapophyses and part of the neural spine. As in other theropods, the arch flares laterally toward the postzygapophyses. The neural spine is remarkably low and has a convex dorsal border in lateral view. A prominent, moundlike epiphysis is present on the dorsal surface of each postzygapophysis. It extends laterally rather than posteriorly, and does not over-

hang the posterior edge of the postzygapophysis as in Dromaeosauridae, Troodontidae, and various other theropod taxa. In this respect, its configuration is closer to the condition seen in Ornithomimidae and Oviraptoridae.

Only the neural arch of one anterior cervical is preserved. Both prezygapophyses have been broken off. In dorsal view, the neural arch is short and broad. It bears a narrow, rectangular neural spine. The spine is thicker along its posterior edge than along its anterior edge, and the posterior groove for the attachment of interspinous ligaments is also more prominent than the anterior one. The epiphyses are located anterior to the postzygapophyses, as in Troodontidae and Oviraptoridae but unlike the condition in Dromaeosauridae.

The posterior region of the cervical column is represented by parts of five vertebrae. Of these, both the centrum and the arch of the probable 7th cervical are complete (fig. 3), although separated from each other, whereas the following vertebra has parts of the centrum and arch preserved in contact. The preserved centra are moderately elongate and platycoelous, rather than truly opisthocelous as suggested by Ostrom (1970). The single complete centrum bears three excavations on either side. One of these is very small and may either be an artifact of preservation or a nutrient foramen. The two other fossae are larger and shallow. They may represent incipient stages of bone resorption by diverticula of the cervical air-sac system, which would have invaded the interior of the centrum later during ontogeny, as indicated by the hollow nature of the centrum revealed by fractures in the more anterior vertebra. Pneumatic invasion of the centrum is present in dorsal vertebrae of *Microvenator*. The larger anterior foramen is positioned just above and behind the parapophyses, as in other coelurosaurs. On the right side of the complete centrum, the larger anterior fossa is expanded and confluent with the small middle foramen. Breakage indicates that the interior of the centrum was hollow, although the state of preservation does not permit positive identification of its pneumatic nature.

The neural arches of the posterior cervical vertebrae are almost devoid of neural spines

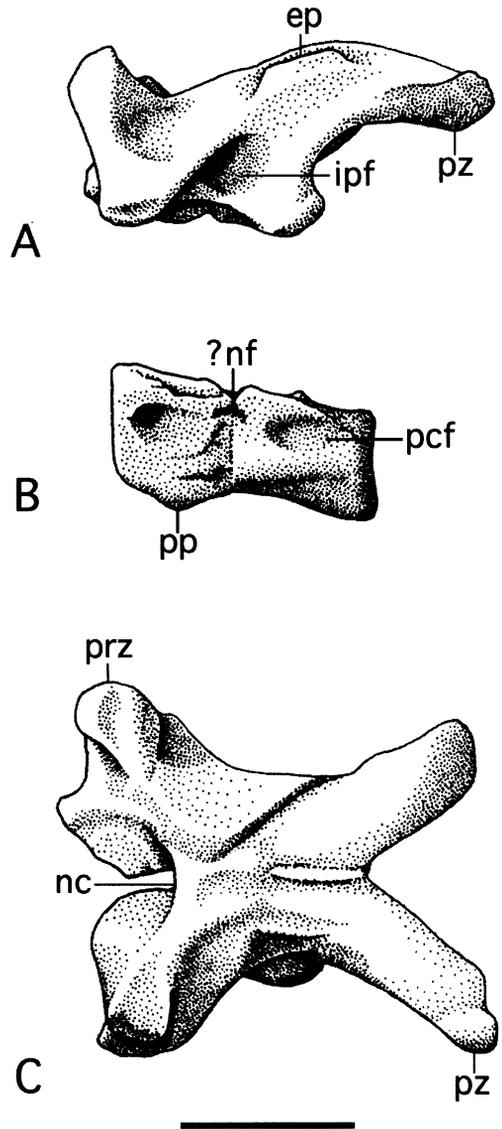


Fig. 3. Posterior cervical vertebra of *Microvenator celer*. (A) Neural arch in lateral view, (B) centrum in lateral view, and (C) neural arch in dorsal view. Abbreviations: ep, epiphysis; ipf, infrapostzygapophyseal fossa; nc, neural canal; ?nf, possible nutrient foramen; pcf, posterior central fossa; pp, parapophysis; prz, prezygapophysis; pz, postzygapophysis. Scale bar equals 1 cm.

and have elongate zygapophyses. The anterior and posterior grooves for attachment of interspinous ligaments are deeply incised between the pre- and postzygapophyses, respectively, so that the neural arches have an X-shaped appearance in dorsal view. The

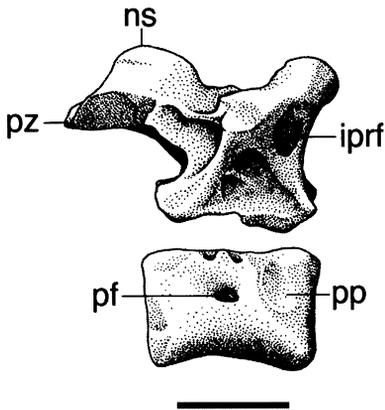


Fig. 4. Anterior dorsal vertebra of *Microvenator celer* (AMNH 3041) in lateral view. Abbreviations: iprf, infraprezygapophyseal fossa; ns, neural spine; pf, pneumatic foramen; pp, parapophysis; pz, postzygapophysis. Scale bar equals 1 cm.

postzygapophyses are longer than the prezygapophyses, which are oriented anterodorsally. A small ridgelike epipophysis extends along the lateral edge of the base of each postzygapophysis, much as in ornithothoracine birds. By homology with the torus dorsalis in extant birds, it probably served for attachment for *Mm. ascendentes* (Baumel et al., 1993). The bases of the pedicels of unfused neural arches bear irregular, transverse ridges and grooves for interdigitating with the centra. In spite of the small size and apparent immaturity of the specimen, the neural arches have clearly defined infraprezygapophyseal, infradiapophyseal, and infrapostzygapophyseal fossae.

At least three neural arches and two centra can be assigned to anterior dorsal vertebrae, in which the parapophyses have not completely migrated onto the neural arches (fig. 4). The two centra probably articulated with the two more anterior neural arches, although crushing of the pedicels of these arches precludes perfect alignment of sutural surfaces. Although Ostrom (1970) claimed that none of the dorsal centra has either a ventral keel or hypapophysis, one of the two centra is keeled and bears a diminutive hypapophysis anteriorly. The 11th presacral vertebra is typically the first to bear a hypapophysis in nonavian theropods, although a hypapophysis is first encountered on the 13th presacral in

Oviraptoridae. We know of no nonavian theropod in which hypapophyses are present beyond the 4th or 5th dorsal. The centrum is moderately constricted at midlength, and the parapophysis is located at midheight at its anterior end.

The neural arch, here considered that of the 1st dorsal (fig. 4), was identified and figured by Ostrom (1970) as that of a middorsal. However, it displays a number of characters that are characteristic of vertebrae from the cervicodorsal transition and preclude its assignment to a more posterior position. The neural spine forms a low, broad mound rising evenly on the medial side of each postzygapophysis. The prezygapophyses are widely separated from each other on either side of the midline as in the cervicals, but the postzygapophyses are smaller and positioned close to the midline as in the dorsal vertebrae. The transverse processes are short and directed laterally. They are angled upward to the extent found on the more posterior dorsal vertebrae of other theropods. All three lateral pneumatic fossae are well-developed. The more posterior dorsal neural arches bear low, rectangular neural spines. The fossa for the interspinous ligaments at the anterior base of the spine is small, whereas the posterior edge is more deeply excavated by a large fossa. The zygapophyses are proportionately smaller than those of the cervicals and are positioned close to the midline. On one of these vertebrae, a slight ventral flexure of the medial margin of each postzygapophysis forms a diminutive hypophene. This feature usually occurs first on the 3rd or 4th dorsal vertebra in other coelurosaurs, indicating a similar position for this arch.

The posterior dorsal centra are markedly wider than high (fig. 5D). In two centra, the width exceeds the height by about one-third, a ratio not found in any other known theropod. Each dorsal centrum bears a pair of large, anteroposteriorly elongate pneumatic openings (fig. 5). The articular faces are platycoelous, and the centra are moderately elongate, unlike the anteroposteriorly short dorsal centra in Dromaeosauridae. The neural spine of a lumbar dorsal is of moderate height and has a subrectangular profile. Its anterior and posterior margins are vertical,

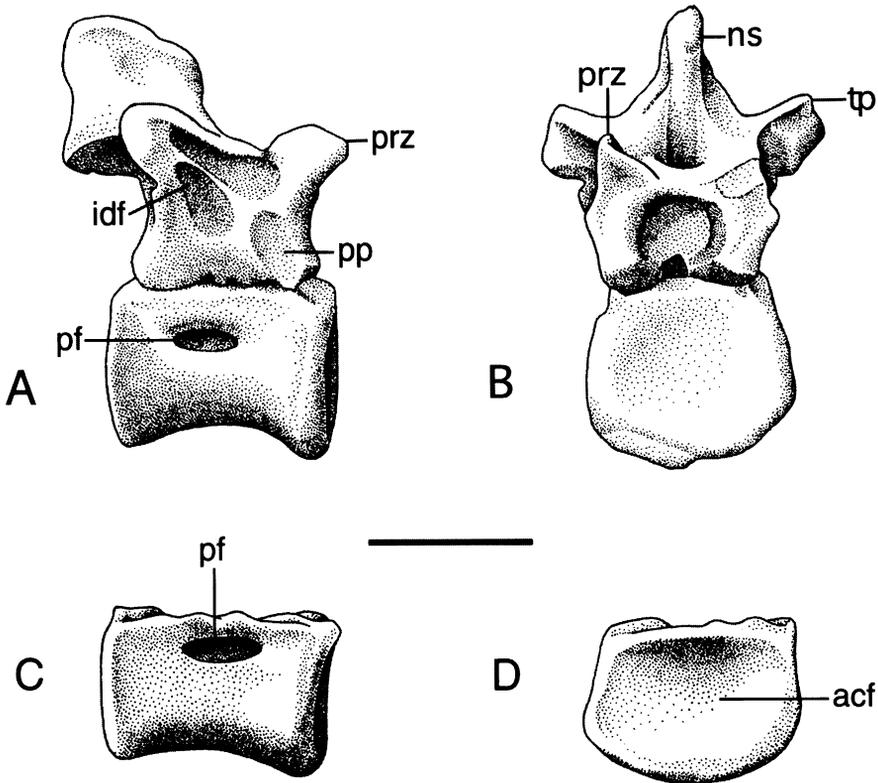


Fig. 5. Posterior dorsal vertebra of *Microvenator celer* (AMNH 3041) in (A) lateral and (B) anterior views. Isolated centrum of posterior dorsal vertebra of *Microvenator celer* (AMNH 3041) in (C) lateral and (D) anterior views. Abbreviations: acf, anterior central face; idf, infradiapophyseal fossa; ns, neural spine; pf, pneumatic foramen; pp, parapophysis; prz, prezygapophysis; tp, transverse process. Scale bar equals 1 cm.

and scars for the attachment of interspinous ligaments extend the full length of both the anterior and posterior edges. The neural spine is not expanded to form a distal spine table, and the dorsal edge forms a low convex arc in lateral view. The subcircular prezygapophysis is medially inclined at an angle of about 45° (Ostrom, 1970). The neural spine and postzygapophysis are located over the posterior half of the centrum, forming a pronounced overhang above the posterior intercentral surface. A comparable overhang is present on the posterior dorsals of *Oviraptoridae*.

The transverse processes of the dorsal vertebrae are proportionately wide anteroposteriorly and very short proximodistally (fig. 5). In dorsal view, they appear somewhat swept back, although less so than in, for example, *Ornithomimidae*. The pronounced dorsal in-

clination of the transverse processes found in many theropod taxa is absent in *Microvenator*. Each transverse process is excavated below by deep infradiapophyseal and infra-postzygapophyseal fossae. The dorsoventrally elongate parapophysis is located at the anterior margin of the pedicel of the neural arch between the base of the prezygapophysis and the neurocentral suture.

Only a single sacral centrum is preserved in AMNH 3041. Several fractures in the bone indicate that the centrum was dorsoventrally flattened by postmortem crushing. This element was explicitly compared to the last sacral vertebra of *Chiostenes* by Currie and Russell (1988), but the presence of rugose sutural surfaces at either end shows that the centrum is derived from within the sacrum. The centrum is wider at one end than at the other, and appears to be constricted at

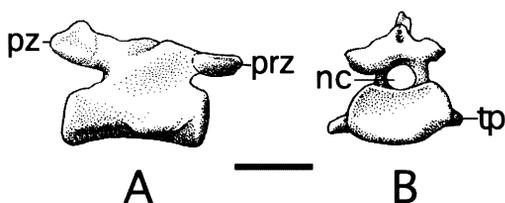


Fig. 6. Caudal vertebra of *Microvenator celer* (AMNH 3041) in (A) lateral and (B) anterior views. Abbreviations: nc, neural canal; prz, prezygapophysis; pz, postzygapophysis; tp, transverse process. Scale bar equals 5 mm.

midlength. Because the element was incorporated into a reconstruction of the sacrum, parts of it are now covered by putty, obscuring details of the neural canal and neurocentral surfaces.

AMNH 3041 includes parts of nine caudal vertebrae. Two isolated, heavily abraded centra are proportionately large and wider than high. Due to weathering, they display no features that would indicate whether or not they are of theropod origin, but they do possess unfused neurocentral sutures as do many of the preserved vertebral elements of *Microvenator*. Of the caudals that can be confidently assigned to *Microvenator*, two centra have unfused neurocentral sutures. One of these can probably be associated with an isolated neural arch. These elements are larger than the other preserved caudals, indicating that they are derived from the proximal region of the tail. The larger of the isolated centra is rounded and has chevron facets only at one end, presumably the posterior. The remaining centra are wider than tall, and each bears a sulcus along the ventral midline. Paired chevron facets are present at either end of the centrum, but the posterior pair is always larger. The isolated neural arch is the largest of those preserved. Its prezygapophyses are short and pointed. The neural arch preserves the bases of both transverse processes. These are wide, flat, and backswept, but their length is uncertain due to breakage. Although the neural spines are not completely preserved on any of the more anterior caudals, they appear to have been relatively short anteroposteriorly but expanded transversely. The anterior and posterior grooves for the attachment of interspinous ligaments are wide. In the more posterior vertebrae, the

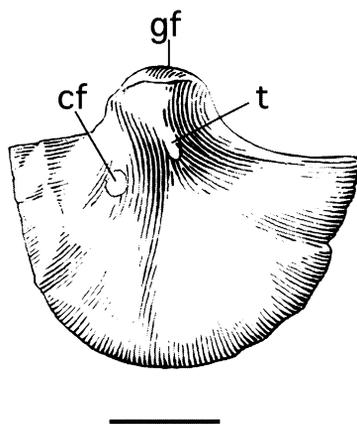


Fig. 7. Left coracoid of *Microvenator celer* (AMNH 3041) in lateral view. Abbreviations: cf, coracoid foramen; gf, coracoid portion of glenoid facet; t, tubercle. Scale bar equals 1 cm.

centra become proportionately lower and wider toward the distal end of the tail (fig. 6). The transverse processes become reduced posteriorly, forming only a lateral tab on two of the centra, and, finally, a slight ridge on the posteriormost preserved caudal. The prezygapophyses do not display progressive elongation in any of the preserved caudals, in contrast to the condition in most other theropods.

Only four partial ribs are preserved with AMNH 3041. Two dorsal ribs were largely covered with putty in an attempt to reconstruct them. Two shorter ribs, probably from one of the posterior cervical vertebrae or perhaps the first dorsal, are still partially embedded in matrix. The proximal portions of the ribs from the cervicodorsal transition are broad and fan-shaped. The shaft of the rib turns sharply ventrally just posterior to the proximal region and then tapers to a fine point distally. A low ridge extends from the tuberculum along the anterior half of the rib. Very little detail is visible on the two preserved dorsal ribs. The capitulum and tuberculum are not widely separated. Neither the length nor the curvature of the rib shaft can be determined with accuracy because the area is covered with putty.

PECTORAL GIRDLE AND FORELIMB: The pectoral girdle is represented only by the left coracoid (fig. 7). The coracoid is a thin, semicircular element, which is wider antero-

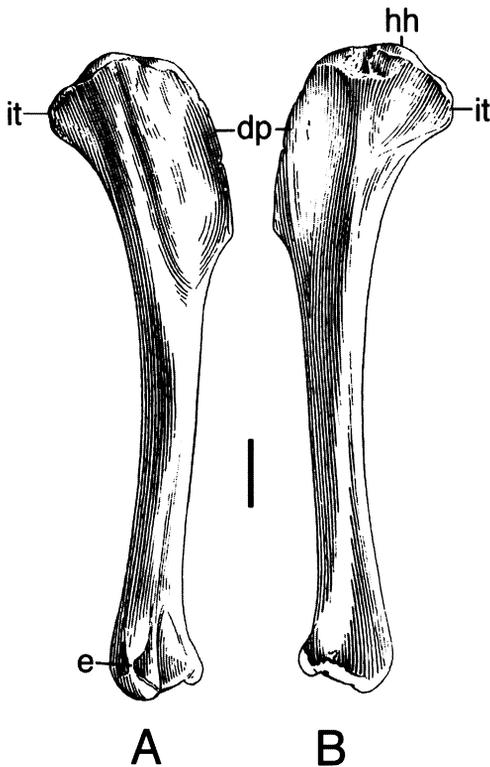


Fig. 8. Left humerus of *Microvenator celer* (AMNH 3041) in (A) medial and (B) lateral views. Abbreviations: dp, deltopectoral crest; e, entepicondyle; hh, humeral head; it, internal tuberosity. Scale bar equals 1 cm.

posteriorly than high dorsoventrally. Although its anterior and ventral margins are very thin, the coracoid plate thickens toward the sutural surface for the scapula and the glenoid region. The contact with the scapula is concave in both lateral and dorsal view. Its posterior edge is formed by a stout process that bears the coracoid portion of the glenoid on its posterior surface. A proportionately large “biceps” tubercle (probably for the origin of a tendinous portion of *M. coracobrachialis* rather than *M. biceps*; Walker, 1990) projects laterally from the base of this process. A large coracoid foramen pierces the coracoid plate just anteroventral to the “biceps” tubercle. The posterodorsal margin of the postglenoid process is thickened.

The well-preserved left humerus (fig. 8) is gently sigmoid in lateral view. The robust head forms a rounded convexity at the prox-

imal end of the bone. Anterior and ventral to the head, the deltopectoral crest extends for about a third of the length of the humeral shaft (fig. 8A). Its thin anterior edge has been damaged, but the deltopectoral crest probably did not extend much further than preserved now. The distal end is slightly offset from the shaft but to a lesser degree than in *Deinonychus*, for example. The medial face of the deltopectoral crest is excavated by a shallow depression (fig. 8B) although the depth of this concavity appears to have been somewhat exaggerated by postmortem crushing. Posterior to the head, the internal tuberosity (Ostrom, 1969), which is probably homologous to the bicipital crest of birds, forms a small subtriangular process. Both its medial and lateral surfaces are shallowly concave. A faint intramuscular ridge extends from below the humeral head to the ectepicondyle along the posterolateral surface of the humerus. The humerus flares at its distal end, reaching a width of 13 mm. The lateral condyle is wider than the medial one and is separated from it by a wide depression. The entepicondyle is formed as a small but distinct medial tubercle, whereas the ectepicondyle is reduced.

The left radius is slightly expanded at either end. Much of the slender shaft has been damaged, and the distal end is badly crushed. The apparent posterior curvature of the shaft is probably an artifact of preservation. The left ulna (fig. 9) is less damaged. Its proximal end is triangular in dorsal view and bears a distinct olecranon process above and behind the articular facet of the humerus. The shaft of the ulna is bowed posteriorly, and it decreases in thickness from the proximal end of the middle of the shaft. Its distal end is anteroposteriorly flattened and mediolaterally expanded. The anterior face of the distal end forms a triangular, concave facet for contact with the radius. The shallow concavity of this facet indicates that the radius could rotate relative to the ulna, and that *Microvenator* was capable of limited antebrachial pronation-supination. The plane of the distal articular facet of the radius is slightly offset from that of the proximal one.

There are four manual bones preserved in AMNH 3041. One of these is the left first metacarpal. It is slightly curved medially,

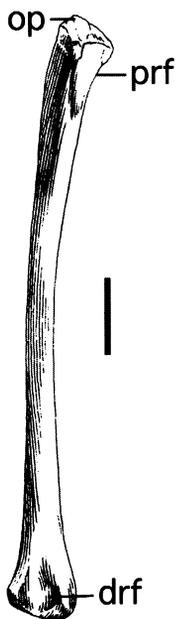


Fig. 9. Left ulna of *Microvenator celer* (AMNH 3041) in oblique anterior view. Abbreviations: drf, distal radial facet; op, olecranon process; prf, proximal radial facet. Scale bar equals 1 cm.

and its shaft is triangular in transverse section. The proximal articular facet is also triangular. The distal articulation is ginglymoid, and its dorsoventral plane of articulation is twisted laterally relative to the proximal articular facet. An elongate, slender phalanx may represent manual phalanx I-1. Its lateral ligament pit is more prominently developed than the medial one. Two unguals are preserved in AMNH 3041. One ungual is about 20% taller at the proximal articulation than the other. The distal tip of the larger ungual has been lost. Both unguals have a moderately pronounced flexor tubercle and a dorso-posterior lip at the dorsal end of the proximal articular surface. In transverse section, each ungual forms a tall oval, and they are moderately trenchant as in Oviraptoridae, Caenagnathidae, and an isolated manus referred to *Ornitholestes* (AMNH 517). Comparisons of the relative proportions of the unguals with those of *Chiropstenotes* (Currie and Russell, 1988), *Oviraptor*, and *Deinonychus* (Ostrom, 1969) indicate that they represent

the first and the second or third manual unguals, respectively.

PELVIC GIRDLE AND HINDLIMB: Only the preacetabular blade, pubic peduncle, and supra-acetabular rim of the left ilium (fig. 10) and the pubic peduncle and much of the preacetabular blade of the right ilium are preserved. The deep preacetabular portion of the iliac blade forms a large, ventrally directed, subtriangular point. On the medial face of the blade, a wide shelf rises from the pubic peduncle toward the anterior edge of the iliac blade. It is widest at the apex of the notch between the pubic peduncle and the ventral point of the blade. The concave ventral surface of this shelf probably served as the site of origin for *M. cuppedicus*, a femoral protractor (Rowe, 1986). The pubic peduncle extends further ventrally than the ischiadic peduncle, and its surface for contact with the pubis is directed anteroventrally, indicating a forward and downward orientation of the pubis. It is also about twice as wide at its base as the ischiadic peduncle, a condition found in many theropods. The pointed ischiadic peduncle is directed ventrally and slightly posteriorly. Situated posterior to it, the brevis shelf is relatively narrow and faces ventromedially. Much of the blade is missing from either ilium, and it is impossible to determine the number of sutural surfaces for the attachment of the sacral ribs. The rim of the acetabulum is wider anteriorly than posteriorly, as noted by Ostrom (1970). No trace of a supra-acetabular buttress is evident, and the antitrochanter was either small or absent.

Neither pubis preserves complete proximal or distal ends (fig. 11). Each bone bears a deep depression on the medial surface at the junction between the main shaft and the ischiadic peduncle. The pubic shafts extend in an anteriorly concave arc as in Oviraptoridae (Barsbold et al., 1990). The transverse pubic apron is relatively short, extending for little more than half of the total length of the pubes. The distal end was expanded, but most of the pubic "boot" has been destroyed by erosion. The ischia are not preserved in AMNH 3041.

Neither femur has a completely preserved proximal head (fig. 12). The orientation of the femoral neck indicates that the head was directed dorsomedially and well set off from

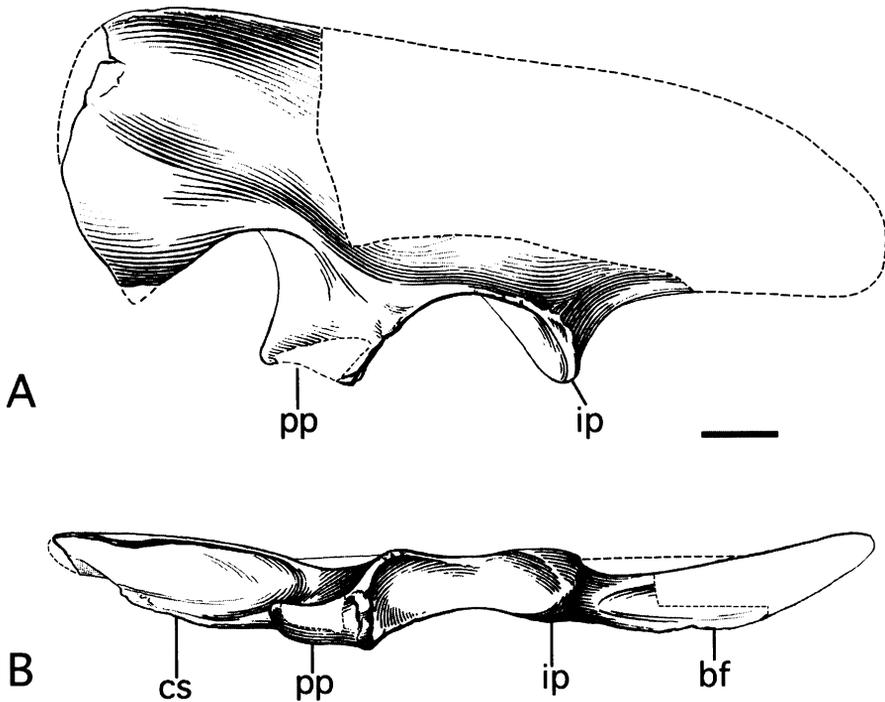


Fig. 10. Left ilium of *Microvenator celer* (AMNH 3041) in (A) lateral and (B) ventral views. Abbreviations: bf, fossa for origin of *M. caudifemoralis brevis*; cs, area for origin of *M. cuppedicus*; ip, ischiadic peduncle; pp, pubic peduncle. Scale bar equals 1 cm.

the shaft. The greater trochanter is broadly separated from the head by a saddle-shaped sulcus. The prominent, fingerlike lesser trochanter is present anterolateral to the greater trochanter, and its apex constitutes the highest point of the femur (fig. 12B, C, lt). It is separated from the greater trochanter by a deep cleft. An accessory crest is developed anterolaterally at the base of the lesser trochanter, and most probably served for the insertion of *M. iliotrochantericus anterior* (fig. 12B, C, at). The shaft of the femur displays a pronounced anterior curvature and bears two rugose muscle scars on its posterior surface (fig. 12A). The more proximal of these scars forms an elongate depression on the posteromedial face of the femur about a quarter of the total length from the proximal end. A prominent, rugose oval scar is visible on the posterior surface of the femur one-third of the way up from the distal condyles. An intramuscular line extends from the base of the lesser trochanter to the point where *M. caudifemoralis longus* probably inserted on

the more dorsal of these muscle scars, which corresponds topographically to the 4th trochanter of other nonavian theropods. The lateral femoral condyle is wider than the medial one, and it bears a large fibular trochlea. The condyles are separated by a wide popliteal fossa.

The proximal end of each tibia is incomplete. Only the ventral edge of the cnemial crest is preserved on the left tibia (fig. 13, cc), and the size of this process is uncertain. The tibia is distinctly longer than the femur (table 1). The fibular crest, located one-fifth of the way down the preserved length of the shaft (fig. 13A, fc), is directed anterolaterally. The diameter of the shaft decreases distally. The shaft is oval in transverse section, but expands mediolaterally and becomes anteroposteriorly flattened distally where it contacts the astragalus. The flattened surface for the reception of the astragalus extends for about a quarter of the length of the tibia, and forms a tall triangle. In posterior view, the articulation for the astragalus is formed as a

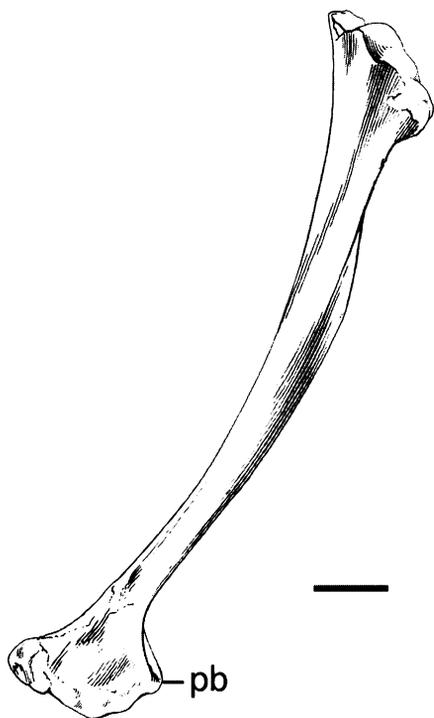


Fig. 11. Lateral view of left pubis of *Microvenator celer* (AMNH 3041). Abbreviations: pb, pubic boot. Scale bar equals 1 cm.

deep, asymmetric notch situated lateral to the center of the distal end.

Only the proximal part of the left fibula is preserved. It corresponds to about one-third of the length of the preserved portion of the tibia (fig. 13). The anteroposteriorly expanded proximal articulation of the fibula is more or less crescentic in dorsal view. Below this point, the fibula tapers rapidly and is very thin at the broken end of the shaft. The slenderness of the fibula led Ostrom (1970) to speculate that it may not have reached the tarsus. The medial face of the fibula is concave for articulation with the tibia, but there is no medial fossa as in Ornithomimidae. About two-thirds of the way down the preserved length of the fibula, the anterior edge is raised to form a tubercle for the insertion of *M. iliofibularis* (Baumel et al., 1993).

The astragalus, represented by the almost complete left element, is distinguished by its tall ascending process, which has steeply inclined lateral and medial edges (figs. 13A, 14). The ascending process is separated from

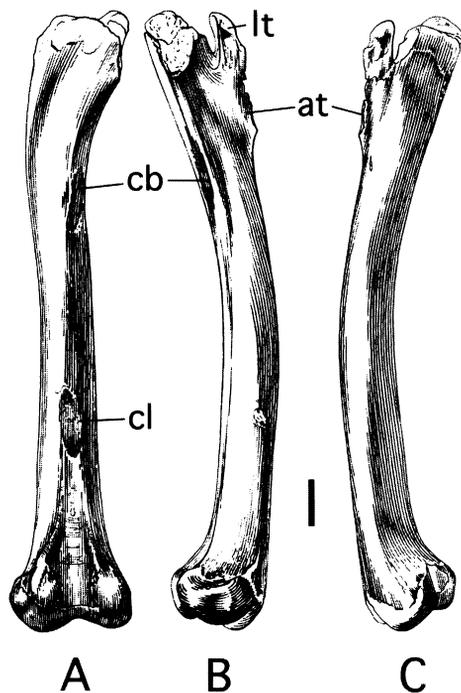


Fig. 12. Left femur of *Microvenator celer* (AMNH 3041) in (A) posterior, (B) medial, and (C) lateral views. Abbreviations: at, accessory trochanteric crest; cb, scar for insertion of *M. caudifemoralis brevis* (depression in place of fourth trochanter); cl, scar for insertion of *M. caudifemoralis longus*; lt, lesser trochanter. Scale bar equals 1 cm.

the condyles by a wide, shallow sulcus, which extends along the dorsal edge of the condyles. The medial condyle is twice as wide as the lateral one, and extends further ventrally. Laterally, the astragalus bears a shallow concavity that probably received a small, disclike calcaneum. Further evidence for the presence of a calcaneum is provided by the fact that the astragalus does not completely cover the anterior face of the tibia. The posterior flange of the astragalus is short and only wraps around the ventral extremity of the tibia.

The pes is documented by two bones from the first digit. Ostrom (1970) identified these elements as a manual phalanx and an unguis, but they compare more favorably with the first metatarsal and the unguis of the first pedal digit of other theropods. The metatarsal is derived from the left foot. The medial sur-

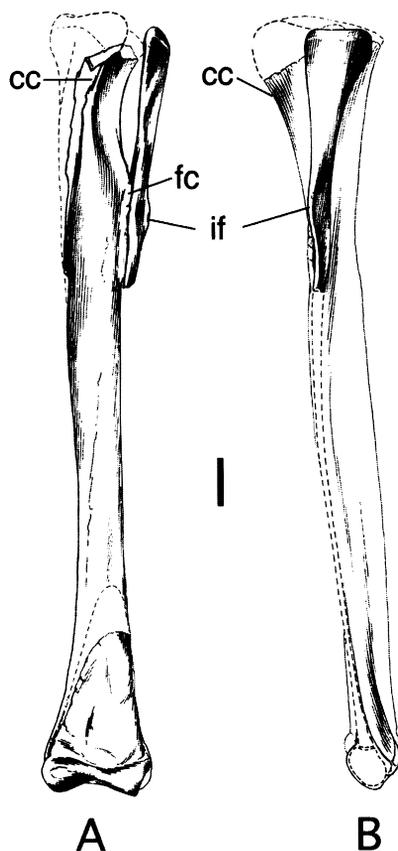


Fig. 13. Left tibia, fibula, and astragalus of *Microvenator celer* (AMNH 3041) in (A) anterior and (B) lateral views. Abbreviations: cc, cnemial crest; fc, fibular crest; if, tubercle for attachment of *M. iliofibularis*. Scale bar equals 1 cm.

face of its short shaft, which was appressed against the shaft of the second metatarsal, is concave. The distal articulation for the phalanx is non-ginglymoid and turned away from the median axis of the metatarsus. The medial ligament pit is large and deep. The ungual is blunt and not trenchant. It is clearly a pedal ungual because it lacks a flexor tubercle. Its proportionately small size indicates that it belongs to the first digit. A shallow groove for the claw sheath extends along the distal two-thirds of either side of the ungual. There is no clear way to determine whether this ungual belongs to the left or right foot, but, because the bones of the left leg are generally better preserved than those of the right (including left metatarsal I), the

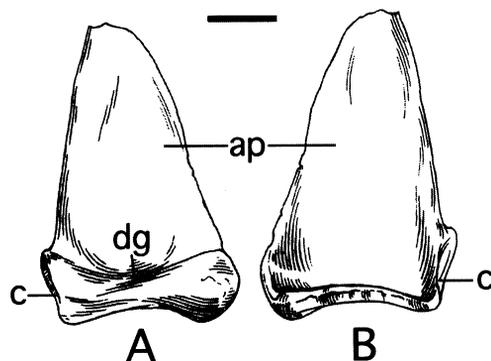


Fig. 14. Left astragalus of *Microvenator celer* (AMNH 3041) in (A) anterior and (B) posterior (internal) views. Abbreviations: ap, ascending process; c, articular facet for the calcaneum; dg, dorsal groove. Scale bar equals 1 cm.

ungual is probably also derived from the left pes.

ONTOGENETIC ASSESSMENT

Several features of the holotype of *Microvenator celer* (AMNH 3041) indicate that it represents a juvenile individual. Most significant is the lack of fusion between the centra and neural arches of the cervical, dorsal, sacral, and anterior caudal vertebrae. There is also no apparent fusion between the scapula and coracoid. The presence of a depression on the posteromedial aspect of the femoral shaft in place of a crestlike fourth trochanter may represent an additional feature indicative of immaturity. Femoral trochanters are known to increase in size during ontogeny in other dinosaurs (Horner and Weishampel, 1988). Given the well-formed proximal trochanters and accessory trochanteric ridge, this inference may or may not be warranted. Sereno et al. (1996) listed "femoral fourth trochanter weak or absent" as a diagnostic character for Coelurosauria, but at least one velociraptorine dromaeosaurid (GI 100/986) has a well-developed fourth trochanter.

The presence of paired depressions, rather than invasive perforations, on the cervical centra may be another juvenile feature. Few observations concerning pneumatic invasion in juvenile dinosaurs exist, and it is difficult to evaluate the significance of this difference from other coelurosaurs. In extant birds,

pneumatic invasion of the postcranial skeleton occurs only after hatching (Müller, 1908).

Similarly, the presence on the cervical centra of a distinct nutrient foramen, which is separated from a pneumatic structure by a wall of bone, may also indicate immaturity (Britt, 1993). A similar separation is visible on the preserved anterior cervical vertebrae of the holotype of the troodontid *Sinornithoides youngi* (IVPP V9612; Britt, 1993) and on an isolated cervical centrum of an immature ornithomimid with unfused neurocentral sutures (RTMP 94.12.817). In adult theropods, the nutrient foramina become confluent with the pneumatic openings (Britt, 1993). Ostrom (1970) was not convinced that open neurocentral sutures are indicative of immaturity in the holotype of *Microvenator celer*, and he claimed that the well-ossified limb bones show that AMNH 3041 represents a small adult. However, more recent finds of juvenile theropods (e.g., Currie and Peng, 1994) demonstrate that the limb bones of these specimens display a high degree of ossification. We do not regard the degree of ossification of the limb bones as a reliable ontogenetic indicator. However, Brochu (1996) demonstrated that closure of the neurocentral sutures is indeed a good indicator of maturity in crocodyliform archosaurs, and that sutural fusion progresses from the tail forward during ontogeny. If this anatomical criterion is also applicable to nonavian theropods, it certainly supports our interpretation of the holotype of *Microvenator celer* as a young animal.

In their description of *Caenagnathasia martinsoni*, Currie et al. (1994) discussed fusion of the mandibular symphysis as a possible indicator of maturity in oviraptorosaurs. Given the results of our phylogenetic analysis, this criterion may well be applicable to the holotype of *Microvenator celer* as further corroboration that it is a juvenile. However, in light of the poor sampling of juvenile oviraptorosaurs and the fact that an unfused mandibular symphysis is plesiomorphic for Theropoda, we place little emphasis on this character at present.

AUTAPOMORPHIES OF *MICROVENATOR CELER*

In his cladistic analysis of avian origins, Gauthier (1986) considered *Microvenator*

celer a metataxon devoid of diagnostic autapomorphies. However, our study revealed that *M. celer* has at least four features that set it apart from all other known theropod taxa.

1. Centra of dorsal vertebrae wider than high. Most theropods have dorsal centra that are higher than wide or subcircular in transverse section. However, *Microvenator* is distinctive in its possession of dorsal centra that are markedly wider than high (fig. 5D). A posterior dorsal of AMNH 3041 is about 30% wider than high, and the succeeding vertebra shows similar proportions.

2. Centra of caudal vertebrae wider than high. Like the centra of the dorsal vertebrae, the caudal centra of *Microvenator* are significantly wider than high (fig. 6). In Allosauridae, Tyrannosauridae, Ornithomimidae, and *Coelurus*, the anterior caudal centra form tall ovals in transverse section. In Dromaeosauridae, Troodontidae, and *Archaeopteryx*, the anterior caudals are subrectangular in transverse section, and in none of these taxa are the caudals wider than high. Consequently, the condition in *Microvenator* appears to be unique among Tetanurae.

3. Accessory trochanteric crest. The femur of *Microvenator* has a distinct accessory crest on the anterolateral margin of the shaft at the base of the lesser trochanter (fig. 12, at). In extant birds, *M. ilirotrochantericus* anterior inserts on this portion of the femur (Baumel et al., 1993), and it seems likely that the accessory crest served a homologous function in *Microvenator*. A similar crest is present on the femur of *Tyrannosaurus* (Osborn, 1906: fig. 9), but it occupies a relatively more proximal position in the latter taxon.

4. Deep concavity on the proximomedial part of the pubis. A deep, oval depression is situated adjacent to the iliac articulation on the proximomedial face of the pubis. A comparable feature is not known in any other coelurosaur where this region of the pubis is preserved. The functional significance of this depression is uncertain, but it may have been the site of origin for a head of *M. puboischiofemoralis internus*.

In addition to these unique anatomical features, a cladistic analysis of the relationships of *Microvenator celer* to other coelurosaur reveals a number of character states that ap-

parently evolved independently in this taxon and in other theropods. These include a shift in the position of the cervical epiphyses toward the bases of the postzygapophyses (character 41) and possibly the secondary loss of an expanded deltopectoral crest (reversal of character 64). Several other features may also have developed convergently in *Microvenator*, but appear ambiguous in our analysis due to missing data.

PHYLOGENETIC RELATIONSHIPS

Ostrom (1970) referred *Microvenator celer* to the family Coeluridae. He based this assignment on alleged similarities in the degree of hollowness of the bones between *Compsognathus*, *Microvenator*, and *Ornitholestes*, similarly high degrees of vertebral pneumaticity in *Coelurus* and *Microvenator*, as well as small body size. The paraphyly of Coeluridae has been established by several recent cladistic analyses of theropod phylogeny (Gauthier, 1986; Holtz, 1994). Currie and Russell (1988) briefly discussed the affinities of *Microvenator* and suggested that it may represent a basal caenagnathid. *Microvenator* was implicitly referred to Oviraptoridae by Russell and Dong (1994). To date, only Gauthier (1986) has considered the affinities of *Microvenator* in a cladistic analysis of theropod interrelationships. In his study, this taxon occupies a position within an unresolved polytomy of basal maniraptorans. The phylogenetic relationships of birds formed the principal focus of Gauthier's analysis, and his study did not present all characters that are potentially useful for resolving the interrelationships of the various taxa of nonavian theropods.

We undertook a numerical cladistic analysis in order to discover the relationships of *Microvenator celer*. Because this theropod taxon displays a number of undisputed coelurosaurian apomorphies, the ingroup was limited to Coelurosauria sensu Gauthier (1986). A set of 95 characters based on transformation series relevant to resolving the relationships of Coelurosauria and the chosen outgroups was compiled and analyzed using PAUP 3.1.1 (Swofford and Begle, 1993). Many of these characters were taken from published sources (Gauthier, 1986; Russell

and Dong, 1994; Clark et al., 1994; Holtz, 1994; Sereno et al., 1996), whereas others were new. Some characters used in earlier studies were omitted, either because they have a wider distribution than previously suggested, or because their validity is questionable. Appendix 1 lists the characters and character states used in our analysis, and appendix 2 shows the data matrix. Most taxa that have been referred to Coelurosauria at some point were included in the analysis, although certain still poorly known forms such as *Compsognathus* and *Deltadromaeus* were omitted. This omission did not affect the phylogenetic position of *Microvenator* in the set of minimum-length trees. In addition, the two oviraptorosaurian clades Caenagnathidae and Oviraptoridae were scored as separate terminal taxa in order to determine whether *Microvenator* is more closely related to either clade. *Herrerasaurus*, *Coelophysis*, and *Allosaurus* were used as outgroups to root the trees, following results of previous analyses by Gauthier (1986), Holtz (1994), and Sereno et al. (1996). Our analysis generated three minimum-length trees (tree length: 201 steps), with an apical trichotomy between the taxa *Microvenator*, Oviraptoridae, and Caenagnathidae. As in the analysis by Sues (1997), Therizinosauroidea is considered the sister taxon of Oviraptorosauria sensu lato. A strict consensus tree is shown in figure 15. The lack of full resolution seen in the consensus tree was almost exclusively due to numerous missing data for *Microvenator*, as revealed in the Adams consensus tree (identical to the strict consensus tree).

A sister-group relationship between Oviraptorosauria and Therizinosauroidea is unambiguously supported by three cranial and three postcranial apomorphies:

1. Premaxilla edentulous (1.1). The premaxillae of Oviraptoridae (Barsbold et al., 1990) and Therizinosauroidea (Perle, 1979; Clark et al., 1994) are edentulous, and may have been covered by a keratinous beak in life. The premaxilla of *Chirostenotes* is still unknown, but it was probably edentulous (Sues, 1997). Plesiomorphically, the premaxilla bears four teeth in Theropoda, and this condition is retained in Dromaeosauridae, Troodontidae, *Ornitholestes*, and the basal ornithomimosaur *Pelecanimimus* among

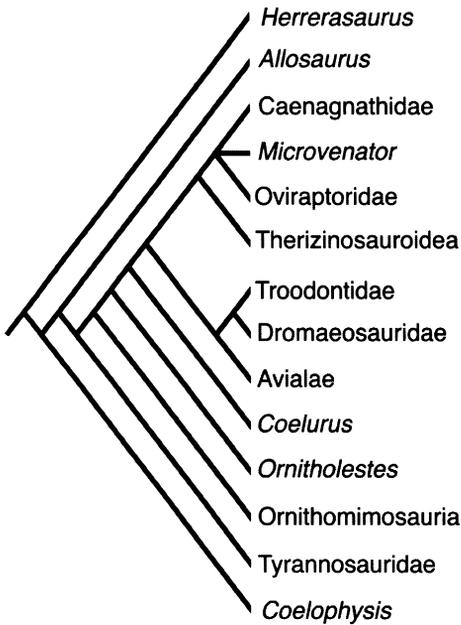


Fig. 15. Strict consensus of the three most parsimonious trees found by PAUP of the matrix in appendix 2. Tree length = 201, consistency index = 0.562, rescaled consistency index = 0.357, homoplasy index = 0.517, retention index = 0.635.

Coelurosauria. The condition in *Microvenator* is unknown, but, given the possible presence of an edentulous dentary, the premaxillae may have also been edentulous.

2. Reduced basipterygoid processes (15.1). In Oviraptoridae (Clark et al., 1994), Caenagnathidae (Sues, 1997), and Therizinosauroida (Clark et al., 1994), the basipterygoid processes are reduced, and their transverse extent is less than that of the basal tubera. In these taxa, the pterygoids appear to overlap the side of the braincase wall (Clark et al., 1994). This condition contrasts with the long, anteroventrally and laterally directed basipterygoid processes plesiomorphically present in theropods. Because no braincase elements have yet been identified for *Microvenator*, this character state cannot be scored for this taxon.

3. Symphyseal region of dentary inflected medially toward midline (28.1). Plesiomorphically in theropods, the mandibular rami are straight and converge anteriorly. In Therizinosauroida and Oviraptorosauria, possi-

bly including *Microvenator*, the anterior portions of the rami curve medially to form an U-shaped mandibular symphysis. Medial inflection of the dentary is also present in some, but not all, troodontids (Russell and Dong, 1994), and may have evolved convergently within this clade. The condition in *Microvenator* appears to be less developed than in other known oviraptorosaurs, although postmortem deformation may account for this difference.

4. Distal caudal vertebrae short (54.1). In Oviraptorosauria, the length and height of the caudal centra progressively decrease toward the distal end of the tail. A similar condition is present in Therizinosauroida (Russell and Dong, 1994) and in *Microvenator*. This contrasts with the typical coelurosaurian condition, where the caudals become low but long past the midpoint of the tail as, for example, in Ornithomimidae (RTMP 93.62.1; RTMP 95.110.1).

5. Presence of posterodorsal "lip" on proximal end of manual unguals (73.1). The manual unguals of *Microvenator* bear a distinct tubercle, possibly for the insertion of digital extensor muscles, at the posterodorsal end of the proximal articular facet. A similar tubercle is developed in *Chirostenotes* (Gilmore, 1924; Currie and Russell, 1988) and the oviraptorid taxa *Oviraptor* and *Conchoraptor* (Barsbold et al., 1990). However, the oviraptorid *Ingenia* lacks this feature (Barsbold et al., 1990), and thus we coded the condition as polymorphic for Oviraptoridae. Nevertheless, parsimony suggests that the presence of a posterodorsal lip on the unguals constitutes a synapomorphy for Oviraptorosauria + Therizinosauroida.

6. Preacetabular portion of ilium deep (75.1). The preacetabular portion of the iliac blade is deep in *Microvenator*, Caenagnathidae, and Therizinosauroida. The iliac blade of *Oviraptor philoceratops* also has a deep preacetabular region. The more shallow profile of the ilium of *Ingenia* may reflect an overall elongation of that bone and may well represent a reversal.

Ambiguous apomorphies linking Oviraptorosauria and Therizinosauroida under ACCTRAN optimization are:

1. No accessory maxillary fenestra (8.0). An accessory maxillary fenestra is diagnostic

of Tetanurae (Gauthier, 1986), but is absent in Therizinosauroida (Clark et al., 1994) and Caenagnathidae (Sues, 1997). Under ACCTRAN optimization this reversal appears diagnostic of the clade Therizinosauroida + Oviraptorosauria, with an apparent reacquisition of the tetanuran character state in Oviraptoridae. Presence or absence of an accessory maxillary opening cannot be ascertained for *Microvenator* at present.

2. Presence of a lateral depression in the middle ear region on the braincase (16.1). This feature is present in Therizinosauroida (Clark et al., 1994) and in *Chirostenotes* (Sues, 1997). It also occurs convergently in Troodontidae (Currie, 1985). The condition in *Microvenator* is still unknown.

3. Two pairs of pneumatic openings on cervical vertebrae (36.1). The better preserved cervicals of *Microvenator* bear three small excavations on either side of the centrum (fig. 3). One of these is probably a nutrient foramen, which may have merged with one of the pneumatopores in more mature individuals, as indicated by the confluence of these openings on one of the cervical centra (Makovicky, 1995). A similar configuration is observed in *Chirostenotes*, where a cervical of a juvenile (RTMP 75.11.33) bears two pneumatic openings on either side of the centrum. The more posterior pair appears to grow over in adult individuals (ROM 43250), producing a shallow lateral depression (Sues, 1997). The cervical vertebrae of *Ingenia* (GI 100/30) also bear two pairs of pneumatic foramina, although the anteroventral pair is the smaller in this taxon, in contrast to *Microvenator*. An isolated midcervical vertebra from the Upper Cretaceous of Kazakhstan, tentatively referred to Therizinosauroida (P. J. Currie, personal commun.), displays a pattern similar to that in *Chirostenotes*. If the taxonomic identification of the latter specimen is correct, this character would represent an unambiguous synapomorphy for Oviraptorosauria and Therizinosauroida.

Our analysis indicates that the presence of two discrete pneumatopores on the cervical centra is not homologous to the condition in ceratosaurian theropods. In *Coelophysis* and *Syntarsus*, each cervical centrum bears two pairs of large depressions. These fossae are

deepest toward the intercentral articular facets, and pneumatization occurred in this region. Cervicals of *Elaphrosaurus* (HMN, holotype of *E. bambergi*) also bear these depressions although there is no clear indication of pneumatic invasion, much as in *Microvenator*. Abelisaurid theropods such as *Carnotaurus* have two small pneumatic foramina (Bonaparte et al., 1990) and resemble derived oviraptorosaurs in this respect. Although secondary pneumatic openings develop in Tyrannosauridae, their presence is variable between individuals (Britt, 1993), and the phylogenetic distribution of this feature in our analysis implies that the tyrannosaurid condition is not strictly homologous to that in oviraptorosaurs.

4. All presacral vertebrae pneumatized (44.1). Under ACCTRAN optimization, the pneumatization of all presacral vertebrae is interpreted as a synapomorphy of the clade Therizinosauroida + Oviraptorosauria. The ambiguity in this character is caused by the polymorphic distribution within Therizinosauroida. The primitive therizinosauroid *Alxasaurus* appears to be devoid of pneumatic foramina on the centra of the dorsal vertebrae, but they are present in *Nanshiungosaurus* (Dong and Yu, 1997).

5. Sacral centra decreasing in width toward the posterior end of the series (51.1). In *Chirostenotes*, the sacral centra become progressively shorter and narrower toward the posterior (caudal) end of the synsacrum (ROM 43250; RTMP 79.20.1; RTMP 84.163.102). Although only a single sacral vertebra is known for *Microvenator*, the disparity between it and the preserved caudals indicates that the posterior sacral vertebrae were markedly smaller than the anterior ones.

6. Manual phalanx III-3 shorter than III-1 + III-2 (72.0). This condition represents a reversal in Oviraptorosauria. The condition in Therizinosauroida and *Microvenator* is still unknown.

7. Broad fossa for origin of *M. cuppedicus* (77.1). A shelf along the anteroventral margin of the ilium forms a broad ventral fossa for the origin of *M. cuppedicus*, which is a synapomorphy of Theropoda (Rowe, 1986). This shelf is secondarily reduced in Ceratosauria (Rowe and Gauthier, 1990) and in

some representatives of Dromaeosauridae and in Avialae among Maniraptora (Novas, 1996; Norell and Makovicky, 1997). The shelf is expanded in Oviraptorosauria and, convergently, in Ornithomimidae. The condition is unknown in Therizinosauroida, but is interpreted as present under ACCTRAN optimization.

8. Pubic boot expanded anteriorly (82.0). The pubic boots of *Microvenator*, Oviraptoridae, *Chiostenotes* (Sues, 1997), and Therizinosauroida (Barsbold and Maryanska, 1990) are expanded anteriorly as well as posteriorly, unlike the pubis of Avialae, *Coelurus*, and Dromaeosauridae (Norell and Makovicky, 1997). The presence of an anterior expansion of the pubic boot is interpreted as a diagnostic reversal of the Therizinosauroida Oviraptorosauria clade under ACCTRAN optimization.

Four unambiguous synapomorphies support a monophyletic clade comprising Oviraptorosauria and *Microvenator*:

1. Edentulous dentary (2.1). The dentary (and probably all other jaw bones) in Oviraptorosauria are edentulous (Barsbold et al., 1990; Currie et al., 1994; Sues, 1997). Therizinosauroida and all more distant outgroup taxa have at least partly dentigerous jaws. Although Ornithomimidae also have edentulous dentaries, teeth are present in the basal ornithomimosaur *Pelecanimimus* (Pérez-Moreno et al., 1994) and *Harpymimus* (Barsbold and Perle, 1984).

2. Neural spines on cervicals short and centered on neural arch, giving neural arches an X-shaped appearance in dorsal view (39.1). In Caenagnathidae, Oviraptoridae, and *Microvenator* (fig. 3C), the neural arches of the posterior cervical vertebrae have long zygapophyses and short, low neural spines, which gives them an X-shaped appearance in dorsal view. This effect is enhanced by the steeply sloping medial faces of the zygapophyseal processes that form a deep incision into the neural arch adjacent to the interspinous ligament scars.

3. Short, wide transverse processes on dorsal vertebrae (45.1). In *Microvenator*, Caenagnathidae, and Oviraptoridae, the dorsal vertebrae have short and wide transverse processes. In Therizinosauroida, Troodontidae, Dromaeosauridae, and more distant out-

groups, the dorsal transverse processes are more elongate and slender, and the transverse processes may exceed the neural spine in proximodistal length.

4. Pubic shaft anteriorly concave in lateral view (79.1). Theropods are characterized by the possession of an elongate pubis that approaches, and in some cases exceeds, the femur in length (Novas, 1996). In most taxa, the slender pubic shaft is either straight or gently curves posteroventrally. Oviraptoridae and *Microvenator* are unusual in that the pubic shaft displays a distinct anteroventral curvature (fig. 11; Barsbold et al., 1990); this feature is not related to the expansion of the distal pubic "boot." (The presence or absence of this feature in *Chiostenotes* cannot be definitely established due to the crushing of the pubes in ROM 43250).

The sister-group relationship between *Microvenator* and Oviraptorosauria is supported by five ambiguous apomorphies under ACCTRAN optimization:

1. Propubic condition (80.0). This character reversal appears to be diagnostic for Oviraptorosauria because of the disjunct distribution of an opisthopubic pelvis among the terminal taxa in this analysis. As discussed elsewhere (Norell and Makovicky, 1997), however, the opisthopubic condition probably represents a complex of pelvic characters, with major differences between Therizinosauroida on one hand and Avialae and Dromaeosauridae on the other. Hence, the apparent reversal in Oviraptorosauria under ACCTRAN optimization may be an artifact of our choice of coding rather than a truly diagnostic feature.

The following four apomorphies are shared by all Oviraptorosauria, but the respective character states are still unknown in *Microvenator*. In our current state of knowledge, they appear to unite the *Microvenator*-Oviraptorosauria clade under ACCTRAN optimization.

2. Paroccipital processes ventrally deflected, pendant (19.1). Most theropods, including all of the outgroup taxa used in this analysis, have straight, laterally directed paroccipital processes. This condition prevails among coelurosaurs, where it is found in the Ornithomimidae, Dromaeosauridae, Troodontidae, and Therizinosauroida. Ovirapto-

rosauria differ in having the paroccipital processes deflected ventrally, in a pendant fashion, at their distal ends.

3. Anteroposteriorly elongate, shallow articular facet on mandible (22.1). Unlike those in the majority of theropods, the articular facet of the mandible is elongate and shallow in Oviraptorosauria (Currie et al., 1994) and would have permitted fore-and-aft motion of the mandible relative to the quadrates. The plesiomorphic condition is the presence of deeply concave, well-defined articular facets that fit tightly around the quadrate condyles.

4. Long, tapering retroarticular process (23.1). A long, tapering retroarticular process characterizes the mandibles of Oviraptorosauria (Currie et al., 1994). Therizinosauroida lack a retroarticular process (Clark et al., 1994), and even in more remote outgroups in which this process is present, such as Dromaeosauridae and Tyrannosauridae, it is short and deep rather than long and pointed.

5. Six or more sacral vertebrae (49.1). This condition is convergently developed in some Ornithomimidae, Dromaeosauridae, and in Troodontidae.

The sister-group relationship between *Microvenator* and Oviraptorosauria is also supported by the following ambiguous apomorphies under ACCTRAN optimization, but the respective character states are unknown in *Microvenator* and/or *Chirostenotes*:

1. Maxilla excluded from margin of external narial fenestra by premaxilla-nasal contact (7.0). This condition represents a reversal in Oviraptorosauria, because maxillary participation in the naris is present in the two outgroups, Therizinosauroida, and ambiguously in the clade Deinonychosauria + Avialae under this optimization.

2. Quadrate pneumatic (12.1). To date, this character state has only been demonstrated in Oviraptoridae (Maryanska and Osmólska, 1997).

3. Dorsal centra wider than high (43.1). The centra of the dorsal vertebrae are markedly wider than high in *Microvenator*, a condition also present in the posterior dorsals of Oviraptoridae. (The posterior dorsal vertebrae of *Chirostenotes* are still unknown.) In other coelurosaurs, the dorsal centra are either elliptical (*Coelurus*, Ornithomimidae) or subcircular (Dromaeosauridae, Troodontidae)

in transverse section. The proportional difference between centrum height and width in *Microvenator* is unusual among theropods, however, and constitutes an autapomorphy for this taxon.

4. No distinct transition point in the tail (53.0). The tail in Oviraptoridae is highly modified relative to the typical condition in Tetanurae. Transverse processes are present along much of the caudal column, and, in *Oviraptor* and *Ingenia*, they appear to be unusually long on the anterior caudals. The anterior caudal vertebrae of *Chirostenotes* (ROM 43250) also have long transverse processes, but no distal caudals can safely be assigned to this taxon. Although the complete caudal series is unknown for *Microvenator*, the size discrepancy between the preserved sacral centrum and caudals indicates that the latter elements originated from near the midcaudal region. In contrast to the generalized coelurosaurian condition where the transition point is located at or anterior to the 15th caudal, the midcaudal vertebrae of *Microvenator* bear transverse processes. This reversal is unique to Oviraptorosauria and is part of a complex of characters resulting in a relatively short but massive tail in these theropod dinosaurs.

One character provides ambiguous support for the *Microvenator* + Oviraptorosauria clade in all trees under DELTRAN optimization:

1. Broad fossa for origin of *M. cuppedicus* (77.1). This character is an ambiguous apomorphy of the Therizinosauroida-Oviraptorosauria clade under ACCTRAN optimization, and is discussed under that heading.

The three alternative resolutions of the *Microvenator*-Oviraptoridae-Caenagnathidae trichotomy are each supported by a single potential synapomorphy under both ACCTRAN and DELTRAN optimization regimes.

One character is potentially diagnostic of an Oviraptorosauria clade that excludes *Microvenator*:

1. All sacral vertebrae pneumatic (44.2). All sacral vertebrae are pneumatic in Oviraptoridae and *Chirostenotes* (Sues, 1997). The single known sacral centrum of *Microvenator* does not display pneumatic features. This may reflect its juvenile age, however, since pneumaticity increases with ontogeny. If this

character state is scored as unknown, *Microvenator* becomes part of Oviraptorosauria as the sister group of either Oviraptoridae or Caenagnathidae.

A possible sister-group relationship between *Microvenator* and Oviraptoridae is supported by the following character:

1. Dentary with widely divergent posterior rami (25.1). If correctly identified, the dentary of *Microvenator* is short and deep, with a large angle enclosed between the posterior rami. In this respect, *Microvenator* would resemble Oviraptoridae more than Caenagnathidae. However, the condition in *Microvenator* may have been exaggerated by mediolateral crushing. In other theropods including *Chirostenotes* ("Caenagnathus"), the rami extend more subparallel and the mandible has a lower and more elongate profile (Currie et al., 1994).

Finally, an apical *Microvenator*-Caenagnathidae clade may be diagnosed by a single character:

1. Posterior cervical postzygapophyses elongate (38.1). The postzygapophyses of the posterior cervical vertebrae are elongate relative to the prezygapophyses in *Microvenator* and *Chirostenotes*, although not in the Oviraptoridae. Elongate posterior cervical postzygapophyses are also present in Ornithomimidae.

In addition to the characters mentioned above, one more ambiguous apomorphy is potentially diagnostic of Oviraptorosauria exclusive of *Microvenator* under DELTRAN optimization:

1. Length of ischium less than two-thirds that of pubis (84.1). Gauthier (1986) originally considered the presence of this character-state a synapomorphy of Maniraptora. The ischium of *Microvenator* is unknown.

Two of the three possible solutions nest *Microvenator* within the Oviraptorosauria sensu Barsbold (1976) (Oviraptorosauria = Oviraptoridae + Caenagnathidae). Additionally, the sister-group relationship between Oviraptoridae and Caenagnathidae is supported by a single apomorphy (pneumatic sacra [44.2]), which may vary with ontogeny, and the possibility that *Microvenator* is a member of the Oviraptorosauria cannot be dismissed. The presumed dentary of *Microvenator* does not display the symphyseal fu-

sion and ventral depression present in the mandibles of Caenagnathidae, however (Currie et al., 1994). The absence of these caenagnathid apomorphies in the possible dentary of *Microvenator* indicates that it is not nested within that group.

DISCUSSION

Our analysis of the phylogenetic position of *Microvenator celer* supports the hypothesis of relationships proposed by Currie and Russell (1988) and substantially increases the number of characters that ally *Microvenator* with Oviraptorosauria. Given the large percentage (47%) of characters that cannot be scored for *Microvenator* at present, any future discoveries of additional material are likely to affect the topology of the relationships found in our analysis.

The record of oviraptorosaurian theropods in North America was previously restricted to the Late Cretaceous Caenagnathidae, which are known from Campanian and Maastrichtian strata of western North America (Currie et al., 1994; Sues, 1997) but have also been reported from Uzbekistan (Currie et al., 1994). Oviraptoridae are currently known only from the Late Cretaceous of Mongolia and China (Barsbold et al., 1990). Our phylogenetic analysis indicates that *Microvenator* represents the earliest record of a true oviraptorosaur or an oviraptorosaur-like theropod from Laurasia.

Traditionally, the close resemblances between Cretaceous terrestrial vertebrates from Asia and North America have been interpreted as the result of dispersal of Asian taxa into North America, principally during the Late Cretaceous (Jerzykiewicz and Russell, 1991). A number of theropod taxa, including Dromaeosauridae, Oviraptorosauria, and Tyrannosauridae, and several ornithischian groups such as Hadrosauridae and Ceratopsia are generally thought to have originated in Asia and migrated to North America during late Early or early Late Cretaceous times. Recently, fragmentary skeletal remains of dinosaurs found in Aptian-Albian strata of the western United States have been referred to several of these groups (Weishampel et al., 1990; Head, 1996; Kirkland, 1996). Kirkland (1996) interpreted the shift in faunas recorded from the Cedar Mountain Formation of

Utah as marking a faunal takeover by taxa of Asian origin. If the various American finds are correctly identified, they represent the oldest known occurrences of lambeosaurine Hadrosauridae and an animal that is either a member or the sister taxon of the Oviraptorosauria in North America. This would have important implications for scenarios advocating an Asian origin for these dinosaurian taxa.

Fragmentary theropod specimens from the Lower Cretaceous of Brazil (Frey and Martill, 1995) and Australia (Currie et al., 1996) have recently been referred to the Oviraptorosauria. Frey and Martill (1995) tentatively identified an incomplete sacrum from the Aptian-Albian Santana Formation of northeastern Brazil as oviraptorosaurian based on the presence of pneumatic foramina on the centra. Although this character is present in Oviraptorosauria, pneumatic openings are also developed on the first and sometimes second sacral vertebrae of Tyrannosauridae, and on the first two sacrals of the dromaeosaurid *Saurornitholestes* and the enigmatic theropod *Ornithodesmus cluniculus* (Howse and Milner, 1993). Furthermore, the theropod sacrum from the Santana Formation differs from oviraptorosaurian sacra in being arched in lateral view and having much expanded intercentral articulations. In Oviraptorosauria, the ventral profile of the sacrum forms a rather straight line, and the intercentral areas are only slightly expanded. Currie et al. (1996) provisionally identified a fragmentary bone from the Aptian-Albian Otway Group of Victoria (Australia) as a possible surangular of an oviraptorosaur, and they also referred an isolated dorsal vertebra from the same strata to Oviraptorosauria. If the iden-

tification of the first bone as a surangular is correct, it does indeed resemble the homologous element in Oviraptorosauria. Similarly, the dorsal vertebra resembles those of Oviraptoridae in having a pneumatic centrum and having short, wide transverse processes, although it displays many features that are plesiomorphic for Theropoda. Until more complete material is found at either of these localities, reference of these specimens to Oviraptorosauria must be considered doubtful in view of the geological and temporal separation.

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APPENDIX 1

List of characters and character states used in the phylogenetic analysis to discover the affinities of *Microvenator celer*.

1. Premaxilla bearing teeth (0) or edentulous (1) (Clark et al., 1994)
2. Dentary bearing teeth (0) or edentulous (1) (Russell and Dong, 1994).
3. Constriction between root and crown of each tooth absent (0) or present (1) (Currie, 1987).
4. Denticles on maxillary and posterior dentary teeth small (0) or large and separated by deep "blood grooves" (1) (Currie, 1987).
5. Carinae of tooth crowns serrated (0) or without serrations (1).
6. Maxillary tooth row terminates below orbit (0) or terminates anterior to orbit (1) (Gauthier, 1986).
7. Maxilla excluded from border of external naris by premaxilla-nasal contact (0) or participating in narial border (1) (Russell and Dong, 1994; coding of character reversed).
8. Accessory maxillary fenestra absent (0) or present (1) (Gauthier, 1986).
9. Secondary bony palate formed by premaxillae and maxillae absent (0) or present (1).
10. Ventral depression on ectopterygoid absent (0) or present (1) (Gauthier, 1986).
11. Prefrontal well developed and forming large part of orbital rim (0) or reduced or absent (1) (Gauthier, 1986).
12. Quadrate nonpneumatic (0) or pneumatic (1) (Molnar, 1985).
13. Lacrimal L-shaped in lateral view (0) or T-shaped in lateral view (1) (Currie, 1995).
14. Parasphenoid flat and nonpneumatic (0) or inflated and pneumatized by anterior tympanic recess (1) (Clark et al., 1994).
15. Basipterygoid processes long and ventrolaterally directed (0) or reduced with a narrower span than the basal tubera (1) (Clark et al., 1994).
16. Lateral depression surrounding opening to middle ear absent (0) or present (1) (Clark et al., 1994).
17. Three tympanic recesses absent (0) or present (1).
18. Branches of internal carotid artery entering hypophyseal fossa separately (0) or entering through common opening (1).
19. Paroccipital processes directed laterally (0) or curving ventrally, pendant (1).
20. Foramen magnum subcircular or wider than tall (0) or taller than wide (1).
21. Occipital condyle without constricted neck (0) or occipital condyle subspherical with constricted neck (1) (Currie, 1985).
22. Articular facet for mandibular joint deeply concave (0) or anteroposteriorly elongate, shallow (1).
23. Retroarticular process short and deep (0) or long and tapering (1) (Currie et al., 1994).
24. Surangular foramen absent (0) or present (1) (Holtz, 1994).
25. Dentary rami subparallel (0) or widely divergent posteriorly (1).
26. Splenial not visible or only slightly visible in lateral view (0) or extensive triangular exposure of splenial between angular and dentary (1) (Currie, 1995).
27. Separate coronoid ossification present (0) or coronoid absent or fused (1) (Clark et al., 1994).
28. Dentary straight in dorsal view (0) or with medially inflected symphyseal region (1) (Clark et al., 1994).
29. Interdental plates distinct (0) or absent or fused (1) (Currie, 1987).
30. Axial epiphyses large and posteriorly directed (0) or moundlike and not extending past posterior rim of postzygapophyses (1) (Gauthier, 1986; coding of character reversed).
31. Axial neural spine flared transversely (0) or compressed mediolaterally (1).
32. Anterodorsal rim of axial neural spine concave in lateral view (0) or forming convex curve in lateral view (1) (Makovicky, 1995).
33. Anterior cervical centra level with or shorter than posterior extent of neural arch (0) or centra extending beyond posterior limit of neural arch (1) (Makovicky, 1995).
34. Anterior cervical centra subcircular or square in anterior view (0) or distinctly wider than high (1) (Gauthier, 1986).
35. Cervical zygapophyses overhang the centrum parasagittally (0) or displaced laterally away from centrum in dorsal view (1) (Makovicky, 1995).
36. Cervical centra with one pair of pneumatic openings (0) or with two pairs of pneumatic openings (1) (Makovicky, 1995; Sues, 1997).
37. Ventral keel on axial centrum present (0) or absent (1).
38. Posterior cervical postzygapophyses short (0) or elongate (1).
39. Cervical neural spines anteroposteriorly long (0) or short and centered on neural arch, so that arch is X-shaped in dorsal view (1) (Makovicky, 1995).
40. Carotid processes on posterior cervical vertebrae absent (0) or present (1).
41. Epiphyses of cervical vertebrae placed distally on the postzygapophyses (0) or placed proximally (1) (Makovicky, 1995).

42. Large hypapophysis in anterior dorsal vertebrae absent (0) or present (1) (Gauthier 1986).
43. Dorsal centra subcircular or oval in transverse section (0) or wider than high (1).
44. Not all presacral vertebrae pneumatic (0) or all presacrals pneumatic (1) or all presacrals and all sacrals pneumatic (2) (ordered).
45. Dorsal transverse processes long and posterodorsally inclined (0) or short, wide, and only slightly inclined (1).
46. Posterior edge of dorsal postzygapophyses level with posterior intercentral articulation (0) or postzygapophyses overhang centrum markedly (1).
47. Apices of dorsal neural spines unexpanded (0) or expanded transversely to form "spine table" (1).
48. Scars for interspinous ligaments terminate at apex of neural spine in dorsal vertebrae (0) or terminate below apex of neural spine (1) (Makovicky, 1995).
49. Less than six sacral vertebrae (0) or six or more sacral vertebrae (1) (Holtz, 1994).
50. Sacral centra round in transverse section (0) or sacral centra flattened ventrally (1) (Makovicky, 1995).
51. Sacral centra subequal in width (0) or centrum width decreasing posteriorly (1).
52. Anterior caudal centra tall, oval in transverse section (0) or boxlike (1) (Gauthier, 1986).
53. Transition point posterior to caudal 15 (0) or transition point at or anterior to caudal 15 (1) or at or anterior to caudal 9 (2) (ordered) (Gauthier, 1986).
54. Distal caudal vertebrae becoming long and low in posterior direction (0) or caudals short and broad throughout tail (1).
55. More than 45 caudal vertebrae (0) or 40 or less (1).
56. Distal caudal vertebrae with low ridgelike neural spine (0) or without neural spine (1) (Russell and Dong, 1994).
57. Proximal gastral segment shorter than distal one in each arch (0) or distal segment shorter than proximal one (1) (Norell and Makovicky, 1997).
58. Proximal chevrons short anteroposteriorly and cylindrical (0) or flattened and platelike (1).
59. Scapula broad and flared widely distally (0) or narrow and straplike (1) (Gauthier, 1986).
60. Coracoid subcircular or axially elongate in lateral view (0) or more or less quadrangular in lateral view (1) (Gauthier, 1986).
61. Coracoid process less than twice the width of the glenoid diameter (0) or elongate and equaling or exceeding twice the diameter of the glenoid (1) (Serenio et al., 1996).
62. Clavicles unfused or unossified (0) or fused to form furcula (1) (Gauthier, 1986).
63. Sternum absent or comprising two small plates (0) or sternum comprising large plates that exceed coracoids in size (1).
64. Deltopectoral crest of humerus low (0) or expanded and offset from humeral shaft (1).
65. Humeral head low and confluent with deltopectoral and bicipital crests (0) or offset and emarginated ventrally by a groove (1).
66. Humeral entepicondyle small (0) or prominent (1).
67. Ulna with straight shaft and small olecranon (0) or ulna with posteriorly bowed shaft and large olecranon (1) (Gauthier, 1986).
68. Ulnar facet for radius small and flat (0) or transversely expanded and concave (1).
69. Distal carpals unfused (0) or distal carpals 1 + 2 fused to form subcrescentic bone (1) (Gauthier, 1986).
70. Manus with more than three digits (0) or with three or fewer digits (1) (Gauthier 1986).
71. Shaft of metacarpal III straight in palmar view (0) or laterally bowed (1) (Gauthier, 1986).
72. Manual phalanx III-3 shorter than III-1 + III-2 (0) or manual phalanx III-3 longer than III-1 + III-2 (1) (Gauthier, 1986).
73. Posterodorsal lip on proximal articular surface of manual unguals absent (0) or present (1) (Currie and Russell, 1988).
74. Iliac blades set lateral to lamina formed by coalesced neural spines of sacrum (0) or medially inclined toward lamina formed by coalesced neural spines of sacrum (1) (Holtz, 1994).
75. Preacetabular part of ilium no deeper than postacetabular part of ilium (0) or (excluding anteroventral extension of iliac blade for origin of *M. iliotibialis*) deeper than postacetabular part of ilium (1).
76. Brevis shelf of ilium narrow (0) or broad (1).
77. Fossa for origin of *M. cuppedicus* on ilium narrow (0) or broad (1) (Rowe, 1986).
78. Pubic apron long and extending for more than 50% of pubic length (0) or short (1).
79. Pubic shaft straight or anteriorly convex in lateral view (0) or concave anteriorly (1) (Barsbold et al., 1990).
80. Pubis propubic (0) or opisthopubic (1) (Ostrom, 1976).
81. Obturator process trapezoidal or quadrilateral in lateral view (0) or triangular in lateral view (1) (Serenio et al., 1996).
82. Pubic boot developed both anteriorly and

- posteriorly (0) or only posteriorly (1) (Gauthier, 1986).
83. Obturator process located proximally on ischium (0) or located distally (1) (Gauthier, 1986).
 84. Length of ischium more than two-thirds length of pubis (0) or less than two-thirds (1) (Gauthier, 1986).
 85. Greater and lesser trochanters of femur separated (0) or trochanters contacting or fused to one another to form crista trochanteris (1).
 86. Lesser trochanter below level of femoral head (0) or level with or above level of femoral head (1).
 87. Fourth trochanter formed as a prominent ridge on posteromedial aspect of femoral shaft (0) or small or replaced by a depression (1) (Gauthier, 1986).
 88. Proximomedial face of fibula only partially occupied by fibular fossa (0) or completely excavated by fibular fossa (1) (Serenó et al., 1996).
 89. Ascending process of astragalus short (0) or tall and broad (1) (Welles and Long, 1974).
 90. Astragalar condyles shallow (0) or deep and separated by deep sulcus (1) (Welles and Long, 1974).
 91. Condylar portion of astragalus confluent with base of ascending process (0) or dorsal groove along condyles separating them from the ascending process (1) (Welles and Long, 1974).
 92. Calcaneum large (0) or calcaneum small and possibly fused to astragalus (1) (Welles and Long, 1974).
 93. Fusion of distal tarsals to each other and to metatarsals absent (0) or present (1) (Osmólska, 1981).
 94. Proximal end of metatarsal III visible in anterior view (0) or proximal portion of metatarsal III dorsally constricted ("arctometatarsal" condition; 1) (Holtz, 1994).
 95. Pedal digit II long and bearing a small claw (0) or short pedal digit II with interphalangeal articulations modified for hyperextension and bearing large claw (1) (Ostrom, 1969).

APPENDIX 2

Character-state/taxon matrix for 14 taxa and 95 characters used to determine the affinities of *Microvenator celer*. The two multistate characters (44 and 53) were treated as ordered. *Herrerasaurus*, *Coelophysis*, and *Allosaurus* were employed as outgroups. The analysis was conducted using the branch-and-bound option of PAUP 3.1.1 (Swofford and Begle, 1993). Coding: 0, 1,

2, ? (data missing), - (character not applicable due to transformation), P (polymorphic character, 0/1). All polymorphic character distributions were treated as polymorphisms rather than as uncertainties. The trees were rooted on the outgroups following the phylogenetic hypotheses by Gauthier (1986) and Sereno et al. (1996).

Taxon	Character states									
	5	10	15	20	25	30	35	40	45	50
<i>Herrerasaurus</i>	00000	00000	00000	00?01	00010	00000	00000	00000	00000	01100
<i>Allosaurus</i>	00000	10100	00000	0?000	10000	00000	00001	00000	00000	00000
<i>Coelophysis</i>	00000	01000	00000	00?00	00000	0?001	00000	11000	10000	00000
<i>Microvenator</i>	?1---	?????	?????	?????	?????	??1-1	11?11	1111?	10111	1001?
Oviraptoridae	11---	-0111	11001	01?10	01101	?11-1	11111	P1010	11121	10011
Caenagnathidae	11---	-001?	???01	11?10	11100	011-?	?????	P1110	?1?21	?0011
<i>Ornitholestes</i>	00000	101??	0?00?	???00	00000	0?00?	??011	0?000	01000	00101
<i>Coelurus</i>	?0???	?????	?????	?????	?00?0	???0?	??001	0?000	1?000	000?1
Ornithomimosauria	001?1	10111	0P010	01000	00000	01011	11111	01100	00000	000P1
Dromaeosauridae	00000	10111	10100	01000	10010	1?010	10011	0100?	01010	111P1
Avialae	001-1	11111	10000	01101	00?00	01000	11?11	01?01	1P001	?0001
Therizinosauroidea	10110	1101?	00001	11?00	10000	0111?	?????	P?000	??0P0	?010?
Tyrannosauridae	00000	10111	01000	0?101	10000	00000	00001	10000	00010	00000
Troodontidae	0011P	1111?	11110	11101	10010	11P10	10111	01101	11000	11111

Taxon	Character states								
	55	60	65	70	75	80	85	90	95
<i>Herrerasaurus</i>	00000	00000	00000	00000	00000	00001	00000	00000	00000
<i>Allosaurus</i>	00000	00010	01000	00001	00000	10000	00000	00000	00000
<i>Coelophysis</i>	00000	00000	00000	00000	00000	00000	00000	00000	00000
<i>Microvenator</i>	1?01?	?????	???01	111??	??111	11110	?0???	11011	11???
Oviraptoridae	?1011	0?010	11110	01111	10P1P	11110	10111	11111	11000
Caenagnathidae	11?11	0???1	?????	?????	1?1?1	?1110	10110	???11	11110
<i>Ornitholestes</i>	00?0?	1?0??	???00	1????	???00	?0000	1?00?	?????	???0?
<i>Coelurus</i>	?0?0?	0??1?	???10	?1011	1?0??	???00	?1??0	00???	?????
Ornithomimosauria	00101	00010	00000	00001	01010	11100	10000	00111	11010
Dromaeosauridae	01201	11111	11111	11111	11000	1P101	1P111	1P011	11101
Avialae	01201	01111	11111	11111	11000	00101	11111	11?11	1110P
Therizinosauroidea	?1111	0?010	???1?	1??01	0?101	1?101	-0100	0??1?	???00
Tyrannosauridae	00101	00010	11000	00001	--010	10100	10000	10111	11010
Troodontidae	01201	11110	10011	01?11	11010	1?100	1?111	01011	11111

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