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3. Redescription of the Small Maniraptoran Theropods *Ornitholestes* and *Coelurus* from the Upper Jurassic Morrison Formation of Wyoming

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Abstract

The small tetanuran–basal maniraptoran theropods *Ornitholestes hermanni* and *Coelurus fragilis* have been described only briefly. Owing to their importance to evolutionary studies of theropods, a detailed description is presented here. *Ornitholestes* has a relatively short neck and body (as indicated by the anteroposteriorly short cervical and dorsal centra); cervicals with opisthocoelous centra; prezygapophyses of distal caudals extending about midway on the preceding caudal; ventrally bifurcated chevrons on distal caudals; a long, low ilium; a posteroventrally curved pubic shaft; an ischium with a large obturator notch and a large, triangular obturator process; and a metatarsal IV longer than metatarsal II and slightly shorter than metatarsal III. In contrast, *Coelurus* is characterized by an elongate neck and body (as indicated by the elongated cervical and dorsal centra); a slender, gracile dentary; very thin walled centra; amphicoelous cervical, dorsal, and caudal centra; long, low neural spines on all vertebrae; short prezygapophyses; a sigmoidal humeral shaft; a posteriorly bowed ulna; a

semilunate carpal with distinct facets for metacarpals; a posteriorly bowed proximal shaft of the pubis; a pubic foot with a short anterior process that is ventrally arcuate; a femur with a low fourth trochanter; an alariform anterior trochanter; an allosauroid-type astragalus; and a very long metatarsal IV, which is nearly as long as the tibia or femur, so that the hind legs are proportionally very long.

Introduction

The Morrison Formation is a widespread Upper Jurassic nonmarine deposit scattered across much of the Western Interior, from northern New Mexico to the Oklahoma panhandle, and north to Montana. The formation has produced a very diverse dinosaur fauna mostly in multi-taxon bone beds (Dodson et al. 1980). Small theropods are rare and include *Coelurus fragilis* Marsh 1879, *Ornitholestes hermanni* Osborn 1903, *Elaphrosaurus?* sp., *Koparion douglassi* Chure 1994, *Tanycolagreus topwilsoni* (Carpenter et al., Chapter 2; previously identified as *Coelurus*, Miles et al. 1998), and another, as yet unnamed theropod reported by Makovicky (1997). Of these, *Coelurus*, *Ornitholestes*, and *Tanycolagreus* are known from partial skeletons. Remarkably, only *Tanycolagreus* has been described in any detail. During our study of *Tanycolagreus*, the material of *Ornitholestes* and *Coelurus* was also studied, and these results are presented below.

The first small theropod from the Morrison Formation to be named was *Coelurus fragilis* by O. C. Marsh (1879). The specimen was apparently widely scattered because it was recovered over a span of several years from Reed's Quarry 13 at Como Bluff, Wyoming, as the quarry was expanded. The locality was an extensive bone bed better known for its numerous specimens of *Stegosaurus* and *Camptosaurus* (Gilmore 1909, 1914). In naming the species, Marsh emphasized the extreme hollowness of the vertebrae and illustrated three of them in 1881. A second species, *Coelurus agilis*, was named a few years later by Marsh (1884) for additional material from Quarry 13, but only a pair of pubes was described and illustrated. As part of our restudy of the *Coelurus* material, it became clear to one of us (JHO), that *C. fragilis* and *C. agilis* are different parts of the same individual (Ostrom 1980). A third species, *Coelurus gracilis*, was erected by Marsh in 1888 for metapodials from the Lower Cretaceous Potomac Formation of Maryland. However, as noted elsewhere, the taxon is a nomen dubium (Ostrom 1980); it is certainly not a species of *Coelurus*.

The other small theropod of our study, *Ornitholestes hermanni*, was named by H. F. Osborn (1903) for a partial skeleton from Bone Cabin Quarry, north of Como Bluff. Osborn figured little of the material at that time, although he did offer a skeletal reconstruction. The skull was figured at a later date, along with a slightly modified rendition of the skeleton (Osborn 1916). In naming this theropod, Osborn noted its small, gracile skeleton and assumed that it was an active, agile hunter. Several years later, Gilmore (1920) synonymized *Ornitholestes hermanni* with *Coelurus fragilis*, arguing that the differences in the vertebrae were minor. However, one of us (JHO) briefly showed later

that numerous characters separate the two taxa (Ostrom 1980). Here, we elaborate upon those differences.

Institutional Abbreviations. AMNH, American Museum of Natural History, New York; USNM, United States National Museum (now National Museum of Natural History), Washington D.C.; YPM, Yale Peabody Museum of Natural History, New Haven, Conn.

Systematic Paleontology

Theropoda
Coelurosauria
Maniraptora
Ornitholestes hermanni Osborn 1903
Coelurus fragilis Gilmore 1920 (in part)
Coelurus hermanni Steele 1970

Holotype. AMNH 619, skull with both mandibles, three cervical vertebrae, eleven dorsal vertebrae, four sacral vertebrae, twenty-seven caudal vertebrae, both ischia, left ilium, both pubes missing the distal ends, incomplete left femur, proximal end of left fibula, both humeri, right metatarsals II, III, and IV, left metatarsal IV, four phalanges of the pes, two pedal unguals, one right tarsal, right metacarpal II or III, fragments of two other metacarpals, two fragments of manus phalanges, one ungual of the manus, and numerous fragments. Date received, Summer 1900.

Type Locality. Bone Cabin Quarry, 13 km north of Como Bluff, Wyoming.

Revised Diagnosis. Distal caudals deep and bifurcated ventrally; pubis bowed, distal end directed posteroventrally; pubic apron without pubic fenestra; ischium with broad obturator notch, triangular obturator process.

Coeluridae

Coelurus fragilis Marsh 1879
Coelurus agilis Marsh 1884
Elaphrosaurus agilis Russell, Béland, and McIntosh 1980

Syntypes. YPM 1991, two proximal caudal vertebrae, one proximal caudal centrum, one proximal caudal neural arch (Marsh 1881, plate 10, fig. 2a,b). YPM 1992, eight mid-caudal vertebrae, one partial mid-caudal centrum (Marsh 1881, plate 10, fig. 3a,b). YPM 1993, cervical vertebra, proximal caudal neural arch (Marsh 1881, plate 10, fig. 1 (composite), 1a (composite), 1b).

Type Locality. Quarry 13 East, Como Bluff, Wyoming.

Referred Specimens. Quarry 13 East, Como Bluff, Wyoming: YPM 1992, eight mid-caudal vertebrae, one partial centrum of a mid-caudal vertebra (Marsh 1881, plate 10, fig. 3, 3a). YPM 1993, one cervical vertebra, one proximal caudal neural arch (Marsh 1881, plate 10, fig. 1, 1a). YPM 1994, one caudal centrum. YPM 1995, one caudal vertebra, plus fragments. YPM 2010 (type specimen of *Coelurus agilis*), right dentary?, three cervical vertebrae, two dorsal vertebrae, five dor-

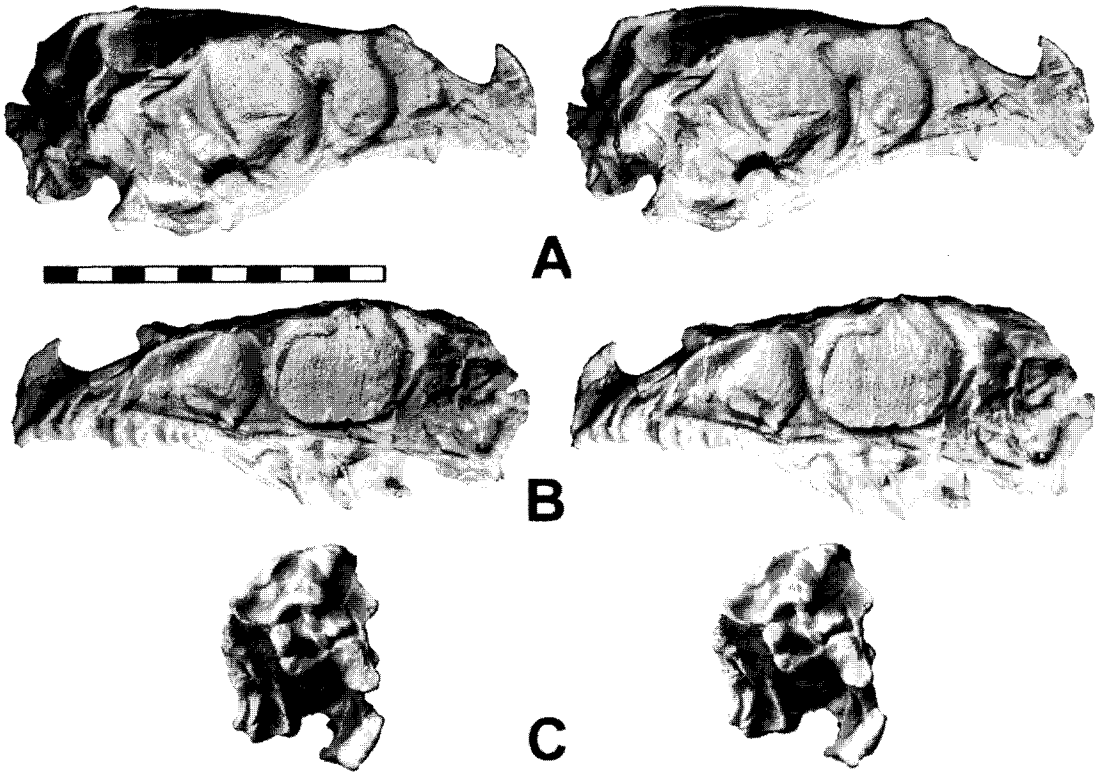


Figure 3.1. Skull of Ornitholestes hermanni *as available to Osborn (1903, 1916) in stereoscopic pairs (YPM 53262 cast): (A) right side showing displacement of bones anteriorly, (B) left side with most bones intact, and (C) posterior view. Scale in cm.*

sal centra, six dorsal neural arches, two indeterminate neural arches, one proximal caudal vertebra, left and right ulnae, distal ends of both radii, left humerus, left femur, proximal end of right femur, both pubes, fragment of an ilium?, distal three-quarters of left tibia, proximal end of left fibula, right scapula, distal end of metatarsal III, metatarsal II or IV, left and right radiale, left and right metacarpal II, right metacarpal III, fragment of right metacarpal IV, seven phalanges of the manus, many unidentified fragments. YPM 9162, one partial sacral vertebra.

Cleveland-Lloyd Quarry, Utah: ?UUVP 11743, 1eft humerus. UMNH 7795, left humerus.

Revised Diagnosis. Very gracile dentary; all centra elongated; all neural spines long and low; all centra very thin walled; paired pleurocoels on some cervicals; triangular diapophyseal ala angled sharply ventrolaterally; centroprezygapophyseal lamina forms fossa lateral to neural canal; centrodiapophyseal lamina present; caudal prezygapophyses very short; pubic foot very arcuate ventrally and projects posterodorsally; pubic fenestra located at middle of pubic apron; very long, gracile metatarsal almost as long as tibia or femur.

Description

Cranial (Figs. 3.1–3.3). The skull of *Ornitholestes* as originally available to Osborn is illustrated in multiple views for the first time in

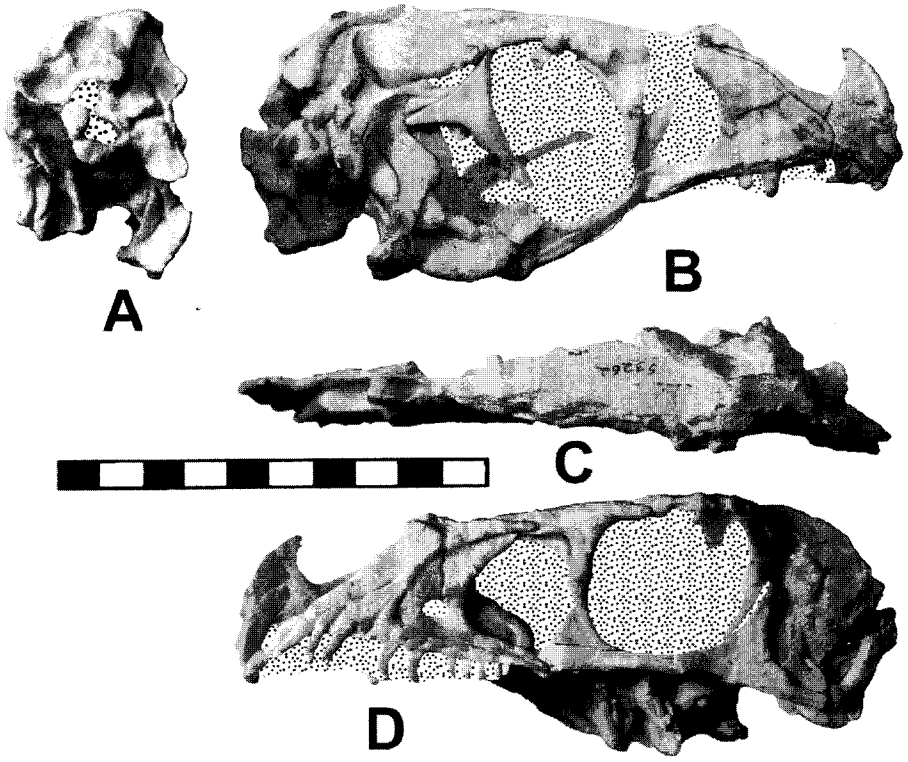


Figure 3.2. Skull of Ornitholestes hermanni *(YPM 53262 cast) in (A) occipital, (B) right, (C) dorsal, and (D) left views. Scale in cm.*

Figures 3.1 and 3.2. The considerable preparation that has been done recently reveals a great deal of detail not previously available to Osborn (Norell, pers. comm.). The skull is presently under study by Mark Norell, and thus little will be written here. The skull is slightly crushed obliquely, resulting in a distortion of the right side. For example, the orbit on the left side is almost circular, whereas it is distinctly ellipsoid on the right. This crushing has displaced the base of the left nasal, which has led to the suggestion that *Ornitholestes* may have had a nasal horn much like *Proceratosaurus* (Paul 1988); clearly it did not (Norell et al. 2001).

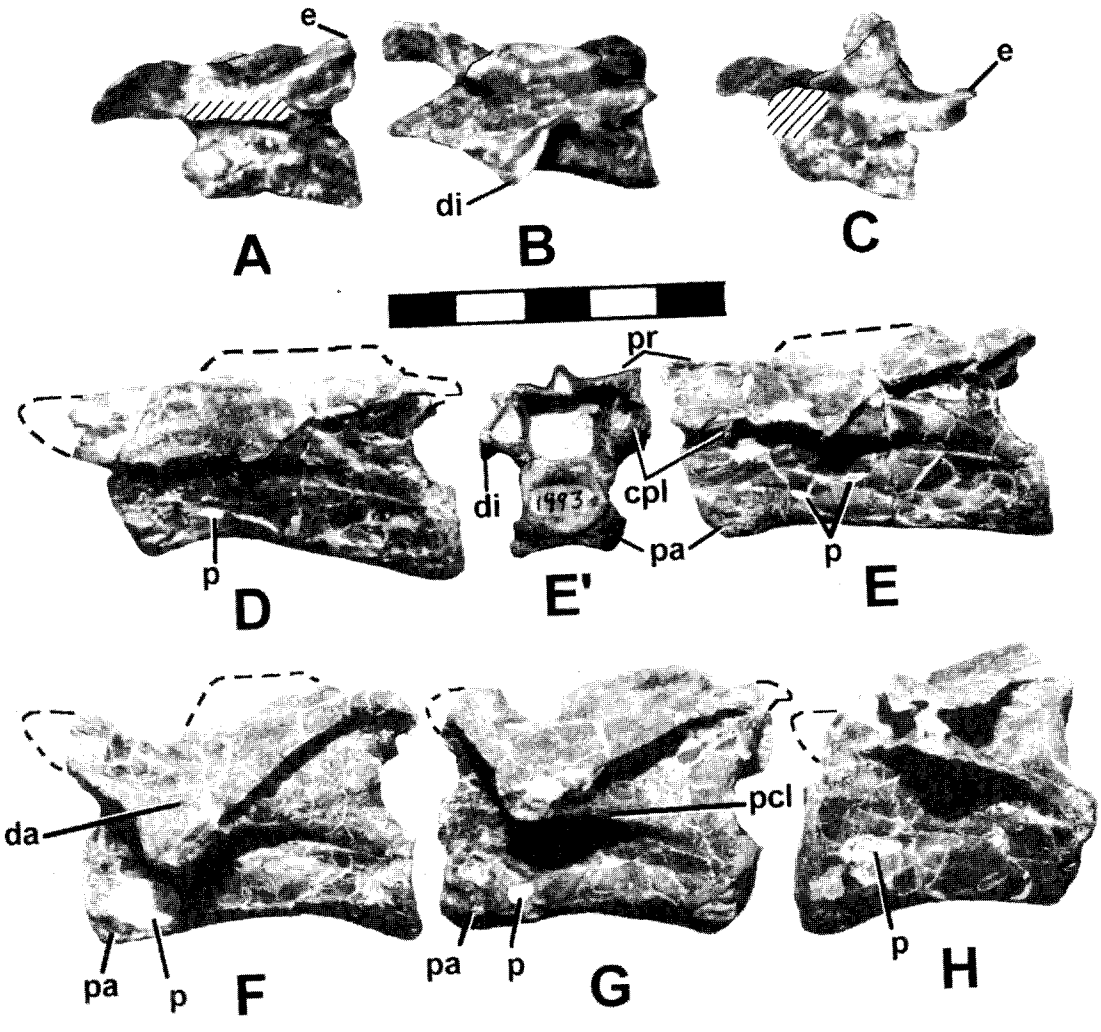
Of *Coelurus,* the only possible cranial fragment is a right dentary (Fig. 3.3). The preservation, including color, is the same as that of most of the rest of YPM 2010, suggesting that the fragment belongs with *Coelurus* as determined by Marsh. However, the fragment is very slender and delicate, measuring 7.9 cm long with a mid-length depth of 1.1 cm. This condition has led us to speculate that perhaps the dentary does not belong with the skeleton, even though it was found in the same general area. In dorsal view, the jaw is slightly sigmoid. There are fourteen alveoli present, as well as interdental plates. It has a large Meckelian groove on the medial side that extends the length of the fragment. On the lateral surface there is a prominent groove connecting the nutrient foramina. If this dentary does belong to *Coelurus,* then the taxon may also be characterized by its unique long, slender dentary.

Figure 3.3. Possible right dentary of Coelurus fragilis *in (top) occlussal, (center) medial, and (bottom) lateral views. Scale in cm.*

A very gracile dentary also characterizes the troodontid *Byronosaurus jaffe,* and it also has a prominent groove on the lateral surface (Norell et al. 2000). A slender, gracile dentary also characterizes *Compsognathus* and *Shuvuuia* (Sereno 2001, fig. 12). Further comparisons may reveal additional similarities with these taxa.

Cervicals (Fig. 3.4). Only three cervicals of *Ornitholestes* are known, and these are crushed or distorted (Fig. 3.4A–C). The neural spines are damaged on the more anterior two, but they were apparently anteroposteriorly longer and lower than the spine on the third cervical. The beveled centra suggest that these are all anterior and mid-cervicals, possibly CV3, CV4, and CV6. The beveling does indicate that the neck was somewhat sigmoidal (contrary to Ostrom 1969, p. 48), as it also was in *Coelurus*. The articular faces of the *Ornitholestes* cervicals are opisthocoelous, whereas they are amphicoelous in *Coelurus* as first observed by Marsh (1881). Marsh (1881, p. 339) also reported that "The first three of four behind the axis [of *Coelurus*] had the front articular face of the centrum somewhat convex, and the posterior one deeply concave." The only vertebrae that match this description are those described by Makovicky (1997) as an unnamed small theropod from the Morrison Formation (see further discussion below). Previously, one of us (JHO) had come to a similar conclusion and had excluded these vertebrae from *Coelurus* (Ostrom 1980, Appendix A). In addition, none of the cervical vertebrae of *Coelurus* can be matched to that figured by Marsh (1881, plate 10, fig. 1). It would appear, therefore, that the figured vertebra is actually a composite of two cervicals (Ostrom 1980, p. 253), including one of the non-*Coelurus* vertebrae described by Makovicky.

The neural spine is preserved long and somewhat low on the anterior two cervicals of *Ornitholestes,* whereas it is anteroposteriorly short and moderately tall in the third cervical. In contrast, the frag-



ments of the neural spines of *Coelurus* suggest that they were all very low and long, extending almost the entire length of the neural arches. Admittedly most of the spines were damaged in collecting; thus it is difficult to know if any were tall. There is a small, triangular depression at the base of the neural spine on the anterior side of the neural spine, and a vertically elliptical one on the posterior side. In addition, there is a peculiar, moderately deep fossa at the base of the prezygapophysis. It is formed by the centroprezygapophyseal lamina. The diapophyseal lamina is a triangular ala that projects ventrolaterally from the neural arch and connects the pre- and postzygapophyses. A posterior centrodiapophyseal lamina is also present connecting the posterior part of the centrum to the diapophysis. In *Ornitholestes*, the diapophysis extends subhorizontally (although it is distorted in the cervical preserving this feature, Fig. 3.4B). The prezygapophyses of *Ornitholestes* project

Figure 3.4. Comparison of cervical vertebrae. Ornitholestes hermanni *(A–C) and* Coelurus fragilis *(D–H). (E') is the anterior view of cervical E showing the matrix filled fossa below the prezygapophyses formed by the centroprezygapophyseal lamina. Abbreviations: cpl—centroprezygapophyseal lamina; da—diapophyseal ala; di—diapophysis; e—epipophysis; p—pleurocoel; pa—parapophysis; pcl—posterior centrodiapophyseal lamina; pr—prezygapophysis. Scale in cm.*

anterodorsally and are slightly flexed in lateral view. In dorsal view, the pre- and postzygapophyses are strongly divergent, forming an X shape. In contrast, the prezygapophyses are horizontal in the anterior cervicals of *Coelurus* and slightly angled anterodorsally in the mid- and posterior cervicals; in dorsal view the pre- and postzygapophyses are moderately divergent. However, the full extent of the prezygapophyses is unknown for most of the vertebrae because they are incomplete. The postzygapophyses overhang the posterior surface of the centrum in *Ornitholestes,* especially in the mid-cervical (contrast Fig. 3.4A,B with 3.4C), but not in *Coelurus.* In addition, the articular facets of the zygapophyses are large in *Ornitholestes* but very small in *Coelurus.* Small, horizontal, prong-shaped epipophyses are present on the cervicals of *Ornitholestes* but apparently not *Coelurus,* although these are probably broken off because most postzygapophyses are incomplete.

None of the centra of *Ornitholestes* or *Coelurus* have a hypapophysis, or keel, ventrally. The centrum of *Ornitholestes* is short relative to the centrum width, whereas in *Coelurus* it is more than four times as long as the width. The anterior articular surface is wider than it is deep in *Ornitholestes,* whereas the articular face is almost circular in *Coelurus.* Pleurocoels are absent on the cervicals of *Ornitholestes* but are present in *Coelurus.* These pleurocoels in *Coelurus* vary considerably in size and number on each side of the centra. Cervical B (Fig. 3.4E) has two small, lenticular pleurocoels on the left side but only one on the right. One cervical, C, has an enormous pleurocoel on one side (Fig. 3.4F), but a considerably smaller one on the other. This asymmetry appears to be real. Another cervical, E (Fig. 3.4H), has a large pleurocoel on the left side, but three smaller pleurocoels on the right side. All of the *Coelurus* vertebrae are very pneumatic. Not only are the centra camellate as noticed by Marsh (1881), but the broken surfaces of the diapophyses suggest that pneumaticity also extended into the diapophyseal ala. Contrary to Marsh (1881), cervical ribs are not fused to the vertebrae in *Coelurus.*

Dorsals (Fig. 3.5A–U). Ten dorsals are preserved in the holotype of *Ornitholestes hermanni,* and nine centra and neural aches in *Coelurus fragilis.* Some of the dorsals of *Ornitholestes* are distorted, and many others have lost their transverse processes (Fig. 3.5A). The neural spines of the anterior dorsals are anteroposteriorly short, and they rise vertically and have a rounded anterior border, whereas those of the mid- and posterior dorsals extend nearly the full length of the neural arch and are almost twice as tall as those of the anterior dorsals. In addition, the neural spine of the last dorsal leans forward. In *Coelurus,* the anterior neural spines are only slightly shorter than the mid- and posterior dorsals. In addition, the spine occupies the length of the neural arch in all of the vertebrae. The apices of the neural spines in both *Ornitholestes* and *Coelurus* are not expanded into a spinal table. Along the anterior and posterior margins, the scars for the interspinous ligaments extend to near the tops of the neural spines in *Coelurus* but terminate well below the tops in *Ornitholestes.*

The transverse processes of *Ornitholestes* are simple horizontal, laterally directed, and subrectangular in dorsal view. In contrast, the

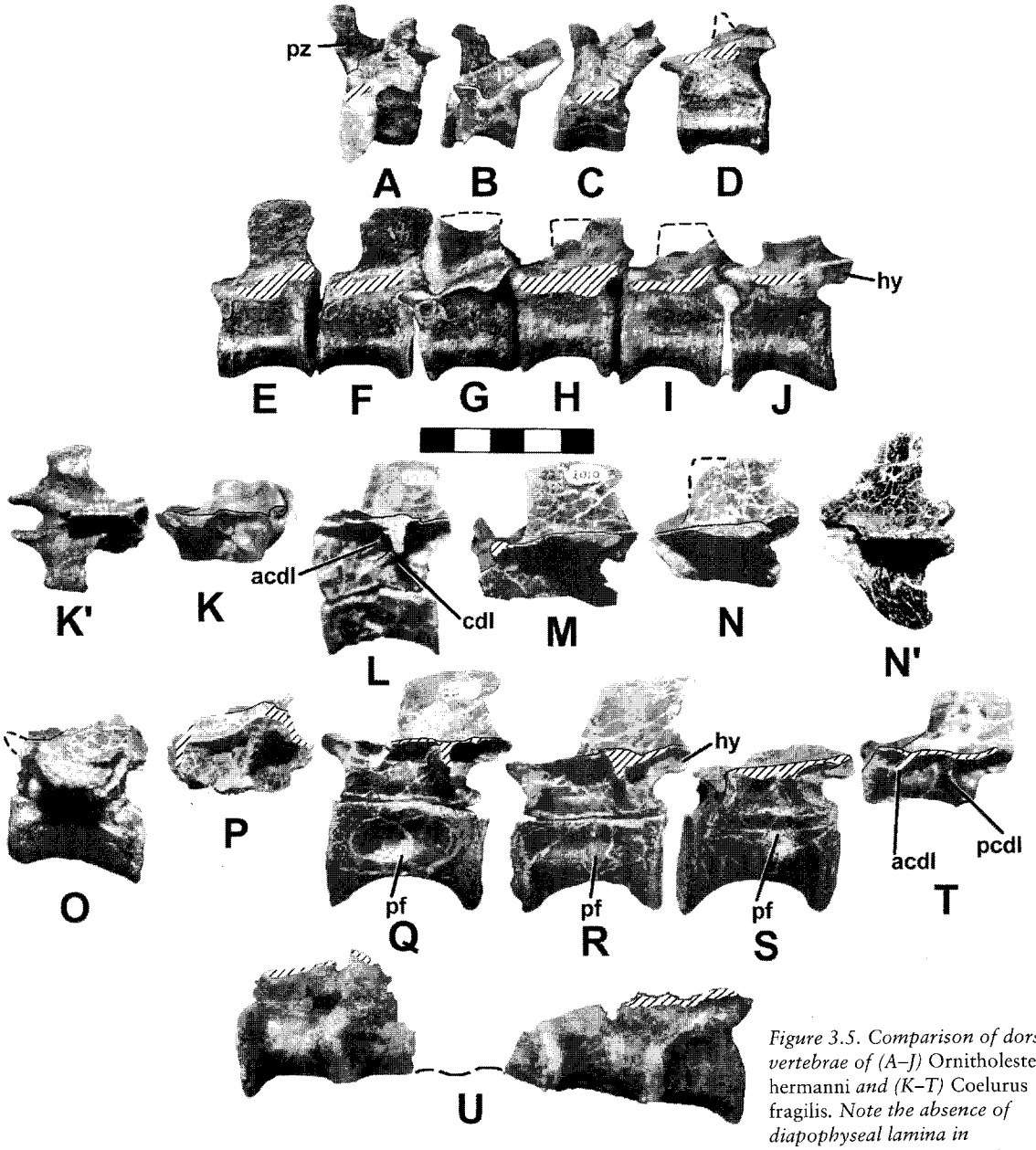


Figure 3.5. Comparison of dorsal vertebrae of (A–J) Ornitholestes hermanni *and (K–T)* Coelurus fragilis. *Note the absence of diapophyseal lamina in* Ornitholestes. *Sequence of vertebrae in* Coelurus *is based upon transverse process shape (compare K' with N'). (U) Sacral vertebrae of* Ornitholestes hermanni. *Abbreviations: acdl—anterior centrodiapophyseal lamina; cdl—centrodiapophyseal lamina; hy—hyposphene; pcdl—posterior centrodiapophyseal lamina; pf—pleurofossa; pz—prezygapophysis. Scale in cm.*

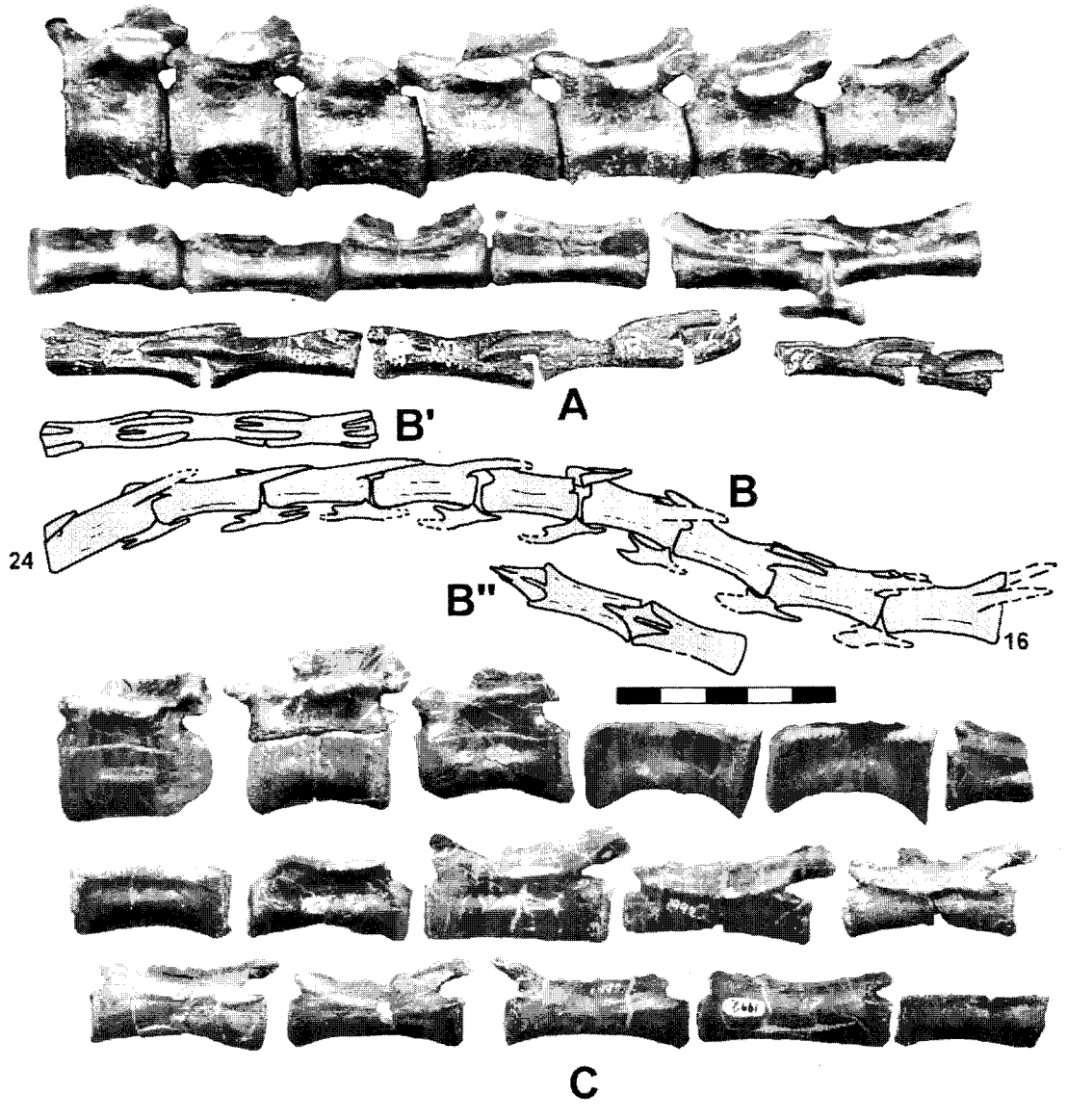
transverse processes of the anterior dorsals in *Coelurus* are horizontal, laterally directed, and subrectangular in dorsal view (Fig. 3.5K') but become strongly back turned and triangular in dorsal view beginning with the mid- and extending to the posterior dorsals (Fig. 3.5N'); a similar change is seen in *Tanycolagreus* (see Carpenter et al., Chapter 2). In addition, there is a well-developed centrodiapophyseal lamina on the ventral side of the transverse process, and this separates two deep diapophyseal fossa. Some transverse processes also have anterior and posterior centrodiapophyseal lamina as well.

The prezygapophyses of *Coelurus* are small, slightly inclined structures that merge laterally into the transverse processes. In contrast, those of *Ornitholestes* are distinct, separate structures. The postzygapophyses in the anterior dorsals of *Coelurus* do not extend beyond the posterior surface of the centrum, whereas they do in the mid- and posterior dorsals. In *Ornitholestes,* the postzygapophyses overhang the centrum of all the dorsals. A hyposphene is developed only on the posterior dorsals of *Ornitholestes* (Fig. 3.5J) and on the mid- and posterior dorsals of *Coelurus* (Fig. 3.5L–T).

In both *Ornitholestes* and *Coelurus,* the centra are taller than they are wide, although the amount of compression varies. In *Ornitholestes,* the centrum is slightly compressed, or spool-shaped, in ventral view, and the cross-section of the mid-section is still over 60 percent the height of the articular face. In contrast, the centrum of *Coelurus* is much more constricted in the middle, being hourglass-shaped in ventral view. The articular faces are amphiplatyan in *Ornitholestes* and somewhat amphicoelous in *Coelurus.* No pleurocoels are present on the dorsals of either taxon.

Sacrals (Fig. 3.5U). Five sacral vertebrae are preserved in *Ornitholestes,* although there is a gap dividing them in half. The neural spines are unfortunately missing on all of them. None of the centra have pleurocoels. The articular face of the first sacrum is amphiplatyan, and its width is subequal to that of the last sacral. There is a damaged centrum that may be a sacral centrum of *Coelurus.*

Caudals (Fig. 3.6). Caudals are the most abundant vertebrae in both specimens. None of them have a pleurocoel, although the centra do have an elongated, shallow groove termed a pleurofossa (Carpenter and Tidwell, in press). In addition, the lateral sides of the centra in *Ornitholestes* have a ridge extending nearly the length of the centra. Ventrally, the centra have a groove separating the paired ridges that connect the chevron facets. The articular faces of the centra are rather boxy, implying less mobility rather than more as stated by Holtz (1998, Appendix 1). The anterior caudals, especially those of *Ornitholestes,* are short. The length of these anterior caudals is about 75 percent the length of the posterior ones in *Ornitholestes* and over 80 percent in *Coelurus.* In addition, the centra faces of these anterior caudals are beveled so that the posterior articular surface is lower than the anterior. Unfortunately, because so many caudals are missing, the transition point between the anterior and posterior portions of the tail cannot be determined in either specimen. The prezygapophyses of the mid- and posterior caudals are proportionally longer in *Ornitholestes* than in *Coelurus,* but even the longest do not extend to mid-centrum (Fig. 3.6B'); in *Coelurus* the prezygapophyses are shorter than in *Tanycolagreus.* The neural spines are damaged in both taxa, but from their remnants they appear to have been longer and lower in *Coelurus* than in *Ornitholestes;* neither show the bifid spines seen in *Sinosauropteryx* (Currie and Chen 2001). The distal chevrons of *Ornitholestes* are elongate, being about as long anteriorly as posteriorly. Structurally, they are unusual in that some of them are bifurcated laterally as well as ventrally (Fig. 3.6B").



There is one odd caudal cataloged with YPM 2010 that we believe does not belong to *Coelurus* and may actually belong to the cervical vertebrae described by Makovicky (1997). In addition, it has the same black color and preservation, suggesting that it also came from the same quarry. This vertebra is amphicoelous but with a thick rim around the articular face. The neural spine is a tall, spike-like structure, as are the horizontal caudal ribs. Ventrally, there are very faint ridges connecting the chevron facets.

Scapula (Fig. 3.7). The only scapula is that of *Coelurus*, and unfortunately, even that is considerably damaged. Nothing about the development of the acromion or about whether the distal end of the

Figure 3.6. Comparison of the caudal vertebrae of Ornitholestes hermanni *(A, B) and* Coelurus fragilis *(C). The distal caudals of* Ornitholestes *shown in articulation in B, two vertebrae in dorsal view in B' and in ventral view in B" (adapted from an unpublished sketch by Erwin Christman). Note the peculiar, boat-shaped chevrons in B". Scale in cm.*

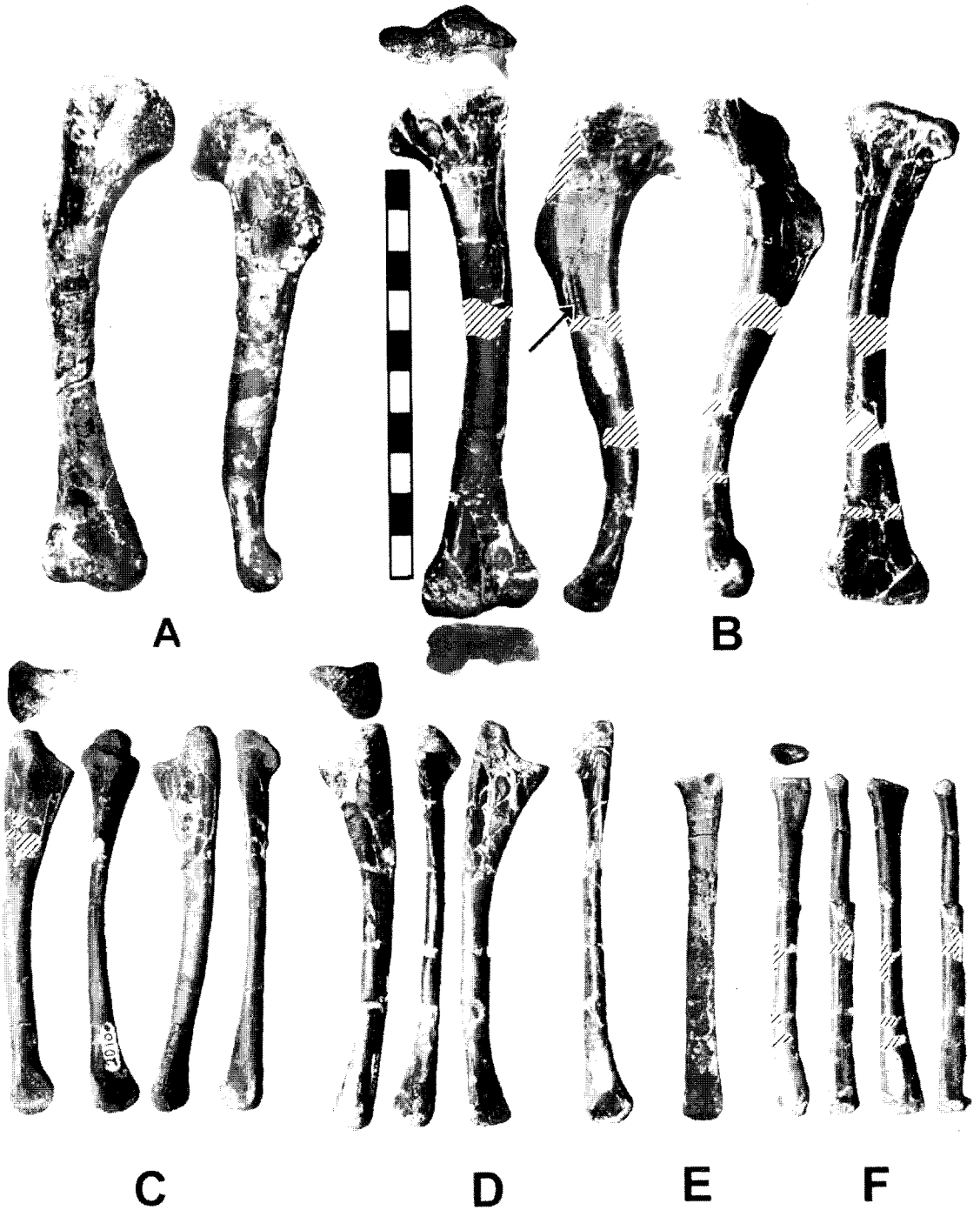
Figure 3.7. Scapular fragment of Coelurus fragilis *in lateral (A), ventral (B), and medial (C) views. Scale in cm.*

scapular blade was expanded can be determined. On the medial side, there is no prominent horizontal ridge as in *Tanycolagreus*. In ventral view (Fig. 3.7B), the scapula is sharply bent medially.

Coracoid. The coracoid is unfortunately missing in both specimens.

Humerus (Fig. 3.8A–B). A right humerus is known for *Ornitholestes* and a left for *Coelurus*. That of *Ornitholestes* (12.4 cm long) is rather straight shafted, whereas that of *Coelurus* is markedly sigmoidal in lateral view (11.9 cm long). The proximal end is rounded in *Ornitholestes* and markedly flat in *Coelurus*. The humeral head is low and confluent with the deltopectoral and bicipital crests in *Ornitholestes* but is offset and emarginated ventrally by a groove in *Coelurus*. The internal tuberosity is well differentiated and angular in both taxa, but it is conical in *Ornitholestes* and elongated and tapering in *Coelurus*. What these differences mean biomechanically is an area in need of research. In lateral view, the internal tuberosities of both taxa project posteriorly and are well separate from the humeral head. The diameters of both the proximal and distal ends are well expanded to over 150 percent of the mid-shaft diameter, and the ends are slightly offset relative to one another; that is, there is slight torsion of the humeral shaft. The deltopectoral crest projects anteriorly and is expanded and offset from the humeral shaft in both taxa. A prominent scar for the M. pectoralis superficialis is present laterally near the base of the deltopectoral crest in *Coelurus*. In *Tyrannosaurus* (Carpenter and Smith 2001) and apparently in *Ornitholestes,* this scar is a slight tuberosity. Distally, the condyles are more anteriorly than ventrally developed, indicating that the relaxed position of the arms was slightly flexed. The entepicondyle is prominent in both taxa also. Ventrally, the ulnar facet is expanded and merges with the entepicondyle.

(Opposite page)
Figure 3.8. Forelimb elements of Ornitholestes hermanni *and* Coelurus fragilis: *(A) right humerus of* Ornitholestes hermanni *in anterior and lateral views; (B) left humerus of* Coelurus *in anterior, medial (showing prominent scar near the deltopectoral crest), lateral, and posterior views, as well as proximal and distal views; (C) right and (D) left ulnas of* Coelurus *in proximal, lateral, anterior, medial, and posterior views; (E) right radius of* Ornitholestes; *and (F) left radius of* Coelurus *in proximal, lateral, anterior, medial, and posterior views. Scale in cm.*


A
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D
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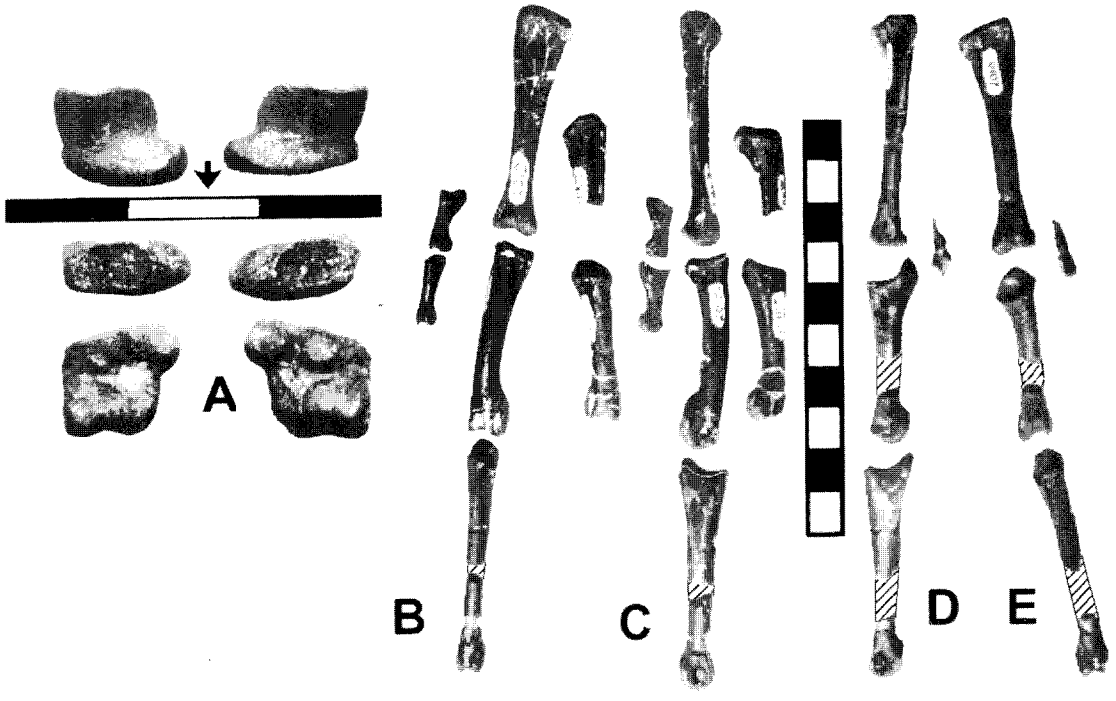

Figure 3.9. Manual elements of Coelurus fragilis: *(A) right and left semilunate carpals (arrow points anteriorly) in proximal, anterior, and ventral views (showing metacarpal facets); (B) right manus in extensor view; (C) right manus in lateral view; (D) left manus in lateral view; and (E) left manus in extensor view. Scale in cm.*

The humerus/ulna ratio is greater than 100 percent in both taxa, and the radius/ulna ratio is less than 75 percent, but greater than 50 percent (Holtz 1998).

Ulna (Fig. 3.8C,D). Both ulnas are known for *Coelurus,* although the left one is slightly crushed laterally (left, 9.6 cm long; right, 9.1 cm). The shafts are bowed posteriorly; and in anterior view, the shafts are bowed laterally. The humeral notch is better developed in the left ulna than in the right; the olecranon is equally developed in both. The radial notch is shallow and is slightly more prominent in the left ulna than in the right. The distal end is arcuate but lacks the anteriorly developed process seen in some theropods, such as *Deinonychus.*

Radius (Fig. 3.8E,F). A single right radius is present for *Ornitholestes* (8.4 cm long), and a left for *Coelurus* (~8.1 cm long), as well as the proximal end of the right. Their shafts are straight, and they differ only in that the shaft is slightly more slender in *Coelurus* than in *Ornitholestes.* The distal ends of the radius and ulna have a loose joint. The distal ends are not expanded as they are in *Deinonychus.*

Carpal (Fig. 3.9A). Both semilunate carpals are known for *Coelurus* (greatest width: left, 1.2 cm; right, 1 cm). The carpal is deeper than in *Tanycolagreus* and has a more prominent trochlear surface (see Carpenter et al., Chapter 2). It has well-developed articular facets on its ventral side, and it broadly overlaps metacarpal II. The carpal differs from that of the contemporary large theropod *Allosaurus* in that it is not restricted to capping metacarpal I, and it lacks the ventral process

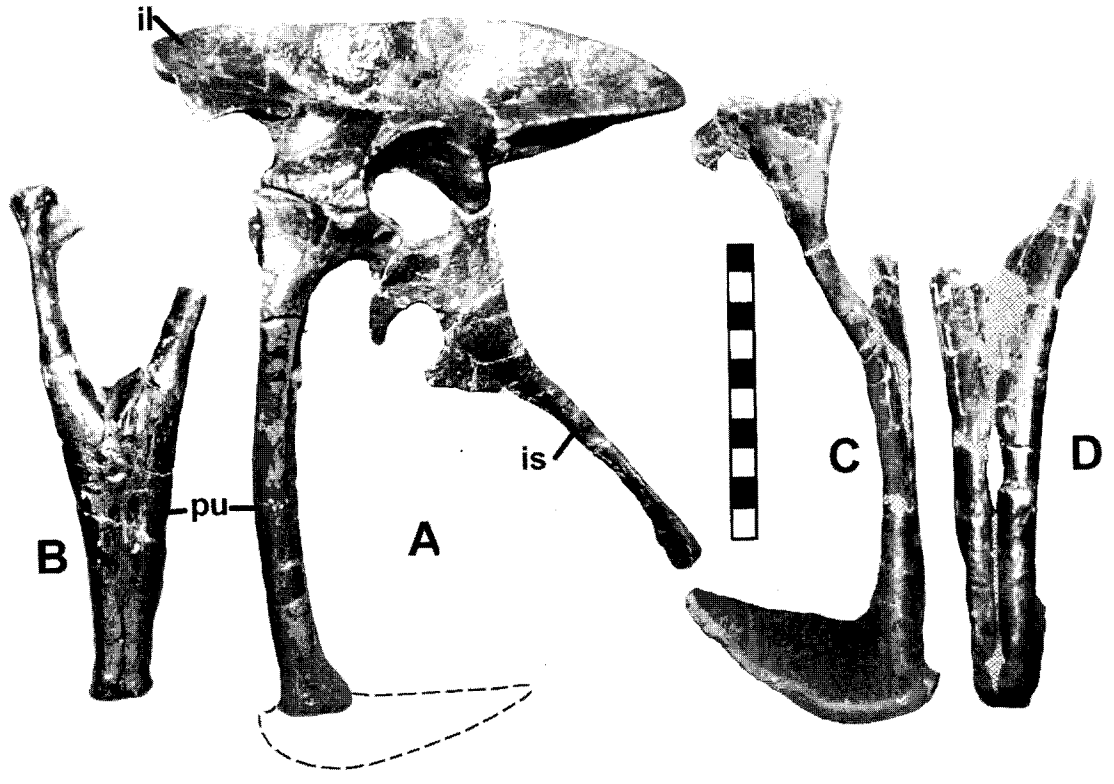

Figure 3.10. Pelvic elements of Ornitholestes hermanni *(A, B) and* Coelurus fragilis *(C, D). (A) Pelvis of* Ornitholestes *in left lateral view showing long, low ilium, anteriorly bowed pubis (foot shown with dashed lines), and ischium with very large obturator notch; (B) pubis of* Ornitholestes *in anterior view show the absence of a pubic fenestra; (C) pubis of* Coelurus *in right lateral view (note bend in shaft in the proximal portion); and (D) pubis of* Coelurus *in anterior view showing slit-like pubic fenestra. Abbreviations: il—ilium; is—ischium; pu—pubis. Scale in cm.*

seen in *Allosaurus* (see Carpenter 2002). It is similar to the carpal of *Deinonychus* in overall shape, although considerably smaller. As noted elsewhere, the manus of theropods could not fold up against the forearm in avian fashion (Carpenter 2002).

Manus (Fig. 3.9B–E). The isolated manus attributed to *Ornitholestes* by Osborn (1916) has been referred to *Tanycolagreus* because of the great similarities between the two, especially in the curvature of the first ungual (Carpenter et al., Chapter 2); the holotype of *Tanycolagreus topwilsoni* comes from a few hundred meters west of the holotype of *Ornitholestes hermanni.* The manual elements of *Coelurus* are long and slender, and parts of both hands are represented. Unfortunately, metacarpal I and IV are missing; metacarpal III is present, and it retains its phalanges. Collateral tendon facets are well developed. Overall, the manual elements resemble those of *Tanycolagreus,* although they are much smaller.

Ilium (Fig. 3.10A). The ilium of *Ornitholestes* is long and low in profile. It has a moderately long preacetabular process that is notched anteriorly, and a much longer, tapering postacetabular process. Ventrally beneath the postacetabular process, the brevis fossa is long and tapering; and anteriorly, a well-developed M. cuppedicus fossa is present along the ventral edge of the preacetabular process. The lateral surface above the acetabulum is smooth, lacking the vertical ridge seen in *Stokesosaurus.* The dorsal lip of the acetabulum flares laterally into

a supra-acetabular crest. The distal end of the ischial peduncle is considerably smaller than that of the pubic one. The pubic peduncle projects slightly anteriorly and is anteroposteriorly longer than it is wide. It also extends ventrally to the level of the ischial peduncle. No ilium is known for *Coelurus*.

Pubis (Fig. 3.10A–D). The pubis is known for both *Ornitholestes* and *Coelurus*. The shaft is bowed in *Ornitholestes* so that the pubic foot is posterior to the vertical plane (Fig. 3.10A), as if it were becoming the precursor to the opisthopubic condition of dromaeosaurids. The shaft is relatively straight in *Coelurus,* except proximally, where it is bowed posteriorly; this bowing appears to be natural and not distortion (Fig. 3.10C). Distally, the left and right pubic feet are in contact in *Coelurus* (Fig. 3.10D). Unfortunately, the distal end for *Ornitholestes* is incomplete, and the damaged end is plastered. It is possible, although doubtful, that the distal end of the pubis retained a rounded, ceratosaur-type pubic expansion. A small part of what is probably the pubic foot is present on the posterior and anterior sides at the distal end (Fig. 3.10A). The pubic foot in *Coelurus* is considerably longer posteriorly than the short anterior projection. The length of the foot is about 46 percent of the length of the pubic shaft as measured just above the foot. The ventral side of the pubic foot is arcuate, whereas it is flat in *Tanycolagreus* (Carpenter et al., Chapter 2) and *Aristosuchus* (Naish et al. 2001, fig. 9.28). The obturator foramen is ventrally open to form an obturator notch in the pubis of both *Ornitholestes* and *Coelurus;* no other foramen is present in the pubis ventral to the notch in lateral view. The pubic apron is relative wide and ventrally long in both taxa. Furthermore, it is pierced about mid-length by a lenticular-shaped pubic foramen in *Coelurus* but not in *Ornitholestes* (compare Figs. 3.10B and D). This foramen is located just above the pubic foot in *Tanycolagreus,* and the pubis from Cañon City previously referred by Gilmore (1920) as *Coelurus;* we therefore transfer this pubis to *Tanycolagreus* (see Carpenter et al., Chapter 2). The contact with the ischium is dorsoventrally narrow.

Ischium (Fig. 3.10A). The ischium for *Ornitholestes* is slightly curved posteroventrally. Proximally, there is no antitrochanter along the posterior margin of the acetabulum. The obturator notch is very wide, and the obturator process is triangular and distally placed; no foramen pierces this process. The anterior margin of the obturator notch is a long, tapering process that extends ventrally from the pubic articulation. A small scar on the posterolateral side of the ischial shaft is present. The distal end of the ischium is slightly expanded but does not have a foot. If we are correct that a *Coelurus-Tanycolagreus*-like foot was present at the end of the pubis, then the ischium/pubis length ratio was 66–68 percent.

Femur (Fig. 3.11A–C). A partial left femur is known for *Ornitholestes* (>20 cm long), and a complete left (~21 cm long) and partial right are known for *Coelurus*. The femur of *Ornitholestes* is anteroposteriorly crushed and is missing its head (Fig. 3.10C). Nevertheless, the shaft is bowed anteriorly and has a slight sigmoid curvature in

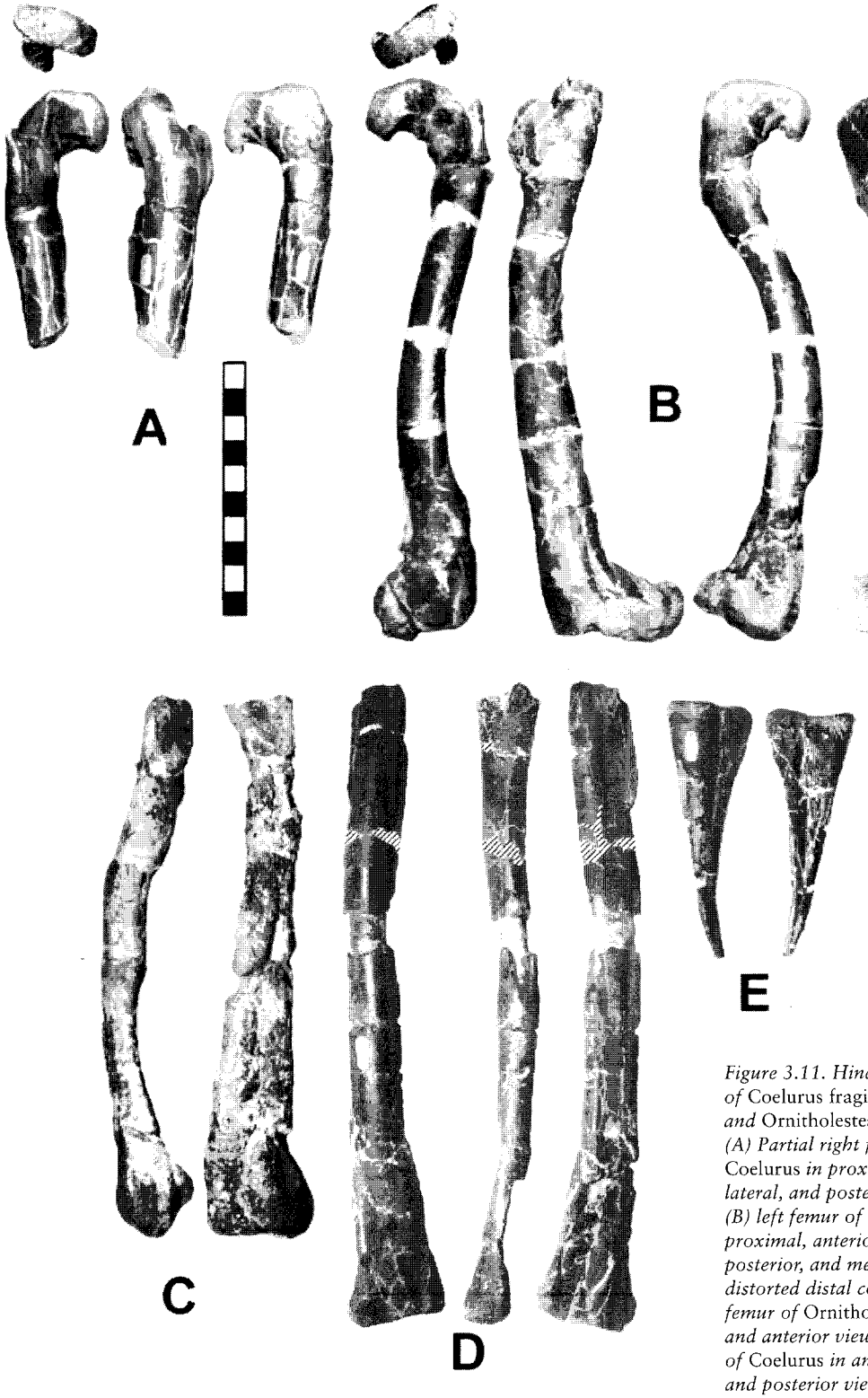

Figure 3.11. Hindlimb elements of Coelurus fragilis *(A, B, D, E) and* Ornitholestes hermanni *(C). (A) Partial right femur of* Coelurus *in proximal, anterior, lateral, and posterior views; (B) left femur of* Coelurus *in proximal, anterior, lateral, posterior, and medial views (note distorted distal condyles); (C) left femur of* Ornitholestes *in lateral and anterior views; (D) right tibia of* Coelurus *in anterior, medial, and posterior views; and (E) fibula of* Coelurus *in lateral and medial views. Scale in cm.*

anterior view. In marked contrast, the femur of *Coelurus* is strongly bowed anteriorly and more strongly curved sigmoidally in anterior view. The femoral head is transversely elongated and rather blocky, or squared; the head is slightly angled ventrally, but less so than in *Nedcolbertia* (Kirkland et al. 1998). The greater trochanter is a mound-like structure in the right femur and less mound-like in the left. In the left femur, the greater trochanter is confluent with the head, giving the proximal end an almost rectangular appearance. The anterior trochanter is alariform, being a plate-like structure that projects anterodorsally below, and separate from, the greater trochanter. The top of the anterior trochanter is well below the top of the greater trochanter, but less so than in *Nedcolbertia*. The fourth trochanter is apparently absent in *Ornitholestes*, although the bone is poorly preserved. It is, however, present in *Coelurus* as a long, low ridge on the right femur (it is broken in the left). The medial epicondyle is short, its length being less than one-quarter the femoral length in *Ornitholestes* but about one-quarter the femur length in *Coelurus*. The distal end of the femur is pathological in *Coelurus*, as evidenced by the filigree on the shaft just above the condyles; the two condyles appear to be approximately the same size. The "patellar" sulcus, or groove, at the anterior surface of the distal end is very shallow in both taxa.

Tibia (Fig. 3.11D). Only the right tibia for *Coelurus* is known, and this is lacking the proximal head. Thus, nothing can be said about the shape of the cnemial crest. The fibular crest (crista fibularis) is present, however, and this is long and low. The presence of the crest and the missing proximal end including the cnemial crest suggest that the crest was distally placed. The shaft is fractured and is missing some of the cortical bone at mid-shaft. Nevertheless, the tibia appears to be laterally bowed. The distal end is fractured in numerous places, as well as slightly crushed. For these reasons, entirely delineating the sutural scar for the ascending process of the astragalus is difficult. The fibular process, or flange, is not as well developed as in *Tanycolagreus*.

Fibula (Fig. 3.11E). The proximal end of the right fibula is known for *Coelurus*. It is triangular and tapers distally. The proximal end is slightly concave. On its medial side, the sulcus, or fossa, is not very well developed, unlike in many theropods.

Tarsal (Fig. 3.12). The only tarsal element available is the right astragalus of *Coelurus*. An astragalus purportedly belonging to *Coelurus* was described by Welles and Long (1974) under its access number, YPM 1252, rather than its catalog number, YPM 9163 (Ostrom 1980). They referred to it as of the allosauroid type, noting that the ascending process does not extend the entire width of the astragalus. Although this is true, it is clear that the ascending process is incomplete and that it projected higher than they acknowledged. In fact, their reported width of 7.4 cm is at odds with our measured width of 3.2 cm. It is unfortunate that they did not figure the specimen. However, their overall description matches the astragalus in Figure 3.12; we can only assume that there is an error in their reported measurements or that there is another, larger astragalus in the Yale collections.

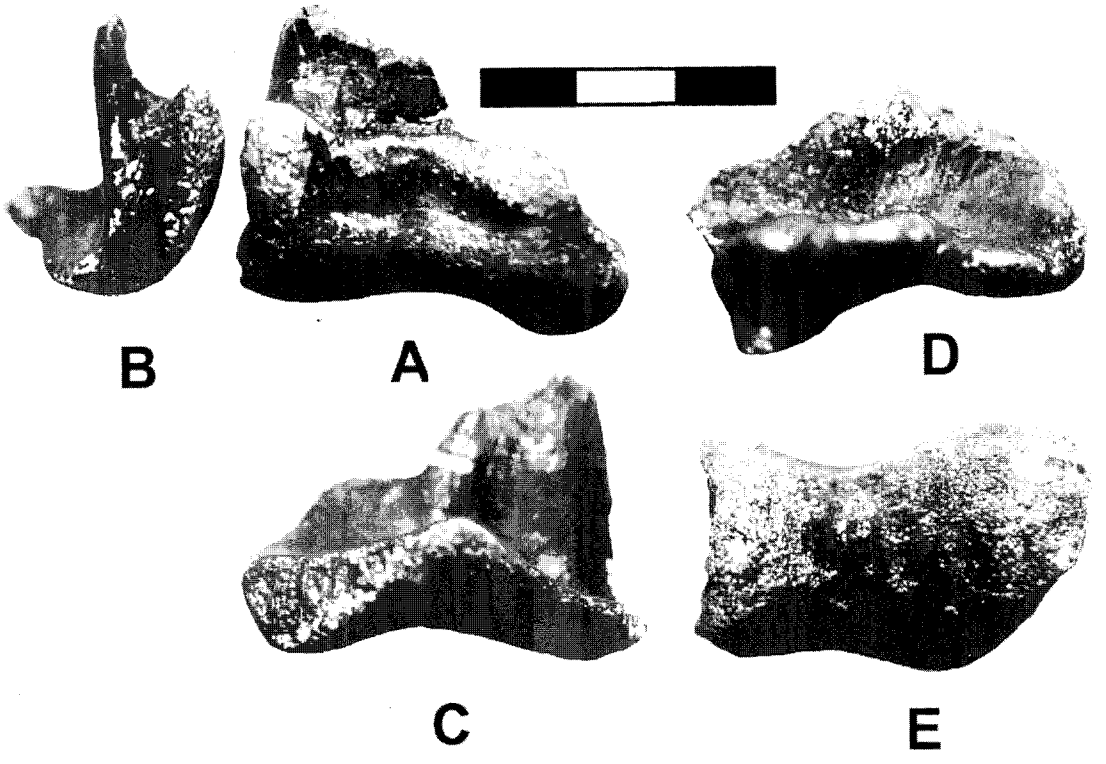

Figure 3.12. Right astragalus of Coelurus fragilis *in (A) anterior, (B) lateral, (C) posterior, (D) proximal, and (E) ventral views. Scale in cm.*

The ascending process occupies the lateral half of the astragalar body (Fig. 3.12A), and it has a prominent, wide groove separating it from a short dorsal projection from the lateral distal condyle (Fig. 3.12B); a fossa is not present at the base of the ascending process. The anterior face of the distal condyles has a shallow horizontal groove, or sulcus, extending across it (Fig. 3.12A). The facet for the calcaneum is not well developed, but it was slightly interdigitating. The condyles are oriented anteroventrally (Fig. 3.12B).

Pes (Fig. 3.13). The foot of *Ornitholestes* is represented by right metatarsals II–IV and phalanges (Fig. 3.13A,B), and that of *Coelurus* only by a left metatarsal IV and the distal end of metatarsal III (Fig. 3.13C,D). Metatarsal IV of *Ornitholestes* is distorted so that it is not appressed against metatarsal III. It is clear, however, from metatarsals II and III that originally the metatarsals were closely appressed, although not fused together. Proximally, metatarsal III is somewhat hourglass-shaped, and it separates metatarsals IV and II; metatarsal IV backs metatarsal III. Metatarsal IV (11.3 cm long) is also longer than metatarsal II (10.9 cm long) but not as long as metatarsal III (11.9 cm long). The width of the cross-section of the metatarsals is about the same as the anteroposterior length. The phalanges and unguals resemble those of other theropods.

In contrast, the only complete metatarsal of *Coelurus* is extremely long and slender and is about the same length as the femur, whereas

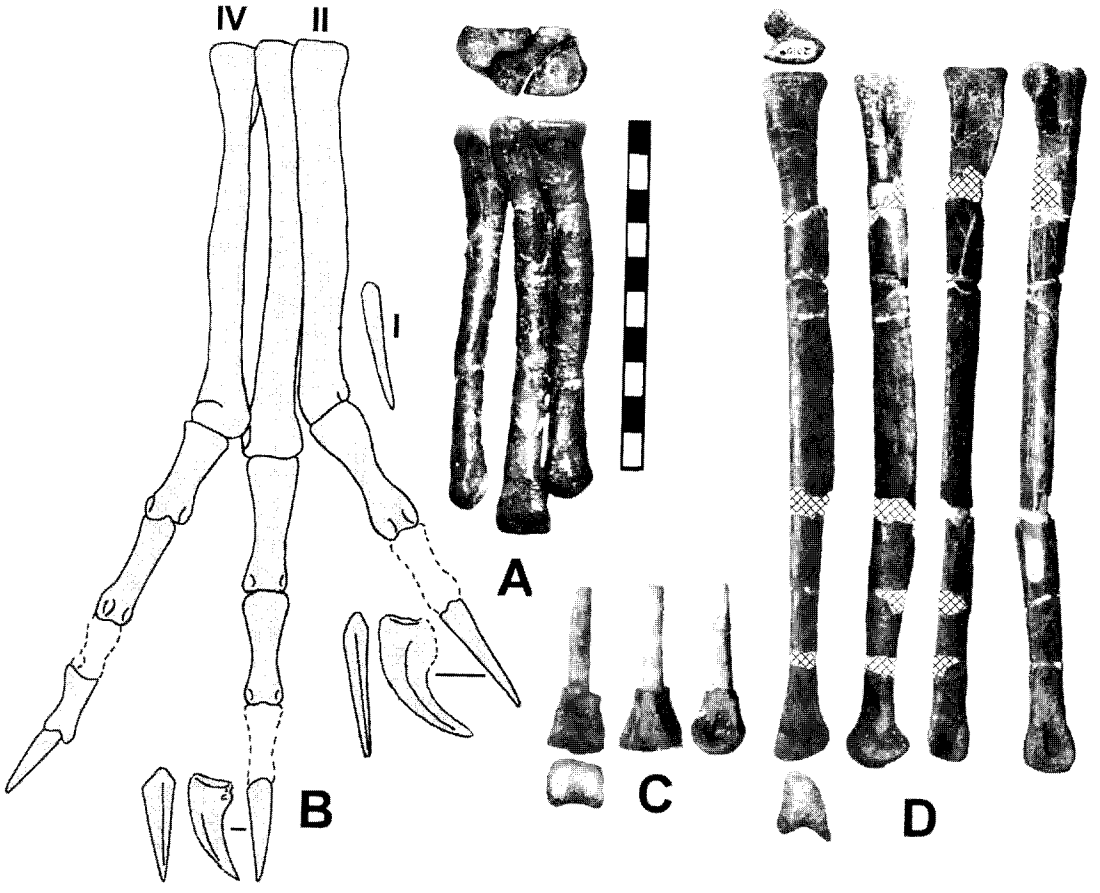

Figure 3.13. Pes elements of Ornitholestes hermanni *(A, B) and* Coelurus fragilis *(C, D). (A) Right metatarsals II–IV of* Ornitholestes *in proximal and anterior views; (B) reconstructed pes of* Ornitholestes *(adapted from an unpublished sketch by Erwin Christman); (C) distal end of metatarsal III of* Coelurus *in anterior, posterior, and lateral views; and (D) left metatarsal IV of* Coelurus *in proximal, anterior, distal, lateral, posterior, and medial views. Scale in cm.*

the length of metatarsal IV is less than 50 percent of the femur length in *Ornitholestes*. In addition, the cross-section of the metatarsal in *Coelurus* is wider than it is anteroposteriorly long.

Discussion

Small theropod remains are known from various sites in the Morrison. Some of these have been referred to *Ornitholestes* or *Coelurus* more because of size than morphology. Makovicky (1997) has identified two vertebrae in the Marsh collection that were apparently considered by Marsh as anterior *Coelurus* cervicals (we note that his "fourth cervical" is dorsoventrally crushed, as indicated by the fracture patterns on the diapophyseal lamina, and that the centrum would normally be visible in lateral view). A posterior cervical, otherwise matching these vertebrae, is also known from the Small *Stegosaurus* locality (Carpenter 1998), indicating that the geographic range of this small theropod was wider than the Como Bluff region. A long slender tibia is also known from the Small Quarry, which size-wise, seems reasonable as belonging to this as yet unnamed theropod. Because the original specimens described by Makovicky came from Quarry 9 (mam-

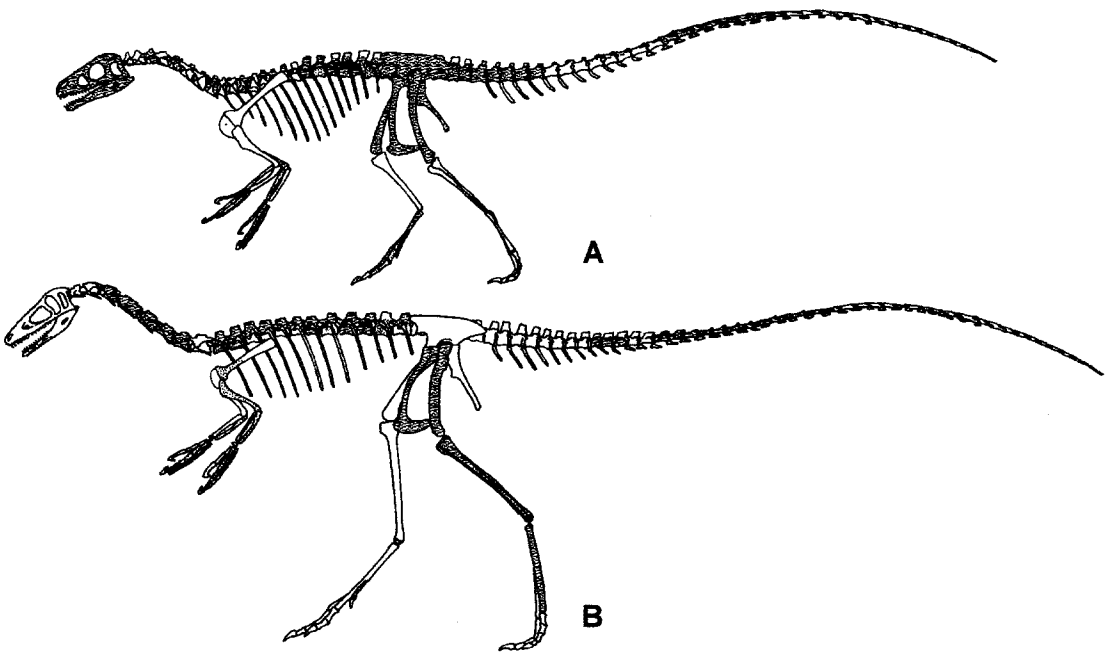

Figure 3.14. Skeletal reconstruction of Ornitholestes hermanni *(A) and* Coelurus fragilis *(B) to same femoral length. Note differences in relative proportions.*

mal quarry), it is possible that some of the small theropod bones from Quarry 9 at the National Museum of Natural History actually belong to this particular individual: USNM 5810 cervical vertebra, USNM 5809 sacral vertebra, USNM 6624 distal caudal, USNM 6625 distal caudal, USNM 6626 mid-caudal, USNM 6627 distal caudal, USNM 6628 anterior caudal, USNM 162447 right femur, and uncatalogued distal end of metatarsal.

Skeletal reconstructions for *Ornitholestes* and *Coelurus* are presented in Figure 3.14 to the same femoral length, which is actually close to being similar in the two specimens. Several important differences are readily apparent. First is that on the basis of the dentary section, the skull of *Coelurus* must have been more slender or gracile than that of *Ornitholestes*. In this, the former is more similar to that of *Mononykus* and *Compsognathus* than to the proportionally more robust skull seen in other small theropod skulls, such as *Deinonychus*. In addition, it may have also been proportionally small relative to body size, as in *Mononychus* as well. Second, the neck and body are proportionally longer in *Coelurus* than in *Ornitholestes*. This difference is due to the longer vertebrae of *Coelurus* as compared with those of *Ornitholestes* (Figs. 3.4 and 3.5). Finally, the hind leg of *Coelurus* is very long and gracile, and it more closely resembles that of *Mononykus*. This extreme long-leggedness is due to the very long metatarsal.

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ham Young University). In addition, we thank Gregory S. Paul for review comments.

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