2005. Carpenter, K. (ed). The Carnivorous Dinosaurs. Bloomington, Indiana University Press.

# 2. New Small Theropod from the Upper Jurassic Morrison Formation of Wyoming

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## Abstract

A partial skeleton from the Upper Jurassic Morrison Formation at Bone Cabin Quarry West, Wyoming, is named *Tanycolagreus topwilsoni.* The taxon is phyletically closest to *Coelurus fragilis* but differs in the absence of pleurocoels in the anterior dorsal centra and in the moderate-length prezygapophyses on the distal caudals, the straight humeral shaft, and the relative length of the metatarsals to the humerus. It differs from *Ornitholestes hermanni* from nearby Bone Cabin Quarry in the presence of a centrodiapophyseal lamina, more elongate dorsals, shorter prezygapophyses on the distal caudals, and a bowed radius. Small theropods during the Late Jurassic were clearly more diverse than previously realized.

## Introduction

Small to medium-size theropods (< ~5 m) from the Upper Jurassic (Oxfordian-Tithonian) Morrison Formation of the western United States are considerably less common and diverse than they are in the Late Cretaceous (Campanian-Maastrichtian). The difference in the number of specimens is multiple orders of magnitude and appears to be real, but research in the area is only preliminary (e.g., Chure et al. 2000;

Foster et al. 2001). The known small to medium-size theropods from the Morrison Formation include *Coelurus fragilis* Marsh 1879, *Ornitholestes hermanni* Osborn 1903, *Elaphrosaurus?* sp., *Stokesosaurus clevelandi* Madsen 1974, *Marshosaurus bicentesimus* Madsen 1976, *Koparion douglassi* Chure 1994, and the new taxon named below as *Tanycolagreus topwilsoni*. Of these taxa, *Coelurus, Ornitholestes,* and *Tanycolagreus* are known from partial skeletons, the rest from isolated bones or teeth.

*Coelurus fragilis* was named by O. C. Marsh (1879) for material recovered from Reed's Quarry 13 at Como Bluff, Wyoming. The locality was an extensive bone bed known for its numerous specimens of *Stegosaurus* and *Camptosaurus* (Gilmore 1909, 1914). In describing the specimen, Marsh emphasized the extreme hollowness of the vertebrae and illustrated three of them in 1881 (repeated again in Marsh 1896). A second species of *Coelurus, C. agilis,* was named a few years later by Marsh (1884) for a partial skeleton, of which only a pair of pubes was described and illustrated (repeated in Marsh 1896). Ostrom (1980) has concluded that *C. fragilis* and *C. agilis* are different parts of the same individual, a conclusion we agree with as well. A third species of *Coelurus, C. gracilis,* was erected by Marsh in 1888 for metapodials from the Lower Cretaceous Potomac Formation of Maryland. However, the taxon is considered a nomen dubium (Ostrom 1980); it is certainly not a species of *Coelurus*.

*Ornitholestes hermanni* was named by H. F. Osborn (1903) for a partial skeleton from Bone Cabin Quarry, north of Como Bluff. The site is also a multi-taxa bone bed, although little of the material from this quarry has been described. Osborn (1903) figured some of the *Ornitholestes* material and offered a skeletal reconstruction. The skull was figured at a later date, along with a slightly modified rendition of the skeleton (Osborn 1916). Gilmore (1920) synonymized *Ornitholestes hermanni* with *Coelurus fragilis,* arguing that the differences in the vertebrae were minor. However, as was shown by Ostrom (1980), numerous characters separate the two taxa (Carpenter et al., Chapter 3). More recently, Western Paleontological Laboratories, Inc., of Lehi, Utah, renewed excavation a few tens of meters west of Bone Cabin Quarry, calling their site Bone Cabin Quarry West (BCQ West; Miles and Hamblin 1999). Among the numerous specimens found was a partial theropod skeleton collected in 1995 (Fig. 2.1), originally identified as *Coelurus fragilis* (Miles et al. 1998). However, a comparison with the holotype material of *C. fragilis* demonstrated that the BCQ West specimen was of a new taxon, described below as *Tanycolagreus topwilsoni*.

Other small theropods from the Morrison are based on a few isolated bones. *Stokesosaurus clevelandi* was named by Madsen (1974) for an ilium from the Cleveland-Lloyd Quarry. The ilium is characterized by a prominent vertical ridge on the lateral surface just dorsal to the acetabulum. Another ilium and a premaxilla were also referred to this taxon; however, as will be shown below, the premaxilla is referable to *Tanycolagreus*. *Marshosaurus bicentesimus* was also named by

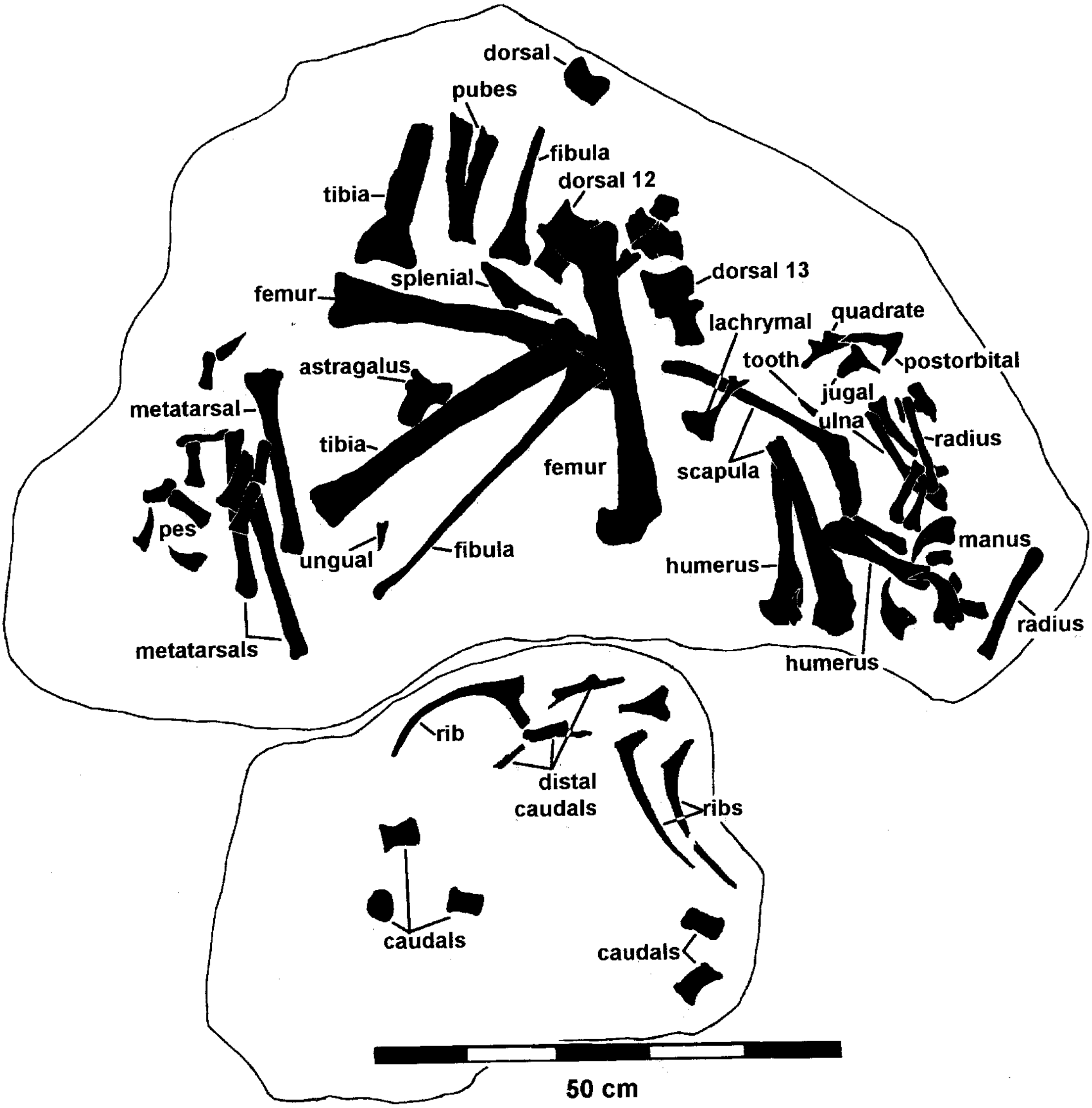



*Figure 2.1. Distribution of the holotype skeleton of* Tanycolagreus topwilsoni *as uncovered in the field jackets (outline).*

Madsen (1976) for an ilium from the Cleveland-Lloyd Quarry; a premaxilla, several maxillae, ilia, pubes, and ischia were also referred to this taxon. An *Elaphrosaurus* sp. was identified in the Morrison Formation by Peter Galton (1982) from a humerus collected at Felch Quarry 1 and from a tibia from the Small Quarry described by Dan Chure (2001). *Elaphrosaurus* was originally described from a partial skeleton from the Tendaguru Formation of Tanzania (Janensch 1925). Russell (1972) suggested that the pubes of *Coelurus agilis* were very similar to those of *Elaphrosaurus,* and later referred to the species as *Elaphrosaurus agilis* (Russell et al. 1980). Russell was apparently not aware that the holotype of *C. agilis* consisted of a partial skeleton, parts of which make the synonymy untenable (Galton 1982).

Chure (1994) named a tooth from Dinosaur National Monument *Koparion douglassi* and considered it the oldest troodontid (although its status as such has yet to be verified). Nothing of the rest of the skeleton is known. Another small theropod is known only from cervical vertebrae from Quarry 9; Ostrom (1980) listed it as *Coelurus,* but Makovicky (1997) demonstrated that it belongs to a different, unnamed taxon, a point with which we agree. Additional specimens of this unnamed taxon probably include the vertebrae from Quarry 9 listed by Gilmore (1920) as *Coelurus agilis,* as well as two vertebrae from the Small Quarry at Cañon City (Carpenter, unpublished).

Numerous isolated, small to medium theropod bones occur in most collections from the Morrison Formation (Carpenter, notes), suggesting that these theropods were more diverse than previously recognized. The main collections are held at the Earth Science Museum of Brigham Young University, the Denver Museum of Natural History, the Yale Peabody Museum of Natural History, and the National Museum of Natural History. Although some of the specimens are of juveniles of known large adults, others cannot be referred to any of the recognized small to medium-size theropods.

*Institutional Abbreviations.* AMNH, American Museum of Natural History, New York; TPII, Thanksgiving Point Institute, Inc. (North American Museum of Ancient Life), Lehi, Utah; UMNH, Utah Museum of Natural History, Salt Lake City, Utah; YPM, Yale Peabody Museum of Natural History, New Haven, Conn.

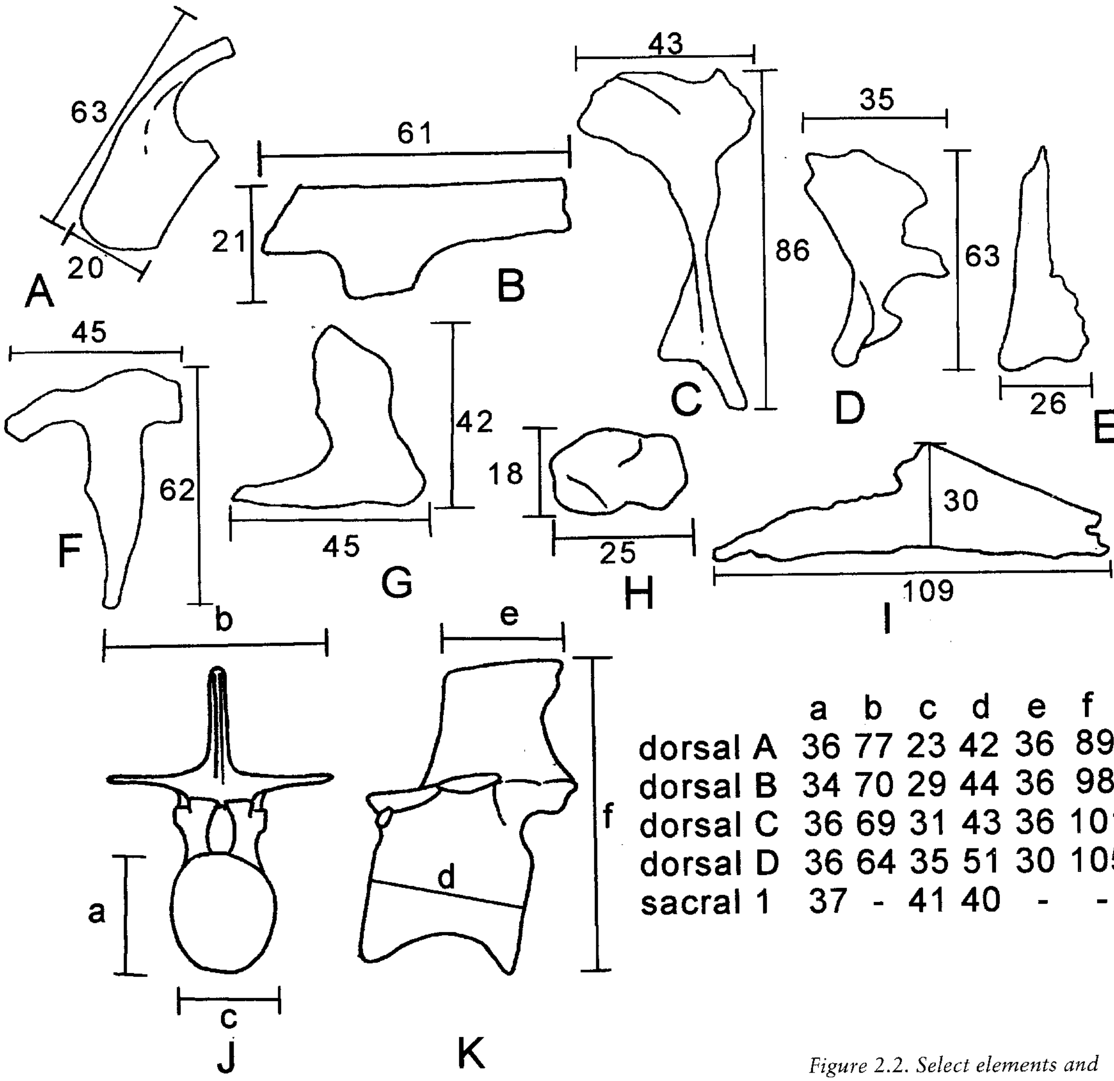
## Systematic Paleontology

Order Theropoda
Maniraptora
Coeluridae
*Tanycolagreus* n. g.

*Etymology.* From Greek *tany-* "long, stretched out" + Greek *kolon* "limb" + Greek *agreus* "hunter."

*Diagnosis.* As for the species.

*Holotype.* TPII 2000-09-29, partial skeleton including left premaxilla, premaxillary tooth, left partial nasal, left lachrymal, left postorbital, left quadratojugal, right quadrate, left squamosal fragment, right splenial, left articular, two cheek teeth, two anterior dorsal centra, four complete posterior-most dorsals, first sacral centrum, two anterior caudal centra, two mid-caudal centra, three distal caudals, fourteen ribs, seven chevrons, gastralia fragments, left and right scapula and coracoid, left and right humeri, left and right ulnae, left and right radii, left capalia and ulnare, right and left mani, distal half of paired pubes, left and right femur, left and right tibiae, proximal half of left fibula, right fibula, right astragalus and calcaneum, right metatarsals I–V, complete right foot. Measurements of select bones are given in Figures 2.2 and 2.3. A cast of this specimen is also housed at the Denver Museum of Nature and Science.




| | a | b | c | d | e | f |
|---|---|---|---|---|---|---|
| dorsal A | 36 | 77 | 23 | 42 | 36 | 89 |
| dorsal B | 34 | 70 | 29 | 44 | 36 | 98 |
| dorsal C | 36 | 69 | 31 | 43 | 36 | 101 |
| dorsal D | 36 | 64 | 35 | 51 | 30 | 105 |
| sacral 1 | 37 | - | 41 | 40 | - | - |

*Figure 2.2. Select elements and their measurements (in mm) for the holotype* Tanycolagreus topwilsoni *(TPII 2000-09-29). Compare with Figures 2.4 and 2.7. (A) Premaxilla, (B) nasal, (C) lachrymal, (D, E) quadrate in lateral and posterior views, (F) postorbital, (G) quadratojugal, (H) articular in dorsal view, (I) splenial, and (J, K) dorsal in anterior and posterior views (measurements of best vertebrae given in the table). Not to scale.*

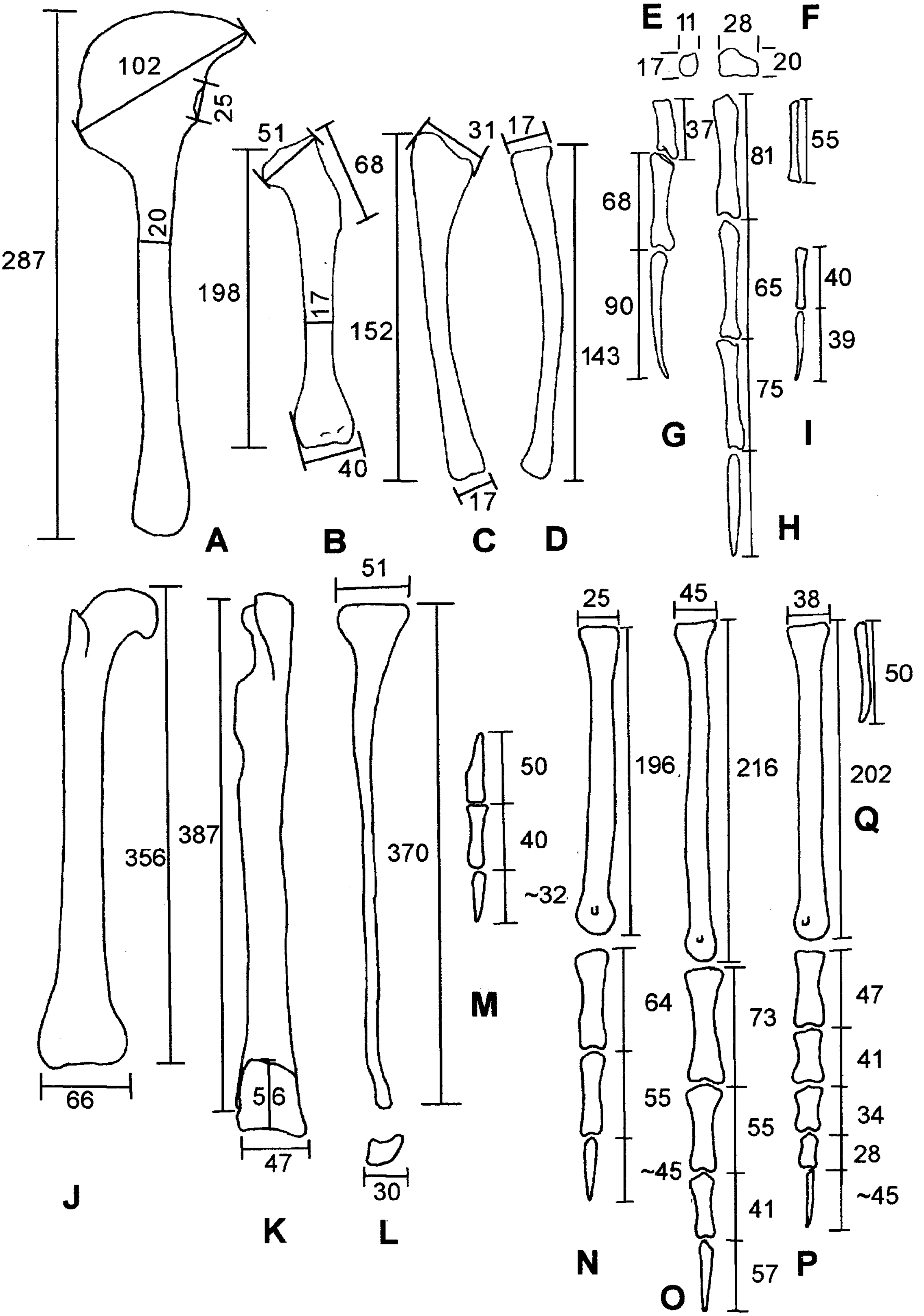
*Tanycolagreus topwilsoni* n. sp.

*Ornitholestes hermanni (in part)*

*Stokesosaurus clevelandi (in part)*

*Etymology.* Named for George "Top" Wilson, retired, United States Marine Corps.

*Diagnosis.* Medium-size tetanuran having short, deep-bodied premaxilla pierced by narial foramen at base of nasal process, orbital process on postorbital, T-shaped quadratojugal, centrodiapophyseal lamina on dorsals. Differs from *Coelurus* in the absence of pleurocoel on anterior dorsals; posterior caudal prezygapophyses elongated to one-third centrum length, rather than short; straight, rather than sigmoidal, humeral shaft; bowed, rather than straight, radius; flat-bottomed rather than arced pubic foot; straight rather than sigmoidal



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femoral shaft; metatarsal length subequal to humeral length, rather than 1.75 times humeral length. Differs from *Ornitholestes* in straight anterior margin of premaxilla, rather than rounded; T-shaped rather than L-shaped quadratojugal; elongate neural spine that overhangs centrum, rather than short neural spine; posterior caudal prezygapophyses only one-third centrum length, rather than one-half centrum length; bowed, slender radius, rather than straight, robust radius.

*Type Locality.* Morrison Formation, Bone Cabin Quarry West, Albany County, Wyoming.

*Paratypes.* AMNH 587, partial manus previously referred to *Ornitholestes hermanni* from Bone Cabin Quarry, Albany County, Wyoming. UMNH 7821 (formerly UUVP 2999), premaxilla previously referred to *Stokesosaurus clevelandi* from the Cleveland-Lloyd Quarry, Emery County, Utah.

## Description

### *Cranial*

The skull of *Tanycolagreus* is known only from a few elements: left premaxilla, premaxillary tooth, left nasal, left lachrymal, left postorbital, left quadratojugal, right quadrate, left squamosal fragment, left articular, right splenial, and two cheek teeth (Fig. 2.4). Unfortunately, nothing of the skull roof or braincase has been found. The tentative reconstruction of the skull presented in Figure 2.5 is long and low as is typical of small to medium-size theropods (i.e., non-"carnosaurian"). Comparisons to the skull of *Ornitholestes* are based on a cast of the skull (YPM 53262). A detailed description of the *Ornitholestes* skull is in development by Mark Norell (AMNH) following additional preparation of this specimen.

*Premaxilla.* The premaxilla is very deep and very short anteroposteriorly (Fig. 2.4A–C) and is similar to that referred to as "*Stokesosaurus clevelandi*" by Madsen (1974) (see Fig. 2.6A–C). Both are anteroposteriorly short and deep, although these need not imply an extremely short-snouted skull as envisioned by Madsen (1974) (see Fig. 2.5). There are four subrectangular alveoli, and the one damaged premaxillary tooth present (Fig. 2.4D) has the asymmetrical cross-section typical of theropods. On the external surface, the narial fossa extends from the external nares onto the lateral surface and is pierced by the narial foramen at the base of the nasal process (Figs. 2.4A, 2.6A,D). The placement of such a foramen is unusual in the theropods. Just dorsal to the dental margin is a series of shallow vertical grooves for the blood vessels and facial nerves to the now missing soft tissue. The narial process is thin and short, and it gently curves dorsoposteriorly. Along the posterior margin of the premaxilla, the maxillary suture extends as a shallow vertical groove that is pierced by a deep fossa (Fig. 2.6B,E). The sutural groove extends more dorsally than as described by Madsen in "*Stokesosaurus clevelandi*" because the groove is damaged in the latter specimen (Fig. 2.4B). On the medial side (Figs. 2.4C, 2.6C,F), the sutural surface for the right premaxilla is a smooth,

*(Opposite page)*
*Figure 2.3. Select elements and their measurements (in mm) for the holotype* Tanycolagreus topwilsoni *(TPII 2000-09-29). (A) Scapulocoracoid, (B) humerus, (C) ulna, (D) radius, (E) semilunate, (F) distal carpal, (G) manus digit I (H) manus digit II, (I) manus digit III, (J) femur, (K) tibia and astragalus, (L) fibula and calcaneum, (M) pes digit I, (N) pes digit II, (O) pes digit III, (P) pes digit IV, and (Q) metacarpal V. Not to scale.*

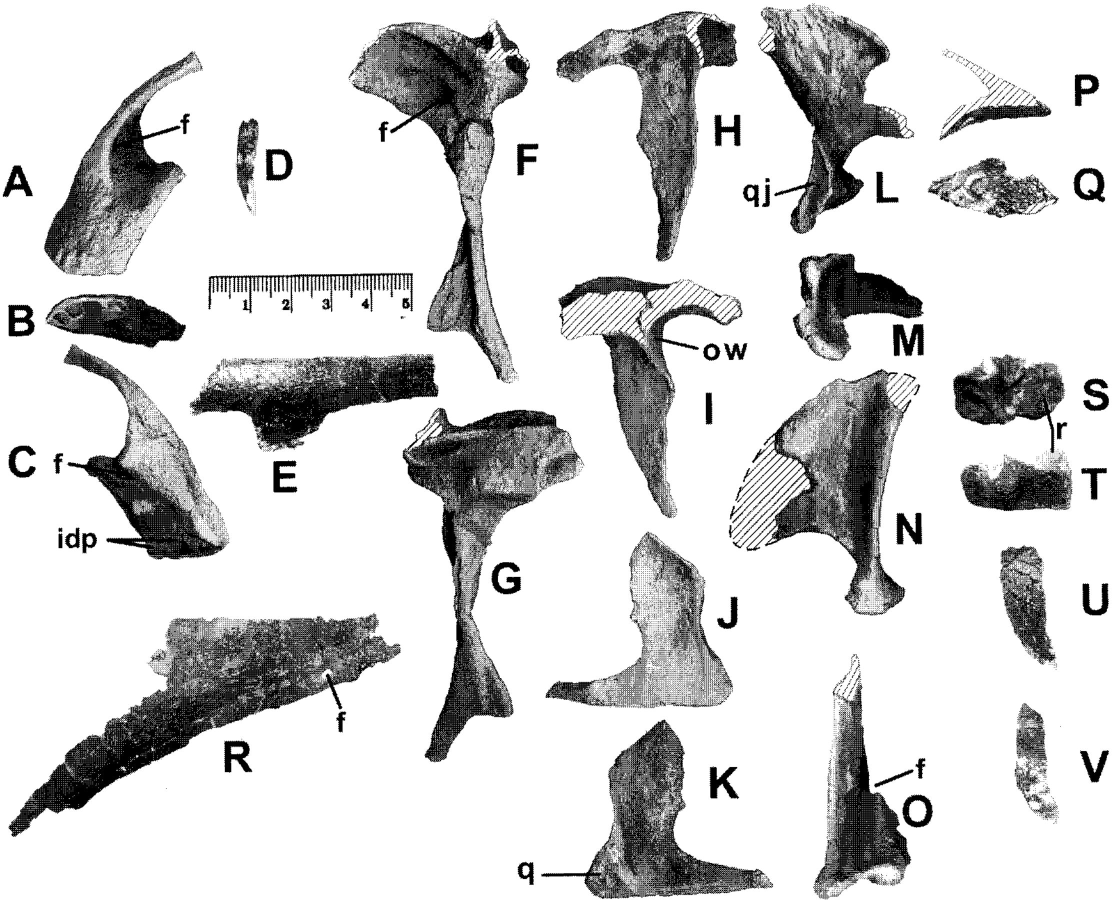
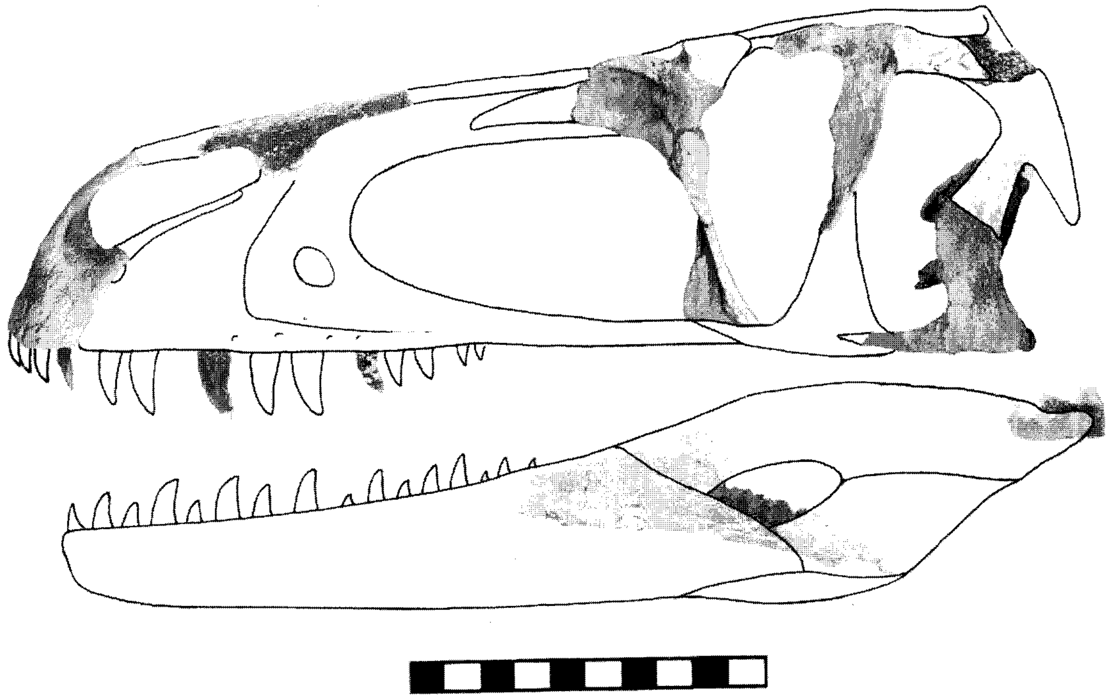



*Figure 2.4. Cranial elements of the holotype* Tanycolagreus topwilsoni *(TPII 2000-09-29). Left premaxilla in lateral (A), occlussal, showing the alveoli (B), and medial (C) views. Premaxillary tooth in lateral view (D). Partial nasal in dorsal view (E). Left lacrimal in lateral (F) and medial (G) views. Left postorbital in lateral (H) and medial (I) views. Left quadratojugal in lateral (J) and medial (K) views. Right quadrate in lateral (L), ventral (M), medial (N), and posterior (O) views. Left squamosal fragment in dorsal (P) and lateral (Q) views. Right splenial (R). Left articular in dorsal (S) and lateral (T) views.*
*(continued on page 31)*

inverted triangle, the widest part being at the level of the external nares. The sutural surface extends to the level of the tooth row, indicating that a subnarial gap was not present. The angle formed by the surface of the symphyseal and the lateral surface is very low, indicating that united, the two premaxillae would form a V shape in ventral view. A large foramen, which Madsen (1974) has referred to as the foramen for the facial nerve, pierces the body of the premaxilla medially below the external nares (Fig. 2.6C,F). Ventral to the foramen is the short, triangular maxillary process, or ala, to which the medial premaxillary process of the maxilla articulates. This ala is unlike the well-developed prong or strap seen in large theropods, such as *Allosaurus* or *Sinraptor* (Currie and Zhao 1993). The interdental plates of both specimens of *Tanycolagreus* are slightly damaged, but enough remains to show that they are fused to each other.

*Nasal.* Most of the left nasal is preserved in the holotype, although it is damaged at each end (Fig. 2.4E). The element is slightly curved along its length. The medial edge is flat for contact with the other nasal. The descending, or ventral, process, which forms the posterior margin



of the external nares, is incomplete; thus it is not known whether the process contacted the premaxilla ventral to the external nares.

*Lachrymal.* The left lachrymal is nearly complete, except for the tip of the horizontal ramus and a small portion of the posterodorsal suture to the prefrontal (Fig. 2.4F,G). The horizontal ramus is deep, and the dorsal margin is arcuate, with a ridge extending its length (seen best on the medial side, Fig. 2.4G); there is no lachrymal horn. Unfortunately, the length of the ramus is unknown, although about half of the anterior portion is believed to be missing. The dorsal surface is relatively wide, indicating that the lachrymal was broadly exposed on the skull roof. The lateral surface of the horizontal ramus contains a large oval depression, the lachrymal fossa, which contains the smaller lachrymal fenestra (Fig. 2.4F). A short ridge occupies the middle of the fossa, effectively dividing the fossa horizontally. The ridge connects the floor of the fossa with the posterior rim of the fossa. The lachrymal fenestra pierces the lachrymal just posteroventral to this ridge. On the medial side, the horizontal ramus has sutures along the posterior portion for the prefrontal, and along the anterodorsal portion for the nasal (Fig. 2.4G). The prefrontal suture extends upward on a short spur of damaged bone. A slight notch along the ventral margin of the horizontal ramus coincides with a very shallow depression on the medial side. These features probably denote the suture for the posterodorsal-most portion of the dorsal ramus of the maxilla (Fig. 2.4F,G; compare with Fig. 2.5). The ventral, or vertical, ramus of the lachrymal is constricted in the

*(continued from page 30)*
*Maxillary teeth (U, V). Scale in mm. Abbreviations: (A) f—foramen at the base of the ascending or nasal process; (C) f—large foramen, idp—interdental plates; (F) f—lacrimal foramen; (I) ow—orbital wall; (K) q—suture for the quadrate; (L) qj—suture for the quadratojugal; (O) f—part of the quadrate foramen; (R)—small splenial foramen; (S, T) r—retroarticular process.*

*(Above)*
*Figure 2.5. Restoration of the skull of* Tanycolagreus. *Parts of the squamosal, articular, and splenial hidden by other (missing) bones are shown faintly. Scale in mm.*

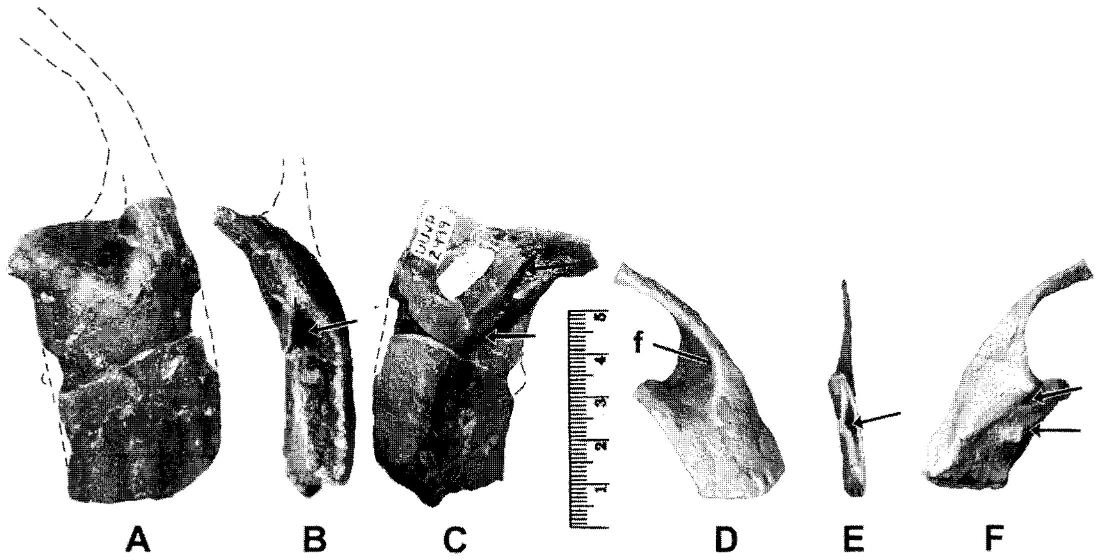



*Figure 2.6. Comparison of the premaxillae of* Tanycolagreus topwilsoni. *(A–C) specimen referred to* "Stokesosaurus clevelandi" *(UMNH 7821) with that of the holotype of* Tanycolagreus topwilsoni *(TPII 2000-09-29) (reversed). Lateral (A, D), posterior (B, E), and medial (C, F) views. In the posterior views (B, E), note the deep fossa within the sutural surface for the maxilla (arrow). Note the paired foramina (arrows) on the medial surface (F). The medial ala, which receives the medial premaxillary process from the maxilla, is damaged in UMNH 7821. Scale in mm. Abbreviation: (D) f—foramen.*

middle, giving it an hourglass shape; it does not have an orbital projection. The ramus is pierced anteroposteriorly by a foramen at its narrowest point, thus connecting the antorbital fenestra with the orbit. The lachrymal is thickest along the orbital border.

*Postorbital.* The postorbital is a T-shaped bone and has a shallow fossa on the external surface (Fig. 2.4H) that may be due to crushing. The horizontal process is incomplete posteriorly and on its medial side, whereas the vertical process is complete (Fig. 2.4I). The horizontal process apparently excluded all except perhaps a small portion of the frontals from the orbital rim. The external surface of the process is smooth, lacking any prominences. Medially, there is a small posterior orbital wall at the junction between the horizontal and vertical processes. The vertical process has a slight orbital projection that would form a slight constriction of the orbit (Fig. 2.5). This feature has previously been suggested as characteristic of large-headed theropods by Chure (1998). The vertical process is longer anteroposteriorly than it is wide. Distally, the ventral process has an oblique suture for the jugal.

*Squamosal.* Most of the squamosal is damaged (Fig. 2.4P,Q), but enough remains to show that in dorsal view it tapered into a V shape posteriorly, rather than a broad U shape as in *Allosaurus* and other large theropods.

*Quadratojugal.* The left quadratojugal is complete, L-shaped, and as tall as it is long (Fig. 2.4J,K); it is not fused to the quadrate. The horizontal jugal process is vertically narrow and projects nearly straight. In contrast, the horizontal squamosal process is slightly arcuate posteriorly, and it slightly widens dorsally. The sutural surface for the squamosal is broad and sloped posteriorly at about 50° relative to the vertical axis. The quadratojugal forms the lateral wall of the quadrate foramen.

*Quadrate.* The right quadrate is nearly complete, lacking only a portion of the pterygoid process and squamosal condyle (Fig. 2.4L–O); the quadrate is not pneumatic. It is slightly arced posteriorly to accommodate the tympanic membrane. On the lateral surface, the facet for the quadratojugal is very prominent and is slightly expanded anteriorly to provide an immoveable suture. The dorsal rim delineates the ventral border of the quadrate foramen (Fig. 2.4O). The foramen is relatively large and walled laterally by the quadratojugal. The pterygoid process apparently arced ventrally, as indicated by the preserved portions (Fig. 2.4N). The posterior face of the quadrate (Fig. 2.4O) is triangular, with a notch for the quadrate foramen located about mid-height on the lateral margin. Distally, the medial mandibular condyle is expanded medially and posteriorly (Fig. 2.4O,N). The medial and lateral condylar surfaces are slightly damaged, the medial one more so. Nevertheless, it is clear that they have an hourglass shape in ventral view (Fig. 2.4M). The two condyles are separated by a slight, oblique groove as in other theropods.

*Splenial.* The splenial is slightly damaged, lacking most of the dorsoposterior process (Fig. 2.4R). Overall, it is shaped like an isosceles triangle. A small foramen pierces the splenial near its anteroventral border.

*Articular.* The articular is a small, rectangular block in dorsal view (Fig. 2.4S). The facets for the quadrate condyles are separated from each other by a low, oblique ridge, which accommodates the groove between the lateral and medial condyles of the quadrate. The retroarticular process is short and vertical (Fig. 2.4T).

*Cheek Teeth.* Two crushed maxillary or dentary teeth are present (Fig. 2.4U,V) but are so damaged that not even the serrations are preserved.

### *Vertebrae*

The vertebrae consist of two anterior dorsal centra, four complete posterior-most dorsals, the first sacral centrum, two anterior caudal centra, two mid-caudal centra, and three distal caudals (Fig. 2.7).

*Dorsals.* The anterior dorsals consist only of the centra, and the neural arches are not fused, indicating that the individual was not fully mature. One of the centra is a parallelogram, with the posterior articular surface lower than the anterior. All of the centra have slightly amphicoelous articular surfaces. The centra are also strongly constricted in the middle, so as to have an hourglass shape in ventral view. In cross-section, the centra are taller than they are wide. The lateral surfaces do not have a pleurocoel; instead they have a shallow, anteroposteriorly elongated fossa, termed pleurofossa ("side fossa") by Carpenter and Tidwell (in press). A representative complete dorsal is presented in Figure 2.7A–D. The suture between the neural arch and centra is visible on most of the dorsals, or else is visible as a faint line. Ventrally, the centra have short parallel ridges near their ends, produced by the ventral horizontal ligament. The capitular facets for the ribs are located just ventrolateral to the prezygapophyses and are connected to the transverse process by a thin paradiapophyseal lamina.

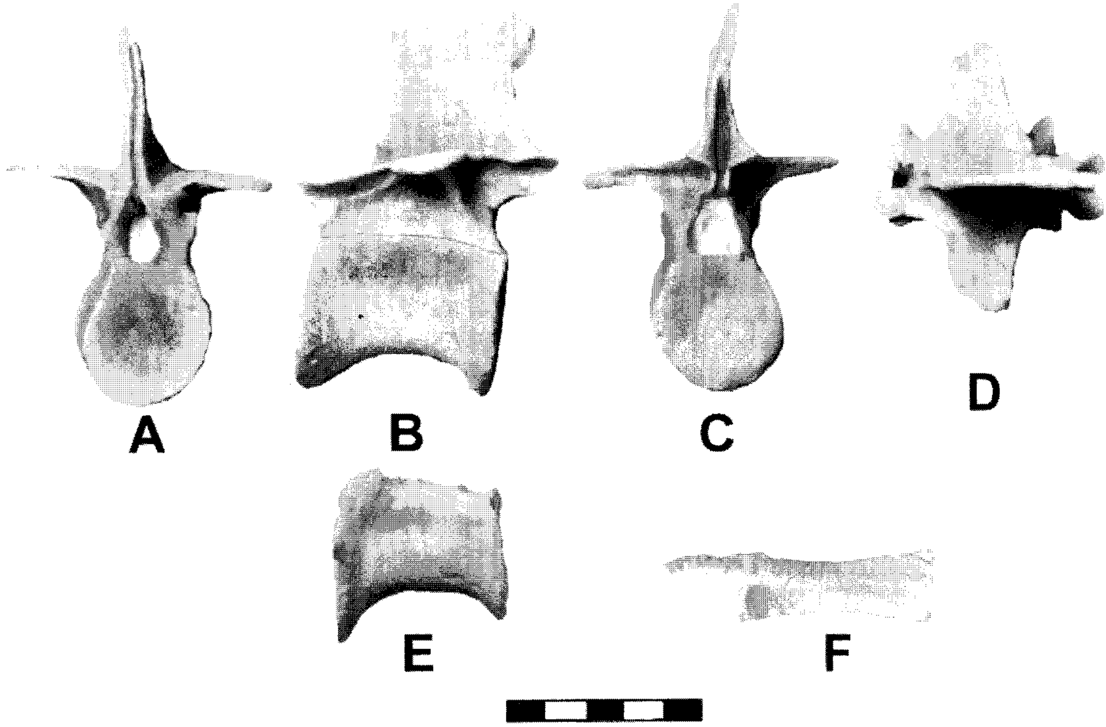



*Figure 2.7. Vertebrae of* Tanycolagreus topwilsoni *(TPII 2000-09-29) Representative posterior dorsal in anterior (A), left lateral (B), posterior (C), and dorsal (D) views. First sacral centrum (E) and distal caudal (F). Scale in cm.*

This lamina is almost non-existent on the anterior-most dorsal (9? 10?) and is most prominently developed on the last dorsal (13? 14?). The neural spines are about the same height as the centra and are simple vertical blades. The groove for the interspinous ligaments extends almost to the top of the spines. The transverse processes vary considerably. The anterior-most complete dorsal (9? 10?) has triangular, posteriorly directed processes that are angled dorsally about 10°. The other dorsals all have laterally directed, horizontal processes that are subrectangular in dorsal view. A well-developed centrodiapophysis is present, connecting the transverse process with the centrum. The postzygapophyses overhang the posterior end of the centra. Well-developed hyposphene-hypantrum accessory articulations are present.

*Sacral.* The sacral (Fig. 2.7E) is slightly procoelus, with the anterior surface concave and the center of the posterior surface very slightly convex. The height of the posterior articular surface is about three-quarters the height of the anterior surface as measured from the neural canal. The floor of the neural canal is hourglass-shaped and has a deep trough. Like the dorsals, the centrum has a pleurofossa, is hourglass-shaped in ventral view, and has scars for the ventral horizontal ligament.

*Caudals.* The anterior and mid-caudal centra are constricted laterally, so are hourglass-shaped in ventral view. They also have pleurofossa, although these are not as prominent as those on the dorsals or sacral; ventral horizontal ligament scars are also present. The posterior caudals are elongated, being about 140 percent longer than the anterior

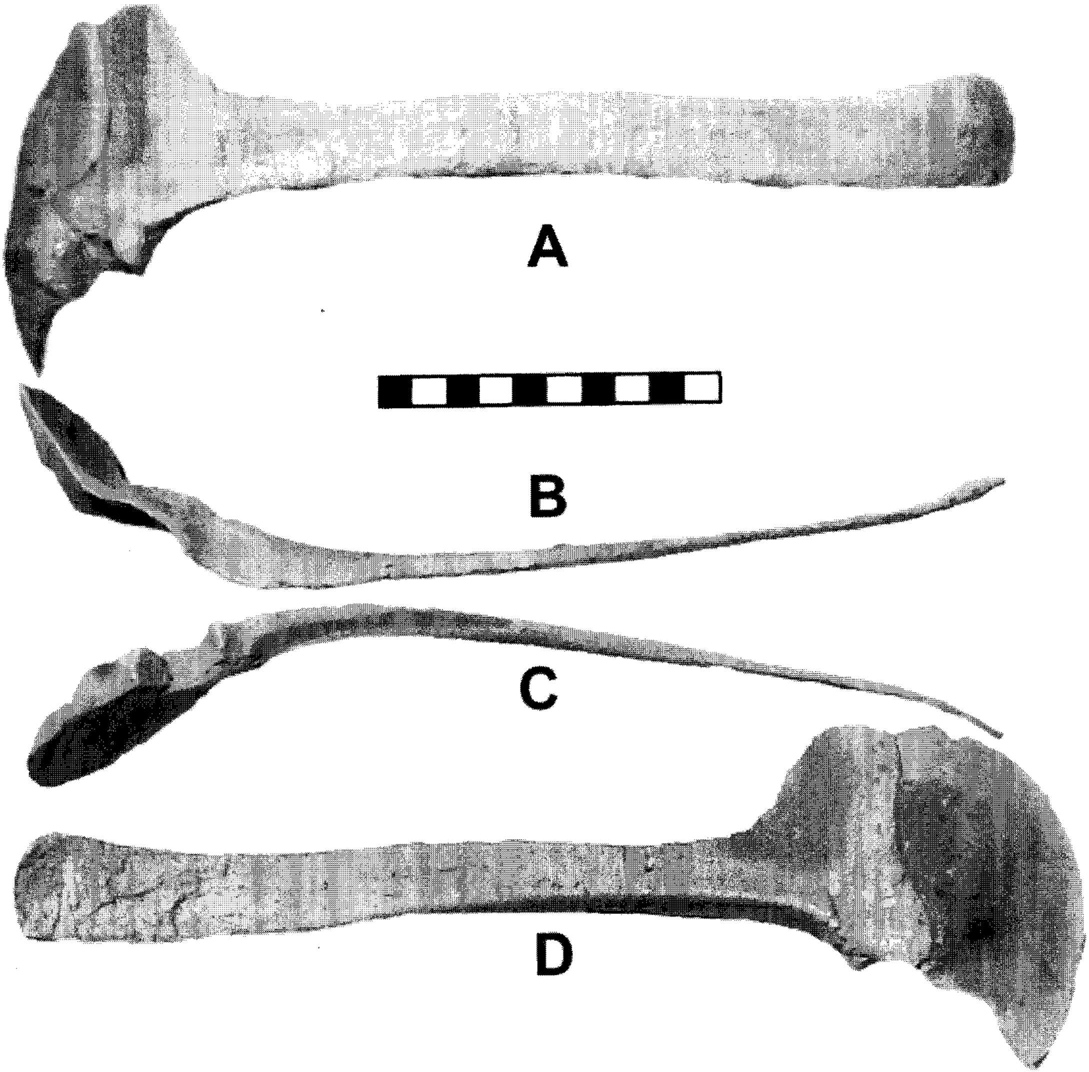



*Figure 2.8. Left scapulocoracoid of* Tanycolagreus topwilsoni *(TPII 2000-09-29) in lateral (A), dorsal (B), ventral (C), and medial (D) views. Sutural contact between the scapula and coracoid has been digitally enhanced. Scale in cm.*

centra. The centra are laterally compressed and have a pair of parallel ridges connecting the anterior and posterior chevron facets. Although the prezygapophyses are long, they do not extend beyond half a centrum length.

*Ribs* (not illustrated). Fourteen complete and partial ribs are present. They are long and slender but otherwise lack any distinctive features.

*Chevrons* (not illustrated). Seven complete or nearly complete anterior and mid-caudal chevrons are present. They are long, slender blades, but they lack any unique features.

*Gastralia* (not illustrated). Several rod-like fragments are thought to be those of gastralia. Unfortunately, they are too incomplete to be diagnostic. A furculum has not been recognized among the fragments.

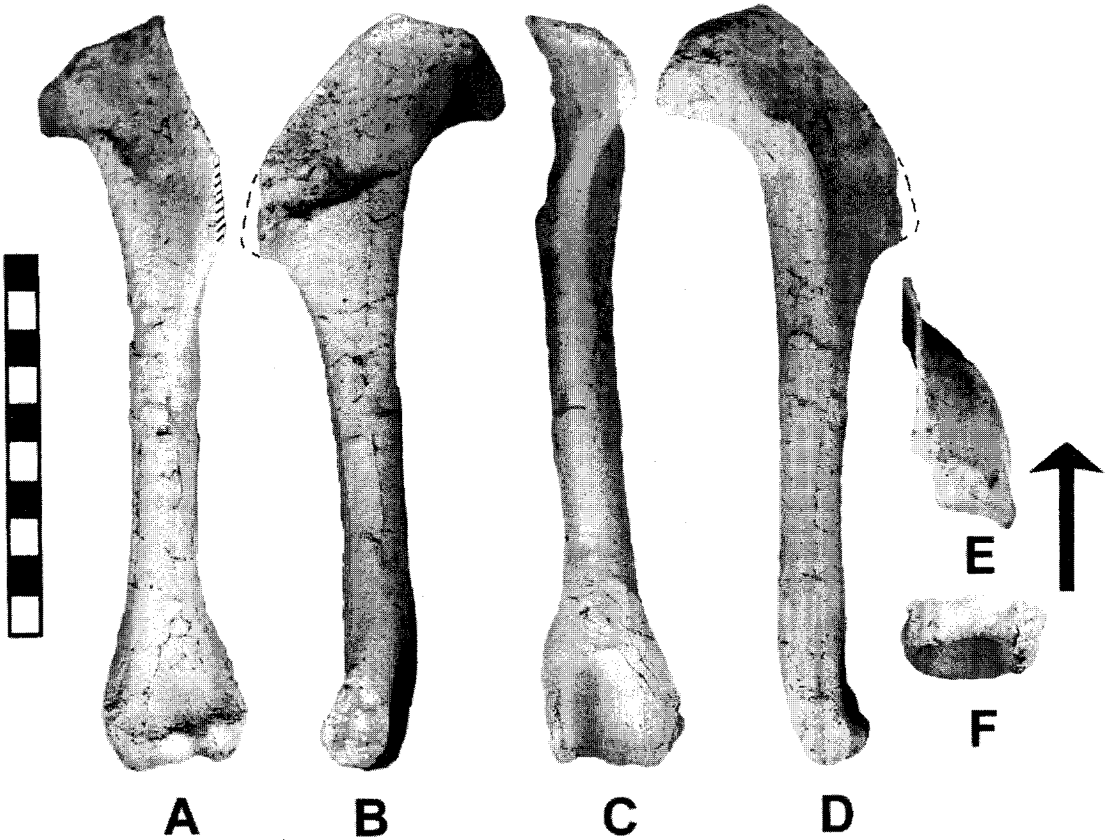



*Figure 2.9. Left humerus of* Tanycolagreus topwilsoni *(TPII 2000-09-29) in anterior (A), lateral (B), posterior (C), medial (D), proximal (E), and distal (F) views. Arrow indicates anterior for E and F. Scale in cm.*

### *Forelimb*

*Scapula* (Fig. 2.8). The scapula is long, and strap-like, with a length almost ten times the mid-shaft vertical height; the distal end is very slightly expanded. The blade is bowed medially just below the posterior edge of the acromion. The acromion is very large, and its height is almost twice the vertical height of the scapular blade at mid-shaft. Its posterior margin is sloped to the scapular blade. There is a slight notch developed between the dorsal margin of the acromion and the coracoid. The length of the scapular portion of the glenoid is twice the length of the coracoid portion, and the glenoid faces ventroposteriorly.

*Coracoid* (Fig. 2.8). The coracoid is large and attached to the scapula, although the suture between them is visible. In profile, the coracoid is over twice as tall as it is anteroposteriorly long. The ventral process is long, although only about as long as the glenoid. The coracoid protuberance (wrongly called the biceps tubercle) is well developed and may be an artifact caused by the coracobrachialis and supercoracoideus (Carpenter 2002). This feature is developed opposite a fossa on the medial side (compare Figs. 2.8A and D). In ventral view, the angle between the coracoid and scapula at the glenoid is about 30°.

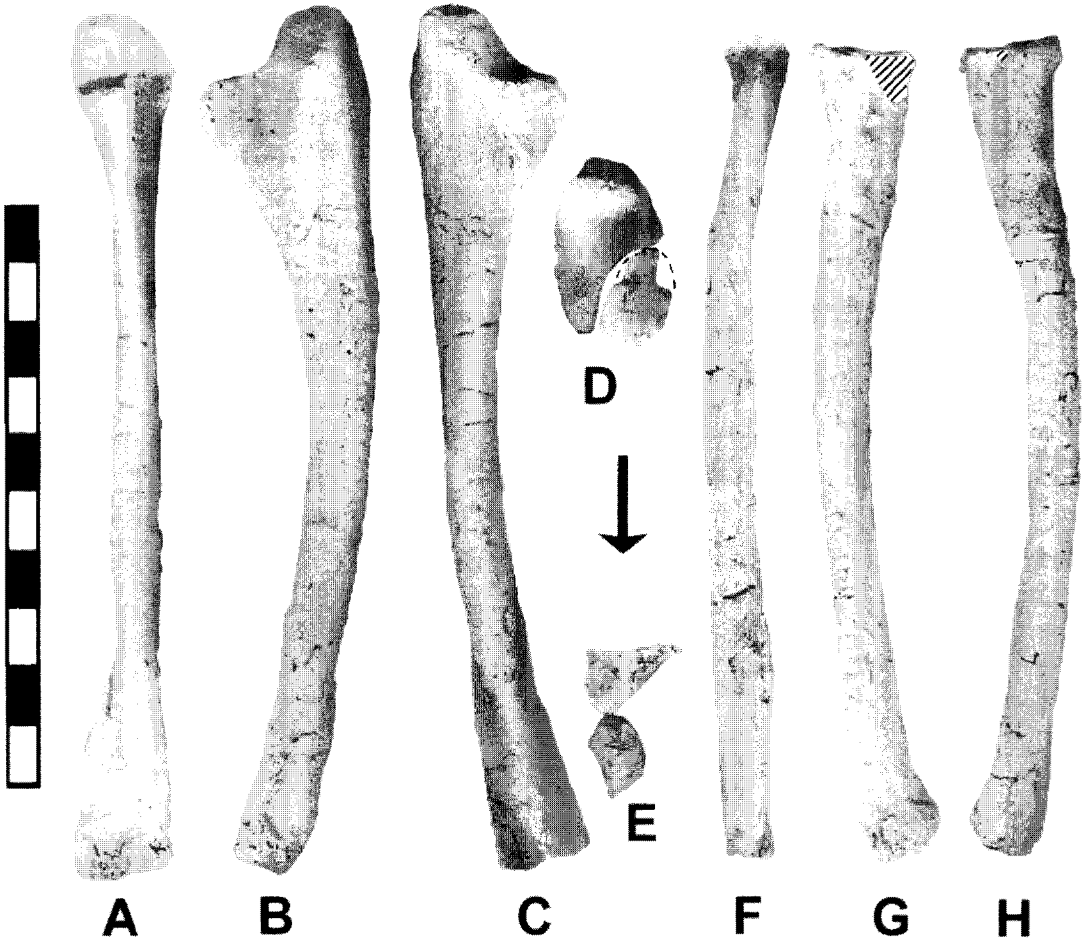



*Figure 2.10. Forelimb elements of* Tanycolagreus topwilsoni *(TPII 2000-09-29). Left ulna in anterior (A), lateral (B), and medial (C) views. Ulna and radius in articulation proximal (D) and distal (E) views (arrow points anteriorly). Left radius in anterior (F), lateral (G), and medial (H) views. Scale in cm.*

*Humerus* (Fig. 2.9). The humerus is straight shafted, although humeral torsion is present, so that the distal end is about 45° relative to the proximal end. The diameters of the proximal and distal ends are over twice the mid-shaft diameter. The humeral head is not well developed, and it is confluent with the medial (=internal) tuberosity and the deltopectoral crest. The medial tuberosity is a triangular process that projects ventromedially, and slightly posteriorly. It is separated from the humeral head by a shallow groove. The deltopectoral crest is expanded anteriorly (Fig. 2.9E) and offset from the shaft in profile (Fig. 2.9D). On the basis of the right humerus, the deltopectoral crest is triangular in profile. The distal condyles are developed on the anterior and ventral surfaces of the shaft. The medial condyle, or entepicondyle, is well developed and is as prominent as the lateral condyle. A shallow ulnar fossa is present dorsal of the lateral condyle, and it extends ventrally toward the notch between the two condyles. On the posterior side, the olecranon fossa is broad and triangular; it is deepest near the lateral margin and shallows medially. Ventrally, it merges with the medial condyle.

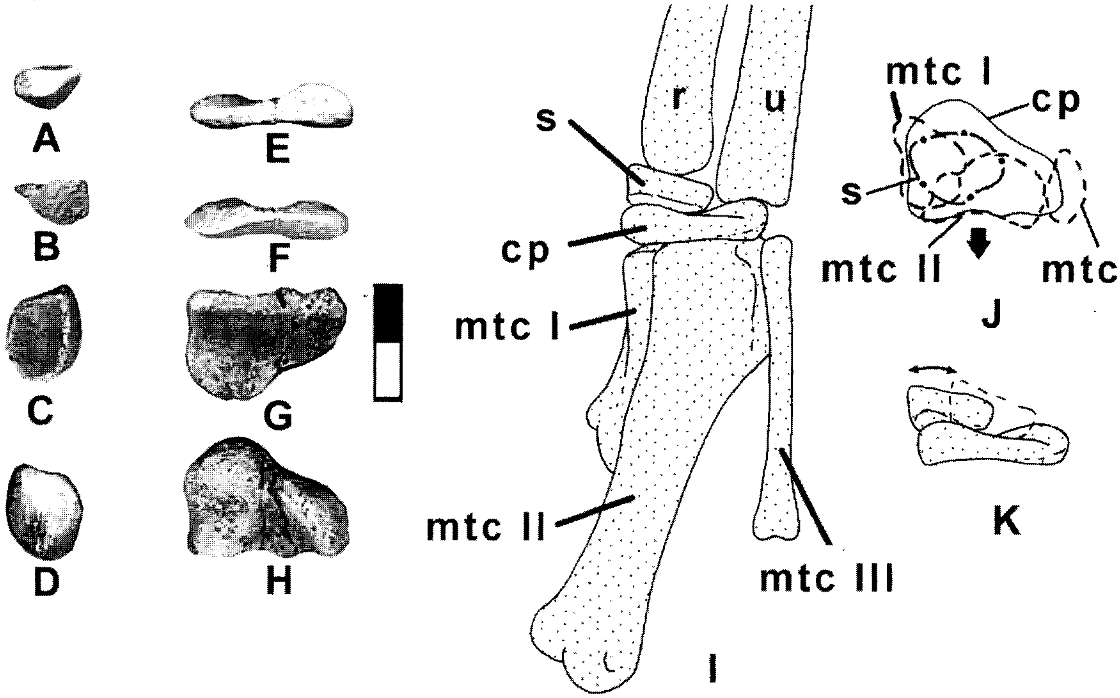



*Figure 2.11. Carpal elements of* Tanycolagreus topwilsoni *(TPII 2000-09-29). Semilunate in anterior (A), posterior (B), proximal (C), and distal (D) views. Distal carpal block in posterior (E), anterior (F), distal (G), and proximal (H) views. Scale in cm. Restored wrist in anterior (I) and proximal (J) views (arrow points anteriorly). Amount of movement possible for the semilunate carpal on the distal carpal block (K). Abbreviations: cp—carpal block; mtc I–III—metacarpals I–III; r—radius; s—semilunate; u—ulna.*

*Ulna* (Fig. 2.10A–C). The ulna is bowed posteriorly, with most of the arching occurring proximally. The olecranon is short and rounded, and it grades anteriorly into the humeral, or medial condylar, notch. The radial notch is well developed, transversely expanded, and concave. The diameter of the radial shaft is about the same as that of the radius. The distal end is triangular in ventral view (Fig. 2.10E) and set at about 60° relative to the proximal end. The contact surface for the radius is small.

*Radius* (Fig. 2.10F–H). The radius is bowed anteriorly. Its proximal end is ellipsoidal, being slightly wider anteriorly than posteriorly (Fig. 2.10D). The distal end is sloped about 50° relative to the axis of the shaft, and its contact with the ulna is small and rounded. The shaft is laterally compressed proximally and is subtriangular at mid-shaft, with the apex on the posterior side.

*Carpals* (Fig. 2.11). The proximal carpal (radiale) is modified into a boat-shaped semilunate carpal (Fig. 2.11A–D) that has a concave dorsal surface for the radius and an elongated convex ventral surface. In end view, it is wedge-shaped, with the tapered edge palmar. The distal carpals (Fig. 2.11E–H) are fused and are functionally a single carpal. The dorsal side has two low, elongate prominences that act as guides to constrain the direction of movement of the semilunate carpal (Fig. 2.11K). The ventral side is slightly concave, with a lip along the palmar side (Fig. 2.11F). The carpal overlies metacarpals I and II and barely overlies metacarpal III (Fig. 2.11J). Movement at the wrist has been discussed elsewhere (Carpenter 2002).

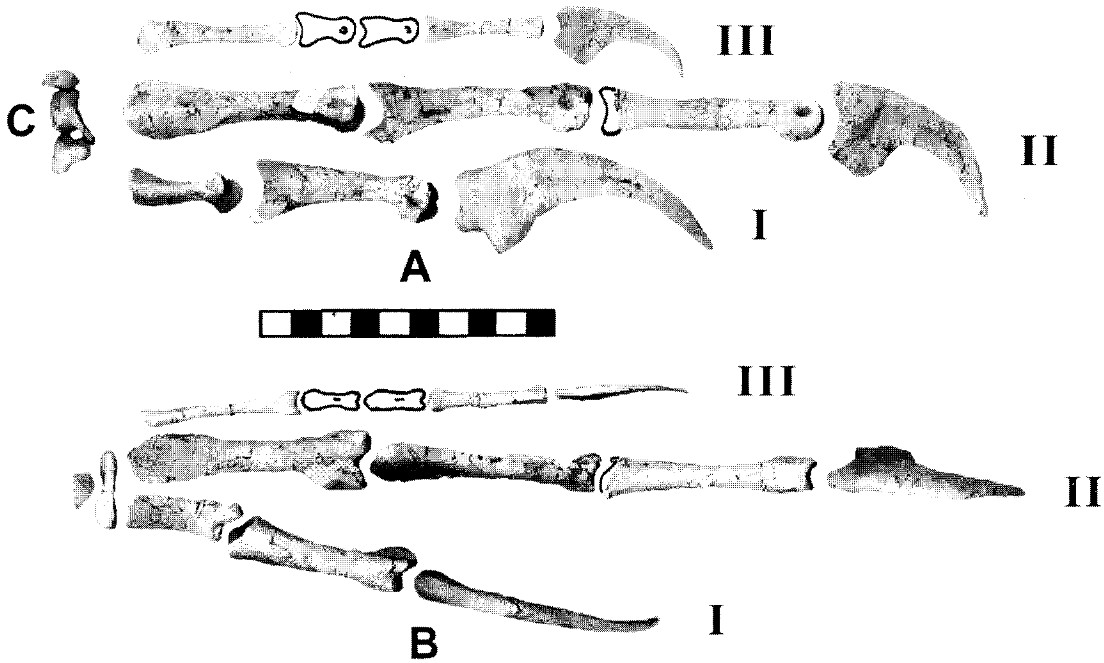



*Figure 2.12. Right manus of* Tanycolagreus topwilsoni *(TPII 2000-09-29) showing digits I–III in lateral (A) and extensor (B) views. Proximal view of metacarpals (C). Scale in cm.*

*Manus* (Fig. 2.12). The manus consists of three digits, all with phalanges and unguals. Digit II is the longest in the manus, followed by digit I and then III. Metacarpal I is slightly less than half as long as metacarpal II. In proximal view it somewhat V-shaped, with a corresponding notch on the proximal end of metacarpal II (Fig. 2.12B). When articulated, the extensor (outer) surfaces of metacarpals I and II form an 80° angle in proximal view (Fig. 2.12B), so that metacarpal I is mostly hidden by metacarpal II (Fig. 2.11I). Distally, metacarpal I is twisted about 35° relative to the extensor surface of the proximal end. The medial and outer lengths are considerably unequal so that the distal condyle is not in the same horizontal plane. The result is that digit I is canted away from digit II. The length of metacarpal II is only 41 percent of humeral length. Metacarpal III is shorter than metacarpal II and has a straight shaft that is significantly narrower than that of metacarpal II. Metacarpal III articulates below the proximal end of metacarpal II, but not on the palmar side. The proximal articulation of metacarpal III is subquadrilateral. The metacarpal-phalangeal joints are hyperextensible (Carpenter 2002), although the extensor pits are not well developed. Digit I extends to the middle of phalanx II-2, which is the longest non-ungual phalanx. The longest ungual is on digit I, and it is five times as long as the height of the articular surface. It is trenchant and rather deep, with an elliptical articular surface. The unguals are moderately curved, and their cross-section at mid-shaft is ovoid, being over twice as deep as it is wide. None of the unguals have a pronounced lip above the articular surface as seen in oviraptorids. On the palmar side, the flexor tubercles of the unguals are well developed and proximally placed. The

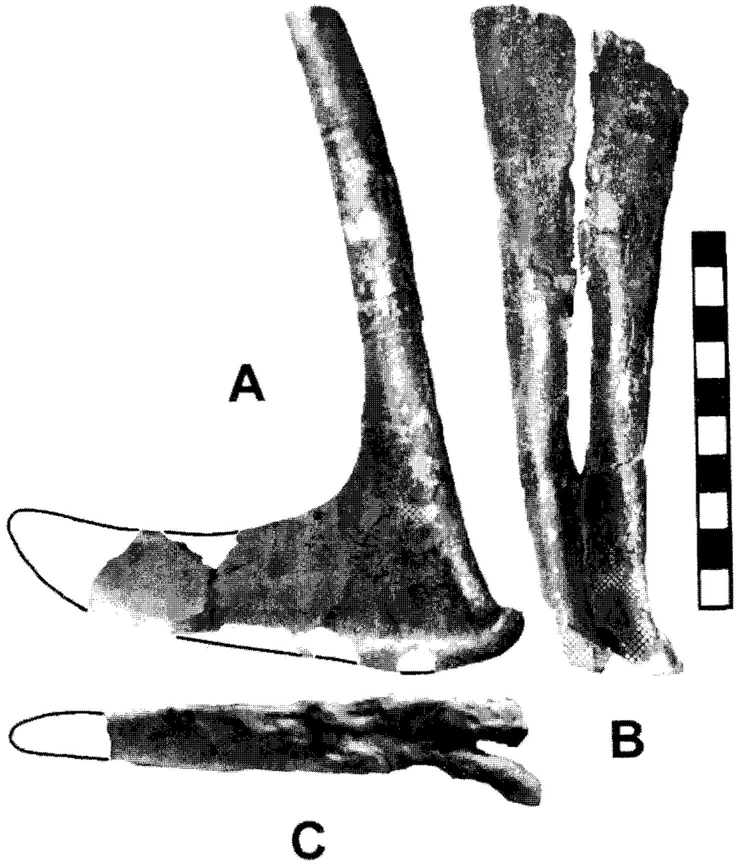



*Figure 2.13. Pubis of* Tanycolagreus topwilsoni *(TPII 2000-09-29) in right lateral (A), anterior (B), and ventral (C) views. Scale in cm.*

ungual grooves divide the unguals equally into palmar and extensor regions.

Previously, Osborn (1916) described a partial manus (AMNH 587) from Bone Cabin Quarry as that of *Ornitholestes hermanni* (it was not found with that skeleton). The specimen was collected about 300 m east of the holotype of *Tanycolagreus topwilsoni* and at approximately the same stratigraphic level. Although we cannot rule out that the manus is that of *Ornitholestes* (the manus is otherwise unknown), we also note that the specimen is indistinguishable from that of *Tanycolagreus*. We therefore consider AMNH 587 as the manus of *Tanycolagreus* until such time as the manus of *Ornitholestes* is known.

*Pelvis*

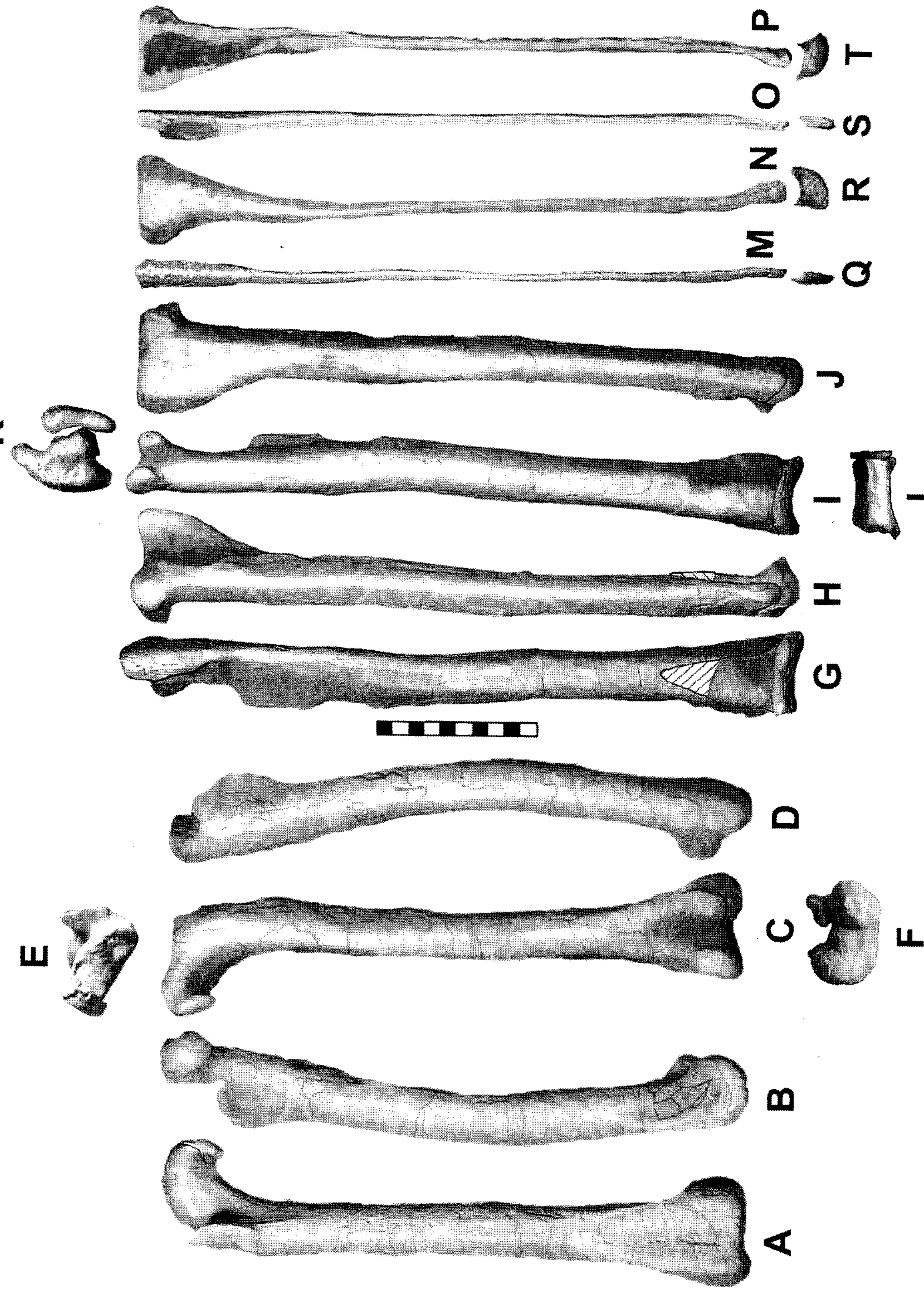
*Pubis* (Fig. 2.13). The pubes are represented by their distal half. In lateral view, the shaft is bowed anteriorly, but it joins the foot at a right angle. The dorsal surface of the foot, where it joins the pubic shaft, is more gently sloped than in *Coelurus*, where the transition is almost abrupt. The pubic foramen is located in the distal half of the pubic shaft and terminates just proximal to the pubic foot (Fig. 2.13B). The foot has a short anterior portion, which is not completely fused (Fig. 2.13C), probably because the individual was not fully mature. The foot is incomplete posteriorly and, in ventral view, is a narrow triangle. The ventral surface of the pubic foot is flat, rather than arcuate or boat-shaped as in *Coelurus* (see Carpenter et al., Chapter 3).

A second pubis from Felch Quarry 1 was previously referred to *Coelurus* by Gilmore (1920), but the ventral surface is flat and the pubic foramen terminates just above the pubic foot as in *Tanycolagreus*, rather than at midway as in *Coelurus* (see Carpenter et al., Chapter 3). We therefore refer this specimen to *Tanycolagreus*.

*Hindlimb*

*Femur* (Fig. 2.14A–F). The femoral shaft is bowed anteriorly and is very slightly sigmoidal (Fig. 2.14B). The femoral head is at right angles to the shaft and is transversely elongated. The dorsal surface of the head is flat and extends laterally toward the greater trochanter, whereas in proximal view (Fig. 2.14E), the head tapers laterally to the greater trochanter. We digress briefly to note that the dorsal surface, lateral to the femoral head, has frequently been misidentified as the greater trochanter. Sometimes there may be a slight crest in that region. However, as Gregory (1918, p. 535) has noted, "the greater trochanter . . . remains on the outer side of the shaft more or less near the proximal end. The outer portion of the head itself has sometimes been wrongly called the 'great trochanter.'" He adds in a footnote, "the proximal surface of the so-called great trochanter was covered by bursa, as is the similar smooth surface above the great trochanter in the Ostrich. . . ; and that the gluteal muscles (i.e., M. iliofemoralis externus) were attached on the outer surface of the great trochanter and not upon its top." Thus, the greater trochanter is on the proximal, lateral surface of the femoral shaft, where this region is frequently marked by faint vertical rugosities or ridges that mark the insertion of the M. iliotrochantericus and M. iliofemoralis externus. The crest that is sometimes developed on the dorsal surface is the trochanteric crest (i.e., crista trochanteris), and in extant birds, it serves to restrict abduction of the femur (see further discussion in Carpenter and Kirkland 1998, p. 249–250).

The anterior trochanter (incorrectly called the lesser trochanter by some; see Carpenter and Kirkland 1998, p. 250), is separated from the proximal end of the femoral shaft by a cleft. Furthermore, the trochanter projects anteriorly as an alariform structure, and its proximal-most point is below the femoral head (Fig. 2.14A,B). On the femoral shaft, the fourth trochanter is little more than a slight, irregular ridge located proximally, beginning opposite the distal end of the anterior trochanter (Fig. 2.14B). Distally on the anterior surface, the origin scar for the tibial extensor, the M. femorotibialis, is elliptical shallow, and bounded medially by the medial distal crest; no extensor groove is present for the tendon of the M. femoro-tibialis, suggesting that the tibial aponeurosis extended dorsally onto the distal end of the femur. On the medial side of the distal end, there is no medial epicondyle, and on the lateral side, there is a groove in the lateral condyle. On the posterior side, the vertical fibular crest (crista tibiofibularis) is short and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is separate from the lateral condyle; lateral to it is a shallow groove. The poptileal fossa is moderately well developed.

*Tibia* (Fig. 2.14G–K). The tibial shaft is long and straight. The cnemial crest is short and projects anterolaterally. The proximal fibular crest is subrectangular and almost as long as the cnemial crest (Fig. 2.14G). In proximal view, the lateral and medial condyles are subequal in size, and the lateral condyle has shifted anteriorly to a lateral position (Fig. 2.14K). There is a conspicuous waist between this condyle and the main body of the tibia. The notch (incisura tibialis) between the cnemial crest and lateral condyle is small relative to the overall size of the femoral platform. Laterally, the fibular crest is low on the shaft and subrectangular, but it is otherwise well developed (Fig. 2.14G). The distal end of the tibia is only slightly expanded relative to the shaft width (Fig. 2.14G), but it does back the calcaneum.

*Fibula* (Fig. 2.14M–P). The fibula is long and slender and is broadly separate from the tibia. The length of the expanded proximal end is almost 75 percent of the anteroposterior length of the femoral platform. Medially, the proximal end is slightly concave, with a sulcus extending ventrally. A slight protuberance is present on the anterior surface of the shaft. Distally, the fibula slightly overlaps the ascending process of the astragalus. The distal terminus is not very expanded.

*Tarsals* (Fig. 2.14G,L,Q–T). The astragalus is anteroposteriorly short, and the distal condyles are more developed ventrally than anteriorly; a transverse groove extends across the anterior face of the astragalus, just proximal to the condyles. The shallow fossa present at the base of the ascending process is not very prominent. The ascending process is not complete, although how much is missing is unknown. The calcaneum is not fused to the astragalus, and is reduced to a small, narrow disk. Medially, the astragalar tuberosity is small.

*Pes* (Fig. 2.15). The metatarsals are elongate, with the length of metatarsal III being about 60 percent of femur length. The mid-shaft cross-sections of metatarsals II–IV are as wide as they are long. Metatarsal I is reduced but still retains phalanges; it is placed posteromedially near the mid-shaft of metatarsal II. Metatarsal III is not reduced proximally, and it separates metatarsals II and IV. Metatarsals II and IV are subequal in length, and both are only a little shorter than metatarsal III. In proximal view, metatarsal III is hourglass-shaped. Metatarsal V is reduced to a slender, laterally compressed structure.

The combined length of the phalanges on pedal digit I is greater than the length of the first phalanx of pedal digit III. Pedal digits II and IV are subequal in length, and the first phalanx of digit II allows some hyperextension of phalanx 2. In cross-section, the pedal unguals are similar in overall shape, laterally compressed, and subtriangular. Ungual II is subequal to ungual IV.

*Figure 2.14. Right hindlimb elements of* Tanycolagreus topwilsoni *(TPII 2000-09-29). Femur in anterior (A), medial (B), posterior (C), lateral (D), proximal (E), and distal (F) views. Tibia and astragalus in anterior (G), lateral (H), posterior (I), and medial (J) views. Tibia and fibula in articulation in proximal view (K). Astragalus and calcaneum in distal view (L). Fibula in anterior (M), lateral (N), posterior (O), and medial (P) views. Calcaneum in anterior (Q), lateral (R), posterior (S), and medial (T) views. Scale in cm.*

## Discussion

The holotype of *Tanycolagreus* is of a submature individual, about 3.3 m long, whereas the premaxilla from the Cleveland-Lloyd Quarry

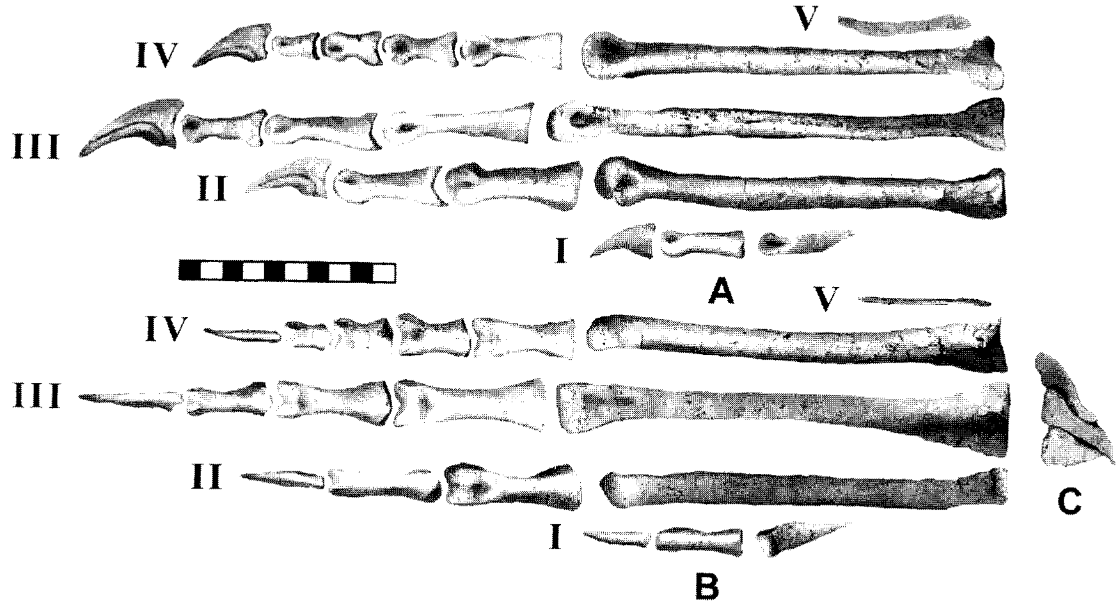


*Figure 2.15. Pes of* Tanycolagreus topwilsoni *(TPII 2000-09-29) showing digits I–V in medial (A) and extensor (B) views. Proximal view of metatarsals (C). Scale in cm.*

suggests an individual about 4 m long (Fig. 2.16). Whether the Cleveland-Lloyd specimen represents a fully mature individual is not known. When initially discovered, the holotype skeleton of *Tanycolagreus* was identified as that of *Coelurus fragilis* (Miles et al. 1998). However, direct comparison with the holotype makes such an identification untenable; nor can it be referred to *Ornitholestes* (Table 2.1). Comparison with another medium-size theropod from the Morrison Formation, *Stokesosaurus clevelandi,* is not possible, because the ilium is unknown for *Tanycolagreus,* and the referred premaxilla is shown above to be that of *Tanycolagreus.* The referred premaxilla of *Marshosaurus,* another medium-size Morrison theropod, differs from that of *Tanycolagreus* in being long and low, rather than short and deep; and the referred pubis lacks the short "toe" at the anterior part of the pubic boot.

Of all the known theropods from the Morrison Formation, *Tanycolagreus* is most similar to *Coelurus,* although the former is more primitive in a number of points, including the absence of pleurocoels on the anterior dorsals, the relatively long prezygapophyses on the caudals, and the straight humeral shaft. Its identification has increased the diversity of theropods in the Morrison and demonstrates that small to medium-size theropods were considerably more diverse than previously thought.

*Acknowledgments.* We thank the following people for access to specimens in their care: Dan Chure (Dinosaur National Monument), Jacques Gauthier and Lyndon Murray (Yale Peabody Museum), Charlotte Holton and Mark Norell (American Museum of Natural History), Robert Purdy (National Museum of Natural History), and Kenneth

TABLE 2.1.

Comparison between *Tanycolagreus*, *Coelurus*, and *Ornitholestes*

| | *Tanycolagreus* | *Coelurus* | *Ornitholestes* |
|---|---|---|---|
| Anterior edge of premaxilla | Straight | Unknown | Rounded |
| Premaxillary body | Deep | Unknown | Shallow |
| Jugal process of lachrymal | Angled sharply downward | Unknown | Horizontal |
| Orbital projection on postorbital | Present | Unknown | Absent |
| Posterior process of quadratojugal | Moderately developed | Unknown | Absent |
| Posterior dorsal neural spine/centrum length | >75% | >75% | <75% |
| Dorsal neural spine | Long, overhangs centrum posteriorly | Long, overhangs centrum posteriorly | Short, does not overhang centrum posteriorly |
| Centrodiapophyseal lamina | Present | Present, with two very deep fossa on each side | Absent |
| Pleurocoel in anterior dorsal centra | Absent | Present | Absent |
| Dorsal centrum height/length | >75% | <75% | <75% |
| Posterior caudal prezygapophysesnot | Moderately long, extending to about 1/3 preceding centrum length | Short, not extending much beyond end of centrum | Long, to about half preceding centrum |
| Lateral side of distal caudal centrum | Smooth | Smooth | Ridge |
| Humeral shaft in lateral view | Straight | Strongly sigmoidal | Straight |
| Proximal internal tuberosity | Sharp corner, angled down below level of humeral head | Sharp corner, nearly level with humeral head | Rounded, lower than humeral head |
| Ulna | Strongly bowed posteriorly | Strongly bowed posteriorly | Unknown |
| Radius | Bowed anteriorly, slender | Straight, slender | Straight very robust for length |
| Semilunate carpal | Present | Present | Unknown |
| Pubic foot | Flat bottomed | Arced bottom (boat shape) | Unknown |
| Femur shaft in anterior view | Straight | Sigmoidal | Straight |
| Medial end of femoral head | Level with greater trochanter | Below greater trochanter (angled ventromedially) | Unknown |
| Metatarsal IV/humeral length | 1.01 | 1.72 | 0.91 |

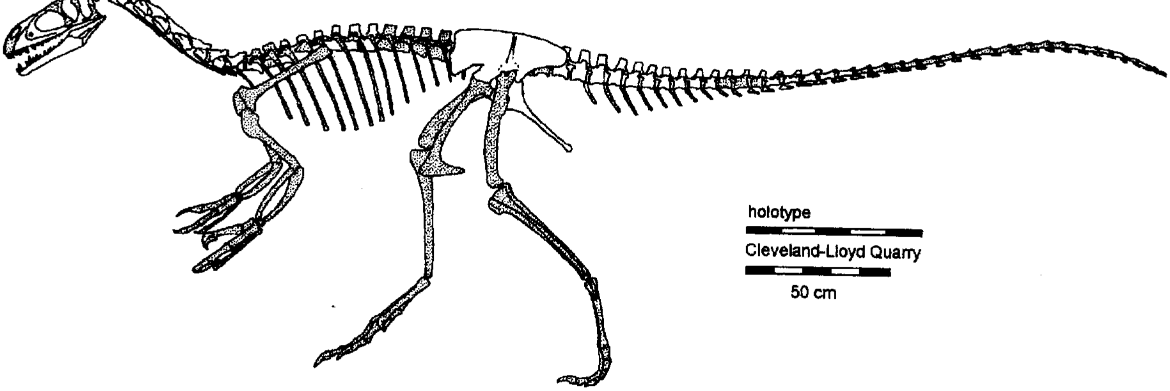


*Figure 2.16. Skeletal reconstruction of* Tanycolagreus topwilsoni. *Shaded bones are known. Scale = 50 cm.*

Stadtman (Brigham Young University Earth Science Museum). Thanks to Ben Creisler for the moniker *Tanycolagreus*. Finally, we thank an anonymous benefactor for donating the holotype skeleton, which is now on display at the North American Museum of Ancient Life.

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