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A CRITICAL RE-EVALUATION OF THE LATE TRIASSIC DINOSAUR TAXA OF NORTH AMERICA

Sterling J. Nesbitt
American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA and
Lamont-Doherty Earth Observatory, Columbia University, 61 Rt. 9W, Palisades, NY 10964, USA

Randall B. Irmis
Museum of Paleontology and Department of Integrative Biology, 1101 Valley Life Sciences Building,
University of California, Berkeley, CA 94720–4780, USA

William G. Parker
Division of Resource Management, Petrified Forest National Park, P.O. Box 2217, Petrified Forest,
AZ 86028, USA

SYNOPSIS The North American Triassic dinosaur record has been repeatedly cited as one of the most complete early dinosaur assemblages. The discovery of *Silesaurus* from Poland and the recognition that *Herrerasaurus* and *Eoraptor* may not be theropods have forced a re-evaluation of saurischian and theropod synapomorphies. Here, we re-evaluate each purported Triassic dinosaur from North America on a specimen by specimen basis using an apomorphy-based approach. We attempt to assign specimens to the most exclusive taxon possible. Our revision of purported Late Triassic dinosaur material from North America indicates that dinosaurs were rarer and less diverse in these strata than previously thought. This analysis concludes that non-dinosaurian dinosauriforms were present in North America in the Late Triassic. Most of the proposed theropod specimens are fragmentary and/or indistinguishable from corresponding elements in the only well-known Triassic theropod of North America, *Coelophysis bauri*. No Triassic material from North America can be assigned to Sauropodomorpha, because none of the purported 'prosauropod' material is diagnostic. Recent discovery of the skull and skeleton of *Revueltosaurus callenderi* from Arizona shows that it is a pseudosuchian archosaur, not an ornithischian dinosaur. As a result, other purported North American ornithischian teeth cannot be assigned to the Ornithischia and therefore, there are no confirmed North American Triassic ornithischians. Non-tetanuran theropods and possible basal saurischians are the only identifiable dinosaurs recognised in North America until the beginning of the Jurassic Period.

KEY WORDS Dinosauria, Ornithischia, Saurischia, Theropoda, Triassic, early diversity

Contents

INTRODUCTION

The origin of the Dinosauria lies in the Late Triassic Period (Gauthier 1986; Langer 2004; Langer & Benton 2006): however, our understanding of the early history and relationships of dinosaurs remains poor because of the absence of well preserved crania and postcrania for most basal dinosaurs and a poor understanding of the character polarities of dinosaurs and their immediate outgroups (Fraser *et al.* 2002). Furthermore, a lack of consensus of the phylogenetic placement of controversial taxa such as *Herrerasaurus* inside Theropoda (Sereno & Novas 1993; Novas 1993), as a stem saurischian (Langer 2004) or outside Dinosauria (Holtz & Padian 1995; Fraser *et al.* 2002)) hampers our understanding of the origin, early biogeography and diversity of the Dinosauria. A new distribution of character states among ornithodirans and basal archosaurs (including crocodile-line archosaurs) has emerged with the discovery of taxa such as *Silesaurus* (Dzik 2003), *Effigia okeeffeae* (Nesbitt & Norell 2006) and *Revueltosaurus* (Parker *et al.* 2005) and has led to new insights regarding the identification of crocodile-line archosaurs, ornithodirans, dinosauromorphs, dinosauriforms and members of the Dinosauria in the Triassic.

Recently, many Late Triassic dinosaur specimens have been described from around the world (see Heckert & Lucas 2000), especially from the western United States (Hunt 1991; Carpenter 1997; Hunt *et al.* 1998; Sullivan & Lucas 1999; Heckert & Lucas 2000). The apparently high diversity of dinosaurs in the western United States (Hunt *et al.* 1998) has been compared with the European (Rauhut & Hungerbühler 2000) and South American (Heckert & Lucas 2000) Triassic dinosaur faunas.

Here, we re-examine each purported Triassic dinosaur from North America on a specimen by specimen basis. We employ a conservative approach in our assignments to specific or more general clades that are unaffected by the various current phylogenetic hypotheses concerning the placement of controversial taxa (e.g. *Eoraptor* and *Herrerasaurus*). Our goal in this study is to determine which specimens in the Late Triassic of North America can be unambiguously identified as members of Dinosauria. We do not specify the exact phylogenetic position of these taxa within Dinosauria, a task that requires a comprehensive specimen-based phylogenetic analysis that is beyond the scope of the present work.

METHODS

Revision of the diagnoses of Dinosauromorpha, Dinosauriformes and Dinosauria is beyond the scope of this paper and can only be completed after a comprehensive phylogenetic analysis. Because there is no consensus regarding the diagnosis of Dinosauria (see Sereno & Novas 1993; Sereno 1999; Holtz & Padian 1995; Fraser *et al.* 2002; Langer & Benton 2006) and its immediate outgroups, we use an apomorphy-based approach. That is, we use specimen by specimen comparisons and highlight character states that have previously been used in phylogenetic analyses to place taxa within specific clades. We cannot always assign a specimen to a species-level taxon, so we assign specimens to the least inclusive clade possible using apomorphies. The most useful character states for identification of members of Dinosauria are illustrated in Fig. 1.

We recognise that some of the taxa considered here may fall within the Dinosauria in future phylogenetic analyses; however, the lack of certain character states that place a taxon within Dinosauria may be a result of reversals (e.g. a nearly closed acetabulum) and/or missing data in other important regions of the body (e.g. the skull of *Chindesaurus* is not known), as exemplified by many of the purported Late Triassic dinosaurs of North America. Only after a rigorous phylogenetic analysis, which is not provided herein,

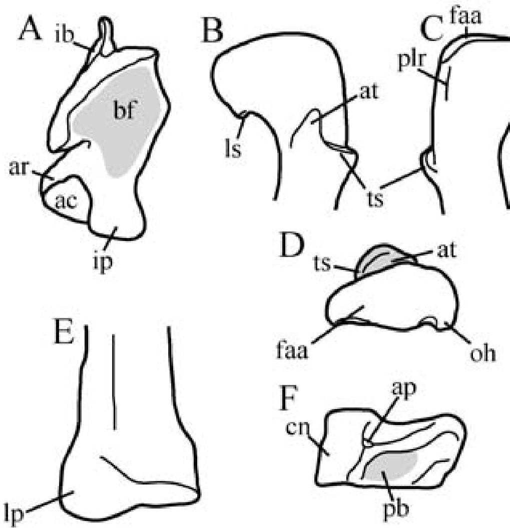

Figure 1 Dinosaur specimens displaying character states used to diagnose Dinosauria in the text. (**A**) left ilium of the holotype of *Dilophosaurus wetherilli* (UCMP 37302) in posterior view showing the brevis fossa. Left proximal femur of *Coelophysis* sp. (UCMP 129618) in anterior (**B**), posterior (**C**) and proximal (**D**) views, showing the presence of a spike-like anterior trochanter, offset head and ligament sulcus. (**E**) right distal tibia of *Coelophysis* sp. (UCMP 129618) in anterior view showing an expanded lateral process. (**F**) left astragalocalcaneum of *Coelophysis bauri* (AMNH FR30576) displaying a posterior basin adjacent to the ascending process of the astragalus. Abbreviations: **ac**, acetabulum; **ap**, ascending process; **ar**, acetabular rim; **at**, anterior trochanter; **bf**, brevis fossa; **cn**, calcaneum; **faa**, facies articularis antitrochanterica; **ib**, iliac blade; **ip**, ischial peduncle; **lp**, lateral process; **ls**, ligament sulcus; **oh**, offset head; **pb**, posterior basin; **plr**, posterolateral ridge; **ts**, trochanteric shelf.

can these ambiguous cases be settled. It is important to take this conservative approach with such specimens and it would be imprudent to consider specimens lacking key dinosaurian character states to be true dinosaurs. Such an approach in the past has inflated the record of Triassic dinosaurs in North America.

In this study, *Saturnalia* is considered to be a basal sauropodomorph, following recent phylogenetic studies (e.g. Langer 2004; Yates 2004). We provisionally agree with Langer & Benton (2006) that *Herrerasaurus* and *Eoraptor* are basal saurischians based on our own observation of the material, but this hypothesis requires further testing. There is still a possibility that *Herrerasaurus* and *Eoraptor* could fall outside Dinosauria *sensu stricto* (e.g. Holtz & Padian 1995), but in Langer (2004), constraining these two taxa to fall outside of the Dinosauria resulted in a most parsimonious tree 14 steps longer than the unconstrained tree that placed them as basal saurischians and 12 steps longer than a tree constraining them to be within Theropoda. Most relevant to this study, *Herrerasaurus* shares several pelvic and hindlimb character states with other saurischians that are not found in basal ornithischians (Langer 2004; Langer & Benton 2006).

We have studied first-hand *Marasuchus*, *Lagerpeton*, *Pseudolagosuchus*, *Agnostiphys*, *Scutellosaurus*, *Eoraptor*, *Herrerasaurus*, *Guaibasaurus*, *Saturnalia*, *Unaysaurus*, *Riojasaurus*, *Coelophysis bauri*, *Coelophysis* sp., *Dilophosaurus, Silesaurus* and all of the specimens being revised below with the exception of *Arctosaurus*. Casts of *Lesothosaurus* tibiae described by Knoll & Battail (2001) were also examined. Descriptions of *Lesothosaurus*, *Thecodontosaurus*, *Plateosaurus*, *Coelophysis rhodesiensis*, '*Syntarsus*' *kayentakatae*, *Liliensternus* and *Arctosaurus* were taken from the literature. Unpublished photographs of *Silesaurus* material were also used.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York, NY; **FMNH**, Field Museum of Natural History, Chicago, IL; **MNA**, Museum of Northern Arizona, Flagstaff, AZ; **NMI**, National Museum of Ireland; **NMMNH,** New Mexico Museum of Natural History, Albuquerque, NM; **PEFO**, Petrified Forest National Park, AZ; **TTUP,** Texas Tech University Paleontology Collections, Lubbock, TX; **UCM**, University of Colorado Museum, Boulder, CO; **UCMP**, University of California Museum of Paleontology, Berkeley, CA; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, MI; **YPM**, Yale Peabody Museum, New Haven, CT.

Putative theropods

New Mexico

Eucoelophysis baldwini Sullivan & Lucas, 1999 (Fig. 2)

Age. Norian, Late Triassic.

Occurrence. Petrified Forest Member, Chinle Formation (Sullivan *et al.* 1996; Sullivan & Lucas 1999), Rio Arriba County, New Mexico, U.S.A.

Holotype. NMNNH P-22298 (Figs 2A–E).

Referred material. Sullivan & Lucas (1999) referred a pubis (AMNH 2706), part of the syntype of *Coelophysis longicollis* (see Padian 1986), to *E. baldwini*.

Taxonomic assignment. Non-dinosaurian basal ornithodiran.

Remarks. The holotype specimen of *Eucoelophysis baldwini* (Sullivan & Lucas 1999) was collected from a small quarry with a mixed assemblage including *Typothorax*, represented by an osteoderm and other numerous unidentifiable fragments. Sullivan & Lucas (1999) assigned most of the material to *Eucoelophysis* based on its proximity to the partially articulated hindlimbs and stated that the scapula may belong to another taxon. They also assigned a pubis from Cope's original material of *Coelophysis* to *Eucoelophysis* based on arguments that it was collected near the type locality of *Eucoelophysis* and the presence of an apomorphy tying it to the pubis assigned to the holotype of *Eucoelophysis*. Originally described as a coelophysoid theropod dinosaur, our re-examination of the holotype and comparisons with other Triassic archosaurs (e.g. *Silesaurus*), suggest that *Eucoelophysis* is not a coelophysoid and not even a dinosaur.

Sullivan & Lucas (1999) used two characters to assign *Eucoelophysis* to the Ceratosauria (*sensu* Rowe & Gauthier 1990): (1) the presence of triangular and posteriorly-directed transverse processes of the dorsal vertebrae and (2)

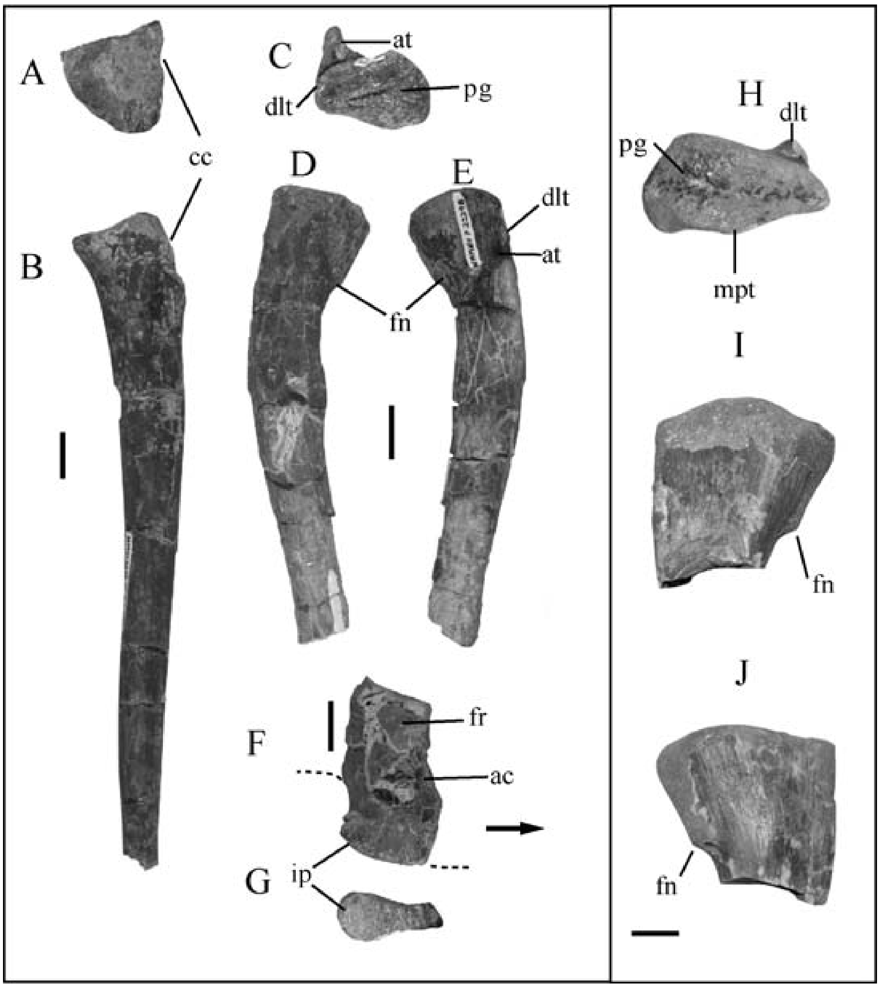

Figure 2 Informative elements from the holotype of *Eucoelophysis baldwini* (NMMNM P-22298). The right tibia in proximal (**A**) and medial (**B**) views and the left femur in proximal (**C**), posterior (**D**) and anterior (**E**) views. Posterorventral portion of the right ilium in lateral (**F**) and ventral (**G**) views. The dashed lines postulate the extrapolation of the finished edges and the small arrow indicates the anterior direction. Proximal portion of the femur of PEFO 34347 in dorsal (**H**), lateral (**I**) and medial (**J**) views. Abbreviations: **ac**, acetabulum; **at**, anterior trochanter; **cc**, cnemial crest; **dlt**, dorsolateral trochanter; **fn**, femoral head notch; **fr**, fragments; **ip**, ischiadic process; **mpt**, mediolateral proximal tuber; **pg**, proximal groove; Scale bars = 1 cm.

the presence of a prominent trochanteric shelf on the anterior trochanter of the femur. The first character is not present in the specimen. The vertebrae that Sullivan & Lucas (1999) identified as dorsal vertebrae are actually posterior cervical vertebrae, because they preserve parapophyses on the ventrolateral sides of the anterior portion of the centrum. The transverse processes of the best preserved cervical are laterally directed and not backswept as in coelophysoids. Second, an isolated neural arch, identified by Sullivan & Lucas (1999) as possibly belonging to a dorsal vertebra, bears processes that are also laterally directed and obscured by matrix in dorsal view. Therefore, none of the vertebrae have triangular, backswept, posteriorly-directed transverse processes. A prominent anteroposteriorly orientated trochanteric shelf on the anterior trochanter of the femur occurs in some coelophysoids and *Ceratosaurus* (Rowe & Gauthier 1990); however, there is no prominent trochanteric shelf on either of the holotype femora of *Eucoelophysis*. The anterior trochanter is a simple spike-like projection (Fig. 2E). Nevertheless, the presence of a trochanteric shelf has a wider distribution in basal Dinosauria and is found in basal taxa such as *Herrerasaurus* (Novas 1993) and *Saturnalia* (Langer 2003).

Both *Eucoelophysis* femora have a small dorsolateral trochanter (=dlt, dorsolateral trochanter in Fig. 2) just posterolateral to the anterior trochanter. This same expansion is present in *Herrerasaurus* and *Chindesaurus* (Bonaparte *et al.* 1999; Langer 2003). In addition, the distal end of the femur of *Eucoelophysis* lacks a sulcus between the lateral and fibular distal condyles, which is found in most basal theropods (Rowe & Gauthier 1990) and a variety of other archosaurian taxa such as *Saturnalia*, *Silesaurus*, *Shuvosaurus* and *Dibothrosuchus* (Wu & Chatterjee 1993). Without these last two crucial characters, *Eucoelophysis* shares no character states with coelophysoids and, thus, cannot be assigned to the coelophysoid or 'ceratosaurid' clade.

Moreover, *Eucoelophysis* cannot be assigned to the Dinosauria because it lacks characters shared by both saurischians and ornithischians. Dinosaurs have a distinct proximal femur with an offset femoral head (Novas 1989) and a prominent facies articularis antitrochanterica (see Langer 2004). The femur of *Eucoelophysis* lacks both of these characters (Figs 2C–E). Instead, the femoral head is roughly triangular in lateral view as in *Silesaurus* (Dzik 2003). The only character that the femora of *Eucoelophysis* shares with the Dinosauria is the presence of an anterior trochanter with a spike-like projection; however, taxa outside the Dinosauria such as *Silesaurus* and even the suchian *Ornithosuchus* (Walker 1964; Sereno 1991) all have similar spike-like anterior trochanters. The proximal head of the femur of *Eucoelophysis* is triangular in proximal view and has a mediolaterally trending sulcus that Sullivan & Lucas (1999) considered an autapomorphy. This sulcus is not unique to *Eucoelophysis* and is present in other archosaurs such as *Silesaurus*, *Saturnalia*, *Coelophysis* sp. (Padian 1986), *Poposaurus*, *Ornithosuchus* and juvenile phytosaurs and aetosaurs (S.J.N., pers. obs.).

The proximal portion of the tibia (Figs 2A,B) is nearly featureless, but has a cnemial crest (Sullivan & Lucas 1999), a character that is shared among ornithodirans, including those outside the Dinosauria (e.g. *Marasuchus*). The appressed surface of the tibia that Sullivan & Lucas (1999) described is unique to *Eucoelophysis*; however, the homology of the appressed surfaces of the tibiae of both *Eucoelophysis* and the small Snyder Quarry coelophysoid advocated by Heckert *et al*. (2000*b*, 2003) is doubtful because the length and morphology of each of the specimens are different from one another.

The holotype includes a partial right metatarsus with most of metatarsal II (missing the proximal end), a nearly complete metatarsal III and the distal portion of metatarsal IV. The proximal end of metatarsal III is symmetrical and similar to other basal ornithodirans and dinosaurs. The distal articular end of metatarsal IV is asymmetrical and deeper than broad, an apomorphic state shared with *Saturnalia*, theropods and some ornithopods (Langer 2003, 2004; Langer & Benton 2006). Dzik (2003) did not figure or describe the distal end of metatarsal IV for *Silesaurus*, so it is unclear what character state is present in *Silesaurus*.

Because the hindlimbs were the only elements of *Eucoelophysis* that were definitely associated (within a multitaxic quarry), we consider the hindlimbs and metatarsals to be the only definite material pertaining to the holotype of *Eucoelophysis*. The other elements may or may not pertain to *Eucoelophysis* and, as discussed below, are non-diagnostic.

The proximal surface of the pubis assigned to *Eucoelophysis* bears an ischio-acetabular groove between the ischial facet and the acetabular facet, which Sullivan & Lucas (1999) considered to be an autapomorphy of the taxon; however, an ischio-acetabular groove is also present in *Saturnalia* (Langer 2003). Examination of the holotype and paratypes of *Saturnalia* indicates that the ischio-acetabular groove in this taxon differs slightly from the *Eucoelophysis* pubis in not piercing the medial wall of the pubis, whereas the groove in *Eucoelophysis* completely pierces both the lateral and medial margins of the pubis. The ischio-acetabular groove used by Sullivan & Lucas (1999) to refer a pubis from the original syntypes of *Coelophysis bauri* (AMNH 2706) to *Eucoelophysis* is much shallower, does not pierce the medial wall of the pubis (similar to *Saturnalia*) and is poorly defined relative to the condition in the holotype of *Eucoelophysis*. Recent repreparation of this pubis (AMNH 2706) also indicates the presence of both an obturator foramen and pubic foramen, a coelophysoid theropod character. We could not determine if the pubis included with the holotype of *Eucoelophysis* also has a pubic foramen. Therefore, the original syntype of *Coelophysis* most probably does not contain *Eucoelophysis* material (i.e. material assignable to the same taxon as the himdlimb material of the holotype of *Eucoelophysis*).

Furthermore, we do not agree with Sullivan & Lucas's (1999) interpretation of the pubis, particularly regarding their identifications of the iliac, ischial and acetabular facets. After a close inspection of the proximal end of the pubis, these three regions cannot be clearly discerned because of the poor preservation of the proximal end. Moreover, the assignment of the acetabular facet implies that *Eucoelophysis* has an open acetabulum: however, the proximal face of the pubis is poorly preserved, so it is not certain if the acetabulum was open. A previously undescribed fragment of the ischiadic process of an ilium (Figs 2F, G) discovered with the type material suggests that if all the pelvic material belongs to *Eucoelophysis*, the acetabulum was mostly or completely closed. Even if the assignment of the three articular surfaces of the proximal surface of the pubis by Sullivan & Lucas (1999) is correct, it is not clear that the pubis found with the hindlimbs of *Eucoelophysis* belongs to the same taxon because it was not found in articulation and other taxa are known from the quarry.

Regardless of whether the bone Sullivan & Lucas (1999) identified as the ischium is referable to *Eucoelophysis*, it does not belong to a dinosaur. The ischium lacks an articular facet with the pubis and does not indicate an open acetabulum.

The right scapulacoracoid assigned to the holotype of *Eucoelophysis* is missing the distal end of the scapula and ventral portion of the coracoid as well as most of the anterior margin of both bones. The small portion of the coracoid seems to be firmly sutured to the scapula as described by Sullivan & Lucas (1999). It is a robust element, but lacks any informative character states except that it appears to have a fully posteriorly directed glenoid fossa, a character state present in dinosaurs (Fraser *et al*. 2002).

In summary, the hindlimb elements preserved in the holotype specimen indicate that *Eucoelophysis* is neither a theropod nor a dinosaur because it shares no apomorphies with these taxa. The morphology and more medial placement of the fourth trochanter and the presence of the anterior trochanter of the femur does indicate that the taxon is more closely related to Dinosauria than to Crocodylomorpha, but, at the moment, the placement of *Eucoelophysis* in a phylogenetic framework is hampered for two reasons: (1) the holotype of *Eucoelophysis* lacks substantial information because it is incomplete and (2) basal archosaur relationships are in a state of flux (Gower & Wilkinson 1996). The preserved elements closely resemble *Silesaurus*, an unambiguous ornithodiran from the Carnian of Poland (Dzik 2003) and *Pseudolagosuchus* from the Middle Triassic of Argentina. All three taxa share the presence of a small femoral head that is triangular in proximal view and the absence of a facies articularis antitrochanterica (Figs 2 C–E), two character states that are derived relative to other ornithodirans. A third possible synapomorphy shared by *Eucoelophysis*, *Silesaurus* and *Pseudolagosuchus* is a non-offset femoral head defined by a small ventral emargination visible in anterior and posterior views (Figs 2 C–E). In addition, *Silesaurus* and *Eucoelophysis* share a deep proximal sulcus and a finger-like anterior trochanter. The anterior trochanter is not visible in the holotype of *Pseudolagosuchus*. The presence of an anterior trochanteric shelf separates *Eucoelophysis* from *Silesaurus*; however, not all *Silesaurus* femora have a trochanteric shelf. In addition, Novas (1992: fig. 4B) illustrates a trochanteric shelf for a referred specimen of *Pseudolagosuchus*. *Eucoelophysis*, *Silesaurus* and *Pseudolagosuchus* also share a well-defined, sharp dorsolateral trochanter (Figs 2C, E) on the proximal portion of the femur. The absence of dinosaurian femoral characters and the presence of ornithodiran femoral characters (presence of an anterior trochanter) suggest that both *Eucoelophysis* and *Silesaurus* are non-dinosaurian ornithodirans, as has also been hypothesised for *Pseudolagosuchus* (Arcucci 1987; Novas 1992). In addition, the continuation of the division of the distal femoral condyles one-third up the shaft, a character absent in other ornithodiran taxa, is present in both *Silesaurus* and *Eucoelophysis*. The distal end of the femur of *Pseudolagosuchus* is too poorly preserved to evaluate this character in that taxon.

The pubes of *Silesaurus* and *Pseudolagosuchus* are nearly identical, but they differ substantially from the pubis found with the holotype of *Eucoelophysis*, which is gracile and rod-like. This suggests that the pubis found with *Eucoelophysis* may not belong to this taxon because the holotype was found among other archosaurian remains and was not articulated with the other bones of the *Eucoelophysis* holotype.

The other elements that cannot be shown to belong with the hindlimbs of *Eucoelophysis* (because the mixed assemblage confuses possible associations) and therefore might pertain to *Eucoelophysis*, another dinosaur or dinosaurs, or one or more basal archosaurs, are the ischium, scapula and the vertebrae.

In conclusion, we consider *Eucoelophysis* to represent a valid taxon because it processes one autapomorphy, an appressed surface of the tibia. Based on preserved character states in the hindlimb elements, we can assign *Eucoelophysis* to a non-dinosaurian basal ornithodiran. Based on several potential synapomorphies and other shared characters in the femur, we hypothesise that *Eucoelophysis*, *Silesaurus* and *Pseudolagosuchus* may form a group of basal dinosauriforms close to, but outside, Dinosauria. This hypothesis requires further testing in an explicit phylogenetic context.

Two other specimens referable to the possible clade containing *Eucoelophysis*, *Silesaurus* and *Pseudolagosuchus* are a complete femur (TMM 31100–185) from the Dockum Group (Otis Chalk quarry 3) of Texas and a well preserved proximal portion of a femur (PEFO 34347) (Figs 2F–G) from the Blue Mesa Member (Chinle Formation) in Petrified Forest National Park, Arizona. First described as a possible ornithosuchian (Long & Murry 1995), the complete femur (TMM 31100–185) has the same derived character states present (i.e. a proximal groove, a small notched offset femoral head that is triangular in proximal view and a well-defined dorsolateral trochanter) as in *Eucoelophysis*, *Silesaurus* and *Pseudolagosuchus*. The proximal portion of the femur from the Petrified Forest also preserves the same suite of derived character states. Unfortunately, the anterior trochanter is not preserved in this specimen. The well-defined dorsolateral trochanter is much more pronounced in PEFO 34347 than in *Eucoelophysis* and PEFO 34347 has a slight, but more pronounced mediolateral proximal tuber in comparison with *Eucoelophysis* (Fig. 2F). The mediolateral proximal tuber is present plesiomorphically in all members of the Archosauria. The stratigraphic position of both PEFO 34347 and TMM 31100-185 suggest that members of the *Eucoelophysis*, *Silesaurus* and *Pseudolagosuchus* clade were present at the base of the Chinle Formation and in the Dockum Group (if the stratigraphy for the Dockum in Texas proposed by Lucas & Anderson (1993) is correct; but see Lehman & Chatterjee (2005) for an alternative interpretation).

Snyder Quarry 'dinosaur' material (Fig. 3)

AGE. Norian, Late Triassic.

OCCURRENCE. Petrified Forest Member, Chinle Formation (Lucas *et al.* 2003), Rio Arriba County, New Mexico, USA.

SPECIMENS. NMMNH P-30852, left premaxilla, left maxilla, right lacrimal, both dentaries and surangulars, left splenial, hyoid elements and two articulated anterior cervical vertebrae and cervical ribs; NMMNH P-30779, dorsal vertebra; NMMNH P-30780, dorsal vertebra; NMMNH P-33691, dorsal vertebra; NMMNH P-31661, sacrum; NMMNH P-31661, partial left scapulocoracoid; NMMNH P-29047, partial right ilium, nearly complete right ischium, and proximal tibia; NMMNH P-29046, right and left femora, complete tibia and proximal tibia and fibula; NMMNH P-31293, nearly complete left tibia; NMMNH P-29168, large tibia, fibula with fused astragalocalcaneum.

TAXONOMIC PLACEMENT. Two, possibly three distinct ornithodirans that are not referable to *Eucoelophysis*.

REMARKS. The Snyder Quarry contains a multitaxic assemblage of Norian vertebrates that is roughly stratigraphically equivalent to the nearby Canjilon Quarry and stratigraphically well below the famous Ghost Ranch *Coelophysis* Quarry (Zeigler *et al.* 2003). During the excavation of numerous phytosaur and aetosaur specimens, several disarticulated dinosaur-like elements were recovered. Heckert *et al.* (2000*b*, 2003) assigned all the dinosaur material from the quarry to *Eucoelophysis* sp. except one specimen, which they considered to represent an unnamed large coelophysoid (NMMNH P-29168). A portion of some of the smaller material was associated and may belong to one individual (NMMNH P-29046. Heckert *et al.* 2000*b*).

It was assumed by the original authors that all material of roughly the same size belonged to the same taxon. Our re-examination of the material suggests that at least two coelophysoids are present (one large and one small that may or may not be the same taxon), as well as a third taxon closely related to, but possibly outside of, Dinosauria.

Heckert *et al.* (2000*b*, 2003) assigned the majority of the material to *Eucoelophysis* based on the similarity of the scapulocoracoid, ischium and an appressed lateral surface of the tibia. This referral is faulty for several reasons. Firstly, the similarities of the scapula between the small Snyder quarry theropod and *Eucoelophysis* are found in all archosauriforms. Secondly, the ischium of *Eucoelophysis* is not typical of any dinosaur because it lacks a rim defining the acetabulum and a distinct articular surface with the pubis; it may not even belong with the rest of the holotype of *Eucoelophysis* as discussed above. Conversely, the ischium of the small Snyder quarry theropod clearly has a rim defining the open acetabulum and a clear articulation with the pubis. Thirdly, as mentioned previously, the lateral position of the appressed surface of the *Eucoelophysis* tibia cannot

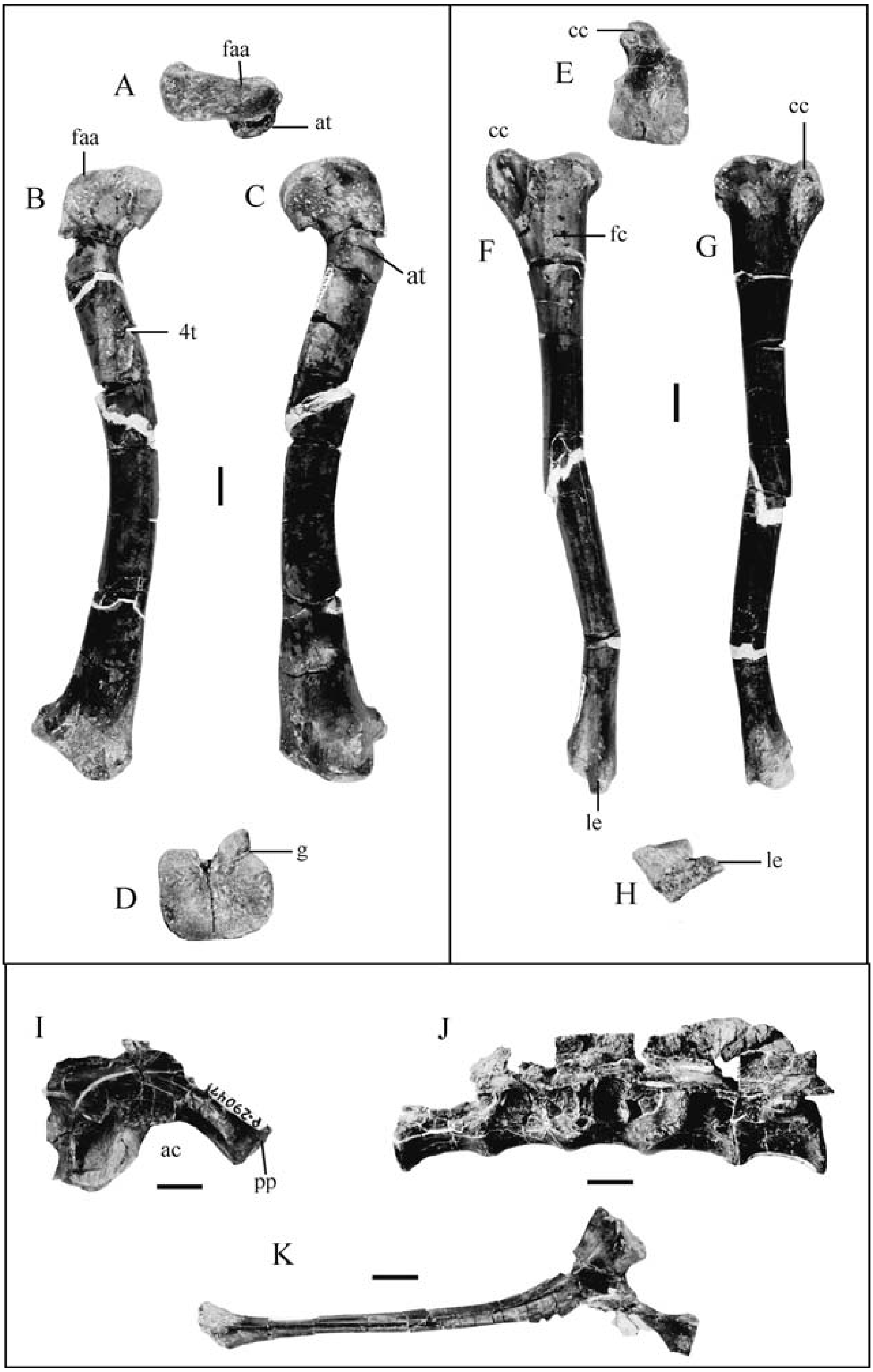

Figure 3 Informative elements from the Snyder Quarry coelophysoid. Left femur (NMMNH P-29046) in proximal (**A**), posterior (**B**), anterior (**C**) and distal (**D**) views. Left tibia (NMMNH P-29046) in proximal (**E**), posterior (**F**), anterior (**G**) and distal (**H**) views. Anterior portion of a right ilium (NMNNH P-29047) in lateral (**I**) view. Fused sacrum (NMMNH P-31661) in lateral (**J**) view. Nearly complete right ischium (NMMNH P-29047) in lateral (**K**) view. Abbreviations: **ac**, acetabulum; **at**, anterior trochanter; **cc**, cnemial crest; **faa**, facies articularis antitrochanterica; **fc**, fibular crest of the tibia; **g**, groove; **le**, lateral expansion of the distal portion of the tibia; **pp**, pubic peduncle; **4t**, fourth trocenter. Scale bars = 1 cm.

be considered homologous to the appressed lateral surface of the tibia of the small Snyder Quarry theropod. Heckert *et al.* (2000*b*, 2003) highlighted the major differences (e.g. difference in the proximal portion of the head) between the femora of *Eucoelophysis* and the Snyder Quarry theropod, but failed to recognise the importance of these differences. As mentioned previously, several characters of the proximal femur of *Eucoelophysis* preclude an assignment to the Dinosauria, whereas femora from the Snyder Quarry theropod are consistent with those of coelophysoids. Thus, in light of our reappraisal of the holotype of *Eucoelophysis*, the referral of the small coelophysoid material to *Eucoelophysis* is not tenable.

Most of the small Snyder Quarry theropod specimens (Figs 3A–I) appear to belong to at least two associated individuals (NMMNH P-30852, NMMNH P-29047 and NMMNH P-29046) of a coelophysoid similar to *Coelophysis bauri* and *Coelophysis rhodesiensis*. The preserved skull material (NMMNH P-30852) can be identified as a non-tetanuran theropod based on the presence of a sub-narial gap between the premaxilla and maxilla. This character may be a synapomorphy of Coelophysoidea (Rowe & Gauthier 1990), although recent analyses suggest that *Dilophosaurus*, which also has this character state, may be closer to Ceratosauria than to Coelophysidae (Carrano *et al.* 2002; Rauhut 2003). Traditionally, the 'L-shaped' lacrimal that is visible in dorsal view (present in the Snyder Quarry specimen) has been used as a dinosaur synapomorphy (e.g. Gauthier 1986), but Rauhut (2003) recognised that other basal archosaurs have a lacrimal exposed in dorsal view.

The cervical vertebrae found in direct association with the skull are clearly theropod, because they have two elongate pleurocoels on the lateral surface of the centrum (one on the anterior centrum and one on the posterior centrum), which are found in *Coelophysis* and other non-tetanuran theropods.

A variety of limb and girdle elements probably pertain to the small coelophysoid taxon. The scapulocoracoid (NMMNH P-31661) has a visible suture between the two elements. This suture closes during ontogeny in coelophysoids (Tykoski & Rowe 2004) and other archosaurs (Brochu 1995). The strap-like morphology of the scapular blade in this specimen is found in many theropods (Rauhut 2003) as well as *Eoraptor* (Sereno *et al.* 1993) and *Herrerasaurus* (Sereno 1993), but it is unclear if the distal end is expanded as in coelophysoids (Tykoski & Rowe 2004) and *Saturnalia* (Langer *et al.* 1999), because this is not preserved. The sacrum (Fig. 3J: NMMNH P-31661) also appears to be from a coelophysoid theropod. It has four fused sacral vertebrae and a caudo-sacral (five sacrals total) that articulated with the ilium. Having at least three sacral vertebrae is generally considered diagnostic of Dinosauria (Fraser *et al.* 2002), but the suchians *Sillosuchus* and *Shuvosaurus* also have at least four sacral vertebrae plus additional dorsosacral vertebrae. The pattern of attachment to the ilium and gracile morphology of the sacral ribs in the Snyder Quarry sacrum is nearly identical to *Coelophysis bauri*, but differs from *Saturnalia*, *Caseosaurus*, *Herrerasaurus*, *Eoraptor*, *Silesaurus*, *Poposaurus*, *Sillosuchus* and *Shuvosaurus*. NMMNH P-29047 includes a partial ilium with a fully open acetabulum (Fig. 3I) and an enlarged overhanging supraacetabular rim. This enlarged rim is present in coelophysoids (e.g. *Coelophysis* sp. (Padian 1986), *Coelophysis bauri*, '*Syntarsus*' *kayentakatae* and *Segisaurus*) as well as many other non-avian theropods (Rauhut 2003). The ischium (Fig. 3K) of NMMNH P-29047 is similar to other coelophysoids such as *Coelophysis bauri* and '*Syntarsus*' *kayentakatae* in that the pubic peduncle of the ischium is part of an elongate process separated from the iliac articulation of the ischium. This character is not present in *Herrerasaurus* (Novas 1993), or *Saturnalia* (Langer 2003), but is present in *Coelophysis bauri*, '*Syntarsus*' *kayentakatae*, *Coelophysis rhodesiensis* and some tetanuran theropods (Rauhut 2003). The anterior border of the proximal ischium is broken, so the position and morphology of the obturator process (Rauhut 2003) cannot be determined. The distal portion of the ischium ends in a small, but distinct posteriorly directed foot. This is similar to the condition in *Saturnalia* (Langer 2003), *Coelophysis rhodesiensis* (Raath 1969), *Segisaurus halli* (Camp 1936) and *Allosaurus* (Madsen 1976), whereas *Coelophysis* sp. (Padian 1986), *Coelophysis bauri* (Colbert 1989) and '*Syntarsus*' *kayentakatae* (Tykoski 1998) have a small symmetrical 'knob.'

The femora of NMMNH P-29046 (Figs 3A–D) have an offset femoral head and spike-like anterior trochanter separated from the femoral shaft, both of which are synapomorphies for Dinosauria. A distinct trochanteric shelf is present adjacent to the anterior trochanter as in *Silesaurus* (Dzik 2003), *Herrerasaurus* (Novas 1993), *Chindesaurus* (this study), *Saturnalia* (Langer 2003), *Coelophysis* sp. (Padian 1986), *Coelophysis bauri* and other basal theropods (Rauhut 2003). The dorsolateral trochanter forms a distinct ridge as in *Saturnalia* (Langer 2003), *Coelophysis* sp. (Padian 1986), *Coelophysis bauri* and other theropods. The fourth trochanter forms a low ridge with a ventral border that gradually grades into the shaft as with *Silesaurus* (Dzik 2003), *Coelophysis* sp. (Padian 1986) and *Coelophysis bauri*. In *Herrerasaurus* (Novas 1993), *Saturnalia* (Langer 2003) and other basal sauropodomorphs, the ventral border of the fourth trochanter terminates abruptly and is perpendicular to the femoral shaft. The distal femur of the small Snyder Quarry coelophysoid is similar to *Silesaurus* (Dzik 2003), *Saturnalia* (Langer 2003), *Coelophysis* sp. (Padian 1986), *Coelophysis bauri* and '*Syntarsus*' *kayentakatae* (among other basal theropods) in having a differentiated lateral and fibular condyle that is separated by a distinct sulcus.

Three small coelophysoid-like tibiae (NMMNH P-29046, NMMNH P-29047 and NMMNH P-31293) are preserved. All of the tibiae (e.g. Figs 3E–H) are identical in morphology and size. The proximal end of the tibia (Fig. 3E) has a well-developed cnemial crest that curves laterally with a blunt, squared-off anterior end. This results in the formation of a distinct, semicircular excavation on the lateral side of the tibia. All of these features are present in *Herrerasaurus* (Novas 1993), *Guaibasaurus* (our pers. obs.), *Saturnalia* (Langer 2003), basal sauropodomorphs (e.g. Galton & Upchurch 2004), *Coelophysis* sp. (Padian 1986), *Coelophysis bauri* and *Allosaurus* (Madsen 1976). In *Silesaurus* and *Eoraptor* (our pers. obs.), the cnemial crest does not arch laterally and has a rounded anterior extremity. In *Ceratosaurus* and tetanurans the lateral excavation widens so that the lateral condyle appears triangular in proximal view (Rauhut 2003). The appressed lateral surface on the tibial shaft described by Heckert *et al.* (2000*b*, 2003) is not present in *Coelophysis* sp. (Padian 1986) and *Coelophysis bauri* and cannot be homologous to a similar feature on *Eucoelophysis* (see previous

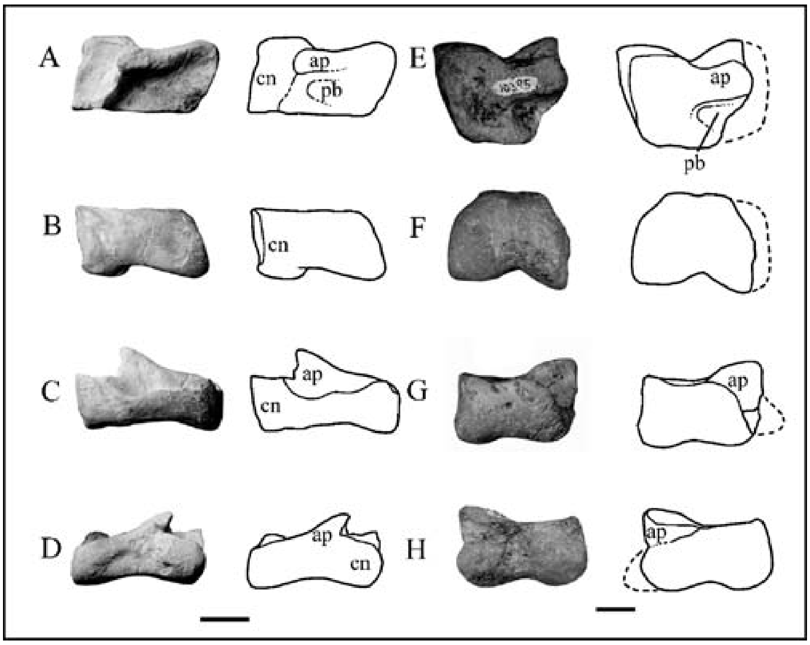

Figure 4 Comparison of the astragalocalcanea of *Coelophysis bauri* (AMNH FR 30576) (left) in dorsal (**A**), ventral (**B**), posterior (**C**) and anterior (**D**) views, with the astragulus of *Chindesaurus bryansmalli* (PEFO 33982) (right) in dorsal (**E**), ventral (**F**), posterior (**G**) and anterior (**H**) views. Abbreviations: **ap**, ascending process; **cn**, calcaneum; **pb**, posterior basin. Scale bars = 1 cm.

discussion). Among the preserved material, the appressed lateral surface is the only tibial character that separates the small Snyder Quarry theropod from *Coelophysis*.

The distal tibia is quadrangular in distal view (Fig. 3H). This shape is a result of a strong ridge on the posterior side with a slightly concave posterolateral face and a slightly convex posteromedial face and a developed descending process of the tibia. This overall quadrangular shape is found in *Saturnalia* (Langer 2003), basal sauropodomorphs (e.g. Galton & Upchurch 2004), *Coelophysis* sp. (Padian 1986), *Coelophysis bauri* and *Dilophosaurus*. In *Silesaurus* (Dzik 2003), *Eoraptor* (our pers. obs.), *Herrerasaurus* and *Chindesaurus*, the distal tibia is sub-rounded with little or no descending process. As in *Coelophysis* sp. and *Coelophysis bauri*, the descending posterolateral process of the tibia extends laterally well beyond the body of the tibia, whereas in *Saturnalia* and basal sauropodomorphs it does not. The anterior portion of the body of the distal tibia is also excavated more dorsally in *Coelophysis* and the Snyder Quarry material than in *Saturnalia* or basal sauropodomorphs.

A second possible dinosaur identified by Heckert *et al.* (2000*b*, 2003) is represented by a fused tibia and fibula that is missing the midshaft and fused with a complete astragalocalcaneum (Figs 5A–C) (NMMNH P-29268). The tibia bears a laterally curved and blunt cnemial crest that is similar to *Herrerasaurus*, *Saturnalia*, *Coelophysis* sp. and *Coelophysis bauri*. The fusion of the proximal tibia with the proximal fibula obscures the identification and morphology of the medial and lateral condyles. For the same reason, the presence or absence of the appressed tibial surface cannot be determined. Thus, the fused distal tibia, fibula and astragalocalcaneum complex cannot be distinguished from that of corresponding fused elements in *Coelophysis bauri*, *Coelophysis rhodesiensis* and '*Syntarsus*' *kayentakatae*. Furthermore, these taxa and NMMNH P-29268 all share the fusion of these elements (Rowe & Gauthier 1990; Tykoski & Rowe 2004). Therefore, this bone is assigned to Coelophysoidea indet.

An isolated ilium (Figs 6E-H) (NMMNH P-35995) assigned by Heckert *et al.* (2000*b*, 2003) to *Eucoelophysis* sp., although missing much of the iliac blade, shows remarkable similarities to the holotype ilium of *Caseosaurus crosbyensis* (Figs 6A–D: Hunt *et al.* 1998). Shared characters include a short, pointed anterior process of the ilium, a strong ridge running anterodorsally from the acetabular rim to the anterior preacetabular process, a wide, open angle between the anterior process and the pubic process, a moderately developed supra-acetabular rim and an ischiadic process with a rounded distal end that is dorsal to the distal end of the pubic process. None of these characters are found in *Coelophysis* sp. (Padian 1986), *Coelophysis bauri*, *Coelophysis rhodesiensis* (Raath 1969), '*Syntarsus*' *kayentakatae* (Rowe 1989), or *Dilophosaurus*. Unfortunately, with only an isolated ilium known for both NMMNH P-35995 and *Caseosaurus*, the affinities of this taxon are unclear. The strong anterodorsal ridge appears to be present in *Saturnalia* (Langer 2003) and *Efraasia minor* (Galton 1984: plate I, fig. 7; Yates 2003*a*), although in *Saturnalia* this ridge twists medially behind the preacetabular process of the iliac blade (our pers. obs.). It is found convergently in *Poposaurus* and *Shuvosaurus* (Long & Murry 1995), but it differs in these taxa in originating on the lateral extent of the dorsal surface of the supra-acetabular rim. The acetabulum in NMMNH P-35995 and *Caseosaurus* is at least partially perforate, but the broken margin makes it unclear to what degree it was open. The only iliac character state that diagnoses the Dinosauria according to Fraser *et al.* (2002) is a 'largely to fully perforate acetabulum.'

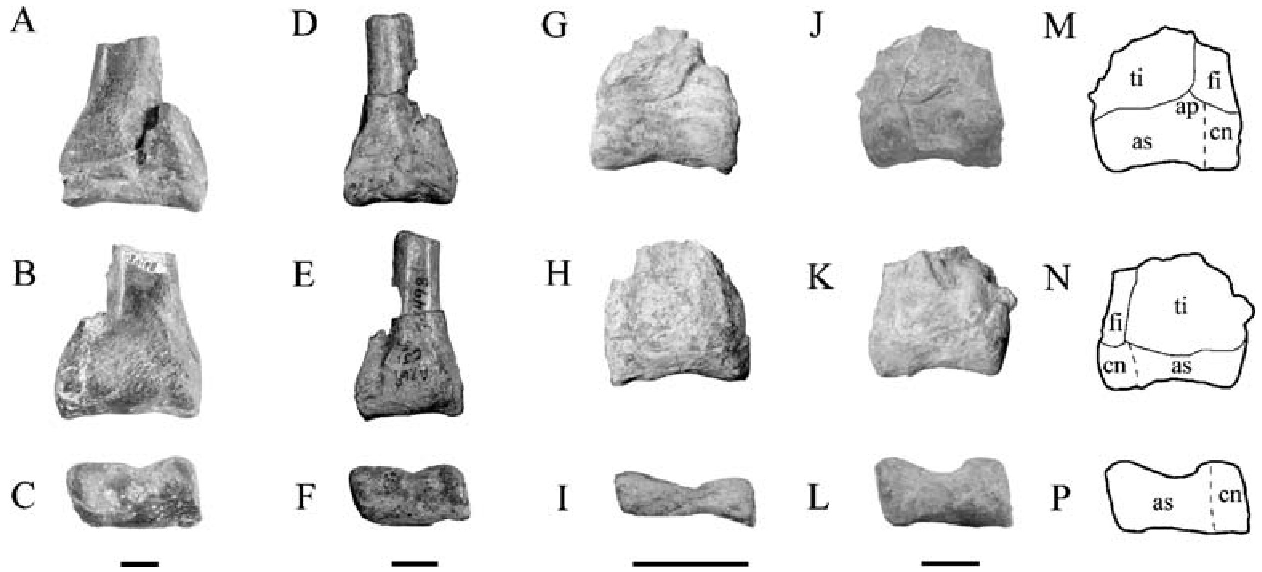

Figure 5 Distal portion of the large coelophysoid (NMMNH P-29168) right (reversed) tibia, fibula and complete astragalocalcaneum in anterior (**A**), posterior (**B**) and ventral (**C**) views. (Note: the proximal portion is not figured, but it is present in the specimen). Distal portion of the holotype left tibia, complete astragalus and calcaneum of '*Camposaurus arizonensis*' (UCMP 34498) in anterior (**D**), posterior (**E**) and ventral (**F**) views. *Coelophysis bauri* (AMNH FR 30614) left, juvenile tibia, fibula and complete astragalocalcaneum in anterior (**G**), posterior (**H**) and ventral (**I**) views. *Coelophysis bauri* (AMNH FR 30615) left, adult tibia, fibula and complete astragalocalcaneum in anterior (**J**), posterior (**K**) and ventral (**L**) views. Line drawing of the relative proportions of the tibia, fibula and astragalocalcaneum in anterior (**M**), posterior (**N**) and ventral (**O**) views (from *Coelophysis bauri* J–K). Abbreviations: **as**, astragalus; **cn**, calcaneum; **fi**, fibula; **ti**, tibia. Scale bars = 1 cm.

Because this is unclear in NMMNH P-35995 and *Caseosaurus*, it cannot be determined whether these specimens represent dinosaurs.

Several isolated vertebrae from the Snyder Quarry were also considered theropod by Heckert *et al.* (2000b, 2003). The large dorsal vertebrae NMMNH P-33691 is poorly preserved and does not possess any dinosaur synapomorphies. Two small dorsal vertebrae (NMMNH P-30779 and 30780) have strongly triangular transverse processes in dorsal view, a character shared with *Coelophysis bauri*, *Coelophysis rhodesiensis*, '*Syntarsus*' *kayentakatae* and other coelophysoids (Rowe & Gauthier 1990; Tykoski & Rowe 2004). Thus, these two specimens probably pertain to the coelophysoid theropod in the quarry. A single distal caudal vertebra catalogued under 'Theropoda' (NMMNH P-29996) is identical to corresponding vertebrae of *Coelophysis* sp. (Padian 1986), but cannot be differentiated from other archosaur distal caudal vertebrae.

In summation, the Snyder Quarry preserves two, possibly three distinct ornithodirans that are not referable to *Eucoelophysis*. The large remains (NMMNH P-29268) probably pertain to a coelophysoid; the smaller, better represented, remains belong to a coelophysoid closely related to *Coelophysis*. The presence of an appressed surface on the lateral side of the tibia in the small Snyder Quarry coelophysoid differentiates it from *Coelophysis*. Unfortunately, most of the phylogenetically informative character states in this material are also present in *Dilophosaurus* (except those listed above for the isolated astragalus). If *Dilophosaurus* is outside Coelophysoidea (e.g. Carrano *et al.* 2002; Rauhut 2003), then these characters only constrain the material to non-tetanuran theropods. Another ornithodiran from the Snyder Quarry is represented by a partial ilium (NMMNH P-35995) that may or may not pertain to a dinosaur and is similar to *Caseosaurus*.

Coelophysis bauri Cope, 1889

Age. Norian, Late Triassic.

Occurrence. 'Siltstone member,' Chinle Formation (Stewart *et al.* 1972), Rio Arriba County, New Mexico, USA.

Neotype. AMNH FR 7224, almost complete articulated skeleton.

Referred material. Numerous specimens from the Ghost Ranch *Coelophysis* quarry in the collections of several North American institutions. See Colbert (1989) for more detail.

Taxonomic placement. A valid taxon and basal member of the Neotheropoda.

Remarks. The tortured nomenclatorial history of *Coelophysis bauri* has been reviewed extensively (Padian 1986; Sullivan & Lucas 1999). As a result of the ICZN ruling, the name-bearing type is now a nearly complete skeleton (AMNH 7224) from the extensive Ghost Ranch assemblage (Colbert *et al.* 1992). It is clear that this spectacular assemblage of specimens represents a theropod taxon that is very similar to other Late Triassic and Early Jurassic coelophysoids. Characters of *Coelophysis bauri* satisfy all of the criteria for referral to Dinosauria.

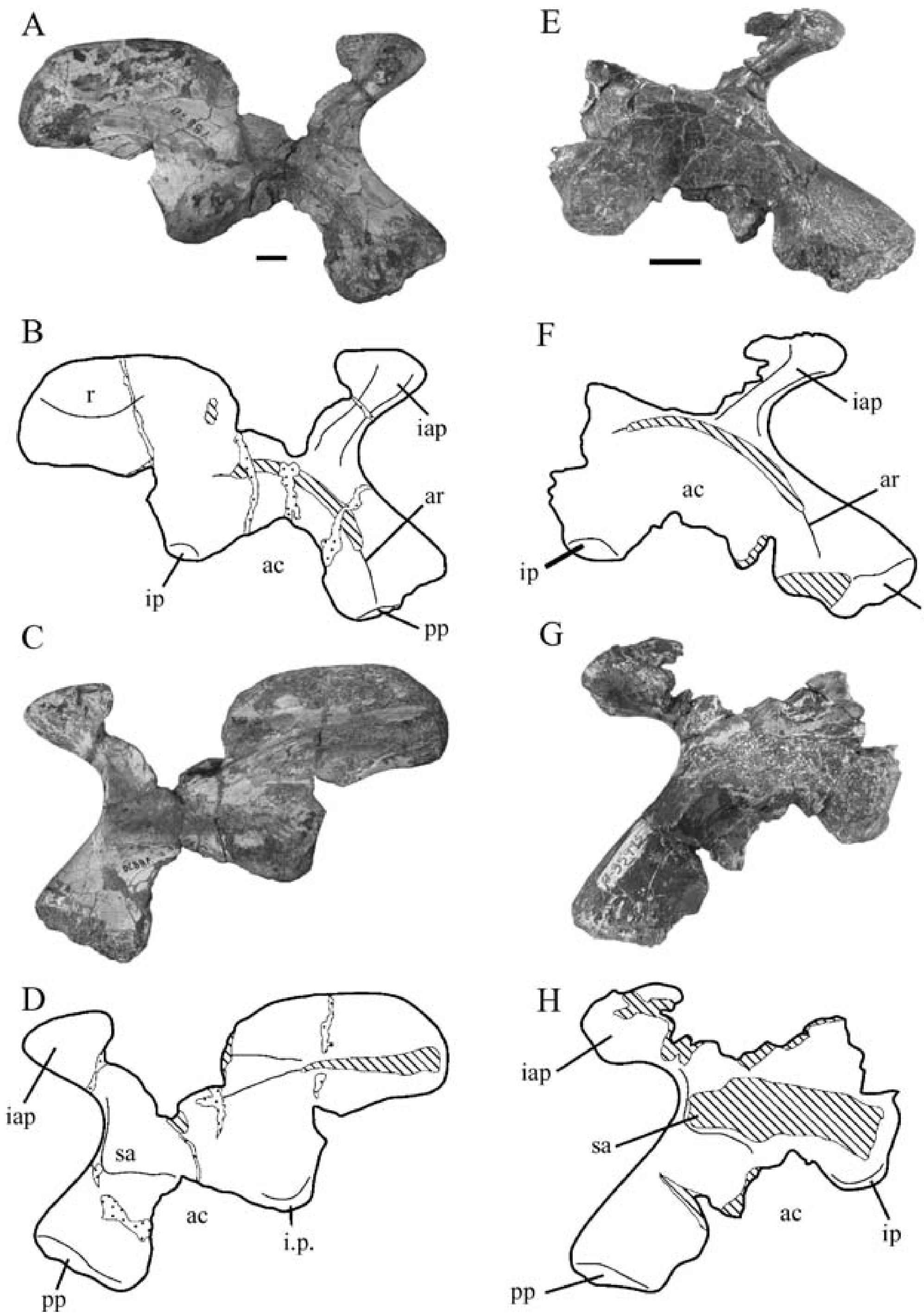

Figure 6 Holotype ilium (UMMP 8870) of *Caseosaurus crosbyensis* in lateral (**A, B**) and medial (**C, D**) views compared to a similar ilium from the Snyder Quarry (NMMNH P-35995) in lateral (**E, F**) and medial (**G, H**) views. Stippling represents breaks and gaps filled with adhesive; cross-hatching indicates broken surfaces. Abbreviations: **ac**, acetabulum; **ar**, acetabular rim; **iap**, anterior process of the ilium; **ip**, ischial peduncle; **pp**, pubic peduncle; **r**, rugosity; **sa**, sacral rib articulation. Scale bars = 1 cm.

Coelophysis bauri is well supported as a basal member of the Neotheropoda in numerous phylogenetic analyses (Gauthier 1986; Rowe & Gautier 1990; Carrano *et al*. 2002; Rauhut 2003). As one of the best known coelophysoids, *C. bauri* consistently falls out as one of the most derived members of the Coelophysidae (Rauhut 2003; Tykoski & Rowe 2004). Because of its unambiguous position as a dinosaur and coelophysoid theropod, the reevaluation of Late Triassic dinosaurs presented here uses *C. bauri* as a reference for comparison with other 'dinosaurian' taxa (Figs 4, 5G–L).

Coelophysis material of Cope

AGE. Norian, Late Triassic.

OCCURRENCE. ?Petrified Forest Member, Chinle Formation, New Mexico, USA.

MATERIAL. Diagnostic material includes AMNH FR 2706, pubis; AMNH FR 2705, a right ilium; AMNH FR 2708, another right ilium; AMNH FR 2722, fused sacral vertebrae.

TAXONOMIC PLACEMENT. The diagnostic portions of Cope's original syntype material belong to a coelophysoid similar to *Coelophysis bauri*.

REMARKS. Sullivan *et al.* (1996) and Sullivan & Lucas (1999) argued that the original *Coelophysis* material collected by Baldwin and described by Cope did not come from the AMNH *Coelophysis* Quarry as suggested by Colbert (1989). They hypothesised that the material was from the Petrified Forest Member rather than the 'siltstone member' (Stewart *et al.* 1972; Schwartz & Gillette 1994) where the *Coelophysis* Quarry lies, and probably from the holotype locality of *Eucoelophysis baldwini* (Sullivan & Lucas 1999). We agree with Sullivan *et al.* (1996) and Sullivan & Lucas (1999) that Baldwin's original material does not match well with the preservation of the *Coelophysis* Quarry material and probably derives from the Petrified Forest Member of the Chama Basin. However, Sullivan and colleagues make an unconvincing argument for placement of Baldwin's 'Arroyo Seco' '*Coelophysis*' material at the *Eucoelophysis* locality. Both the *Eucoelophysis* locality and the *Coelophysis* Quarry are equally remote from Arroyo Seco proper. Furthermore, fossiliferous outcrops of the Petrified Forest Member that have produced dinosaur material are found directly adjacent to Arroyo Seco (Downs 2005) and are near the historically main transportation routes in the valley. These represent more viable possibilities for the locality of Baldwin's material.

The designation of a neotype specimen of *Coelophysis bauri* from the Ghost Ranch *Coelophysis* Quarry left Cope's original syntype material of *Coelophysis* without a name. Sullivan & Lucas (1999) referred one specimen (AMNH FR 2706) to *Eucoelophysis baldwini* but, as discussed above, this referral cannot be substantiated.

Much of Cope's original '*Coelophysis*' material is well preserved. In the next section, we discuss some of the more diagnostic material from the original collection. Because the original syntypes are assignable to at least two taxa (see below), we will treat each element as a separate specimen to prevent future confusion.

Most of the original syntype material consists of limb fragments, pedal elements and vertebrae. The association of the material is not clear, but the similar preservation and similar coloured matrix around some of the elements suggest that the material was found in one area, possibly the same horizon. The limb fragments and pedal elements are undiagnostic within Archosauria as isolated elements. Moreover, AMNH FR 2725, a femur without a fourth trochanter and a small sulcus on the distal surface precludes an assignment to Dinosauria. This femur possibly belongs to a *Shuvosaurus*-like taxon because of the absence of the fourth trochanter and indicates that other archosaurs were discovered mixed together with the original *Coelophysis* syntype material. The limb fragments and pedal elements cannot be unambiguously assigned to the Theropoda. The vertebrae suffer from the same problem. None of the dorsal vertebrae preserve the neural arches, which are needed to differentiate archosaur vertebrae. Most of the cervical vertebrae have both anterior and posterior excavations of the centrum that have been previously referred to as pleurocoels (Colbert 1989; Rowe & Gauthier 1990; Rauhut 2003). These cervicals are indistinguishable from other coelophysoids.

The pelvic elements can be referred to the Theropoda. AMNH FR 2705, a right ilium, has non-tetanuran theropod or coelophysoid character states (depending on whether *Dilophosaurus* is a coelophysoid or a taxon closer to Tetanurae than to coelophysoids) including: a well developed supra-acetabular rim (or crest) that arcs ventrally at its lateral margin; a 'squared-off' distal portion of the posterior iliac process; a deep brevis fossa where the lateral ridge originates near the supra-acetabular rim; flattened dorsal margin of the iliac blade; and a fully perforated acetabulum. All of these features are also found in AMNH FR 2708, another right ilium. A right pubis (AMNH FR 2706), referred by Sullivan & Lucas (1999) to *Eucoelophysis baldwini*, has a small distally expanded boot that is identical to *Coelophysis bauri*. In proximal view, three regions of articulation are clearly defined: one that articulates with the ilium, one that indicates that the acetabulum which was at least partially open and one that articulates with the ischium. Recent repreparation of this element reveals the presence of both an obturator foramen and a pubic foramen, a coelophysoid character (Rowe & Gauthier 1990; Rauhut 2003; Tykoski & Rowe 2004). An anterior portion of an ilium attached to four fused sacral vertebrae (AMNH FR 2722) is identical to corresponding elements of *Coelophysis bauri* and the small Snyder Quarry coelophysoid. The ilium fragment indicates that the acetabulum was partially open and that the supra-acetabular rim was well developed.

Although none of the characters are directly diagnostic of *Coelophysis bauri*, there are no contradictory characters that would separate Cope's original syntype material from that of the neotype of *Coelophysis bauri* (AMNH FR 7224). In sum, the diagnostic portions of Cope's original syntype material belong to a coelophysoid similar to *Coelophysis bauri*.

Gojirasaurus quayi Carpenter, 1997

[='*Revueltoraptor lucasi*'; Hunt 1994; ='Herrerasaurid A'; Hunt *et al.* 1998]

AGE. Norian, Late Triassic.

OCCURRENCE. Bull Canyon Formation (= Cooper Canyon Formation), Dockum Group, Quay County, New Mexico, USA (Carpenter 1997).

HOLOTYPE. UCM 47221, partial skeleton.

REFERRED MATERIAL. Hunt (1994) referred the following isolated postcranial material to this taxon, none of which is diagnostic. NMMNH P-4666, pubis; NMMNH P-16607, teeth fragments; NMMNH P-16656, dorsal and caudal centra; NMMNH P-17258, vertebrae and fragmentary scapula; NMMNH P-17134, fragments of pelvis and dorsal and caudal vertebrae; UMMP 7274 (in part), two dorsal centra.

TAXONOMIC PLACEMENT. Coelophysoidea *incertae sedis*.

REMARKS. The holotype and only known specimen of *Gojirasaurus* (Parrish & Carpenter 1986: figs 11.5–11.7; Carpenter 1997: figs 2–8) was collected from the Bull Canyon (=Cooper Canyon) Formation in Quay County, New Mexico, from a bone bed containing microvertebrates, aetosaurs, a phytosaur (*Pseudopalatus* sp.) and *Shuvosaurus* sp. (Parrish & Carpenter 1986; Carpenter 1997). From this mixed assemblage of disarticulated bones, a tooth, four dorsal vertebrae, a scapula, a pubis, ribs, a chevron and a complete tibia were assigned to the holotype of *Gojirasaurus* (Carpenter 1997). Hunt *et al.* (1998) referred to this taxon as 'Herrerasaurid A' and referred several NMMNH specimens from the Bull Canyon Formation of New Mexico to this taxon. In his dissertation, Hunt (1994) named UCM 47221 '*Revueltoraptor lucasi*' and referred numerous NMMNH specimens to it. None of the specimens (listed above) from the Bull Canyon Formation referred to this taxon can be distinguished from those of *Shuvosaurus* or other archosaurs and, therefore, cannot be referred to *Gojirasaurus*. Hunt (1994) referred UCM 47221 to the Herrerasauridae based on the strap-like scapular blade, an elongate pubis and shortened posterior dorsal vertebrae.

Because the holotype of *Gojirasaurus* is from a mixed, disarticulated assemblage (Parrish & Carpenter 1986), the association of the fossil material remains problematic. The tibia and pubis of the holotype of *Gojirasaurus* belong to a coelophysoid theropod, whereas some of the included material cannot be differentiated from the contemporaneous *Shuvosaurus*-like taxon and most of the remaining material is non-diagnostic. The tooth was found isolated and spent tooth crowns are common in fossil quarries and cannot be assigned by proximity to a certain taxon in a mixed assemblage. Moreover, mediolaterally compressed, serrated teeth are present in a variety of archosaurs (e.g. 'rauisuchians') that lived contemporaneously with theropod dinosaurs (e.g. Long & Murry 1995).

The four centra and one neural arch cannot be clearly assigned to the Dinosauria and are not diagnostic to a more specific clade within Archosauria. Rauhut (2003) scored the vertebrae of *Gojirasaurus* into his basal theropod matrix, but none of the character states scored for the vertebrae of *Gojirasaurus* were unambiguous synapomorphies of any theropod clade. In addition, the vertebrae assigned to *Gojirasaurus* cannot be differentiated from the vertebrae of the suchian archosaur *Shuvosaurus*. The vertebrae of *Shuvosaurus* have a deep lateral fossa on the centrum, coarse ridges along the centrum face rims and the diapophysis and parapophysis are both on the transverse process, features also found in dinosaurian vertebrae. Even though many of the neural spines of the dorsal vertebrae of *Shuvosaurus* are low, the posterior dorsal neural spines are taller and comparable to those assigned to *Gojirasaurus*. Carpenter (1997) described hyposphene–hypantrum articulations on the single neural arch of a posterior dorsal vertebra of *Gojirasaurus*. However, the dorsal vertebrae of *Shuvosaurus* and other suchians (e.g. *Batrachotomus*, *Arizonasaurus* and *Desmatosuchus*) also have hyposphene–hypantrum articulations between the vertebrae. Therefore this character is not exclusive to dinosaurs.

In addition, Parrish & Carpenter (1986) described an edentulous premaxilla (UCM 52081) from the same quarry that is identical to the premaxilla of *Shuvosaurus* (Hunt 1994). New specimens from the Ghost Ranch *Coelophysis* Quarry (Nesbitt & Norell 2006) indicate that the skull of *Shuvosaurus* belongs to the postcranial skeleton of '*Chatterjeea*' (see full discussion below) as postulated by Long & Murry (1995). The size of the premaxilla suggests that the vertebrae of the animal would be smaller than those assigned to *Gojirasaurus*, but it is possible that a larger *Shuvosaurus*-like taxon would have vertebrae identical to those assigned to *Gojirasaurus*. Therefore, the dorsal vertebrae cannot be confidently assigned to a theropod. The ribs, gastralia and chevron are not diagnostic and also cannot be assigned to the Theropoda, let alone clades within Archosauria.

The scapula, represented by a nearly complete element, cannot be assigned directly to the Theropoda or Dinosauria, although it is not inconsistent with such an assignment. The scapula of *Gojirasaurus* shares no apomorphies with theropods such as *Coelophysis bauri*, '*Syntarsus*' *kayentakatae* and *Coelophysis rhodesiensis*. Although coelophysoids have an expanded distal margin of the scapula as found in *Gojirasaurus*, this feature is also found in a variety of other Triassic archosaurs such as stagonolepidids and taxa such as *Postosuchus* (Chatterjee 1985). Carpenter (1997) assigned a pubis with a pubic fenestra to *Gojirasaurus* that was later used by Rauhut (2003) to infer a close relationship to *Coelophysis bauri* and other coelophysoids. The presence of a pubic fenestra is not completely clear as most of the area is broken around the pubic fenestra; however, a small region of finished bone suggests that a pubic fenestra was present and, hence, it indicates that at least the pubis belongs to a coelophysoid (Rauhut 2003). The other character states of the pubis scored by Rauhut (2003) are symplesiomorphies within the Theropoda and probably Archosauria. The size of the pubis and scapula suggest that they belong to the same animal as the tibia, yet we are hesitant to assign all the bones to one taxon in the absence of unambiguous synapomorphies and the presence of other non-dinosaur archosaurs in the holotype quarry.

The tibia can be assigned to the Dinosauriformes based on the presence of a cnemial crest, two proximal posterior condyles and a well-developed slot at the distal end of the tibia that accepts the ascending process of the astragalus. All of these characters are present in *Silesaurus*, a non-dinosaur dinosauriform (Dzik 2003), and *Marasuchus* (Sereno & Arcucci 1994). The laterally-curved blunt cnemial crest is found in *Saturnalia*, basal sauropodomorphs, *Coelophysis bauri* and other theropods. The distal end is subrectangular with a small posterolateral process in distal view. Rauhut (2003: character 208) used this character to unite *Gojirasaurus*, *Dilophosaurus*, *Coelophysis bauri*, *Coelophysis rhodesiensis* and *Liliensternus*. A subrectangular distal end of the tibia is also found in basal sauropodomorphs such as *Plateosaurus* (Galton & Upchurch 2004) and *Riojasaurus* (R.B.I., pers. obs.); however, the *Gojirasaurus* tibia shares with *Coelophysis bauri*, *Coelophysis* sp., *Coelophysis rhodesiensis*, '*Syntarsus*' *kayentakatae*, *Liliensternus liliensterni*, *Dilophosaurus* and the Snyder Quarry small coelophysoid taxon a posterolateral process of the tibia that extends laterally well beyond the body of the tibia, and the anterior portion of the body of the distal tibia is also excavated more dorsally than in basal sauropodomorphs such as *Riojasaurus*. Tetanuran theropods and some neoceratosaurs lose the subrectangular shape in distal view (Rauhut 2003), so the *Gojirasaurus* tibia can be identified as a non-tetanuran theropod.

Our analysis indicates that the holotype of *Gojirasaurus* may include several taxa. Part of the holotype material, the tibia in combination with the pubis, can be assigned to a coelophysoid theropod. The only character that separates *Gojirasaurus* from *Coelophysis* is the robustness of the tibia; however, the *Coelophysis* specimen described by Padian (1986), although smaller, has very similar tibial proportions. Therefore, it is entirely possible, though not certain, that the material Padian (1986) described and *Gojirasaurus* belong to the same taxon. Because *Gojirasaurus* has no autapomorphies or a unique combination of character states, we consider it a metataxon, following Rauhut (2003), and Coelophysoidea *incertae sedis*. Furthermore, we restrict only the diagnostic material to the holotype, the tibia and pubis.

Bluewater Creek Member 'theropod' material

[= '*Cinizasaurus hunti*' Heckert 1997; = 'Theropoda, probable new genus and species' Heckert 1997; =Theropoda indet. Heckert *et al.* 2000*a*]

AGE. ?Late Carnian, Late Triassic.

OCCURRENCE. Bluewater Creek (= Mesa Redondo) Member of the Chinle Formation near Fort Wingate, New Mexico, USA.

MATERIAL. NMMNH P-18400, vertebrae, tibia, fragments; NMMNH P-18401, dorsal vertebrae.

TAXONOMIC PLACEMENT. Archosauriformes indet.

REMARKS. Heckert (1997) considered NMMNH P-18400 a distinct theropod, but later considered it 'not generically determinate' (Heckert *et al.* 2000*a*). There are no derived character states that it shares with theropods such as *Coelophysis bauri*, *Coelophysis* sp., *Coelophysis rhodesiensis*, or *Dilophosaurus*. The vertebrae cannot be differentiated from other basal archosaurs. The proximal tibia does not have a differentiated cnemial crest or lateral and medial condyles. The rest of the limb elements cannot be differentiated from those of other basal archosaurs.

Heckert *et al.* (2000a) concluded that NMMNH P-18401 represented a distinct theropod with 'highly derived' dorsal centra that had a ventral keel. The centra have no characteristics they share with *Coelophysis* and other theropods to the exclusion of all other archosaurs. Furthermore, a ventral keel on dorsal vertebrae is found in *Postosuchus* (Long & Murry 1995) and basal crocodylomorphs such as *Hesperosuchus* (Parrish 1991). Therefore, a ventral keel is not unique to theropods. Accordingly, both of these specimens should be considered Archosauriformes indet.

Santa Rosa Formation 'theropod' material

AGE. ?Late Carnian, Late Triassic.

OCCURRENCE. Los Esteros Member of the Santa Rosa Formation, Dockum Group, New Mexico.

MATERIAL. NMMNH P-13006, two fused sacral centra; NMMNH P-25749, fragmentary 'femur' and pubis; and NMMNH P-25750, metatarsals.

TAXONOMIC PLACEMENT. Archosauria indet.

REMARKS. Heckert *et al.* (2000*a*) considered this material to belong to theropods, most probably coelophysoids. NMMNH P-13006 consists of two fused sacral centra that Heckert *et al.* (2000*a*) referred to the Theropoda on the basis of being hollow. Hollow centra are also found in crocodylomorphs and *Shuvosaurus*, so this specimen should be considered Archosauria indet. The femur of NMMNH P-25749 may not be a femur because it is eroded and typical distinguishing features of the femur are not present. The proximal end of the pubis of this specimen has an obturator foramen, but this is plesiomorphic for Archosauria. There is no evidence for an acetabular rim on the proximal pubis that is present in dinosaurs with an open acetabulum. Therefore, NMMNH P-25749 cannot unambiguously be considered a dinosaur. Heckert *et al.* (2000*a*) compare NMMNH P-25750 to the metatarsals of *Eucoelophysis*, but because these elements cannot be differentiated from other archosaurs, neither specimen can be considered a theropod or dinosaur.

Arizona

Coelophysis sp. (Padian, 1986)

AGE. Norian, Late Triassic.

OCCURRENCE. Petrified Forest Member, Chinle Formation, Petrified Forest National Park, Arizona, USA.

MATERIAL. UCMP 129618, most of the pelvis and hindlimb, posterior dorsal vertebrae and caudal vertebrae; PEFO 33981, fragmentary skeleton with parts of the posterior vertebral column, pelvis and most of the hindlimbs; PEFO 33983, most of the posterior portion of the skeleton, under preparation. All of these specimens represent a coelophysoid of the same size and with a similar morphology.

TAXONOMIC PLACEMENT. *Coelophysis* sp.

REMARKS. Padian (1986) described a partial skeleton of *Coelophysis* from the Petrified Forest Member of the Chinle Formation of Petrified Forest National Park, Arizona. Whereas he recognised many similarities with *Coelophysis bauri* from Ghost Ranch, he also noted some small differences, especially in the robustness of the hindlimb. Recent recovery of new specimens of the same taxon from equivalent strata in Petrified Forest National Park suggests that the Petrified Forest taxon is generally larger and more robust than the Ghost Ranch material. We recognise that these are not features that can be used alone to distinguish separate taxa, but combined with the lengthy temporal gap between the Petrified Forest and Ghost Ranch specimens, we refrain from referring the Petrified Forest material to *C. bauri* pending additional preparation and detailed study.

Hunt (1998) attributed a proximal portion of a tibia (NMMNH unnumbered) from the Blue Mesa Member near Blue Mesa inside the Petrified Forest National Park to a theropod about the same size as the *Coelophysis* specimen described by Padian (1986). The proximal portion of the tibia bears a cnemial crest and two divided posterior condyles. These features are not diagnostic to Theropoda; thus, this specimen cannot be assigned to the Theropoda.

'Camposaurus arizonensis' Hunt *et al.*, 1998 (Fig. 5)

AGE. Late Carnian, Late Triassic.

Occurrence. Mesa Redondo Member, Chinle Formation (Lucas *et al.* 1997; Heckert & Lucas 2003), Apache County, Arizona, USA.

Holotype. UCMP 34498, fused tibiae, fibulae and astragalocalcanea of the right and left sides.

Referred material. Hunt *et al.* (1998) referred additional material (e.g. MNA V3091) to this taxon; however, see discussion below.

Taxonomic placement. Coelophysoidea indet.

Remarks. Long & Murry (1995) referred several isolated elements from the *Placerias* Quarry to Ceratosauria indet. Hunt *et al.* (1998) considered all of this material to represent a single theropod taxon, perhaps even a single individual. They concluded that this taxon was distinct from other Triassic theropods and designated matching right and left fused distal tibiae, fibulae and astragalocalcanea (Figs 5D–F) as the holotype of a new taxon, '*Camposaurus arizonensis*,' with the other *Placerias* Quarry 'theropod' material as paratypes. Because all the material is disarticulated and disassociated in the quarry, the referred material will be considered separately below.

Hunt *et al.* (1998) distinguished '*Camposaurus*' from *Coelophysis bauri* and '*Syntarsus*' (it is unclear whether they compared it to *Coelophysis rhodesiensis*, '*Syntarsus*' *kayentakatae*, or both) in having a ventral margin of the astragalus that is horizontal rather than concave in anterior and posterior view. We could not corroborate this difference when directly comparing '*Camposaurus*' to *Coelophysis bauri* (AMNH FR 30614 and AMNH FR 30615) material. One difference between '*Camposaurus*,' some specimens of *Coelophysis bauri* and all other theropods is that in ventral view, the concave depression on the anterior side of the astragalus is much stronger and more abrupt in *Coelophysis bauri*; however, some specimens of *Coelophysis bauri* have a morphology identical to '*Camposaurus*'. This is illustrated in Fig. 5, which shows that the range of variation between juvenile and adult *Coelophysis bauri* is comparable to the small difference between the ankle regions of most *Coelophysis bauri* specimens and '*Camposaurus*'. Therefore, we refer '*Camposaurus*' to Coelophysoidea indet. and consider it a *nomen dubium* following Downs (2000), Heckert (2001) and Rauhut (2003).

Other *Placerias* Quarry material

Additional isolated material was assigned to Ceratosauria indet. by Long & Murry (1995) and referred to '*Camposaurus*' by Hunt *et al.* (1998). None of these assignments can be substantiated. The femur figured by Long & Murry (1995: figs 191, 192A–E), UCMP 139622, is badly weathered, but has an offset proximal head, an apparent ventral sulcus on the femoral head, a moderately developed trochanteric shelf of the anterior trochanter and a facies articularis antitrochanterica. Therefore, we refer it to Saurischia indet. None of the dorsal vertebrae figured by Long & Murry (1995: fig. 192) (UCMP 177317, MNA V3091 [incorrectly listed as V2777 in Long & Murry 1995: fig. 192]) are diagnostic – they are equally comparable to many dinosauriforms as well as *Shuvosaurus*. The same is true for the sacral vertebrae (UCMP 138591, 178047, 178048, 178049) figured and listed by Long & Murry (1995: fig. 192Y; pp. 189, 238). The distal left tibia (UCMP 25793) that Long & Murry (1995) refer to '?Prosauropoda indet.' is not quadrangular in ventral view as present in *Saturnalia* (Langer 2003), other basal sauropodomorphs (e.g. Galton & Upchurch 2004) and *Coelophysis bauri*, but is very similar to *Silesaurus* (Dzik 2003), *Eoraptor* (R.B.I. pers. obs.) and *Herrerasaurus* (Novas 1993) in possessing a posterolateral process of the distal tibia that has an unexpanded distal tibial margin that is convex in distal view. Therefore, we refer UCMP 25793 to Dinosauriformes indet.

An unpublished distal femur from the *Placerias* Quarry (UCMP 25834), although similar to a *Shuvosaurus*-like taxon distal femora, is referable to Dinosauriformes indet. on the basis of a fibular groove that opens at an obtuse angle and a rounded fibular condyle (Parker & Irmis 2005). This is identical to the distal femur morphologies of *Silesaurus* (Dzik 2003), *Herrerasaurus* (Novas 1993) basal sauropodomorphs and coelophysoids. A second unpublished specimen from the *Placerias* Quarry (UCMP 25820) is a distal tibia. Although broken, it has a well-developed descending posterolateral process, a concave posterolateral margin in distal view and a well developed dorsal excavation for insertion of the ascending process of the astragalus. These features, in combination with a posterolateral process that extends well beyond the body of the tibia laterally, allow us to refer this specimen to Theropoda indet. It is possible that these two elements belong to '*Camposaurus*.'

Texas

Protoavis texensis Chatterjee, 1991

Age. Norian, Late Triassic.

Occurrence. Tecovas and Bull Canyon (= Cooper Canyon) Formations, Garza County, Texas, USA.

Holotype. TTUP 9200, partial skull and postcranial material of a large individual from the Post Quarry (Bull Canyon Formation).

Referred specimens. TTUP 9201, partial skull and skeleton of a small individual from the Post Quarry (Bull Canyon Formation); TTUP 9350–9380, various isolated elements from the Kirkpatrick Quarry (Tecovas Formation) (Chatterjee 1999). Many authors (Ostrom 1987, 1991, 1996; Chiappe 1995, 1998; Padian & Chiappe 1998; Witmer 2001, 2002) believe the associated specimens do not belong to a single individual.

Taxonomic placement. Non-tetanuran theropod in part.

Remarks. *Protoavis* Chatterjee,1991 is a problematic taxon that has been heavily discussed in the last decade because of its possible importance in understanding the origin and evolution of birds. Many skeletal elements and partial elements of '*Protoavis*' were collected from above the Post (Miller) Quarry in the 1980s and other specimens referred to *Protoavis* were collected from the underlying Tecovas Formation. The bones have been completely freed of matrix, some are heavily reconstructed and the identification of some of the elements have been questioned (Ostrom 1987, 1991, 1996; Chiappe 1995, 1998; Witmer 2001, 2002).

Most authors (e.g. Chiappe 1998; Padian & Chiappe 1998) consider *Protoavis* to represent a 'fauna' rather than a single taxon. The cervical vertebrae, which have been proposed to be unambiguously avian (Chatterjee 1991), are remarkably similar to the cervical vertebrae of the drepanosaurid *Megalancosaurus* (Renesto 2000) and isolated three-dimensionally preserved drepanosaurid cervical vertebrae from the Late Triassic fissure fills at Cromhall Quarry, England (Renesto & Fraser 2003). Moreover, other drepanosaurid bones are known from the *Protoavis* locality. Therefore, it is quite possible that parts of *Protoavis*, particularly the cervical vertebrae, belong to a drepanosaurid.

Witmer (2001) suggested that the braincase of the holotype of *Protoavis* is not avian, but may be coelurosaurian, noting that the braincase of *Protoavis* shares the following characters with coelurosaurs: cranial pneumatic recesses, specifically the caudal tympanic recess; a large cerebellar auricular fossa; a metotic strut; and a vagal canal opening onto the occiput (Chatterjee 1991; Witmer 1997, 2001). The presence of a coelurosaur in the Bull Canyon Formation would pull the hypothetical first appearances of theropod groups such as the spinosauroids and carnosaurs into the Late Triassic, in contrast to our findings that only coelophysoids are present in North America at that time. Theropod taxa remain rare in Late Triassic deposits and it is possible that representatives of the spinosauroids and carnosaurians were present in the Norian, but have not been found to date. Alternatively, the *Protoavis* braincase could belong to an aberrant taxon convergent upon coelurosaur braincase morphology. This would not be unprecedented, as the convergent case of *Shuvosaurus* and theropods has shown (Nesbitt & Norell 2006). Confirmation of the coelurosaurian position of the *Protoavis* braincase requires an extensive redescription and analysis of the material.

A redescription of *Protoavis* is beyond the scope of this paper; however, we wish to note the systematic implications of observations made by us during an inspection of the holotype and referred specimens suggesting that the astragalus/calcaneum (TTUP 9201) and the femur (TTUP 9200) of the holotype belong to a theropod. The femur exhibits the following dinosaur and theropod characters: offset femoral head, ligament sulcus, strongly developed facies articularis antitrochanterica of the femur (from Langer 2004), anterior trochanter with strong trochanteric shelf and a small posterior trochanter. Chatterjee (1999) remarked on the absence of a fourth trochanter; however, the area where the fourth trochanter would be present is not preserved in any specimen. The proximal portion of the femur is similar to that of coelophysoids as noted by Hutchinson (2001).

The astragalus and articulated calcaneum are also much like those of a coelophysoid or basal tetanuran theropod. The calcaneum is rectangular in dorsal view like that of all theropods. The astragalus retains a deep fibular facet, a character retained in basal dinosaurs and basal theropods, but lost in maniraptoran theropods (Holtz 1994; Rauhut 2003: character 213). Additionally, the fibular facet is formed by the calcaneum and the astragalus, another character lost in neoceratosaur and tetanuran theropods (Sereno *et al.* 1996; Rauhut 2003: character 219). The ascending process of the astragalus is small and is much more like that of a coelophysoid rather than *Allosaurus*. In addition, the astragalus and calcaneum articulated directly distal to the tibia and fibula; a character present in *Silesaurus*, *Eoraptor*, *Herrerasaurus*, ornithischians, *Saturnalia*, sauropodomorphs and coelophysoids (Sereno *et al.* 1996; Rauhut 2003: character 217). The astragalus of tetanuran theropods articulates with the anterior face of the distal end of the tibia. Therefore, we consider the femur and astragalocalcaneum to belong to a theropod most similar to a coelophysoid, but this identification can only be constrained to a non-tetanuran theropod. Much of the rest of the *Protoavis* material is fragmentary and may not be diagnostic; nevertheless, we refrain from discussion of this material pending a thorough redescription and review of all *Protoavis* material.

Shuvosaurus inexpectatus Chatterjee, 1993

AGE. Norian, Late Triassic.

OCCURRENCE. Bull Canyon (= Cooper Canyon) Formation, Dockum Group, Garza County, Texas, USA.

HOLOTYPE. TTUP 9280; the right and left premaxilla, the left maxilla, the right ectopterygoid, portions of the right pterygoid, a partial braincase, the left lacrimal, left and right frontal, the left and right prefrontal, portions of the left and right postorbital, the left quadratojugal, the left squamosal, the left quadrate, the left and right dentary and the left articular region including parts of the angular, articular and surangular, from the Post Quarry, Garza County, Texas, USA.

REFERRED MATERIAL. TTUP 9281 left squamosal and left palatine, TTUP 9282 braincase and partial skull, TTUP 10969, right quadrate, from the Post Quarry.

TAXONOMIC PLACEMENT. Suchian.

REMARKS. The holotype of *Shuvosaurus* is represented by an articulated skull and questionably associated postcrania (Rauhut 1997). The skull is highly autapomorphic; the jaws are edentulous, the maxilla is highly reduced, the orbit is large and the back of the skull is reduced (Chatterjee 1993; Rauhut 1997). This strange suite of characters persuaded Chatterjee (1993) to assign *Shuvosaurus* to the Ornithomimosauria, a group of Cretaceous coelurosaur theropods. As a consequence of Chatterjee's assignment, the Ornithomimosauria would have originated in the Norian. In addition, the presence of an ornithomimosaurid in the Late Triassic implies that many theropod lineages (e.g. Coelurosauria, Tyrannosauroidea, Tetanurae) must have also been present in the Late Triassic.

Chatterjee's (1993) interpretation was challenged by Long & Murry (1995) and Murry & Long (1997) for five reasons: (1) disarticulated *Chatterjeea* (a crocodile-line archosaur known only from the postcrania) postcrania and the cranium of *Shuvosaurus* were found intimately associated at the Post Quarry and at UCM locality 82021 (*Gojirasaurus* holotype quarry); (2) the relatively similar size of *Chatterjeea* and *Shuvosaurus*; (3) the lack of any other ornithomimosaurid remains in the Post Quarry; (4) the failure of Chatterjee (1993) to present a clear case for the ornithomimosaurid affinities of the skull of *Shuvosaurus* in his original publication; and (5) the similar stratigraphic ranges of both *Shuvosaurus* and *Chatterjeea*. According to Long & Murry (1995), if the *Shuvosaurus* skull material belongs to the postcrania of *Chatterjeea*, *Chatterjeea* would become a subjective junior synonym of *Shuvosaurus*.

In a re-analysis of the skull of *Shuvosaurus*, Rauhut (1997, 2003) also disagreed with Chatterjee's original assignment to Ornithomimosauria, but concluded that *Shuvosaurus* is probably an early theropod. Rauhut (1997, 2003) cites the following characters that place *Shuvosaurus* in the Theropoda: loss of the postfrontal; paraoccipital process directed ventrolaterally; lacrimal dorsoventrally elongated, inverted L-shaped and exposed on the skull roof; presence of a deep basisphenoid recess; and ectopterygoid with expanded medial part and deep ventral fossa. Rauhut (1997) notes that the first three characters have a wider distribution among archosaurs and that the last three characters represent synapomorphies of the Theropoda (Gauthier 1986).

Osmólska (1997) agreed with Chatterjee (1993) that *Shuvosaurus* possesses some similarities with advanced ornithomimosaurids; however, she noted that *Shuvosaurus* differed significantly in some key cranial characters (e.g. the lack of a parasphenoid capsule and the anterior extent of the antorbital fossa) from ornithomimosaurids.

Current work by Nesbitt & Norell (2006) and Nesbitt (2007) on a nearly complete holotype skeleton and referred specimens of *Effigia okeeffeae*, a *Shuvosaurus*-like taxon from the Late Triassic of New Mexico corroborates Long & Murry's (1995) hypothesis that the skull of *Shuvosaurus* and the postcranium of '*Chatterjeea*' belong to the same taxon. The 'crocodile-normal' ankle and presence of five unreduced metatarsals preclude an assignment to Theropoda for *Shuvosaurus* and suggest a relationship to suchians (Nesbitt & Norell 2006). Therefore, the theropod characters Rauhut (1997) used to place *Shuvosaurus* in Theropoda are convergent. In summary, *Shuvosaurus* is a suchian and not a dinosaur.

***Spinosuchus caseanus* von Huene, 1932 (Case 1927: figs 1–6, pl. 1)**

AGE. ?Late Carnian, Late Triassic.

OCCURRENCE. Tecovas Formation, Dockum Group, Crosby County, Texas, USA.

HOLOTYPE. UMMP 7507, articulated vertebral column.

TAXONOMIC PLACEMENT. Valid: Archosauriformes *incertae sedis*.

REMARKS. Case (1922) first studied UMMP 7507, a partial cervical and dorsal vertebral column that he referred to *Coelophysis* based on similarity with Cope's original '*Coelophysis*' material as described and figured by Huene (1906, 1915). Case (1927) later described and figured this specimen (Case 1927: figs 1–6, pl. 1), reiterating its referral to *Coelophysis*. Huene (1932) recognised that this specimen was distinct from Cope's '*Coelophysis*' material and named it the type of a new species of 'podokesaurid' theropod, *Spinosuchus caseanus*. Padian (1986) and Murry & Long (1989) both disputed the dinosaurian affinities of this specimen. Hunt *et al.* (1998) referred *Spinosuchus* to 'cf. Theropoda *incertae sedis*' on the basis of hollow vertebral centra because '*Spinosuchus* is clearly not a flying reptile,' referring to the notion that hollow centra are only found in pterosaurs and theropod dinosaurs. However, hollow centra are found in a variety of non-ornithodiran archosaurs (e.g. basal crocodylomorphs and *Shuvosaurus*). Furthermore, recrystallisation of the interior of vertebrae can make them appear hollow. Although the preserved cervical vertebrae in UMMP 7507 have marked fossae, they lack any clear excavations or pleurocoels, which are found in *Coelophysis bauri*, *Coelophysis rhodesiensis*, '*Syntarsus*' *kayentakatae* and nearly all other theropods (Rauhut 2003). There are no other vertebral character states that distinguish *Spinosuchus* from other archosauriforms other than the autapomorphic neural spines. Richards (1999) considered *Spinosuchus* to be a trilophosaurid, possibly even synonymous with *Trilophosaurus buettneri*. It is clear that the vertebrae of *Spinosuchus* differ from those of *Trilophosaurus* (Gregory 1945) and the other characters (developed interzygapophyseal laminae and abrupt progression of dorsal displacement of the parapophyses in the cervico-dorsal transition) that Richards (1999) used to ally *Spinosuchus* with *Trilophosaurus* are archosauromorph symplesiomorphies or are not restricted to only in *Spinosuchus* and *Trilophosaurus*. In summary, *Spinosuchus* is valid as it bears an autapomorphy, but cannot be assigned to the Dinosauria and must be considered Archosauriformes *incertae sedis*.

PUTATIVE HERRERASAURIDS

***Caseosaurus crosbyensis* Hunt *et al.*, 1998 (Fig. 6)**

AGE. ?Late Carnian, Late Triassic.

OCCURRENCE. Tecovas Formation, Dockum Group, Crosby County, Texas, USA.

HOLOTYPE. UMMP 8870, partial left ilium.

TAXONOMIC PLACEMENT. Dinosauriformes.

REMARKS. *Caseosaurus crosbyensis* (Figs 6A–D) was named by Hunt *et al.* (1998) for an isolated partial ilium collected by E. C. Case from the Tecovas Formation of Crosby County, Texas. Although he noted differences, Case (1927) referred the specimen to *Coelophysis* sp. based on comparison with Huene's (1906, 1915) figures of Cope's original type material. Long & Murry (1995) referred the specimen to *Chindesaurus bryansmalli* because they concluded that the fragment of the posterior iliac blade in the holotype was identical to the Texas ilium. Hunt *et al.* (1998) created the new taxon *Caseosaurus crosbyensis* because they suggested that it was distinct from *Chindesaurus* in having a reduced brevis fossa, differently placed medial longitudinal ridge and a thinner posterior blade. Both Long & Murry (1995) and Hunt *et al.* (1998) hypothesised that UMMP 8870 was a herrerasaurid.

We cannot substantiate the differences between the holotype of *Chindesaurus* and *Caseosaurus* identified by Hunt *et al.* (1998). The thickness of the posterior blade and the differences in the medial ridge are probably consequences of size differences between the two specimens. There is no brevis fossa (see Fig. 1A for illustration of a true brevis fossa) on either specimen (*contra* Hunt *et al.* 1998; *contra* Langer 2004). There is a posterolateral depression on the ilium, but it is not associated with a distinct ridge as in our (and Novas's (1992)) definition of a true brevis fossa. In fact, *Caseosaurus* and *Chindesaurus* appear to be united by a possible single synapomorphy, the presence of a triangular rugosity on the posterior iliac blade. Unfortunately, *Chindesaurus* does not preserve the anterior portion of the ilium, which has a distinct anterodorsal ridge that is shared with a specimen from the Snyder Quarry (NMMNH P-35995). As noted above, this ridge is found in *Saturnalia* and *Efraasia minor*. In the ilium of a referred specimen of *Saturnalia* (MCP 3846-PV), this anterodorsal ridge twists to form the anterior margin of the preacetabular process, whereas the ridge is posterolateral to the anterior margin of the preacetabular process in *Caseosaurus* and *Efraasia*. *Efraasia* differs from the *Saturnalia* and *Caseosaurus* ilia in having a distinct brevis fossa (Yates 2003*a*). Interestingly, *Plateosaurus*, a basal sauropodomorph, has apparently lost the brevis fossa (Yates 2003*a*). The current incompleteness of *Caseosaurus* and *Chindesaurus* prevents us from formally synonymising them. The ilium of *Caseosaurus* also cannot be differentiated from a partial ilium (NMMNH P-35995) from the Snyder Quarry. The incompleteness and equivocal distribution of present character states means that *Caseosaurus* cannot be unambiguously assigned to the Herrerasauridae or Dinosauria. The specimen is assignable to Dinosauriformes because it has at least a partially open acetabulum, but position within this clade is ambiguous because it lacks a brevis fossa. If *Caseosaurus* is assignable to *Chindesaurus*, it would be a saurischian dinosaur as a consequence and the lack of a brevis fossa would represent the retention of the plesiomorphic state in some basal saurischians.

***Chindesaurus bryansmalli* Long & Murry, 1995** (Fig. 7)

AGE. Norian, Late Triassic.

OCCURRENCE. Petrified Forest Member, Chinle Formation, Petrified Forest National Park, Arizona, USA.

HOLOTYPE. PEFO 10395, fragmentary skeleton including vertebrae from the cervical, dorsal, sacral and caudal regions; complete right femur; proximal left femur; proximal right tibia; distal right tibia; right astragalus; pelvic fragments; ribs; chevrons.

REFERRED MATERIAL. PEFO 33982, proximal femur; nine vertebrae; ilium fragment, bone fragments; TMM 31100–523, a proximal end of a femur.

TAXONOMIC PLACEMENT. Valid taxon: probably a basal saurischian dinosaur.

REMARKS. The holotype specimen (PEFO 10395) of *Chindesaurus bryansmalli* was collected from the Dinosaur Hollow Locality (PFV 20) in the Petrified Forest Member of Petrified Forest National Park. Long & Murry (1995) tentatively described this taxon as a herrerasaurid based on the morphology of a referred ilium (UMMP 8870; the holotype of *Caseosaurus*) and a radial pattern of ridges located on the centra rims of the posterior dorsal vertebrae. Novas (1997) considered *Chindesaurus* a sister taxon of *Herrerasaurus* (within Theropoda) based on the presence of two sacral vertebrae (considered a reversal), anteroposteriorly short dorsal vertebrae and a transversely narrow pubic apron. Novas (1997) considered UMMP 8870 referable to *Chindesaurus* and noted herrerasaurid characters such as the lack of a brevis shelf and an anterior iliac notch with a lateral vertical ridge.

Hunt (1996) considered *Chindesaurus* and a few other undescribed 'herrerasaurs' to represent a new clade of herrerasaurs, distinct from *Herrerasaurus* and *Staurikosaurus*. However, the other putative herrerasaurs are not diagnosable (see discussion below). Hunt *et al.* (1998) also referred *Chindesaurus* to the Herrerasauridae, but they removed UMMP 8870 from the hypodigm and referred it to a new taxon, *Caseosaurus crosbiensis* (see *Caseosaurus* discussion above). Rauhut (2003) considered *Chindesaurus* to represent a *nomen dubium* and did not consider it in his analysis. Conversely, Langer (2004) suggested that *Chindesaurus* represents a basal saurischian that is closer to Herrerasauridae than Eusaurischia (the most exclusive saurischian clade containing Sauropodomorpha and Theropoda). Langer (2004) defined this stem as Herrerasauria, but the placement of *Chindesaurus* in this taxon is only tentative because Langer did not include *Chindesaurus* in his phylogenetic analysis. Langer (2004) also considered UMMP 8870 referable to *Chindesaurus* (*contra* Hunt *et al.* 1998).

The incompleteness of *Chindesaurus*, like most of the fossil specimens discussed herein, hinders determination of its precise taxonomic affinities. When first recovered, it was considered a sauropodomorph (Meyer 1986) and several characters, such as a more distally placed fourth trochanter and an ascending process of the astragalus that is situated laterally, strongly support this affinity. However, the lack of a pronounced lip just anterior to the ligament sulcus on the ventral surface of the femoral head and a weakly formed groove for the crista tibiofibularis suggest that it is more basal than *Saturnalia* (considered by Langer (2003) the basal-most sauropodomorph) and *Coelophysis bauri*. With the exception of the single cervical centrum in the holotype, Long & Murry (1995) did not provide comparisons with sauropodomorphs in their original description of *Chindesaurus*.

No identifiable skull material, with the exception of an incomplete, laterally compressed, recurved serrated tooth, is present in the holotype. Although Long & Murry (1995) did not mention this tooth, it was described by Hunt *et al.* (1998) who referred it to the holotype. This assignment is questionable, given the lack of comparable material and the taphonomic tendency for isolated teeth to be deposited with unrelated remains during burial.

The cervical region of PEFO 10395 is only represented by an incomplete cervical centrum (Long & Murry 1995: figs A–C). This bone consists of only the anterior and posterior ends but enough is preserved to show that the vertebrae are elongate (centra are at least twice as long as high) as in *Marasuchus*, *Herrerasaurus*, basal theropods and sauropodomorphs. The dorsal vertebrae are axially shorter than in dinosaurs and most basal archosaurs, although not as much as the posterior dorsal vertebrae of *Herrerasaurus* and *Staurikosaurus* (Langer 2004). However, only a few dorsal vertebrae are preserved, precluding precise placement in the axial column; therefore, the character uniting *Herrerasaurus*, *Staurikosaurus* and *Chindesaurus* (axial shortened posterior dorsal vertebrae) cannot be unequivocally evaluated. The dorsal vertebrae have oval-shaped fossae just ventral to the neurocentral suture that are also present in nearly all archosaurs.

At least four iliac fragments are present in PEFO 10395, including the pubic peduncles of the right and left side, a dorsal portion of the iliac blade and a portion of the left posterior iliac blade (Long & Murry 1995: figs 183a–f). As previously mentioned, Long & Murry (1995) considered

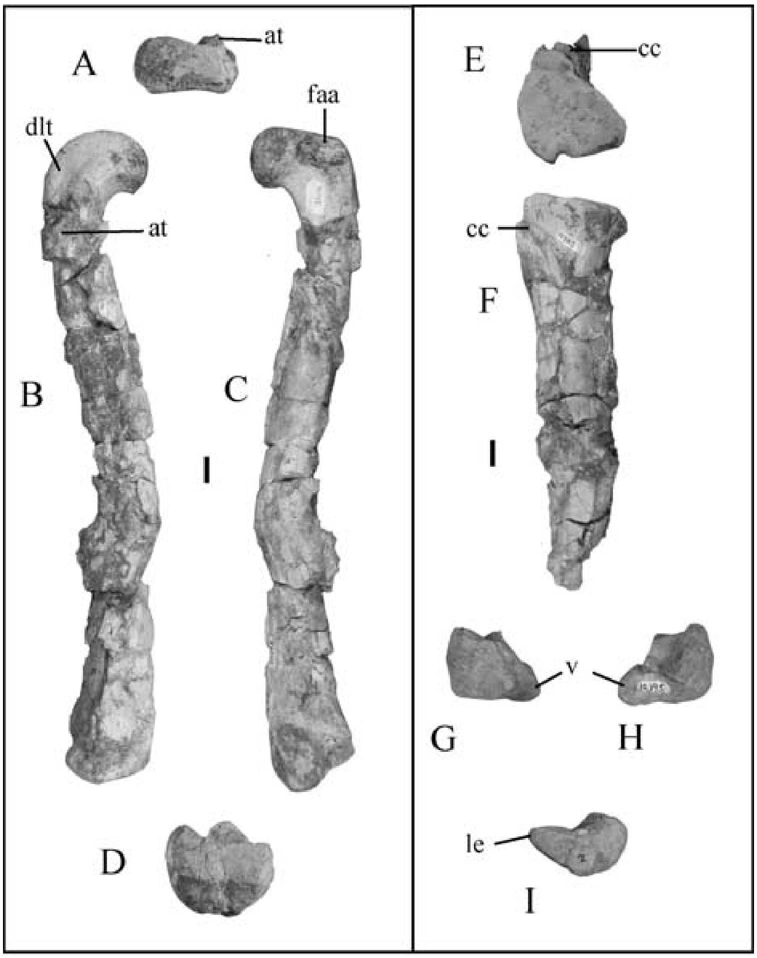

Figure 7 Informative elements from the holotype of *Chindesaurus bryansmalli* (PEFO 33982). The right femur in proximal (**A**), anterior (**B**), posterior (**C**) and distal (**D**) views. The right proximal portion of the tibia in proximal (**E**) and medial (**F**) views and the right distal portion of the tibia in posterior (**G**), anterior (**H**) and distal (**I**) views. See Figs 4E–H for the ankle and Figs 6E–H for the ilium fragments of *Chindesaurus*. Abbreviations: **at**, anterior trochanter; **cc**, cnemial crest; **dlt**, dorsolateral trochanter; **faa**, facies articularis antitrochanterica; **le**, lateral expansion of the distal portion of the tibia. Scale bars = 1 cm.

UMMP 8870 to be identical to the preserved iliac elements of *Chindesaurus* and used this specimen as the basis of their description and referral to the Herrerasauridae. The fragments of PEFO 10395 superficially resemble portions of UMMP 8870, but only a triangular rugosity on the dorsolateral surface of the posterior iliac blade is a potential synapomorphy that links the two specimens. Despite this possible synapomorphy, the stratigraphic and geographical separation between PEFO 10395 and UMMP 8870 combined with the fragmentary condition of the *Chindesaurus* holotype material warrants caution in assigning UMMP 8870 to *Chindesaurus*. A referred specimen (PEFO 33982) contains another iliac fragment, but this specimen is too incomplete to offer any further resolution. Beyond the posterior iliac blade character described above, the preserved iliac fragments are mostly uninformative. They indicate that the acetabular rim extended down most of the length of the pubic peduncle and that the acetabulum was not completely open as in theropods and most sauropodomorphs.

The pubis is fragmentary and contains little information; however, a proximal fragment confirms the presence of an obturator foramen. Elements identified by Long & Murry (1995) as the ischium are uninformative.

The femur (Figs 7A–D) possesses several dinosaur-like features such as a posterior expansion of the femoral head and a facies articularis antitrochanterica. However, the proximal end of the femur lacks a ligament sulcus on the posterior side of the medial femoral head, precluding assignment to any specific clade within Dinosauria. The proximal articular surface is completely convex. The lateral edge between the dorsal extent of the femur and the anterior trochanter is flat and slightly expands anteriorly. This is also present in *Saturnalia* and *Coelophysis bauri*. A ventrally arched trochanteric shelf very similar to that of *Herrerasaurus*, *Coelophysis bauri* and *Saturnalia* is present and is confluent with a spike-like anterior trochanter. The anterior trochanter is spike-like and appressed to the lateral face of the femur as in *Herrerasaurus*, but does not form the dorsally projecting, finger-like process that is separated from the femoral shaft as in *Coelophysis bauri, Dilophosaurus, 'Syntarsus' kayentakatae* and *Coelophysis rhodesiensis*. The fourth trochanter is low, located on the posterior side and has a distinct, dorsoventrally elongated fossa for the *m. caudofemoralis longus* on the medial side. Overall, the femur (Fig. 7; Long & Murry 1995: figs 184–187) is similar to that of *Herrerasaurus*. The femur differs from that of *Herrerasaurus* in a more distally situated fourth trochanter and a fourth trochanter that is low and lacks the abrupt ventral (pendant-shaped) border present in *Herrerasaurus*. There may be an anteroproximally located keel on the proximal femur shaft as in *Herrerasaurus* (Novas 1993); however, the poor preservation of the femoral shaft does not allow confirmation. The posterior surface of the proximal portion of the femur bears a rugose tuber that was reported only in the femur of *Herrerasaurus* (Novas 1993). Furthermore, although the distal portion of the femur of *Chindesaurus* is broken, a weakly developed groove between the lateral and fibular condyles is present, differing from the condition in *Herrerasaurus* and similar to that of *Saturnalia*, *Coelophysis bauri* and more derived saurischians.

The proximal portion of the right tibia (Figs 7E, F) is poorly preserved (Long & Murry 1995: fig. 188). The curvature of the medial surface suggests that a cnemial crest was present, although the anterior portion of this element is missing (Langer 2004: fig. 2.9l). Overall the form of the tibia in proximal view resembles that of *Marasuchus* and *Lagerpeton*, as well as *Coelophysis bauri*, sauropodomorphs and ornithischians. *Chindesaurus* is unique in that the posterior groove separating the fibular and internal condyles is strongly situated medially so that the medial condyle is approximately one-third the size of the lateral condyle. The posterior edge of the lateral condyle is straight in proximal view, unlike any other dinosauromorph or dinosaur.

The distal portion of the right tibia (Figs 7G–I) is also present. The anterior margin of the distal tibia is broken, so it is not clear if it was subrounded and mediolaterally expanded in distal view as in *Coelophysis bauri*, or like the more equant condition in *Herrerasaurus*, *Saturnalia* and *Staurikosaurus*. *Chindesaurus* differs from *Coelophysis bauri*, other basal theropods, *Saturnalia*, *Plateosaurus* and *Riojasaurus* in that the posteromedial margin of the distal tibia is convex in distal view rather than concave. This is the plesiomorphic state and is also found in *Herrerasaurus*, *Silesaurus*, *Marasuchus* and *Lagerpeton*. The posterolateral margin of the distal tibia is also convex in distal view as in *Saturnalia*, *Herrerasaurus*, *Silesaurus* and basal dinosauriforms. In *Lesothosaurus* (and other ornithischians), most basal sauropodomorphs (e.g. *Plateosaurus* and *Riojasaurus*) and basal theropods (e.g. *Coelophysis bauri* and *C. rhodesiensis*), this margin is either straight or slightly concave.

Long & Murry (1995) considered the right astragalus (Figs 4E–H) to be complete and described the overall shape in ventral view as 'glutealiform' (i.e. buttocks-shaped), considering this an autapomorphy of the taxon. Murry & Long (1997) also considered the absence of a fibular facet on the astragalus an autapomorphy. We agree that the large ventral cleft is unique; however, the lateral portion of the element, including the fibular facet, is broken and worn, giving the appearance of a mediolaterally shortened element and a fibular facet that is directed laterally (and easily mistaken for an articular surface for the calcaneum). Although it is unclear how much of the lateral portion is missing, it is apparent that the fibular facet is directed dorsolaterally as in *Marasuchus*, *Herrerasaurus*, *Saturnalia* and *Coelophysis bauri* and unlike the condition in basal sauropodomorphs such as *Riojasaurus* (Fraser *et al.* 2002) and *Plateosaurus* (Galton & Upchurch 2004) in which the lateral face of the ascending process is flush with the lateral face of the astragular body. The astragalus is almost twice as wide as tall (Long & Murry 1995: figs 189f–l) and subrectangular in anterior view. The anteromedial corner is acute in proximal view, a synapomorphy of Dinosauromorpha (Sereno 1991), although not as acute as in *Agnostiphys* (Fraser *et al.* 2002). The ascending process is low. An anterior hollow in the base of this process is present in *Chindesaurus*, *Agnostiphys*, *Herrerasaurus*, *Silesaurus* and *Marasuchus*, but absent in *Lagerpeton* (Fraser *et al.* 2002; Dzik 2003). Posterior to the ascending process is a deep 'dorsal basin' (= posterior basin) that receives the descending process of the tibia (Novas 1989). This posterior articulation with the tibia is found in *Herrerasaurus*, *Agnostiphys*, *Saturnalia*, ornithischians, basal sauropodomorphs and theropods (Novas 1989; Fraser *et al.* 2002; Langer 2004), but a deep dorsal basin separated from the rest of the tibial facet by a small ridge is only present in *Agnostiphys*, *Herrerasaurus*, *Saturnalia* and some basal sauropodomorphs (e.g. *Unaysaurus*). It is absent in basal theropods and some sauropodomorphs (e.g. *Riojasaurus* (specimen number PVL unnumbered '6'): Langer 2004). Langer (2004) stated that this basin with a dividing ridge was absent in *Guaibasaurus*, but this feature is obscured in the only well preserved astragalus (in the paratype MCN-PV-2356) because it partially articulates with the distal tibia.

The mélange of preserved character states in *Chindesaurus* makes for a difficult and ambiguous phylogenetic placement. Characters shared by *Chindesaurus* and *Saturnalia* are also present in *Herrerasaurus* and other taxa, or are plesiomorphic (two sacral vertebrae). *Chindesaurus* differs from *Saturnalia* in the presence of a distal tibia that has a convex posteromedial margin in distal view. Autapomorphies of *Chindesaurus*, in addition to the ventral cleft of the astragalus described by Long & Murry (1995), include a proximal tibial intercondylar groove that is strongly situated medially and a posterior edge of the fibular condyle of the proximal tibia that is straight in proximal view. The 'glutealiform' outline of the astragalus, considered an autapomorphy by those authors, cannot be confirmed given the incomplete lateral margin.

Currently, the herrerasaurid affinities of *Chindesaurus* cannot be substantiated because of the great similarity of the preserved parts with *Saturnalia* and the absence of much of the skeleton. According to our dinosaur criteria and shared character states with *Herrerasaurus*, *Chindesaurus* is a valid taxon and is a member of the Dinosauria and possibly a basal saurischian. Unfortunately, until more complete material is recovered for *Chindesaurus* and an explicit phylogenetic analysis is completed, its exact affinities cannot be determined.

Long & Murry (1995) assigned TMM 31100-523, a proximal femur, to *Chindesaurus* based on very similar measurements and morphology. Conversely, Hunt *et al.* (1998) argued that Long & Murry's (1995) assignment was not based on apomorphies and concluded that the femur belongs to an indeterminate dinosaur. Although Long & Murry (1995) did not explicitly state the similar features, TMM 31100-523 and the holotype of *Chindesaurus* share a combination of characters not present in other ornithodirans. These include the absence of a ligament sulcus, a rounded medial head, a weakly developed posterolateral condyle and a completely convex proximal articular surface with a facies articularis antitrochanterica of the femur. Therefore, we conclude that TMM 31100-523 is referable to *Chindesaurus*.

NMMNH P-4569 (Hunt, 1994: fig. 39; Hunt, 2001: figs 7A–C)

[=cf. *Coelophysis* sp. (Lucas *et al.* 1985); =large podokesaurid (Hunt & Lucas 1989); =*Plateosaurus*-sized anchisaurid (Murry & Long 1989); =‘*Comanchesaurus kuesi*’ (Hunt 1994); =Herrerasaurid (Hunt *et al.* 1998); =Herrerasauridae gen. et sp. nov. 2 (Hunt 2001)]

Age. Norian, Late Triassic.

Occurrence. Bull Canyon Formation, Dockum Group; Guadalupe County, New Mexico, USA.

Specimens. NMMNH P-4569, partial skeleton including dorsal centra, proximal left femur, partial astragalus, metatarsal fragments and phalanges.

Taxonomic assignment. Possible indeterminate saurischian.

Remarks. Hunt (1994) described an associated partial skeleton referable to the Herrerasauridae. Other specimens assigned by Hunt (1994: fig. 39) to this taxon are all non-diagnostic vertebral centra. Hunt (1994) differentiated this taxon from *Herrerasaurus* using characters of the fragmentary astragalus. The astragalus possesses the ‘dorsal basin’ of Novas (1996) posterior to the ascending process; however, this character is also present in *Chindesaurus*, *Herrerasaurus*, *Saturnalia,* ornithischians and some sauropodomorphs (e.g. *Unaysaurus*). In overall morphology the astragalus is more similar to those of *Coelophysis* sp., *Coelophysis bauri* and *Liliensternus* than to those of other taxa inside or outside Dinosauria. Furthermore, Hunt (1994) used the hollow and constricted centrum to assign the specimen to a theropod. As mentioned before, hollow centra are non-diagnostic to any particular clade outside or inside Dinosauria. Smaller pseudosuchians such as *Hesperosuchus* and *Shuvosaurus* also have hollow centra. The proximal femur is rectangular in dorsal view, with a facies articularis antitrochanterica and an offset femoral head. If this material does in fact belong to a single individual, the characters of the femur and partial astragalus show it to represent at least an indeterminate saurischian because of the presence of a ‘dorsal basin’ of the astragalus.

NMMNH P-17375

[=‘*Cryptoraptor lockleyi*’ (Hunt 1994); =‘small theropod of unknown affinities’ (Hunt *et al.* 1998); =Theropoda incertae sedis gen. et sp. nov. 3 (Hunt 2001)]

Age. Norian, Late Triassic.

Occurrence. Bull Canyon Formation, Dockum Group, Quay County, New Mexico, USA.

Material. NMMNH P-17375, fragmentary skeleton including pubis, proximal portions of the femora, and vertebrae.

Taxonomic placement. Archosauria indet.

Remarks. None of this material is diagnostic to Dinosauria. The proximal portions of the femur are fragmentary and little can be discerned because they are so incomplete and weathered. One large piece cannot even be confidently identified as a femur. The vertebrae are represented by centra that cannot be differentiated from those of *Shuvosaurus*. The pubis indicates that the acetabulum was not open. The proximal portion of the pubis indicates that the pubes were conjoined almost to their proximal ends, a character state present in *Shuvosaurus*-like taxa. NMMNH P-17375 cannot be assigned to the Dinosauria because it lacks any clear synapomorphies with the clade. We are hesitant to assign the material to any clade other than Archosauria indet.

Arctosaurus osborni **Adams, 1875**

Age. Late Triassic.

Occurrence. Heiberg Formation, Bathurst Group, Cameron Island, Nunavut, Canada.

Holotype. NMI 62 1971, cervical vertebra.

Taxonomic placement. Archosauriformes indet.

Remarks. *Arctosaurus osborni* (Galton & Cluver 1976; fig. 13) was originally described as a reptile of unknown affinities (Adams 1875). Subsequently it was considered to represent an anchisaurid sauropodomorph (Lydekker 1889), a chelonian (Huene 1906; White 1973), a melanorosaurid sauropodomorph (Huene 1956), or a thecodontosaurid (Romer 1966). Galton & Cluver (1976) demonstrated that *Arctosaurus* was not a sauropodomorph and provisionally referred it to the Theropoda following Steel (1970).

The centrum is parallelogram-shaped and elongate with dorsoventrally offset articular faces resembling the cervical vertebrae of crocodylomorphs, dinosauromorphs, the pseudosuchian *Arizonasaurus* (Nesbitt 2003), and the proterosuchian *Xilousuchus* (Wu 1981). The neural arch is complete and the prezygapophyses extend well anterior to the centrum body. The incomplete neural spine lies dorsal to the posterior half of the centrum. The extent of the neural arch is unknown. The articular faces of the centrum are elliptical in anterior and posterior views, unlike the more rounded faces in crocodylomorphs and *Herrerasaurus* and more like those of *Arizonasaurus*, *Poposaurus* and *Shuvosaurus*. The postzygapophyses possess weakly developed epipophyses. Gauthier (1986) considered the presence of epipophyses on the anterior cervical vertebrae a saurischian synapomorphy, but as Sereno & Novas (1993) noted, they are usually absent in the post-axial cervicals of sauropodomorphs, prominent only among theropods. In a recent investigation of the character, Langer & Benton (2006) argue that epipophyses are present not only in saurischians, but also in basal ornithischians. Therefore, the presence of epipophyses is probably a symplesiomorphy for taxa within the Dinosauria (Langer & Benton 2006). In addition, cervical epipophyses are also present in pseudosuchians (e.g. *Revueltosaurus* and on the neural arch of the axis in *Shuvosaurus*). The wide and sporadic distribution of epipophyses indicates that the presence of the character has little phylogenetic importance for isolated specimens.

Galton & Cluver (1976) noted the presence of ‘pleurocoels’ on the ventrolateral surfaces of the centrum, ventral to the posterior centrodiapophyseal lamina (pcdl of Wilson, 1999), as grounds for tentatively assigning *Arctosaurus* to the Theropoda. However, the term pleurocoel is now restricted to a cavity rimmed with bone containing or leading to a pneumatic space (Britt 1993; Wedel *et al.* 2000). This restricted definition does not describe the concave region of *Arctosaurus,* and therefore *Arctosaurus* bears no true pleurocoels. The concave region ventral to the posterior centrodiapophyseal lamina also occurs in the pseudosuchian *Arizonasaurus* (Nesbitt 2003).

Whereas the overall morphology of the vertebrae along with the presence of epipophyses suggests placement in the Theropoda, these characters have a much wider distribution among archosaurs. Therefore, *Arctosaurus* can only be considered Archosauriformes indet. at this time.

Putative ornithischians

Nearly the entire record of purported Triassic ornithischians from North America is based upon isolated teeth. This is especially problematical, because teeth often evolve convergent features in unrelated taxa, causing tooth taxa to be assigned to incorrect clades. This problem is exemplified by the case of *Revueltosaurus callenderi*, which was long thought to be an ornithischian dinosaur, but is now known to be a pseudosuchian archosaur (Parker *et al.* 2005). We recently reviewed the Triassic record of ornithischian dinosaurs elsewhere using the same apomorphy-based approach as found in this paper (Irmis *et al.* 2006). Because we discuss and revise the record of North American Triassic ornithischian dinosaurs in detail in that work, we will only briefly summarise our conclusions below. An extensive discussion of the possible phylogenetic position of *Technosaurus smalli* is presented here because it was only briefly reviewed in Irmis *et al.* (2006).

Hunt (1989) described *Revueltosaurus callenderi* (Figs 8A, B) as a possible ornithischian dinosaur from the Bull Canyon Formation of the Dockum Group based on isolated teeth, noting the similarity of these teeth with other known ornithischians. Since then, many additional Triassic North American tooth taxa have been assigned to ornithischians, particularly by Hunt & Lucas (1994) and Heckert (2004). These taxa include *Revueltosaurus hunti*, *Galtonia gibbidens*, *Pekinosaurus olseni*, *Tecovasaurus murryi*, *Lucianosaurus wildi*, *Protecovasaurus lucasi*, *Crosbysaurus harrisae* and *Technosaurus smalli*. Parker *et al.* (2005) documented the discovery of numerous partial skeletons containing both cranial and postcranial elements of *R. callenderi* from the Chinle Formation of Petrified Forest National Park. This material conclusively demonstrated that *Revueltosaurus callenderi* is not an ornithischian dinosaur, but a pseudosuchian. This referral is supported by the presence of postfrontal, rectangular dorsal paramedian osteoderms with an anterior bar and a 'crocodile-normal' ankle. As a result, the characters previously used to assign the teeth of *Revueltosaurus* and other isolated Triassic 'ornithischian' teeth to ornithischians (low triangular tooth crown in lateral view; recurvature absent from maxillary and dentary teeth; well-developed neck separating crown from root; prominent large denticles arranged at 45° or greater to the mesial and distal edges; premaxillary teeth distinct from the maxillary/dentary teeth; and maxillary and dentary teeth asymmetrical in mesial and distal views) cannot be used to assign isolated teeth to the Ornithischia and none of these character states can be considered on their own to be synapomorphies of the Ornithischia (Parker *et al.* 2005). Only the presence of an asymmetric basal swelling of the crown ('cingulum') is possibly diagnostic of ornithischian teeth, but even this character may be difficult to evaluate (Irmis *et al.* 2006). Therefore, the assignments of other 'ornithischian' tooth taxa from the Triassic of North America need revision.

In our recent revision of Triassic ornithischians (Irmis *et al.* 2006), we used unambiguous apomorphies to assign teeth to the most exclusive clade possible. *Revueltosaurus hunti* shares several character states with *Revueltosaurus callenderi* (Heckert 2002); furthermore, it has been found in association with osteoderms (described by Heckert & Lucas 2002 as juvenile *Stagonolepis* osteoderms) and cranial elements that are identical to corresponding elements in *Revueltosaurus* (Irmis *et al.* 2006). Thus, we retain *R. hunti* in *Revueltosaurus* and provisionally consider it a pseudosuchian archosaur, *contra* Hunt *et al.* (2005) and Heckert (2005). The taxa *Galtonia gibbidens* (Figs 8E, F) and *Pekinosaurus olseni* (Figs 8K, L) from the Newark Supergroup of eastern North America display the same unique combination of character states as *Revueltosaurus*, so we refer them to *Revueltosaurus* sp. (Irmis *et al.* 2006). Although *Tecovasaurus murryi* (Figs 8I, J) and *Lucianosaurus wildi* (Figs 8O, P), *Protecovasaurus lucasi* (Figs 8M, N) and *Crosbysaurus harrisae* (Figs 8G, H) are diagnosable and valid, they can only be assigned to Archosauriformes *incertae sedis* (Irmis *et al.* 2006), in part because all lack a 'cingulum'. These taxa do not share any unambiguous synapomorphies with ornithischian dinosaur teeth. Similarly, the Wolfville Formation 'ornithischian' (Galton, 1983) can only be assigned to Archosauriformes *incertae sedis* (Irmis *et al.* 2006).

***Technosaurus smalli* Chatterjee, 1984** (Fig. 9)

Age. Norian, Late Triassic.

Occurrence. Bull Canyon (= Cooper Canyon) Formation, Dockum Group, Texas, USA.

Holotype. TTUP P9021: left premaxilla; right dentary fragment; posterior lower jaw fragment; a dorsal vertebra; 'astragalus'.

Referred material. None.

Taxonomic placement. Valid taxon of Archosauriformes.

Remarks. The original description by Chatterjee (1984) included a posterior lower jaw fragment, premaxilla, partial dentary, a dorsal vertebra and an astragalus within the holotype. Sereno (1991) removed the premaxilla and posterior lower jaw fragment on the basis of size differences with the dentary and tentatively assigned these elements to an indeterminate 'prosauropod' based on features that are 'consistent' with that taxon but no clear synapomorphies. The dorsal vertebra is not diagnostic to the Ornithischia and the identification of the astragalus could not be substantiated. As a result, Sereno (1991) restricted the type materials to the dentary fragment, while Hunt & Lucas (1994) designated this element as a lectotype.

The posterior portion of the lower jaw assigned to the holotype of *Technosaurus* belongs to *Shuvosaurus* because: (1) it has an extremely large mandibular fenestra and a large surangular foramen, character states only present in *Shuvosaurus* and *Shuvosaurus*-like taxa (Nesbitt & Norell 2006);

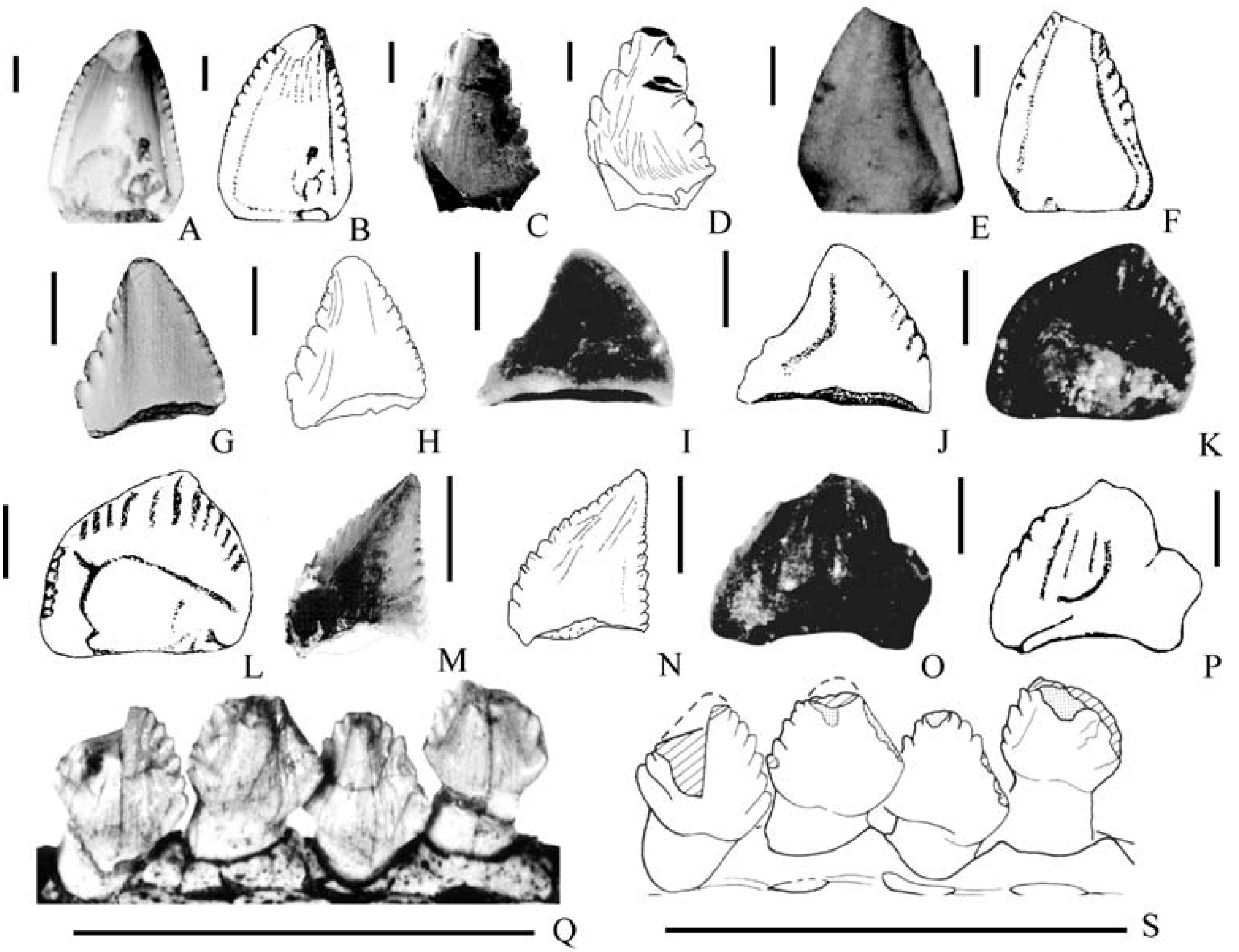

Figure 8 Teeth assigned to Triassic ornithischians. (**A**) *Revueltosaurus callenderi* premaxillary tooth (NMMNH P- 4959) in lingual view; (**B**) Interpretive drawing of NMMNH P-4959; (**C**) *Revueltosaurus hunti* holotype tooth (NMMNH P-29356) in labial view; (**D**) Interpretive drawing of NMMNH P-29356; (**E**) cast of *Galtonia gibbidens* holotype tooth (AMNH 2339) in lingual view; (**F**) Interpretive drawing of AMNH 2339; (**G**) *Crosbysaurus harrisae* paratype tooth (NMMNH P-34201) in labial view; (**H**) Interpretive drawing of NMMNH P-34201; (**I**) *Tecovasaurus murryi* holotype tooth (NMMNH P-18192) in labial view; (**J**) Interpretive drawing of NMMNH P-18192; (**K**) *Pekinosaurus olseni* holotype tooth (YPM 8545) in lingual view; (**L**) Interpretive drawing of YPM 8545; (**M**) *Protecovasaurus lucasi* holotype tooth (NMMNH P-34196) in labial view; (**N**) Interpretive drawing of NMMNH P-34196; (**O**) *Lucianosaurus wildi* holotype tooth (NMMNH P-18194) in labial view; (**P**) Interpretive drawing of NMMNH P-18194; (**Q**) *Lesothosaurus diagnosticus* maxillary teeth (SAM unnumbered) in labial view; (**R**) Interpretive drawing of the teeth of *Lesothosaurus*. Scale bars = 1 mm (**C, D, G–J, M–P**), 2 mm (**A, B, E, F, K, L**) and 10 mm (**Q, R**). **Q, R** from Sereno (1991). **B, E, F, I, J, K, L, O** and **P** from Hunt & Lucas (1994). **A, C** and **D** from Heckert (2002). **G, H, M** and **N** from Heckert (2004).

and (2) abundant *Shuvosaurus* material occurs within the same quarry as *Technosaurus*.

Detailed comparisons between the dentary and premaxilla of *Technosaurus* and *Silesaurus* (Figs 9A–E: Dzik 2003) indicate that the proportions of the *Technosaurus* elements are of the appropriate size to belong to the same individual (*contra* Sereno 1991). Therefore, because there is no duplication of elements, the premaxilla is reassigned to the holotype. Shared characters with the premaxilla of *Silesaurus* include alveoli that extend to the distal margin, lack of a rugose anterior margin, a symphyseal facet that covers almost the entire medial surface and straight non-recurved crowns. Examination of the holotype demonstrates that *Silesaurus* possesses five alveoli in the premaxilla, not four as described by Dzik (2003). *Technosaurus* also appears to possess five alveoli in the premaxilla, although the posterior margin is broken. Nevertheless, all of these characters can be found in basal sauropodomorph dinosaurs (Galton & Upchurch 2004). This indicates that although the premaxilla cannot be conclusively referred to a *Silesaurus*-like taxon, it also cannot be referred to the Sauropodomorpha.

The partial right dentary contains six teeth. Hunt & Lucas (1994) differentiated *Technosaurus* from other ornithischian dinosaurs on the basis of accessory cusps on the dentary teeth (which cannot be confirmed because the teeth are poorly preserved) and the presence of longitudinal striations at the base of the crown. These striations are present in *Silesaurus*, whereas the accessory cusps are not (Dzik 2003). Sereno (1991) recognised the following 'ornithischian' characters in *Technosaurus*: subtriangular crowns, well-developed neck separating crown and root and an increase in tooth size towards the posterior centre of the tooth row. All of these characters are present in *Silesaurus* (Dzik 2003) and at least the first two are present in the pseudosuchian

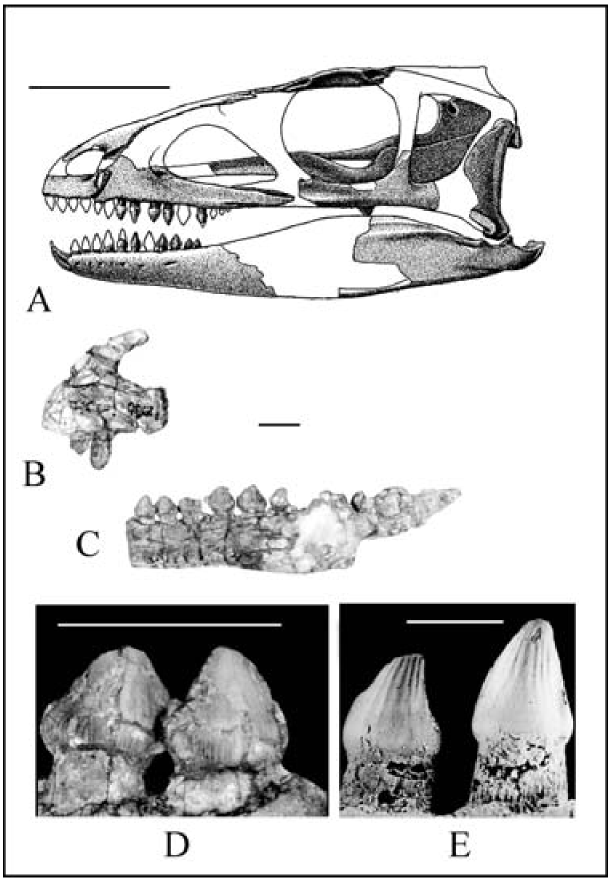

Figure 9 Reconstruction of the skull of *Silesaurus* (**A**) (modified from Dzik 2003) compared with the premaxilla (**B**) (reversed) and dentary (**C**) of the holotype of *Technosaurus smalli* (TTUP P9021). Close up of the dentary teeth of *Technosaurus* (**D**) and *Silesaurus* (**E**). Scale bars = 5 cm in **A** and 1 cm in **B**–**E**.

Revueltosaurus (Parker *et al.* 2005). *Technosaurus* does not possess a 'cingulum' (=basal asymmetric swelling) like Early Jurassic ornithischians such as *Lesothosaurus* (Sereno 1991) and *Scutellosaurus* (Colbert 1981). The dentary provides the best evidence for *Technosaurus* belonging to a *Silesaurus*-like taxon. The dentary teeth of *Silesaurus* and *Technosaurus* are bulbous with highly-reduced denticles and a well-developed neck between the crown and root. Although some basal sauropodomorph dentary teeth have a well-developed neck, they generally have enlarged denticles with lanceolate teeth (Barrett 2000; Galton & Upchurch 2004). In addition, *Silesaurus* and *Technosaurus* have a dentary tooth count of 10–12 teeth (estimated in *Technosaurus*), whereas basal sauropodomorphs have dentary tooth counts of 17–28 teeth. Nevertheless, these character states have a somewhat ambiguous distribution throughout the rest of Archosauria, but if the dentary and premaxilla belong to the same taxon, it appears unlikely that they belong to an ornithischian or sauropodomorph dinosaur.

Despite the possible presence of small accessory cusps in the dentary teeth (Fig. 9D), *Technosaurus* does not possess any ornithischian synapomorphies. Although the anterior dentary is broken and the presence of an anterior dentary 'beak' cannot be confirmed as in *Silesaurus*, the overall morphology of the premaxilla and derived characters of the teeth suggests that *Technosaurus* may represent an archosaur similar to *Silesaurus*. We do not refer *Technosaurus* to *Silesaurus* because the teeth of *Technosaurus*, although they share many characters with *Silesaurus*, can be differentiated by the presence of larger denticles, the possible presence of accessory cusps, a shorter overall height and a slightly more expanded base. However, the discussion above of ornithischian-like teeth suggests that shared ornithischian-like tooth characters may not indicate a true phylogenetic relationship. The teeth of *Technosaurus* are diagnosable and thus, *Technosaurus* is valid, but because the holotype material consists only of a dentary and premaxilla with 'thecodont tooth' implantation, a robust assignment more inclusive than Archosauriformes is not possible.

TTUP unnumbered

Age. Late Triassic.

Occurrence. Bull Canyon Formation (= Cooper Canyon) Formation, Dockum Group, Texas, USA.

Taxonomic placement. Theropoda indet.

Remarks. Cunningham *et al.* (2002) assigned a tibia (TTUP unnumbered) to Ornithischia. The well-preserved tibia has developed medial and lateral condyles, a prominent cnemial crest and a defined lateral ridge on the tibial shaft for the articulation with the fibula. The shaft is nearly circular in cross-section and slightly bows laterally. A slight ridge is present on the anterolateral edge of the shaft starting halfway down the shaft and ending at the distal end. The distal end is eroded but still discernable. The anterior surface bears a hollowed area that fits the ascending process of the astragalus. It is subrectangular with a small posterolateral process in distal view. Rauhut (2003; character 208) used this character to unite *Gojirasaurus*, *Dilophosaurus*, *Coelophysis bauri* and *Liliensternus*. Because *Dilophosaurus*, which is placed outside of the Coelophysoidea in some recent analyses, has this character, the subrectangular shape with small lateral process in distal view may represent a symplesiomorphy within Theropoda. The presence of this shape of the distal end of the tibia does place the tibia within Theropoda, but it is indistinguishable from other non-tetanuran theropods. Furthermore, it is indistinguishable from the tibia of *Gojirasaurus* and the smaller, less robust, tibiae of *Coelophysis*. Most importantly, the morphology of the tibia excludes it from the Ornithischia because it shares an unambiguous apomorphy with theropods. Therefore, we refer this tibia specimen to Theropoda indet.

Putative 'prosauropods'

No unambiguous sauropodomorph fossils have been collected from North American Triassic sediments. Long & Murry (1995) reported two 'prosauropod' (= basal sauropodomorph) fossils from the Chinle Formation of Arizona, a distal tibia (UCMP 25793) from the *Placerias* Quarry of Arizona and a proximal femur (UCMP unnumbered) from the Battleship NW (PFV 169) locality in Petrified Forest National Park. The distal end of the tibia bears a slot for the ascending process of the astragalus, but lacks any synapomorphy of sauropodomorphs. Hunt *et al.* (1998: 513) argued that a proximal femur (UCMP 139487) identified by Long & Murry (1995) as 'prosauropod' is not dinosaurian based on the lack of a 'subrectangular and perpendicularly offset femoral head'. We agree with this assessment, in fact, this element is not diagnostic and cannot be identified as any specific archosaurian element.

Hunt *et al.* (1998) report a single dorsal centrum (no number listed) that they assign to the 'Prosauropoda.' The centrum shares no synapomorphies with the basal Sauropodomorpha and therefore cannot be assigned to this clade. Sereno (1991) referred the premaxilla and posterior jaw fragment from the holotype of *Technosaurus* to a 'prosauropod,' but could not supply any synapomorphies allying these elements to the 'Prosauropoda' (see above).

Harris *et al.* (2002) described a single tooth (NMMNH P-26400) that they argue pertains to a 'prosauropod.' The tooth from the lower part of the Tecovas Formation of Texas has all of the characteristics that Galton (1990) attributes to 'prosauropods' including: (1) spatulate shape; (2) symmetrical crown; (3) numerous; obliquely-angled marginal serrations; (4) poorly developed 'neck;' (5) and straight and narrow shape in mesio-distal views. Recently evidence from non-prosauropod archosaurs (*Silesaurus opolensis* and *Revueltosaurus callenderi*) and two forms from the Carnian of Madagascar (Goswami *et al.* 2005) suggests that the five synapomorphies of 'prosauropod' teeth described by Galton (1990) have a larger distribution among archosaurs. For example, the teeth of *Silesaurus opolensis* exhibit characters 2, 3 and 4 of Galton (1990). Moreover, the three non-prosauropod archosaurs listed above occur in Late Triassic sediments where enigmatic basal archosaur teeth with herbivorous-like morphology are common (Parker *et al.* 2005). Therefore, the evidence is ambiguous as to whether the tooth from Texas actually belongs to a basal sauropodomorph dinosaur.

DISCUSSION

Our critical analysis suggests several conclusions regarding the Late Triassic of North America: the dinosaur record is much poorer than previously indicated; ornithodiran taxa closely related to Dinosauria were present in North America; no sauropodomorphs or ornithischians have been found prior to the Jurassic; and coelophysoids seem to be the only identifiable theropods present in the Triassic of North America.

It is possible that some of the more fragmentary taxa may turn out to be true dinosaurs if more fossils are found. Our analysis places taxa and specimens into the most exclusive clade possible. It is therefore possible that critical character states that place taxa outside or inside Dinosauria are just missing because of incomplete material.

Western North America has been suggested to have 'one of the most extensive fossil records of Late Triassic dinosaurs' (Hunt *et al.* 1998) and recent authors have used the North American Triassic dinosaur record for comparison with other 'incomplete' Triassic dinosaur faunas (Rauhut & Hungerbeuhler 2000). Other recent studies (Hunt 1998; Hunt *et al.* 1998) identify new dinosaur localities in North America based on isolated centra, podials, unguals and teeth. However, we demonstrate that most of these elements are not referable to Dinosauria or Archosauria. It is possible that some of these elements are from dinosaurs, yet they cannot be assigned to the Dinosauria because they lack synapomorphies directly observable in isolated elements. Consequently, our apomorphy based approach forces a low estimate of dinosaur diversity; an estimate that is as accurate as the data allow.

The fundamental problems that created an inflated dinosaur record for the Late Triassic of North America are: poorly preserved, incomplete specimens and the previous lack of understanding of convergences with other Late Triassic archosaur taxa. Of the taxa/specimens listed above, eight (*Caseosaurus*, '*Camposaurus*,' *Gojirasaurus*, *Shuvosaurus*, *Technosaurus*, *Eucoelophysis,* NMMNH P-17375 and NMMNH P-4569) are known only from the holotype or a single specimen and all are incomplete. In addition, at least six taxa/specimens (*Gojirasaurus*, the Snyder Quarry taxa, *Eucoelophysis*, *Protoavis*, *Shuvosaurus* and *Technosaurus*) are found in multitaxic bonebeds, where assignment of elements to a particular specimen and taxon has been somewhat subjective without supporting evidence from contextual information such as quarry maps. *Protoavis*, *Chindesaurus*, *Coelophysis* sp. and the Snyder Quarry coelophysoids are known from more than one specimen; nevertheless, many bones of the skeleton are still unknown for each of these taxa. *Coelophysis bauri* is the only Late Triassic theropod known from complete specimens, but it still remains incompletely described. All of the purported ornithischian taxa, with the exclusion of *Technosaurus*, are known only from isolated teeth. Our taxonomic assignments here are conservative because of the incompleteness of most specimens. Additional specimens of some of the more incomplete taxa may allow the assignment of these taxa to less inclusive clades or a different phylogenetic placement. Thus, we urge caution when naming Triassic archosaur taxa and, more specifically, dinosaurian taxa. Apomorphies must be used to justify taxonomic assignments.

Prior to this study, no non-dinosaurian ornithodirans were recognised from the Late Triassic of North America. *Technosaurus* may represent a form similar to *Silesaurus* from the Late Triassic of Poland, based on dental characters and overall similar morphology of the jaws, but we are suspicious of the phylogenetic signal in archosaur teeth (see Parker *et al.* 2005). The holotype of *Eucoelophysis* also resembles *Pseudolagosuchus* and *Silesaurus*. *Eucoelophysis*, *Pseudolagosuchus* and *Silesaurus* all share ornithodiran characters including the presence of an anterior trochanter and an ascending process of the astragalus (not preserved in *Eucoelophysis*). All of these taxa lack character states that diagnose Dinosauria, but are more closely related to Dinosauria than *Marasuchus*. Therefore, they are best considered non-dinosaurian dinosauriforms. In addition, *Eucoelophysis*, *Pseudolagosuchus* and *Silesaurus* share three possible derived characters (division of the distal condyles at least 1/3 along the length of the femur, small femoral head separated by small 'notch' from femoral shaft and proximal portion of the femur triangular in proximal view) of the femur that suggest that these three taxa may form a clade. If this were the case, the clade would have a nearly worldwide distribution (*Eucoelophysis*, western United States; *Pseudolagosuchus*, Argentina; *Silesaurus,* Poland) and Middle to Late Triassic temporal distribution (*Eucoelophysis*, Upper Norian; *Pseudolagosuchus*, Middle Triassic; *Silesaurus*, Carnian). Moreover, if Langer & Benton's (2006) phylogenetic position of *Silesaurus* is accurate, a clade containing *Eucoelophysis*, *Pseudolagosuchus* and *Silesaurus* would be the sister-group to Dinosauria. Alternatively, the position of this potential group may also be at the base of Ornithischia because our knowledge of character polarities at the base of Dinosauria remains poor. Two additional steps allow *Silesaurus* to fall at the base of Ornithischia in Langer & Benton's (2006) analysis. However, the character states that allow this placement are from teeth that have already been shown to have a wider distribution (Parker *et al.* 2005).

The position of *Herrerasaurus* as a stem saurischian (Langer 2004; Langer & Benton 2006) suggests that *Chindesaurus* is also a stem saurischian, although there is little evidence that *Herrerasaurus* and *Chindesaurus* are united in a monophyletic Herrerasauridae. The position of *Caseosaurus* and a similar ilium from the Snyder Quarry is equivocal because none of the dinosaur character states (Fraser *et al.* 2002) can be determined in these specimens.

Previous reports of Late Triassic ornithischians and sauropodomorphs are based on isolated dental remains or vertebrae; however, before the end of the Triassic, isolated vertebrae, teeth, limb bones and most tooth bearing elements cannot be assigned to the Dinosauria or, in many cases, to specific clades of the Archosauria because of the high degree of plesiomorphic features in basal archosaurs, convergences between different clades (e.g. *Shuvosaurus* and theropods) and the lack of any diagnostic characters in certain regions (e.g. dorsal vertebrae). Only after the extinction of nearly all of the basal archosaur clades ('rauisuchians,' phytosaurs, aetosaurs and basal ornithodirans outside Dinosauria and Pterosauria) after the Triassic–Jurassic boundary are dinosaurs more recognisable from isolated elements, although character states should still be used for identification. The first unambiguous ornithischians and basal sauropodomorphs in North America occur in the Early Jurassic where more complete material is known (Colbert 1981).

The problems listed above also hinder the assignment of Late Triassic material to theropod dinosaurs. Characters once believed to represent dinosaur synapomorphies, such as the presence of three or more sacral vertebrae, hollow vertebrae and limb bones, the presence of an enlarged pubic boot, hyposphene–hypantrum articulations of the dorsal vertebrae and an elongated parabasispenoid are present in more inclusive taxa, including pseudosuchians. The majority of diagnostic theropod specimens from the southwestern United States are referable to *Coelophysis*, including the Ghost Ranch Quarry specimens (Colbert *et al.* 1992) and three partial skeletons from Petrified Forest National Park (Padian 1986; Parker & Irmis 2005). Other material, including the Snyder Quarry coelophysoid(s), the holotype of '*Camposaurus*' and a portion of the *Gojirasaurus* holotype possess coelophysoid characters that are all present in *Coelophysis*. Specimens such as *Protoavis*, with its plesiomorphic and probably chimaeric character suite, cannot be assigned to a clade less inclusive than non-tetanuran Theropoda. As a result, the only unambiguous Late Triassic North American dinosaurs are coelophysoid theropods, although *Chindesaurus* may be a stem saurischian.

Other evidence

Dinosaur ichnotaxa from the Triassic of North America indicate a very similar result to the body fossils. Trackmakers must be identified using discrete synapomorphies, as with body fossils (Olsen & Baird 1986; Olsen *et al.* 1998; Carrano & Wilson 2001; Wilson 2005; Padian 2003). No clearly identifiable ornithischian tracks are known before the Triassic–Jurassic boundary. *Atreipus*, originally referred to the Ornithischia, can be equally parsimoniously assigned to a dinosauriform taxon outside Dinosauria, as illustrated by Olsen & Baird (1986).

The tracks *Tetrasauropus* and *Pseudotetrasauropus* have been identified in the Late Triassic of the western United States (Lockley & Hunt 1995; Lockley *et al.* 2001; Rainforth 2003). They have previously been considered 'prosauropod' tracks (e.g. Lockley & Hunt 1995), but there are no synapomorphies supporting this referral. *Pseudotetrasauropus* is possibly synonymous with *Brachychirotherium* (Rainforth 2003), a non-dinosaur ichnotaxon. Recently, several tracks from the Upper Triassic of New Mexico, Colorado and Utah that were originally assigned to *Chirotherium* sp. and *Brachychirotherium* sp. (Conrad *et al.* 1987) have been reassigned to *Tetrasauropus* and considered to have been made by a sauropod trackmaker (Lockley *et al.* 2001; Wilson 2005). Rainforth (2003) considered these records of *Tetrasauropus* to be definitely referable to *Brachychirotherium*. The tracks are poorly preserved in the substratum and the separate digits and phalangeal formulae cannot be differentiated.

In a synapomorphy-based approach integrated with stratocladistic methods, Wilson (2005) suggested that two of the above Late Triassic trackways assigned to *Tetrasauropus* by Lockley *et al.* (2001) were made by a sauropod. Wilson (2005) listed the following characters to assign these particular *Tetrasauropus* tracks to a sauropod: large size, quadrupedal posture, digitigrade manus, semi-digitigrade pes, laterally directed pedal unguals. Even though these characters separate *Tetrasauropus* from other dinosaur trackway makers, they do not separate them from supposed pseudosuchian ichnotaxa such as the contemporaneous *Brachychirotherium*. *Brachychirotherium* prints cannot be differentiated from *Tetrasauropus* based on large size and quadrupedal posture. The digitigrade manus print of the *Tetrasauropus* trackways (Wilson 2005: figs 5A, B) are equally assignable based on morphology to the smaller manus of *Brachychirotherium*. The same is true for the semi-digitigrade pes of both *Tetrasauropus* and *Brachychirotherium*. Tracks are an interaction between the sediments, the morphology of the foot and the behaviour of the animal (Padian & Olsen 1984). Therefore, it is possible for many different taxa to create morphologically identical imprints. The laterally directed pedal unguals present in *Tetrasauropus*, but not in basal sauropods (*Tazoudasaurus*, *Vulcanodon* and *Gongxianosaurus*) suggest that *Tetrasauropus* acquired this feature in parallel and that it is not homologous with other sauropods (Wilson 2005).

The trackmaker of the *Tetrasauropus* tracks could be the same trackmaker as that for *Brachychirotherium* based on the morphological characters that Wilson (2005) used to assign the tracks to the Sauropoda (i.e. the characters of Wilson (2005) are all found in *Brachychirotherium* and would classify it as a sauropod dinosaur). Furthermore, these prints appear to lack a laterally divergent digit IV, which is a diagnostic character state of the Dinosauria (Carrano & Wilson 2001). Although the reversal of this character is a synapomorphy of Sauropoda, the lack of a laterally divergent digit IV in other Late Triassic tracks that are indistinguishable from the *Tetrasauropus* tracks makes it an ambiguous character for identification of these tracks as sauropods.

Regardless of whether these tracks can be referred to *Tetrasauropus*, we consider their maker indeterminate based upon the characters cited by Wilson (2005). In addition, the poor preservation of the two trackways of *Tetrasauropus* that Wilson (2005) discussed adds further ambiguity. For example, the Peacock Canyon *Tetrasauropus* trackway was created on an incompetent surface, as evidenced by the large displacement of sediment on the edges of the tracks, the absence of clear impressions of the pads and scales and large variation of the orientation of the digits. Assignment of these tracks to a body fossil taxon suffers, like the body fossil record, from the abundance of convergence among Triassic archosaurs.

These two *Tetrasauropus* trackways are from the upper portion of the Upper Triassic sediments of the western sequence (Lockley *et al.* 2001). In these sediments, body fossils remain elusive and, therefore, sauropod dinosaurs may have been present, but not preserved. It is still possible that these trackways were made by sauropod dinosaurs, but this cannot be confirmed from the morphology of the present trackways. If this were the case, it suggests that sauropods were extirpated in the area because they are not yet known in the well-sampled Lower Jurassic Kayenta Formation.

Triassic tridactyl footprints such as *Grallator* spp. cannot be directly assigned to Theropoda because *Herrerasaurus*, *Eoraptor* and *Silesaurus* also have functionally tridactyl pedes with the same phalangeal formula. Based on our criteria for characters diagnosing Dinosauria (Fraser *et al.* 2002), these three taxa cannot be considered theropods and therefore neither can Triassic tridactyl prints.

Timing of the early diversity of dinosaurs in North America

The oldest of the taxa evaluated here is '*Camposaurus*' from the *Placerias* Quarry near the base of the Mesa Redondo Member (= Bluewater Creek Member) (Stewart *et al.* 1972; Heckert *et al.* 2003), located above the Shinarump Member at the base of the Chinle Formation. The relationship to other Triassic sections and age of the Mesa Redondo Member is uncertain, but is generally regarded as upper Carnian (Lucas *et al.* 1997; Lucas 1998). If the age of the Mesa Redondo Member is correct, '*Camposaurus*' would be the oldest confirmed theropod yet found.

The majority of the theropods from the North American Late Triassic lie in the Petrified Forest Member of the Chinle Formation of Arizona and central New Mexico and the Bull Canyon Formation of the Dockum Group. These three roughly equivalent rock units are generally thought to be Norian in age (Lucas 1998; Lehman & Chatterjee 2005). *Coelophysis* sp. (Padian 1986) and *Chindesaurus* from the Petrified Forest National Park were found in nearly equivalent strata in the same geographical region (Heckert & Lucas 2002; Stocker *et al.* 2004). The Snyder Quarry coelophysoids, *Eucoelophysis* and the Hayden Quarry taxon are from the same general stratigraphic interval and geographical area (Downs 2005). *Protoavis* and *Gojirasaurus* are from the Bull Canyon Formation of the Dockum Group, but their precise relative position cannot be determined with accuracy without more extensive correlations.

Coelophysis bauri is known from the 'siltstone member' of the uppermost Chinle Formation strata, (Stewart *et al.* 1972; Colbert 1989; Schwartz & Gillette 1994). The mass accumulation of *Coelophysis bauri* probably does not represent an increased abundance of theropods in the Late Triassic because this quarry is a unique taphonomic situation and theropods are still rare outside the *Coelophysis* Quarry in the uppermost Chinle Formation.

Figure 10 demonstrates that the dinosaurs from North America are sparsely distributed in geographical area and time. The limited data restrict a clear understanding of the early history of the theropods of North America during the Late Triassic, but suggest two ideas: theropods were never a common component of the Late Triassic faunas of North America and were not taxonomically diverse (*contra* Hunt *et al.* 1998; Heckert & Lucas 2000). Alternatively, this pattern can be an artifact of sampling environments that were somehow unfavourable to early theropods; however, neither idea can be confirmed or denied with current palaeontological evidence.

This analysis shows that the taxonomic diversity of dinosaurs is low in the Late Triassic of North America; only coelophysoid theropods have been confirmed and most appear to be of the same size and to differ little in morphology. Even after the Triassic–Jurassic boundary, the taxonomic diversity of theropods remains low in North America. Theropods from the Moenave Formation (Early Jurassic (Lucas & Heckert 2001)) consist of two specimens, both pelves (MNA V2588 and MNA V1968) of coelophysoids (Lucas & Heckert 2001). Moving forward in time, the Kayenta Formation (Sinemurian) contains a more diverse theropod fauna, but all specimens represent coelophysoids ('Shake n' Bake' coelophysoid and '*Syntarsus*' *kayentakatae*: Tykoski 1998; Tykoski & Rowe 2004) or a non-tetanuran, non-ceratosaurid theropod (*Dilophosaurus*: see Carrano *et al.* 2002; Rauhut 2003). Interfingering with and directly overlying the Kayenta Formation, the Navajo Sandstone (?Pliensbachian) contains a single small coelophysoid, *Segisaurus halli* (Camp 1936). Middle Jurassic rocks that preserve dinosaur body fossils are not present in North America. The extensive Late Jurassic Morrison Formation is the next theropod-bearing unit in North America. There, a 'ceratosaur' (*Ceratosaurus*), tetanuran (*Allosaurus*), spinosauroid (*Torvosaurus*), tyrannosauroid (*Stokesosaurus*) and small coelurosaurs (*Coelurus*, *Tanycolagreus* and *Ornitholestes*) are present and signify that a radiation of Theropoda had already taken place by the Late Jurassic.

A strict interpretation of the Late Triassic and Early Jurassic record of theropods in North America indicates that theropod diversity remained low until the Late Jurassic. The absence of many vertebrate fossils from the Navajo Sandstone combined with the absence of other fluvial Middle Jurassic deposits leaves a crucial gap in the theropod record in North America. This gap obscures a critical time in theropod evolution, as indicated by the presence of tetanurans in Middle Jurassic deposits at other localities outside North America (e.g. China, Europe and Argentina: Weishampel *et al.* 2004) and ghost lineages in phylogenetic analyses (Rauhut 2003). Nevertheless, the Early Jurassic record of theropods in North America mimics the theropod diversity of the Late Triassic. The only major difference between the Late Triassic and Early Jurassic theropods is size; on average, Early Jurassic theropods are larger than any Late Triassic theropods, as indicated by body fossils and footprints from the Newark Supergroup (Olsen *et al.* 2002). In addition, the pattern of low taxonomic diversity of the Late

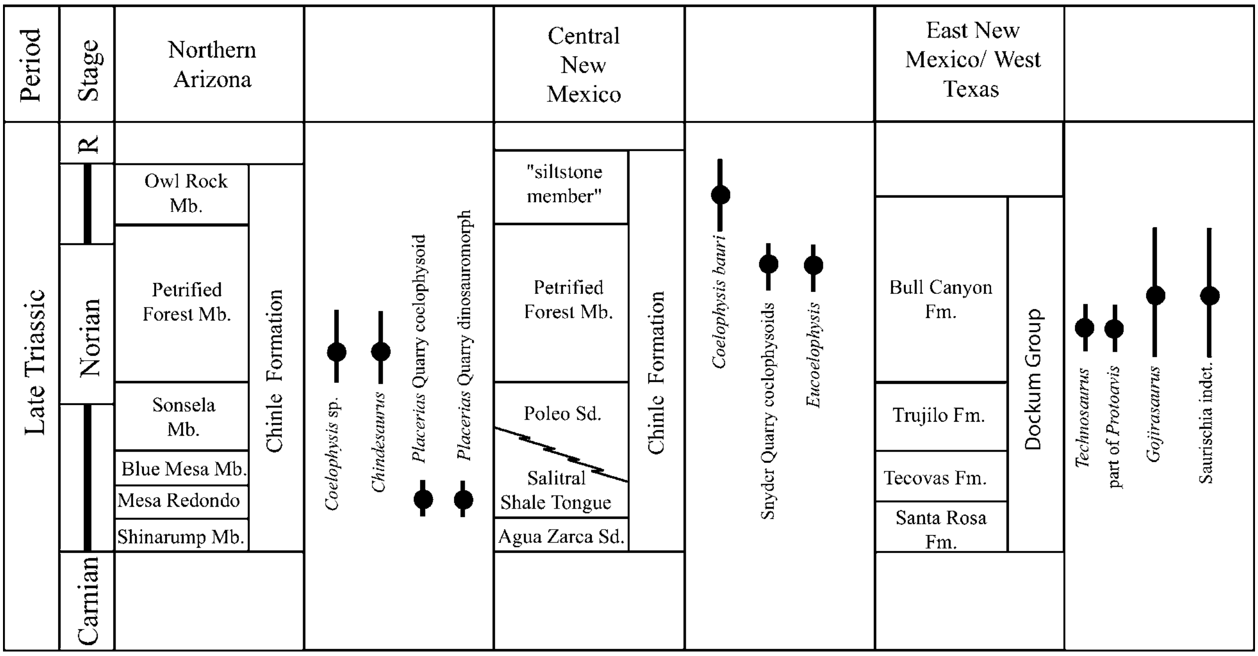

Figure 10 The temporal distribution of Triassic dinosauriform taxa in North America. Error bars indicate uncertainty. **R**, Rhaetian; **Mb**, member; **Fm**, formation.

Triassic–Early Jurassic theropod fossil record (taxonomically restricted to coelophysoids and non-tetanuran theropods) also occurs in South Africa and Europe (Carrano & Sampson 2004). The combination of these data suggests that theropods were not taxonomically diverse until the end of the Early Jurassic or sometime in the Middle Jurassic worldwide.

There is no confirmed evidence for ornithischians and sauropodomorphs in the Triassic of North America. Both clades first appear unequivocally in the Early Jurassic. The first confirmed records of ornithischians in North America are the basal thyreophorans *Scutellosaurus* and *Scelidosaurus* from the Kayenta Formation (Colbert 1981; Parker *et al.* 2005). The first confirmed record of sauropodomorphs in North America includes specimens from the Kayenta and Navajo Formations of Arizona (Galton 1971; Attridge *et al.* 1985), and *Anchisaurus polyzelus* from the Portland Formation of eastern North America (Yates 2004). The lack of ornithischians in the Triassic of North America is not unexpected, considering their worldwide rarity during the Triassic (Parker *et al.* 2005; Irmis *et al.* 2006). They nevertheless suggest a long ghost-lineage in North America because theropods are clearly present. The lack of sauropodomorphs is puzzling considering their abundance in Europe (Yates 2003*a*), Africa (Yates 2003*b*) and South America (Bonaparte 1972).

The Triassic record outside North America

The taxonomic revisions that we have proposed for the Late Triassic of North America have important implications for the global Triassic dinosaur record. Our recognition of several non-dinosaurian ornithodirans suggests that a worldwide reconsideration of Late Triassic dinosaur taxa is needed. For example, *Procompsognathus* from the Norian of Germany may be a non-dinosaurian ornithodiran (Allen 2004). It is also not clear if *Aliwalia* from the Lower Elliot Formation of South Africa (Galton 1985) actually forms a clade with *Herrerasaurus*; recent work by Yates (2005) indicates the femur belongs to an early sauropodomorph. In addition, the phylogenetic position of *Staurikosaurus* from the Santa Maria Formation of Brazil (Colbert 1970) also needs to be revisited. Based on the characters outlined above for inclusion in Dinosauria, these taxa may not represent dinosaurs *sensu stricto*. It is difficult to assess *Alwalkeria* from the Maleri Formation of India from the published figures (Chatterjee 1987), but the femur appears to have an offset femoral head, which is a dinosaur character. The fourth trochanter has an abrupt ventral border as in *Herrerasaurus*, *Saturnalia* and other basal sauropodomorphs. The astragalus of *Alwalkeria* has a posterodorsal basin according to Langer (2004), which is shared with *Herrerasaurus*, *Saturnalia* and *Chindesaurus*. In summary, there are no characters that *Alwalkeria* shares with theropods such as *Coelophysis bauri*, *Coelophysis rhodesiensis* and '*Syntarsus*' *kayentakatae* that are not found in other dinosauriform taxa. In addition, a recent re-analysis of the specimen suggests that it is probably a chimaera (Remes & Rauhut 2005).

Azendohsaurus from the Upper Triassic of Morocco has variously been considered an ornithischian or 'prosauropod' dinosaur (e.g. Dutuit 1972; Bonaparte 1976; Gauffre 1993) based on characters of its dentition. This taxon also needs re-evaluation considering that character states of herbivorous-like archosaur teeth have been shown to be misleading for assessing phylogenetic position (Parker *et al.* 2005). Gauffre (1993) assigned *Azendohsaurus* to the 'Prosauropoda' on the basis of a single character state from each of the dentition and the maxilla. The dental character of a dentition with the largest teeth in the anterior third of the jaw is possibly a reflection of feeding adaptation rather than phylogeny and is also present in *Revueltosaurus callenderi*, a pseudosuchian archosaur. Whether or not the ascending process of the maxilla is 'fully individualized' (Gauffre 1993) is difficult to evaluate because it is broken in the single referred maxilla and its position on the anterior third of the maxilla is an archosaur plesiomorphy, not unique among 'prosauropods.' Other characters of the dentition are not diagnostic of the Dinosauria (see character evaluation in Parker *et al.* 2005). Therefore, there are no unambiguous characters supporting the placement of *Azendohsaurus* within Sauropodomorpha or Dinosauria. Jalil & Knoll (2002) and Galton & Upchurch (2004) arrived at a similar conclusion, arguing that postcranial material referred to *Azendohsaurus* possesses no dinosaur autapomorphies and instead represents an indeterminate ornithodiran.

It is clear that coelophysoid theropods are present in Europe (Rauhut & Hungerbühler 2000), but they seem to be absent from southern Africa during the Triassic. *Zupaysaurus* from the Late Triassic Los Colorados Formation of Argentina (Arcucci & Coria 2003) was described as the earliest tetanuran theropod, but it may be a coelophysoid (Carrano & Sampson 2004; Ezcurra & Novas 2005) or a non-coelophysoid non-tetanuran theropod allied with *Dilophosaurus* (Yates 2005).

Although sauropodomorphs are conspicuously absent from North America during the Late Triassic, they are well known from Europe (Yates 2003*a*), southern Africa (Yates 2003*b*) and South America (Bonaparte 1972). Ornithischians are not known from North America, Europe and Asia in the Triassic (Parker *et al.* 2005; Irmis *et al.* 2006). *Pisanosaurus* from the Ischigualasto Formation of Argentina shows some affinities to ornithischian dinosaurs in its dentition, but the postcrania are ambiguous (Norman *et al.* 2004; Irmis *et al.* 2006). The unnamed heterodontosaurid from Argentina (Báez & Marsicano 2001) is very poorly preserved and fragmentary and can only be assigned to that clade based on ambiguous dental characters. Thus, no dinosaur clade has a fully global distribution during the Late Triassic.

CONCLUSIONS

Late Triassic dinosaurs of North America are not as diverse as previously thought; this is indicated by an apomorphy-based approach to specimen identification. Ornithischians and basal sauropodomorphs are apparently absent in North America until after the Triassic–Jurassic boundary. Non-dinosaurian ornithodirans were present in North America during the Late Triassic. Theropods, although rare in the faunas, seem to represent the only confirmed Triassic dinosaurs in North America. Furthermore, all of the Late Triassic theropods seem to be coelophysoids. A revision of the global Late Triassic dinosaur record is needed using similar methods to this study (i.e. an apomorphy-based approach).

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Appendix

Summary of the taxonomic status of previously identified Late Triassic dinosaurs. The designation to a specific clade is the most exclusive possible given the material.

Specimen Number or taxon	Element(s)	Previous Assignment	This Study
Putative Theropod dinosaurs			
Eucoelophysis baldwini	Partial skeleton	Theropoda	Dinosauriformes (possible chimaera)
PEFO 34347	Proximal end of femur	N/A	Dinosauriformes indet.
TMM 31100-185	Femur	Ornithosuchia	Dinosauriformes indet.
NMMNH P-30852	Partial skull; postcrania	Theropoda (*Eucoelophysis* sp.)	Coelophysoidea indet.
NMMNH P-31661	Scapulocoracoid/sacrum	Theropoda (*Eucoelophysis* sp.)	probable coelophysoid
NMMNH P-29047	Ilium	Theropoda (*Eucoelophysis* sp.)	Coelophysoidea indet.
NMMNH P-29046	Femora	Theropoda (*Eucoelophysis* sp.)	Coelophysoidea indet.
NMMNH P-29047	Tibia	Theropoda (*Eucoelophysis* sp.)	Coelophysoidea indet.
NMMNH P-31293	Tibia	Theropoda (*Eucoelophysis* sp.)	Coelophysoidea indet.
NMMNH P-29268	Tibia/fibula/astragalocalcaneum	Theropoda indet.	Coelophysoidea indet.
NMMNH P-35995	Ilium	Theropoda (*Eucoelophysis* sp.)	cf. *Caseosaurus crosbyensis*
NMMNH P-33691	Dorsal centrum	Theropoda indet.	Archosauria indet.
NMMNH P-30779	Dorsal centrum	Theropoda indet.	Archosauria indet.
NMMNH P-30780	Dorsal centrum	Theropoda indet.	Archosauria indet.
NMMNH P-29996	Caudal vertebrae	Theropoda indet.	Archosauria indet.
Coelophysis bauri	Nearly complete skeleton	Coelophysoidea	Coelophysoidea
AMNH FR 2706	Pubis	*Coelophysis longicollis*	Coelophysoidea indet.
AMNH FR 2705	Right ilium	*Coelophysis longicollis*	Coelophysoidea indet.
AMNH FR 2708	Right ilium	*Coelophysis longicollis*	Coelophysoidea indet.
AMNH FR 2722	Sacral vertebrae	*Coelophysis bauri* (lectotype)	Coelophysoidea indet.
Gojirasaurus quayi	Partial skeleton	Coelophysoidea	Coelophysoidea *incertae sedis* (in part)
NMMNH P-18400	Partial skeleton	Theropoda indet.	Archosauriformes indet.
NMMNH P-13006	Sacral centra	Theropoda indet.	Archosauria indet.
NMMNH P-25749	?Femur/proximal pubis	Theropoda indet.	Archosauria indet.
NMMNH P-25750	Podials	Theropoda indet.	Archosauria indet.
UCMP 129618	Partial skeleton	Coelophysoidea (*Coelophysis bauri*)	Coelophysoidea (*Coelophysis* sp.)
PEFO 33981	Partial skeleton	N/A	Coelophysoidea (*Coelophysis* sp.)
PEFO 33983	Partial skeleton	N/A	Coelophysoidea (*Coelophysis* sp.)
NMMNH unnumbered	Proximal end of tibia	Theropoda indet.	Archosauria indet.
Camposaurus arizonensis	Tibia/fibula/astragalocalcanei	Coelophysoidea	Coelophysoidea indet. (nomen dubium)
UCMP 139622	Femur	Ceratosauria indet.	Saurischia indet.
UCMP 177317	Dorsal centrum	Ceratosauria indet.	Archosauria indet.
MNA V3091	Dorsal centrum	Ceratosauria indet.	Archosauria indet.
UCMP 138591	Sacral centrum	Ceratosauria indet.	Archosauria indet.
UCMP 178047	Sacral centrum	Ceratosauria indet.	Archosauria indet.
UCMP 178049	Sacral centrum	Ceratosauria indet.	Archosauria indet.
UCMP 178048	Sacral centrum	Ceratosauria indet.	Archosauria indet.
UCMP 25834	Distal end of femur	N/A	Dinosauriformes indet.
UCMP 25820	Distal end of tibia	N/A	Theropoda indet.
Protoavis texensis	Partial skeleton	Avialae *incertae sedis*	Coelophysoidea indet. (in part)
Shuvosaurus inexpectatus	Skull	Theropoda	Suchian (non-dinosaur)
Spinosuchus caseanus	Vertebrae	Theropoda/Trilophosauridae	Archosauriformes *incertae sedis*
Caseosaurus crosbyensis	Ilium	Herrerasauridae	Dinosauria
Chindesaurus bryansmalli	Partial skeleton	Herrerasauridae	Saurischia
NMMNH P-4569	Partial skeleton	Herrerasauridae	Saurischia indet.
NMMNH P-17375	Partial skeleton	Herrerasauridae	cf. *Shuvosaurus*
Arctosaurus osborni	Cervical vertebra	Saurischia indet.	Archosauriformes indet.
Grallator/*Anchisauripus*	Tracks	Theropoda	Dinosauriformes

Appendix: continued.

Specimen Number or taxon	Element(s)	Previous Assignment	This Study
Putative Ornithischian dinosaurs			
TTUP unnumbered	Tibia	Ornithischia indet.	Theropoda indet.
Revueltosaurus callenderi	Teeth	Ornithischia *incertae sedis*	Pseudosuchia
Revueltosaurus (“Krzyzanowskisaurus”) hunti	Teeth	Ornithischia *incertae sedis*	probable pseudosuchian
Galtonia gibbidens	Teeth	Ornithischia *incertae sedis*	*Revueltosaurus* sp.
Pekinosaurus olseni	Teeth	Ornithischia *incertae sedis*	*Revueltosaurus* sp.
Tecovasaurus murryi	Teeth	Ornithischia *incertae sedis*	Archosauriformes *incertae sedis*
Lucianosaurus wildi	Teeth	Ornithischia *incertae sedis*	Archosauriformes *incertae sedis*
Wolfville Formation taxon	Teeth	Ornithischia *incertae sedis*	Archosauriformes *incertae sedis*
Protecovasaurus lucasi	Teeth	Ornithischia *incertae sedis*	Archosauriformes *incertae sedis*
Crosbysaurus harrisae	Teeth	Ornithischia *incertae sedis*	Archosauriformes *incertae sedis*
Technosaurus smalli	Dentary/premaxilla	Ornithischia *incertae sedis*	possibly Dinosauromorpha
Atreipus	Tracks	Ornithischia/Dinosauriformes	Dinosauriformes
Putative Sauropodomorphs			
UCMP 25793	Distal end of tibia	?Prosauropoda indet.	Dinosauriformes indet.
UCMP unnumbered	Proximal end of femur	?Prosauropoda indet.	?Archosauria indet.
NMMNH P-26400	Tooth	Prosauropoda indet.	Archosauriformes indet.
Tetrasauropus	Trackways	Sauropoda	Archosauria indet.