

LATE TRIASSIC DINOSAURS FROM THE WESTERN UNITED STATES

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ABSTRACT - Western North America has one of the most extensive fossil records of Late Triassic dinosaurs. All Upper Triassic strata are assigned to the Chinle Group which yields four successive, dinosaur-bearing faunas. Otischalkian (early Tuvanian) dinosaur specimens are fragmentary and indeterminate. Adamanian (late Tuvanian) dinosaurs include a herrerasaurid, *Camposaurus arizonensis* nov. gen. et sp., *Caseosaurus crosbyensis* nov. gen. et sp., *Tecovasaurus murreyi*, a new ornithischian and an indeterminate prosauropod. Revueltian (early-middle Norian) dinosaurs include *Chindesaurus bryansmalli*, two new herrerasaurids, a prosauropod, *Revueltosaurus callenderi*, *Technosaurus smalli*, *Lucianosaurus wildi*, *Protoavis texensis* and the original syntypes of *Coelophysis bauri*. Apachean (Rhaetian) evidence for dinosaurs is principally ichnological (*Grallator*, *Pseudotetrasauropus*, *Tetrasauropus*), but at least three dinosaurs are known from osseous remains, including the neotype of *Coelophysis bauri*. Dinosaurs define three biogeographic provinces in the Late Triassic. In North America, dinosaurs are rare before the late Tuvanian (late Carnian) and appear to become increasingly numerous through the remainder of the Late Triassic.

KEYWORDS: DINOSAURS, LATE TRIASSIC, WESTERN UNITED STATES, DIVERSITY.

RÉSUMÉ - En Amérique du Nord occidentale se trouvent les plus importants gisements de dinosaures du Trias terminal. Tous les niveaux du Trias supérieur appartiennent au groupe de Chinle qui a fourni quatre faunes successives de dinosaures. Les exemplaires de dinosaures otischalkiens (Tuvanian inférieur) sont à l'état de fragments et indéterminés. L'Adamaniens (Tuvanian terminal) contient un herrerasauridé, *Camposaurus arizonensis* nov. gen. et sp., *Caseosaurus crosbyensis* nov. gen. et sp., *Tecovasaurus murreyi*, un nouvel ornithischien et un prosauropode indéterminé. Les dinosaures revueltiens (Norian inférieur et moyen) comprennent *Chindesaurus bryansmalli*, deux nouveaux herrerasauridés, un prosauropode, *Revueltosaurus callenderi*, *Technosaurus smalli*, *Lucianosaurus wildi*, *Protoavis texensis* et les syntypes originaux de *Coelophysis bauri*. Dans l'Apachéen (Rhétien), l'existence de dinosaures est principalement déduite des traces mais au moins trois dinosaures sont connus de restes osseux, y compris le néotype de *Coelophysis bauri*. On peut mettre en évidence d'après les dinosaures trois provinces biogéographiques dans le Trias terminal. En Amérique du Nord, les dinosaures sont rares, avant le Tuvanian supérieur (Carnien supérieur) et semblent plus nombreux dans le reste du Trias supérieur.

MOTS-CLÉS: DINOSAURES, TRIAS SUPÉRIEUR, OUEST DES ETATS-UNIS, DIVERSITÉ.

INTRODUCTION

The Late Triassic record of dinosaurs is very uneven in both quality and quantity of fossils, and this hinders study of the early evolutionary diversification of dinosaurs. The vast majority of articulated Late Triassic dinosaur specimens have come from only two quarries, Ghost Ranch in New Mexico and Trossingen in Germany. Contemporaneous Upper Triassic stratigraphic units have dramatically dif-

ferent proportions of dinosaurs in their vertebrate faunas. For example, the Norian vertebrate faunas of the upper Stubensandstein and Knollenmergel of Southwestern Germany are dominated by dinosaurs (Benton 1994, fig. 9), whereas dinosaurs only form a small component of the well-known, contemporaneous fauna of the Bull Canyon Formation of eastern New Mexico (Hunt 1994a).

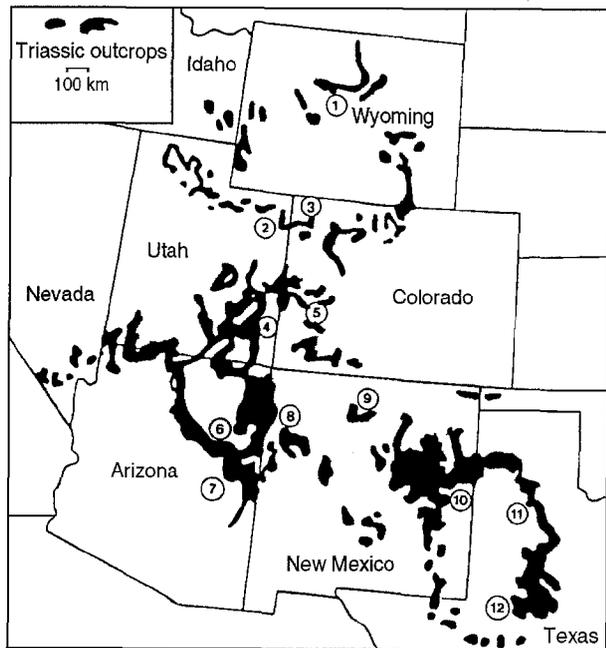


FIGURE 1 - Distribution of Upper Triassic Chinle Group strata in western North America and location of important dinosaur localities. Locations are: 1, Big Horn Mountains (Papo Agie Formation: Otischalkian); 2, Dinosaur National Monument (Bell Springs Formation: Apachean); 3, northwestern Colorado (Bell Springs Formation: Apachean); 4, southeastern Utah (Rock Point Formation: Apachean); 5, southwestern Colorado (Rock Point Formation: Apachean); 6, Petrified Forest National Park (Blue Mesa and Painted Desert Members of Petrified Forest Formation: Adamanian-Revueltian); 7, *Placerias* and Downs' quarries and St. Johns area (Bluewater Creek Formation: Adamanian); 8, Fort Wingate (Bluewater Creek Formation: Adamanian); 9, Ghost Ranch area (Petrified Forest Formation: Reveultian/Rock Point Formation: Apachean); 10, east-central New Mexico (Bull Canyon Formation: Revueltian; Redonda Formation: Apachean); 11, Crosby County (Tecovas Member of Dockum Formation: Adamanian); 12, Otis Chalk (Colorado City Member of Dockum Formation: Otischalkian). *Répartition des niveaux du groupe de Chinle du Trias supérieur dans l'Ouest de l'Amérique du Nord et localisation des sites à dinosaures importants.*

However, for evolutionary studies the greatest drawback to the Late Triassic dinosaur record is that there are few places where a succession of dinosaur-bearing vertebrate fossil assemblages can be studied. In Western Europe and South America there are superposed Carnian and Norian vertebrate faunas, but in each area there was a major ecological change at the boundary between the fossil assemblages of these stages. Thus, in Germany the late Carnian fauna is totally composed of aquatic/semiaquatic temnospondyls and phytosaurs, whereas late Norian faunas are almost entirely terrestrial dinosaurian (Benton 1986, 1994). In Argentina, the Carnian Ischigualasto fauna includes aquatic/semiaquatic proterochampsids and temnospondyls, whereas

the Norian Los Colorados fauna is dominated by dinosaurs. Moreover, virtually all of the dinosaurs in the Norian of both Europe and South America represent a small number of prosauropod genera which are undoubtedly "dryland" facies fossils (Hunt 1991). It is thus clear that there a major ecological change during the Late Triassic in both Europe and South America. Strata in other areas with both Carnian and Norian tetrapod faunas are either poorly dated (South Africa, fissure fills of Britain), have few dinosaur body-fossils (eastern North America), or have inadequate documentation of existing collections (India, Morocco).

To understand early dinosaur evolution we need a geographic area where there is a sequence of Late Triassic dinosaur-bearing faunas that are well documented, known from many specimens, and show no evidence of a major ecological change at the Carnian/Norian boundary (Fig. 1). These criteria are only met in the Chinle Group of western North America. The object of this paper is twofold: to present an overview of the dinosaurian components of Chinle vertebrate faunas that represent the best data base for studying early dinosaur evolution; and to comment briefly on some aspects of early dinosaur radiations.

We note that there is much disagreement at present about the relationships of the Herrerasauridae and whether they are theropods (e. g., Sereno et al. 1993) or a sister group to Saurischia plus Sauropodomorpha or even not within Dinosauria (e. g., Holtz & Padian 1995). We accept the hypothesis that herrerasaurs are basal theropods.

Abbreviations are: FMNH, Field Museum of Natural History, Chicago; MDM, Mesalands Dinosaur Museum and Natural Science Laboratories, Tucumcari; MNA, Museum of Northern Arizona, Flagstaff; NMMNH, New Mexico Museum of Natural History, Albuquerque; PEFO, Petrified Forest National Park, Arizona; SMP, The State Museum of Pennsylvania, Harrisburg; UCM, University of Colorado Museum, Boulder; UCMP, University of California Museum of Paleontology; Berkeley; UMMP, University of Michigan Museum of Paleontology, Ann Arbor.

GEOLOGIC SETTING

All Upper Triassic nonmarine strata in the western United States have recently been united in the Chinle Group (Lucas 1993) although this usage is not yet ubiquitous. Rocks of the Chinle Group are divided into about 25 formations and extend from west Texas in the south to northern Wyoming in the north to western Oklahoma on the east and as far west as eastern Nevada (Lucas 1993). These strata were deposited in a large

basin that covered most of the western United States, had essentially no major internal topographic barriers and represented a fairly homogeneous floodplain environment. The majority of Chinle units are fine-grained siliciclastic redbeds, although other lithologies (sandstones, conglomerates, limestone) are also present. These strata were deposited primarily on river floodplains that drained to the north-northwest, in floodplain lakes and some larger lakes where drainage was locally impounded, and in the uppermost Chinle Group, on paralic sandflats and by minor eolianite sandsheets (Dubiel 1989; Lucas 1993).

BIOCHRONOLOGY

Chinle Group strata range from late Carnian (early Tuvanian) to Rhaetian in age (Lucas 1993; Lucas & Hunt 1993b). Vertebrate fossil assemblages represent four land-vertebrate faunal zones: the Otischalkian (late Carnian: early Tuvanian), Adamanian (late Carnian: late Tuvanian), Revueltian (early-late Norian: Lacin-Sevastian) and Apachean (Rhaetian) (Lucas & Hunt 1993b). Thus, the Chinle Group spans the entire range of ages from which Late Triassic dinosaurs are known. (Note we believe that there is no substantive evidence that the dinosaurs of the Ischigualasto Formation are pre-late Carnian in age: Lucas et al. 1992; Lucas & Hunt 1993a; but see Rogers et al. 1993; Padian & May 1993).

OTISCHALKIAN DINOSAURS

The majority of Otischalkian vertebrates derive from the type fauna from the Colorado City Member of the Dockum Formation in Howard County, west Texas (Lucas & Anderson 1993; Lucas et al. 1994), and the Popo Agie Formation of the Wind River Mountains and southern Bighorn Mountains of Wyoming (Lucas 1994). Several authors (Gregory 1945; Elder 1978, 1987) have referred to specimens from University of Texas quarries 1, 3 and 3A at Otis Chalk, Howard County as coelurosaurian or as *Coelophys* sp., but most of these specimens pertain to *Trilophosaurus buettneri*. The only possible dinosaur specimen is an isolated proximal femur (Long & Murry 1995, figs 186D-H). This specimen has a subrectangular and perpendicularly offset femoral head and thus represents a dinosaur (Novas 1993; Sereno et al. 1993). Long and Murry (1995) referred this specimen to the herrerasaur *Chindesaurus bryansmalii*. However, the femoral head of the Otis Chalk specimen and that of *Chindesaurus* are only similar in gross morphology and share no apomorphies, so we cannot confirm Long and Murry's (1995) generic identification, although the specimen is undoubtedly dinosaurian.

A single podial (NMMNH specimen) from the Popo Agie Formation of the southern Bighorn Mountains, near the type locality of *Heptasuchus*, appears to represent a theropod. *Poposaurus gracilis* was described by Mehl (1915) from the Popo Agie in the Wind River Range and has been considered a phytosaur, an ornithischian, a saurischian, or a "thecodont" (= basal archosaur) (Lees 1907; Mehl 1915; Colbert 1961; Galton 1977) but it is obviously a crurotarsan (e.g., Long & Murry 1995). Dinosaur footprints that were previously attributed to the Popo Agie Formation (e.g., Lockley & Conrad 1989) actually derive from the Bell Springs Formation (sensu Lucas 1993). No Otischalkian footprints are known from the Chinle Group.

ADAMANIAN DINOSAURS

Adamanian vertebrate faunas are well known from northeastern Arizona, north-central and east-central New Mexico and West Texas (Murry 1989; Hunt & Lucas 1993b). Two stratigraphic units in the Petrified Forest National Park (PFNP) in northeastern Arizona have yielded dinosaurian fossils: the Adamanian Blue Mesa Member and the Revueltian Painted Desert Member of the Petrified Forest Formation. Several dinosaurian specimens have been reported from the Blue Mesa Member.

Parrish & Carpenter (1986) reported a large theropod from the Blue Mesa Member in the PFNP based on an uncatalogued scapula, but Long (pers. commun., 1989) identified this as rauisuchian. Colbert (1989) reported fragmentary theropod specimens from near the Lot's Wife locality in the Blue Mesa Member that he assigned to *Coelophys* (Hunt & Lucas 1991), but these specimens (elongate centra) represent the aberrant reptile *Trilophosaurus* (Long, pers. comm., 1989). One proximal left femur from UCMP locality 82261 has been assigned to the ?Prosauropoda by Long & Murry (1995, fig. 193A-E). However, this specimen is dissimilar to prosauropod femora (e.g., Weishampel & Chapman 1990, fig. 3.1) and cannot be assigned to Dinosauria as it lacks a subrectangular and perpendicularly offset femoral head (Novas 1993; Sereno et al. 1993). In the summer of 1997, APH and colleagues found a theropod locality in the Blue Mesa that has yielded several specimens of two taxa, currently under study, including vertebrae and dentulous jaw fragments (uncatalogued PEFO specimens) (Hunt et al. 1996).

Charles Camp did much collecting for UCMP southeast of the Petrified Forest National Park in the Blue Hills and at the *Placerias* quarry in the vicinity of St. Johns, Arizona. All the Blue Hills spe-

cimens are from the Blue Mesa Member, whereas the *Placerias* quarry is in the underlying Bluewater Creek Formation (Lucas et al. 1994). He assigned several isolated teeth from the Blue Hills (UCMP locality 7307) to prosauropods (Camp 1930). However, these teeth are not narrow and symmetrical in anterior view like those of Triassic prosauropods (Hunt & Lucas 1994; Hunt et al. 1995a). The teeth have crowns wider than roots, large, oclusally directed denticles, cingulae and are asymmetrical in anterior and posterior view. In all these features these teeth resemble those of ornithischian dinosaurs. Long and Murry (1995, fig. 193F-G) assigned the Blue Hills teeth

to *Revueltosaurus callenderi*, but they differ from this taxon in possessing well-developed, denticulated cingulae. Identical teeth have recently been collected from the Adamanian Los Esteros Member of the Santa Rosa Formation in central New Mexico (Hunt & Lucas 1995). Camp's specimens and those from New Mexico represent the same unnamed taxon of ornithischian.

Several theropod specimens are known from the *Placerias* quarry (and the adjacent Downs' quarry), which is named for the abundant remains of this dicynodont therapsid. Murry and Long (1989, p. 42) identified some isolated teeth as "cf. *Coelophysis*" which represent "probably some

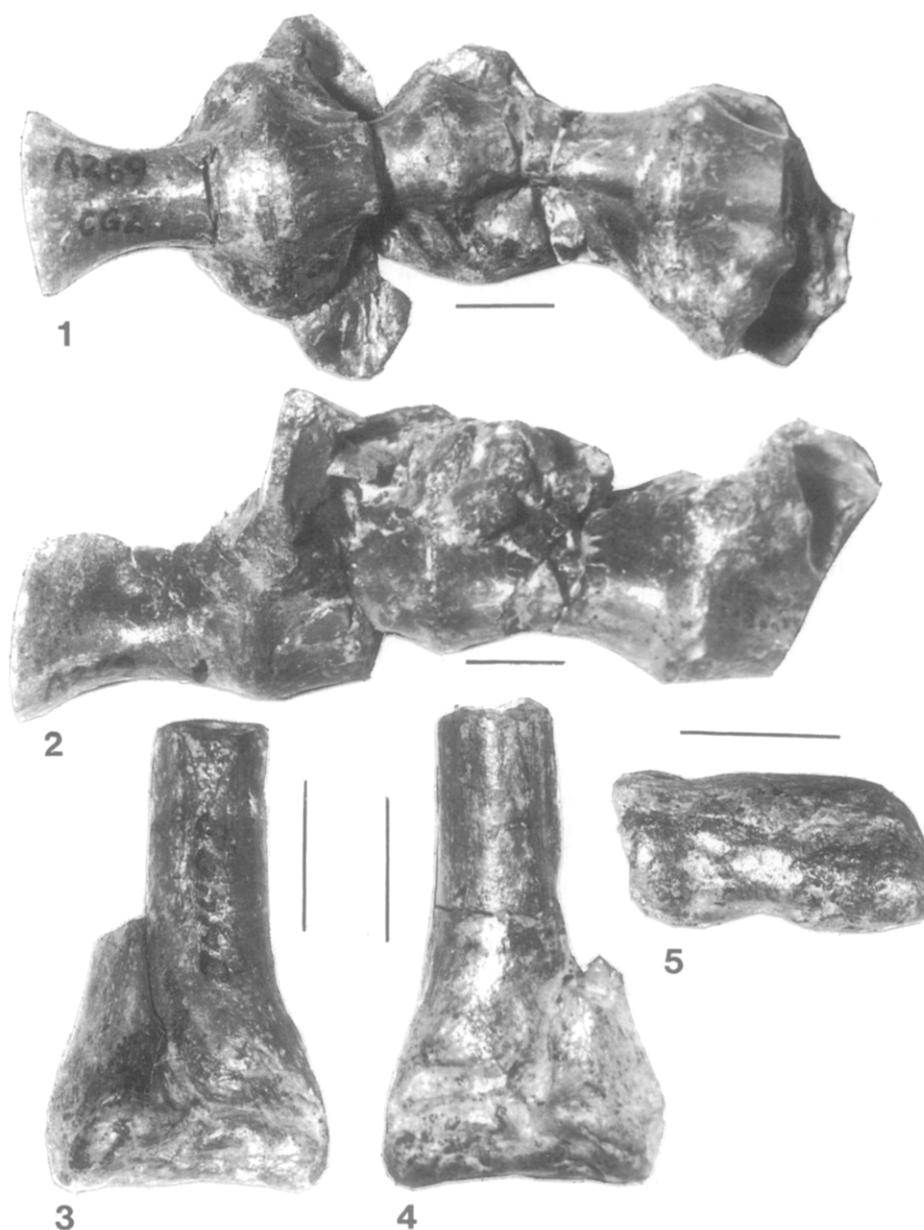


FIGURE 2 - Holotype and paratypes of *Camposaurus arizonensis* nov. gen. et sp. Scale bars are 1 cm. 1-2. Paratype partial sacrum (UCMP uncatalogued but field number is A269/cg2). 1. Ventral view. 2. Lateral view. 3-5. Holotype fused right tibia/fibula/astragalus/calcaneum (UCMP 34498). 3. Posterior view. 4. Anterior view. 5. Distal view. *Holotype et paratypes de Camposaurus arizonensis* nov. gen. et sp. Echelle = 1 cm. 1-2. Paratype d'un sacrum fragmentaire (UCMP non répertorié mais le n° de terrain est A269/cg2). 3-5. Holotype d'un tibia droit avec fibula, astragale et calcaneum soudés.

variety of thecodont or primitive saurischian." However, these teeth are indeterminate. A large number of dissociated, similar-sized theropod postcranial specimens, with no duplication of elements, represent a small theropod (Lucas et al. 1992, fig. 1; Long & Murry 1995, fig. 192 [includes corrected specimen numbers]: Fig. 2). These include a proximal right femur (Long & Murry 1995, figs 191, 192A-E), associated, fused right and left tibiae-fibulae-astragale-calcaneeae (Lucas et al. 1992, fig. 1a-c; Long & Murry 1995, fig. 192F-J: Fig. 2.3-5), a sacrum preserving portions of four fused centra (Lucas et al. 1992, fig. 1D; Long & Murry 1995, fig. 192Y: Fig. 2.1-2) and numerous vertebral centra (Long & Murry 1995, figs 192M-U). As there is no duplication of elements and all specimens are of comparable size the most parsimonious explanation is that they represent a single individual. In support of this hypothesis we also note that the most diverse late Carnian theropod fauna, from the Ischigualasto Formation of Argentina, only contains two genera (*Eoraptor*, *Herrerasaurus*) that are of markedly different sizes.

The number of sacral vertebrae in the *Placerias* quarry theropod and the presence of a high ascending process on the astragalus preclude assignment to the Herrerasauridae (Novas 1993). The number of fused sacral vertebrae (four) and the fusion of the distal limb elements suggest that this specimen represents a ceratosaur (sensu Rowe & Gauthier 1990). The *Placerias* quarry theropod differs from all ceratosaurs except *Coelophysis* and *Syntarsus* in having tarsals fused to the tibia and fibula. (Note that this condition may be variable in *Coleophysis*: Colbert 1989). It differs from *Coelophysis* and *Syntarsus* in that the ventral margin of the astragalus in anterior/posterior view is horizontal rather than deeply concave (Long & Murry 1995). Other distinguishing characters are discussed in the Appendix. The *Placerias* quarry theropod is obviously distinct and we propose the binomial *Camposaurus arizonensis* nov. gen. et sp. for this taxon (Appendix). The name honors Charles Camp who excavated the *Placerias* quarry and also refers to the state of Arizona, which yielded the holotype. The holotype is associated right and left distal hindlimbs and fused astragali and calcanea (UCMP 34498: Fig. 2.5-6). *Camposaurus* differs from other theropods in the character discussed above and in others (Appendix). The following specimens are considered paratypes of *Camposaurus* as their association with the holotype cannot be absolutely demonstrated: UCMP uncatalogued, proximal right femur (Long & Murry 1995, figs 191, 192A-E: Fig. 2.3-4), partial sacrum (Lucas et al. 1992, fig. 1d; Long & Murry 1995, fig. 192Y: Fig. 2.1-2), dorsal centrum (Long & Murry 1995, fig. 192Q-T), 3 incomplete sacra; and

MNA Pl. 2777, dorsal centrum (Long & Murry 1995, fig. 192M-P). Other theropod specimens from the *Placerias* quarry represent a smaller individual(s) and include a proximal left pubis (Long & Murry 1995, fig. 192K-L) and dorsal centra (Long & Murry 1995, fig. 192). These specimens cannot be unequivocally assigned to *Camposaurus*.

Murry & Long (1989) and Long & Murry (1995) list the occurrence at this quarry of the herrerasaurid *Chindesaurus bryansmalli*. However, this occurrence is based on five dorsal centra (Long & Murry 1995) that are not generically determinate, but are herrerasaurid.

Tannenbaum (1983) and Kaye & Padian (1994) described the microvertebrate fauna of the *Placerias* and Downs quarries. Tannenbaum (1983) assigned one tooth (MNA V3690) to the Prosauropoda. However, this tooth is not symmetrical in anterior view and therefore it represents an ornithischian. The Arizona tooth (Tannenbaum 1983, fig. 71) is similar to a tooth referred to *Lucianosaurus* by Hunt & Lucas (1994, fig. 12.6H-I). Kaye & Padian (1994) assigned the same tooth to *Revueltosaurus*. However, the MNA tooth differs from *Revueltosaurus* in a number of features including: (1) much smaller size, (2) much finer denticulations; and (3) more pointed apex. Kaye & Padian (1994, figs 9.104-105) also tentatively assign two fragmentary teeth (V 3682, V3683) to *Revueltosaurus*. We consider these teeth to represent indeterminate ornithischians.

Teeth of herbivorous dinosaurs from the *Placerias* quarry and a distal tibia have been identified as prosauropod (Tannenbaum 1983; Murry & Long 1989; Long & Murry 1995). However, all the teeth represent the ornithischian *Tecovasaurus murryi* (Hunt & Lucas 1994: Fig. 3.1-2). The partial tibia (UCMP A269/25793; Murry & Long 1995, fig. 193H-K) is not assignable to Prosauropoda because this specimen does not exhibit any prosauropod synapomorphies of the distal tibia (Novas 1989) and could represent a primitive theropod (compare Novas 1989, fig. 2.2-3).

In the 1920s, E.C. Case collected a number of specimens from the Tecovas Member of the Dockum Formation in west Texas that he considered dinosaurian (Case 1922, 1927, 1932: UMMP catalogue). Padian (1986) and Murry (1989) have stated, without explanation, that all these specimens, with the possible exception of an ilium, are not dinosaurian.

Case (1922) referred three specimens to the Dinosauria. UMMP 7473 is a basicranium that Chatterjee (1985) demonstrated belongs to a rauisuchian. Case gave an initial (Case 1922) and later a more detailed description (Case 1927) of a

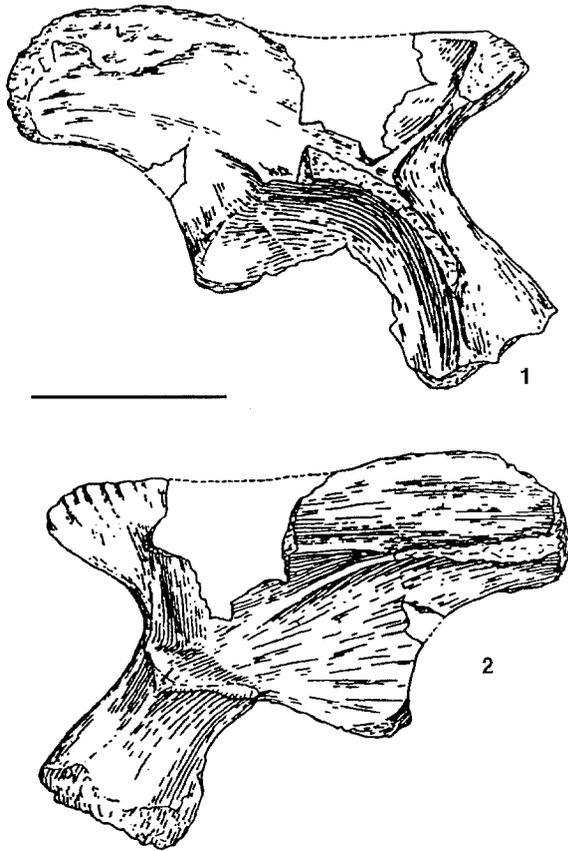


FIGURE 3 - Holotype ilium of *Caseosaurus crobyensis* nov. gen. et sp. (UMMP 8870) in lateral (1) and medial (2) views (after Case 1927). Scale bar is 5 cm. *Holotype d'un ilion de Caseosaurus crobyensis* nov. gen. et sp. en vues latérale et médiane (d'après Case 1927). Echelle = 5 cm.

partial vertebral column that is distinguished by very high neural spines, which he assigned to *Coelophysis* sp. Huene (1932, p. 37) named this specimen *Spinosuchus caseanus* (UMMP 7507), which he considered to be a podokesaurid theropod. Padian (1986) and Murry & Long (1989) do not consider it a dinosaur. Recent analyses of synapomorphies within Dinosauria (e.g., Novas 1993; Sereno & Novas 1993) allow a reconsideration of the taxonomic status of this species.

UMMP 7507 consists of 22 vertebrae and is now mounted in half-relief in plaster at UMMP. Most of the vertebrae are damaged to some extent. It is difficult to clearly distinguish the cervical and dorsal series because of probable "cervicalization" (Rowe & Gauthier 1990) of the anterior dorsals. There are five transitional vertebrae with the parapophysis at the neurocentral suture in vertebrae 9 and 10 (counting the anteriormost preserved vertebra as 1). The curve formed by the neural spines suggests that vertebra 22 is near the sacrum. It is probable that about 8 cervical and 14

dorsal vertebrae are preserved. Only a limited number of dinosaurian synapomorphies are present in a vertebral column (Sereno & Novas 1993). The hollowness of the centra in UMMP 7507 (Case 1922) suggests that *Spinosuchus* is a theropod. Sereno et al. (1993) listed extreme hollowing of centra and long bones as synapomorphies of Theropoda. Novas (1993) noted that hollow *long bones* are characteristic also of lagosuchids, pterosaurs and some basal sauropodomorphs, but did not demonstrate that hollow centra occur in these other groups. Hollow centra do occur in pterosaurs, but *Spinosuchus* is clearly not a flying reptile. A possible synapomorphy that *Spinosuchus* shares with Herrerasauridae is the presence of spine tables on the posterior dorsal vertebrae (Novas 1993). The top of the neural spine of vertebra 22 in *Spinosuchus* is notably expanded compared to others in the series. However, the neural spines in this taxon are so unusual that this may not be a valid character. Other possible dinosaur synapomorphies that might be present in *Spinosuchus* are not visible because of poor preservation or the present enclosure of the specimen in plaster (e. g., postaxial cervical epiphyses and hyposphene-hypantrum articulations: Novas 1993; Sereno & Novas 1993). Further preparation of the specimen is necessary before the taxonomic affinities of this specimen can be adequately evaluated. So, at present we tentatively assign *Spinosuchus* to cf. Theropoda *incertae sedis* on the basis of hollow centra. Note that Case (1927) considered that an isolated bone found with the vertebral column represented a cervical intercentrum (by inference postaxial). If this identification as to element and association is correct, then *Spinosuchus* is a proterosuchid-grade archosaur (Benton & Clark 1988) of a very derived and unusual kind. Recent discoveries of dorsal vertebrae with elongate neural spines (private collection) suggest that *Spinosuchus* is also present in the Adamanian Los Esteros Member of the Santa Rosa Formation in central New Mexico (Santa Fe County).

Case's (1922) third dinosaurian specimen is a left femur (UMMP 3396) that obviously pertains to an aetosaur, possibly *Desmatosuchus*. Case (1927, 1932) assigned various caudal vertebrae (UMMP 7277, 9805, 13670) and isolated teeth (e.g., UMMP 2680, 13766, 13765) to the Dinosauria or *Coelophysis* sp. The theropod-like caudal vertebrae exhibit no synapomorphies of dinosaurian taxa, and potential characters such as elongate prezygapophyses (Novas 1993) cannot be evaluated because of poor preservation (e.g., Case 1932, fig. 1). All the isolated teeth are serrated, laterally compressed and some are slightly recurved (e.g., Case 1932, figs 4-5). These specimens could repre-

sent theropods, rauisuchians or the "canine" teeth of a heterodont phytosaur.

Case (1927) described an isolated dinosaur ilium (UMMP 8870: Fig. 4) from the Tecovas Member that Long (in Murry 1989; Long & Murry 1995) assigned to the herrerasaurid *Chindesaurus bryansmalli*. This specimen bears a strong resemblance to the corresponding element in *Staurikosaurus* (Colbert 1970, fig. 8A) and *Herrerasaurus*

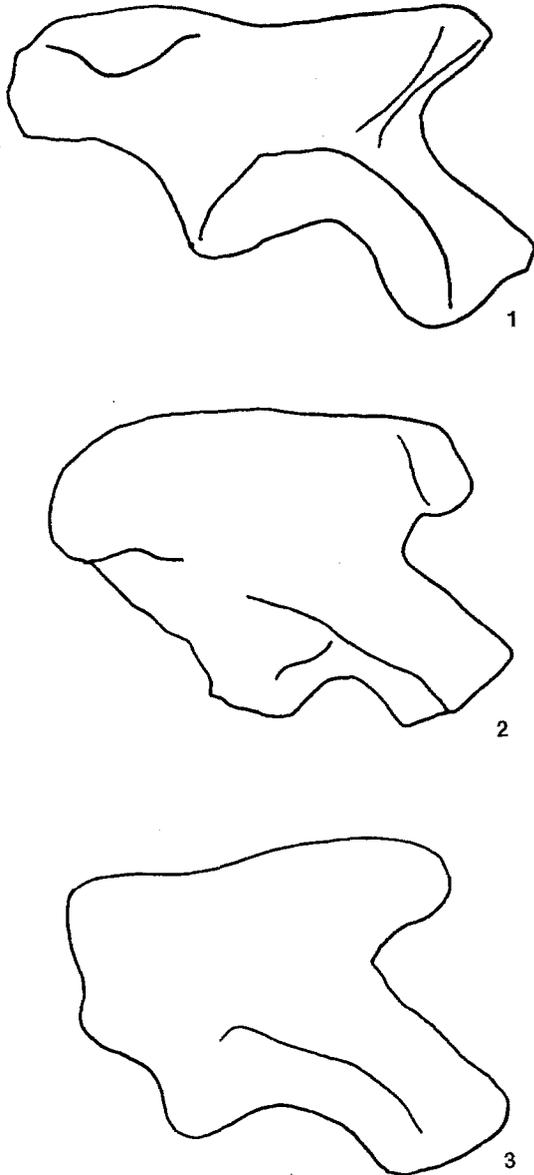


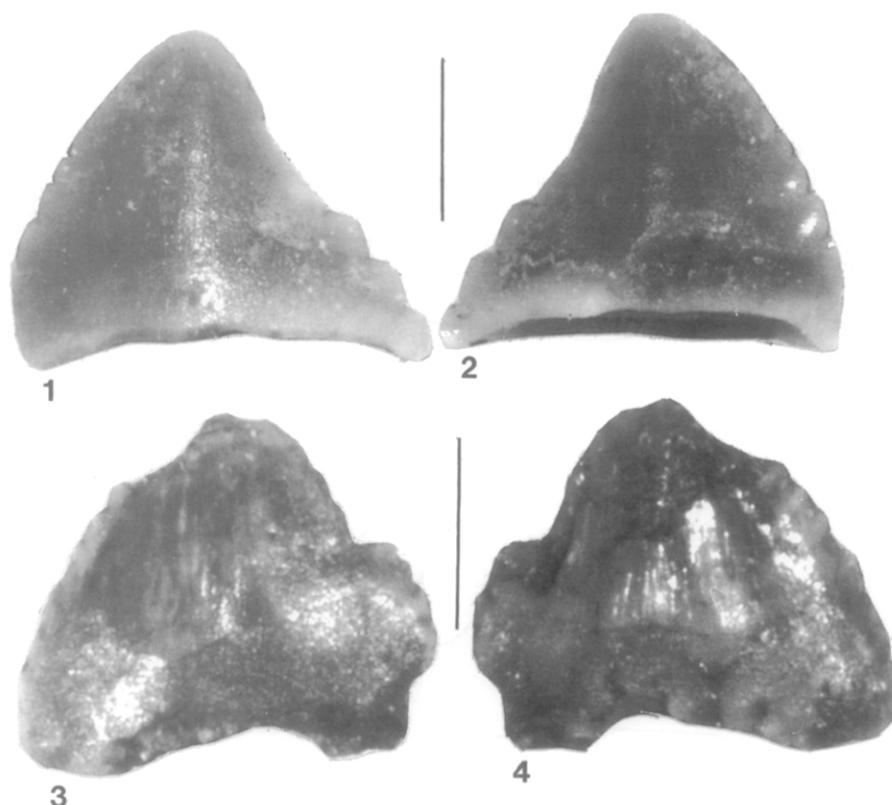
FIGURE 4 - Right ilia of herrerasaurids in lateral view. 1, *Caseosaurus crosbyensis* nov. gen. et sp. (after Case 1927). 2, *Herrerasaurus ischigualastensis* (after Novas 1993). 3, *Staurikosaurus pricei* (reversed after Colbert 1970). Drawn to same scale. *Ilion droit d'herrerasauridés en vue latérale. Tous à la même échelle.*

(Novas 1993, fig. 5) in being anteroposteriorly short and dorsoventrally high with a partially perforate acetabulum. Specifically, UMMP 8870 represents a dinosaur because it has a brevis shelf and a medially opened acetabular wall (Novas 1993). Further, it represents a herrerasaur because the brevis shelf is reduced to a slight ridge, and the brevis fossa is small (Novas 1993). UMMP 8870 differs from *Staurikosaurus* and *Herrerasaurus* in possessing (Fig. 5): (1) an elongate and dorsoventrally narrow posterior blade; (2) a narrow ridge on the lateral margin that extends from the anterodorsal margin of the acetabulum to the anterodorsal anterior spine (sensu Novas 1993); (3) a highly reduced brevis fossa; and (4) a semicircular margin dorsal to the acetabulum. Long (in Murry, 1989; Long & Murry 1995) assigned UMMP 8870 to *Chindesaurus bryansmalli*. The holotype of *Chindesaurus* (PEFO 10395) includes only two small fragments of the ilium, that Long and Murry (1995) consider to be indistinguishable from UMMP 8870 - a fragment of the pubic process of the left ilium (Long & Murry 1995, figs 182A-C, 183A-C) and a portion of the left posterior iliac blade (Long & Murry 1995, figs 182D-F, 183D-F). The pubic process possesses no diagnostic characters but the iliac blade fragment can be directly compared to the Texas ilium. The posterior iliac blade of PEFO 10395 differs from that in UMMP 8870 in possessing a deep brevis shelf that extends to the posterior margin, a lateral longitudinal ridge (for sacral rib articulation) that is placed more dorsally and a much thicker (more than twice) posterior blade in dorsal view. It is clear that the Texas specimen represents a herrerasaurid, but that it cannot be referred to *Chindesaurus* or any other described member of this family. Thus, we propose the new binomen *Caseosaurus crosbyensis* nov. gen. et sp. for this ilium (Appendix) in recognition of the discoverer, E.C. Case, and Crosby County, Texas which yielded the holotype (UMMP 8870) from the Tecovas Member of the Dockum Formation (late Carnian). This taxon differs from other herrerasaurs in the features cited above.

Hunt & Lucas (1994: Fig. 3.1-2) described the ornithischian *Tecovasaurus murryi* for a number of isolated teeth from the Tecovas Member of Crosby County and Harris et al. (1997) identified a single prosauropod tooth from the same locality. The latter is the only evidence for pre-Norian prosauropods in North America. ABH has recently collected a tooth of *Tecovasaurus* from a locality in the Bluewater Creek Formation of western New Mexico.

In New Mexico, the best Adamanian dinosaur specimen is a partial skeleton of a small non-herrerasaurid theropod from the Bluewater Creek Formation in McKinley County (Heckert et al.

FIGURE 5 - Selected Late Triassic ornithischian teeth from western North America. Scale bars are 1 mm. 1-2, Holotype maxillary/dentary tooth of *Tecovasaurus murreyi* (NMMNH P-18192). 1, Buccal view. 2, Lingual view. 3-4, Holotype maxillary/dentary tooth of *Lucianosaurus wildi* (NMMNH P-18194). 3, Buccal view. 4, Lingual view. *Dents d'ornithischiens du Trias supérieur d'Amérique du Nord occidentale*. Echelle = 1 mm. 1-2. Holotype d'une dent maxillaire de *Tecovasaurus murreyi* (NMMNH P-18192). 3-4. Holotype d'une dent maxillaire de *Lucianosaurus wildi* (NMMNH P-18194).



1994) at the same stratigraphic level as the *Placerias* quarry (Heckert et al. 1994). This may be the most completely preserved dinosaur of late Carnian age in North America with numerous vertebral centra and fragmentary limb and girdle elements recovered so far. This specimen will be described elsewhere. Small vertebrae associated with this skeleton appear to represent a second taxon of theropod. Tridactyl dinosaur tracks are also known from the Bluewater Creek Formation which may represent an ornithischian (Hasiotis et al. 1994). Case's (1916) report of a dinosaur from the San Pedro Arroyo Formation (sensu Lucas 1991) of Socorro County, New Mexico is based on phytosaur specimens (UMMP specimens).

Hunt & Lucas (1995, fig. 2D-E) described fragmentary theropod specimens (metapodials, caudal centra, ungual) from the Lamy amphibian quarry, Santa Fe County, New Mexico (Garita Creek Formation). They also described theropod podials from a nearby locality in the Los Esteros Member of the Santa Rosa Formation.

REVUELTIAN DINOSAURS

Revueltian dinosaurs are the most diverse in the Chinle Group and are known from Arizona, Texas

and New Mexico. The most diverse dinosaur fauna occurs in the Bull Canyon Formation, which is widely exposed in east-central New Mexico and West Texas and contains a large but generally fragmentary, dinosaur record. The vertebrate fauna of the Bull Canyon Formation in New Mexico contains eight dinosaur taxa that are described in an unpublished dissertation and will be described in detail elsewhere (Hunt 1994, 1995). The largest theropods are two new herrerasaurids (herrerasaurids A, B). Herrerasaurid A is known from several partial skeletons (e.g., UCM 47221, NMMNH P-17134, 17258), whereas specimens of herrerasaurid B consist of one partial skeleton (NMMNH P-4569) and various isolated elements were erroneously referred to the Prosauropoda by Long & Murry (1995). A third, smaller herrerasaurid (C) is only known from posterior dorsal centra and is the basis of the identification of *Chindesaurus bryansmalli* from New Mexico by Murry & Long (1989) and Long & Murry (1995). These specimens only indicate the occurrence of a *Chindesaurus*-sized herrerasaur. Three other specimens referred by Long & Murry (1995) to *Chindesaurus* (NMMNH P-4415, P-16656, P-17325, P-22494) are incorrectly identified and actually pertain to the new herrerasaurid A, a ?theropod and an indeterminate herrera-

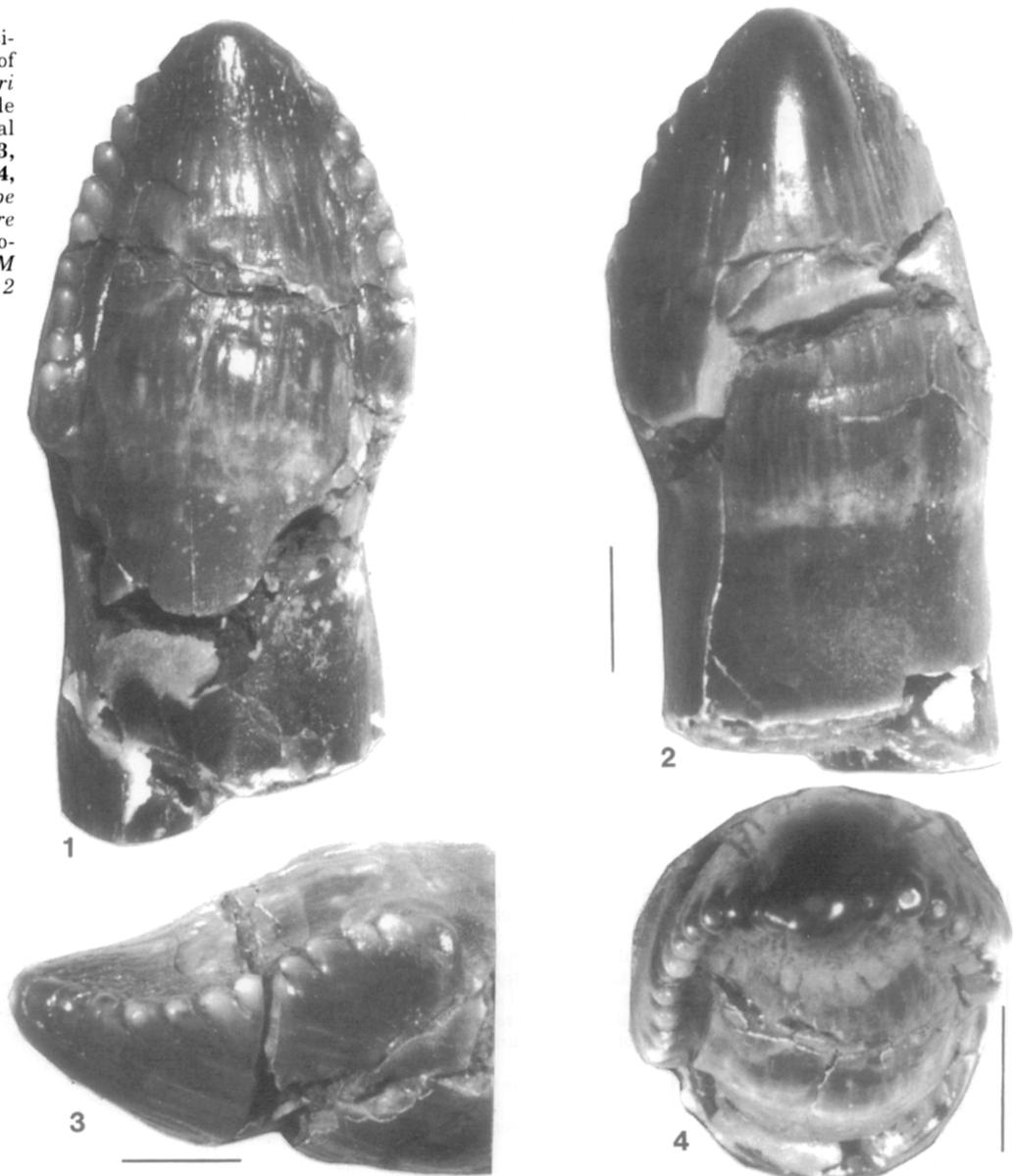
Land vertebrate faunchron	Theropoda	Sauropodomorpha	Ornithischia
Otischalkian (early Late Carnian)	indeterminate proximal femur (TX) indeterminate podial (WY)		
Adamanian (late Late Carnian)	<i>Camposaurus arizonensis</i> (partial skeleton - AZ) undescribed partial skeleton (NM) herrerasaurid vertebrae (AZ) ? <i>Spinosuchus caseanus</i> (vertebral column - TX + vertebrae - NM) <i>Caseosaurus crosbyensis</i> (illum - TX) indeterminate caudal vertebrae, metapodials, podials (NM) unstudied partial skeleton (AZ)	indeterminate tooth (TX)	<i>Tecovasaurus murreyi</i> (teeth - TX, AZ + NM) new genus (teeth - AZ + NM)
Revueltian (early-middle Norian)	new herrerasaurid (several partial skeletons - NM) new herrerasaurid (partial skeleton - NM) small herrerasaurid (centra - NM) new taxon (partial skeleton - NM) <i>Chindesaurus bryansmalli</i> (partial skeleton - AZ) "Coelophysis bauri" of Padian (1986)(partial skeleton - AZ, femur - NM) syntypes of <i>Coelophysis bauri</i> including many vertebrae and other elements described by Cope (e.g., Cope, 1887) and partial skeleton of Sullivan et al. (1996). All represent different taxon than neotype of <i>C. bauri</i> . <i>Protoavis texensis</i> (two partial skeletons - TX) inadequately described postcrania and teeth (AZ)	indeterminate centrum (NM) indeterminate partial lower jaw, premaxilla (TX)	<i>Revueltosaurus collenderi</i> (teeth - NM + AZ) <i>Technosaurus smalli</i> (dentary - TX) <i>Lucianosaurus wildi</i> (teeth - NM)
Apachean (Rhaetian)	<i>Coelophysis bauri</i> - lectotype and numerous other skeletons (NM) cf. <i>Syntarsus</i> sp. skull and postcrania (NM) indeterminate femora, podials, teeth (NM)		

TABLE 1. Distribution of dinosaurian taxa based on body fossils from the Chinle Group of western North America. Abbreviations refer to states: AZ, Arizona; NM, New Mexico; TX, Texas; WY, Wyoming. *Répartition des taxons de dinosaures d'après les fossiles du Groupe de Chinle, Ouest de l'Amérique du Nord. Les abréviations correspondent aux noms des états.*

saurid, respectively (Hunt 1994). Another smaller theropod (D) represents a new taxon of uncertain affinities and is only known from one partial skeleton (NMMNH P-17375). An isolated premaxilla (UCM 52081) demonstrates the presence of the edentulous putative theropod (see below) *Shuvosaurus inexpectatus* CHATERJEE, 1993. A single dorsal centrum identified by C.E. Gow (pers. comm., 1993) is the only evidence for a prosauro-

pod, as teeth assigned by Hunt (1988) to this taxon were later identified as pertaining to *Revueltosaurus* by Hunt (1989). Ornithischian teeth represent two species, *Revueltosaurus collenderi* HUNT, 1989 (Fig. 6) and *Lucianosaurus wildi* HUNT & LUCAS, 1994 (Fig. 3.3-4). *Revueltosaurus* is unusual in that the holotype premaxillary tooth has an incisiform shape more pronounced than in other basal ornithischians (Fig.

FIGURE 6 - Holotype incisi-form premaxilla tooth of *Revueltosaurus callenderi* (NMMNH P-4957). Scale bar is 2 mm. 1, Lingual view. 2, Labial view. 3, Anterior/posterior view. 4, Occlusal view. *Holotype d'une dent prémaxillaire incisiforme de Revueltosaurus callenderi* (NMMNH P-4957). Echelle = 2 mm.



6), which suggests that it may have been located at the anterior end of the jaw (e.g., no edentulous tip to premaxilla)

All dinosaurs from the Bull Canyon Formation in West Texas come from the Post quarry and include the edentulous putative ornithomimosaurian theropod *Shuvosaurus inexpectatus*, which is based on skull fragments, a dentary and a dorsal vertebra. Chatterjee's (1993) description of *Shuvosaurus* does not include mention of any synapomorphies which are diagnostic of Dinosauria (e.g., Gauthier 1986; Benton 1990; Sereno et al. 1993; Novas 1993; Sereno 1992; Sereno & Novas 1993; Padian & May 1993). Possible characters that might be present in the type material include epiphysis on the atlas (Novas 1993, p. 423) and temporal musculature overlapping the

frontal (Gauthier 1986). However, the atlas was neither described nor illustrated by Chatterjee (1993) and his reconstruction of the skull indicates that the frontal portion is poorly preserved. Thus, there is no evidence that *Shuvosaurus* represents a dinosaur. Supposed ornithomimosaurian characters are unconvincing due to poor preservation of the holotype skull. The edentulous nature of the jaws is surprising, because the most plesiomorphic ornithomimosaur (*Pelecanimimus*), which is 100 million years younger than *Shuvosaurus*, retains small teeth (Perez-Moreno et al. 1994; Barsbold & Osmolska 1990). Long & Murry (1995) surmise that *Shuvosaurus* may represent the skull of the enigmatic ?rauisuchian that they name *Chatterjeea elegans* based on size, unusual morphology and association in the Post quarry.

We tentatively support this synonymy and note the association of a premaxilla of *Shuvosaurus* and an ilium of *Chatterjeea* in the Bull Canyon Formation of east-central New Mexico (Hunt 1994a,b; Long & Murry 1995).

Technosaurus smalli was originally described as an ornithischian (Chatterjee 1984), but the holotype is now known to contain elements of both an ornithischian and a prosauropod which are of different size (Serenio 1992). The right dentary is ornithischian, whereas the premaxilla and posterior lower jaw are prosauropod (Serenio 1992). *T. smalli* has been restricted to the ornithischian specimen (Hunt & Lucas 1994). The prosauropod elements are indeterminate.

The putative bird *Protoavis texensis* (Chatterjee 1991) strongly resembles a basal non-avian theropod, as would be expected in an early avian (note that Chatterjee [1986] initially identified the specimens as a juvenile *Coelophysis*). Chatterjee (1991) described the skull of *Protoavis* and illustrated the postcrania, which are to be described in a later paper. The principal difficulty in identifying the relationships of this taxon is that the skull is fragmented. There may also be problems with the association of elements. Chatterjee (1991) provided a generic description in his systematic section but no differential diagnosis. Later in the paper he lists two apomorphies of this taxon: teeth restricted to the tips of jaws and the maxilla is edentulous. However, these apomorphies are relative to *Archaeopteryx*, *Avimimus* and later avians and assume that *Protoavis* is a bird. We are not convinced that *Protoavis* possesses any of the cranial synapomorphies of Aves listed by Chatterjee because of the fragmentary nature of the holotype skull of this genus. Similarly, we cannot support most of the supposed synapomorphies that link *Protoavis* and Ornithurae. The morphology of the quadrate of *Protoavis* is the most convincing evidence for avian affinity, if this element is correctly identified. The postcrania of *Protoavis* (as preliminarily described) appear either to be theropod-like (e.g., astragalus) or unconvincing in their identification (putative furcula and sternum). In summary, we conclude that *Protoavis* probably represents an aberrant theropod.

Two dinosaur-bearing faunas can be distinguished in the Bull Canyon Formation. The lower fauna, which encompasses the lower 50 m of the 95-m-thick unit, includes herrerasaurids A and C, theropod D, a prosauropod, *Revueltosaurus* and *Technosaurus*. The upper fauna includes herrerasaurids B and C and *Lucianosaurus* (Hunt 1994, 1995).

The original syntypes of the various species of *Coelophysis* (Colbert 1989; Hunt & Lucas 1991;

Sullivan 1994; Sullivan et al., 1996) were collected from at least two localities in the Petrified Forest Formation in Rio Arriba County, New Mexico by David Baldwin in the late 1880's (Colbert 1989; Hunt & Lucas 1991). Sullivan et al. (1996) described apparent topotypes of *Coelophysis* that have similar preservation to the syntypes, occur at about the same stratigraphic level, and are morphologically indistinguishable from the syntypes. These specimens apparently differ from the neotype of *Coelophysis* (AMNH 7224) from the Ghost Ranch quarry that is the younger (Apachean) Rock Point Formation in this area (Hunt & Lucas 1991; Sullivan et al. 1996). Therefore, the syntypes of *Coelophysis bauri* (Cope 1887) from the Petrified Forest Formation may represent a different taxon than the neotype from the Rock Point Formation. The Petrified Forest Formation specimens are from eight localities in the upper part of the Petrified Forest Formation, which include the "Cross quarry" of Long & Murry (1995) (locality 3 of Sullivan et al., [1996] that yielded partial skeleton NMMNH P-22298). Another nearby locality that occurs at about the same stratigraphic level is the Canjilon quarry, which has yielded a theropod dorsal centrum (Long & Murry 1995). A single caudal centrum from the upper portion of the Petrified Forest Formation of Sandoval County, New Mexico is very hollow and pertains to a theropod (Hunt & Lucas 1989; Hunt & Lucas 1993b).

The upper dinosaur-bearing unit at Petrified Forest National Park is the Painted Desert Member of the Petrified Forest Formation. This contains partial skeletons of a ceratosaurian and a herrerasaurid and many teeth of an ornithischian. The herrerasaurid was named *Chindesaurus bryansmalli* by Long & Murry (1995). Surprisingly, Long & Murry did not mention the teeth that are included in the holotype (PEFO 10395). The most complete tooth has a broken tip. It is laterally compressed and recurved with a concave posterior margin. As preserved, the height is 22 mm with a basal length of about 12.5 mm. The posterior and anterior margins are finely serrated with about 5 serrations per mm. We assume that this tooth pertains to *Chindesaurus bryansmalli*. Two other tooth fragments are, respectively, nondinosaurian and indeterminate. We have recently collected fragmentary topotype specimens of this taxon (PEFO specimens). Long & Murry (1995) refer a dorsal centrum (PEFO 4849) from a nearby locality to this taxon, but it is not generically determinate.

The ceratosaurian was referred to *Coelophysis bauri* by Padian (1986). This specimen apparently differs from the neotype (AMNH 7224) and associated skeletons of *Coelophysis bauri*, that are from the younger Apachean-age Ghost Ranch quarry, in possessing a well-developed obturator

foramen (Hunt & Lucas 1991). However, examination of AMNH 7224 by RMS indicates that, contrary to previous descriptions, the neotype of *Coelophysis bauri* does possess an obturator foramen. This fragmentary specimen is similar to *Syntarsus* (sensu Rowe & Gauthier 1990) and is apparently identical to an undescribed specimen from the Bull Canyon Formation of east-central New Mexico (NMMNH P-4415). One specimen referred to *Coelophysis* by Cope (1887), from the Revueltian Petrified Forest Formation in New Mexico, has a similar pubis to the PFNP specimen with a well-developed obturator foramen (plesiomorphic feature). The Petrified Forest specimen is from the Dinosaur Hill locality (UCMP V82250) (= Bolt quarry = Lacey Point of some authors). Several other theropod specimens (femur, vertebrae) have recently been collected by APH from this locality (uncatalogued PEFO specimens).

All the ornithischian teeth from the Painted Desert Member, some of which have been previously reported as representing an anchisaurid prosauropod (Murry & Long 1989), pertain to *Revueltosaurus callenderi* (Padian 1991, fig. 1A-H; Hunt & Lucas 1994), which is known from four localities at Petrified Forest National Park (FMNH, PEFO collections).

There are few Revueltian vertebrate tracks (e.g., Hunt et al. 1993), and none represent dinosaurs.

The Owl Rock Formation contains a diverse vertebrate fauna only in northeastern Arizona (Kirby 1991, 1993). Kirby (1991, 1993) assigned various isolated postcrania and teeth to the Theropoda or cf. ?Herrerasauridae (cf. Staurikosauridae? of Kirby 1993). Many of these specimens, including an astragalus and a proximal femur, are undoubtedly dinosaurian (Kirby 1991, pl. 15, figs B-L). These specimens are in need of more detailed description. Kirby (1991, 1993) also noted, on the basis of isolated teeth, the occurrence of a possible ornithischian at one locality. These specimens do not have the coarse, dorsally oriented denticles of ornithischian or non-yunannosaurid prosauropods (Kirby 1991, pl. 16) and are not dinosaurian.

APACHEAN DINOSAURS

In contrast to older portions of the Chinle Group, Apachean strata contain many vertebrate tracks (Fig. 7) and relatively few body fossils. Tetrapod fossils are only common in east-central and northeastern New Mexico and at one quarry (Ghost Ranch) in the north-central part of the state (Hunt & Lucas 1993). Fossil fishes are locally abundant in southeastern Utah, southwestern Colorado and east-central New Mexico. However, vertebrate tracks are known from east-central

and northeastern New Mexico, southeastern and northeastern Utah, southwestern, southeastern and northwestern Colorado and central Wyoming (Baird 1964; Lockley 1986; Conrad et al. 1987; Lockley et al. 1992, 1993; Lockley & Hunt 1993, 1995).

The most important dinosaur body fossils from Apachean age rocks are from the Ghost Ranch quarry (Rock Point Formation) in Rio Arriba County, New Mexico. Some of the many skeletons and isolated bones from this quarry represent the small ceratosaur *Coelophysis bauri* (Colbert 1989). This taxon has an obturator foramen and may lack the pubic fenestrae and pubio-ischiac plate of *Syntarsus*. A number of specimens from the Ghost Ranch quarry have two pubic foramina, incipient cranial crests and fused tarsals that cannot be distinguished from *Syntarsus kayentakatae* (Rowe & Gauthier 1990; Paul 1993; Sullivan 1994) other than on the basis of smaller size. Reisz and others (in prep.) are currently restudying the cranial and postcranial specimens from Ghost Ranch.

Dubiel et al. (1989) reported a theropod podial from what is now recognized as the Rock Point Formation of southeastern Colorado. This undescribed specimen could not be located in the collections of the University of Colorado Museum where it was deposited. Fragmentary theropod specimens (femur, podials, teeth) have recently been collected from the Redonda Formation of east-central New Mexico (Hunt et al. 1997).

Vertebrate ichnofaunas are very diverse in Apachean strata and include a number of dinosaurian tracks from many localities (Table 2). The most common is a small form (10 cm long pedal imprint) of tridactyl track assigned to *Grallator* and interpreted to be the trace of a theropod dinosaur. The names *Agialopous* and *Coelurosaurichnus* have also been applied to this morphotype but these ichnotaxa are probably junior subjective synonyms of *Grallator* (e.g. Leonardi & Lockley 1995). Some larger tridactyl tracks, with pedal imprint lengths of up to 25 cm, are also assignable to *Grallator* (e.g., Lockley & Hunt 1993). All Chinle tridactyl tracks, with the possible exception of *Atreipus* (Olsen & Baird 1986), that is only known from the shores of Lake Powell in Utah, represent theropods. *Atreipus* is probably the track of an ornithischian (Olsen & Baird 1986).

Two morphotypes of tetradactyl tracks occur in Apachean strata. The first is the track of a bipedal animal with a tetradactyl foot, but often only three digit impressions are preserved (Lockley et al. 1993, fig. 2B; Lockley & Hunt 1995, fig. 3.17). These tracks most resemble some specimens described as *Pseudotrasauropus* by Ellenberger from Lesotho.

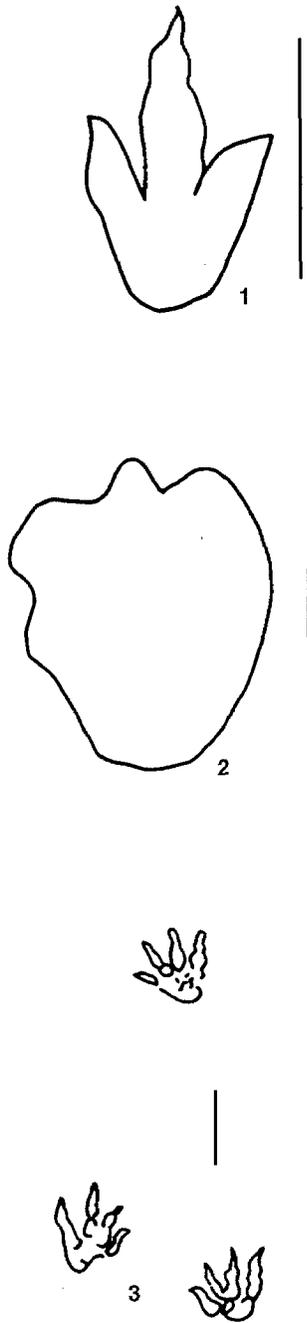


FIGURE 7 - Principal Apachean vertebrate ichnotaxa. Scale bars are 10 cm. 1. Pes print of *Grallator* sp. 2. Pes print of *Tetrasauropus* sp. 3. Partial trackway of *Pseudotetrasauropus*. (after Hunt et al. 1993). *Ichnotaxons principaux de vertébrés apacheens. Echelles = 10 cm. 1. Empreinte de pied de Grallator sp. 2. Empreinte de pied de Tetrasauropus sp. 3. Piste fragmentaire de Pseudotetrasauropus (d'après Hunt et al. 1993).*

revision of the Lesotho material. Other Chinle tetradactyl tracks represent a quadrupedal track-maker who left padded elephantine- or sauropod-like tracks (Lockley & Hunt 1995, fig. 3.13). The manus prints are semilunate like sauropod tracks. These tracks are similar to some specimens that Ellenberger described as *Tetrasauropus* that we feel were unjustly synonymized by Olsen & Galton (1984). Both *Tetrasauropus* and *Pseudotetrasauropus* are probably tracks of prosauropods (Lockley et al. 1993; Lockley & Hunt 1995).

DISCUSSION

Chinle dinosaurs are known from early Tuvanian to Rhaetian strata that encompasses the entire time interval from which dinosaurs are known in the Triassic (Hunt 1991). Dinosaurs are consistently rare members of vertebrate faunas in the Chinle Group, except apparently during the Apachean (Rhaetian). However, there is no major faunal turnover or evidence of large environmental change during the Late Triassic in western North America. Thus, the record of dinosaurs in the Chinle Group is arguably the most representative of the early evolution and diversification of this group. For example, the late Carnian and Norian dinosaur faunas of the Chinle are the most diverse in the world. Taphonomic and faunal studies indicate that Triassic dinosaurs were restricted to drier environments (Hunt 1991; Newell 1992), which explains their rarity in the Chinle Group, which is dominated by semiaquatic/aquatic vertebrate communities (Hunt 1991).

The Chinle dinosaur record (Fig. 8) indicates that early Tuvanian dinosaurs were very uncommon, but that by the late Tuvanian, dinosaur faunas were diverse and included theropods, ornithischians and prosauropods - the three principal clades of dinosaurs.

Early Tuvanian dinosaurs are rare outside North America and are restricted to the Ischigualasto Formation of Argentina the Santa Maria Formation of Brazil the Maleri Formation of India and the Argana Formation of Morocco. It is notable that these dinosaurs include several theropods, an ornithischian and a prosauropod, indicating that all the major dinosaurian clades (Theropoda, Sauropodomorpha, Ornithischia) were present in the late Carnian, so they must have had their origin earlier in the Triassic. Unfortunately, early Carnian vertebrate faunas are rare, and the only diverse one is from the Schilfsandstein of Germany, which is dominated by semiaquatic/aquatic amphibians and reptiles (Hunt 1993). The enigmatic Turkey Branch fauna from Virginia is of this age (Sues & Olsen 1990; Huber et al. 1993; Olsen 1997).

Ellenberger's work has been extensively critiqued by Olsen & Galton (1984). It seems clear that Ellenberger erected too many new ichnotaxa for his collections, but it also our opinion that Olsen & Galton (1984) were too quick to synonymize most of the Lesotho tracks with existing ichnotaxa. Notably some of the *Pseudotetrasauropus*, tracks represent distinct morphotypes that represent neither *Batrachichnus* nor *Otozoum*. Therefore, we follow recent authors in placing the tetradactyl tracks in *Pseudotetrasauropus* pending a thorough

Location	Stratigraphic unit	Ichnotaxa
Panhandle OK	Sheep Pen Formation	<i>Grallator</i> sp.
East-central NM	Redonda Formation	<i>Grallator</i> sp. <i>Pseudotetrasauropus</i> sp.
Northeastern NM	Sloan Canyon Formation	<i>Grallator</i> sp., large tridactyl <i>Tetrasauropus</i> sp.
Northeastern NM	Sheep Pen Formation	<i>Grallator</i> sp. <i>Pseudotetrasauropus</i> sp.
West-central CO	Rock Point Formation	<i>Grallator</i> sp.
Southeastern CO	Sheep Pen Formation	<i>Grallator</i> sp.
Northwestern CO	Bell Springs Formation	<i>Grallator</i> sp.
East-central UT	Rock Point Formation	<i>Grallator</i> sp.
Southeastern UT	Blue Mesa Member of Petrified Forest Formation	<i>Atreipus</i> sp.
Northeastern UT	Bell Springs Formation	<i>Grallator</i> sp. <i>Tetrasauropus</i> sp.
Central WY	Bell Springs Formation	<i>Grallator</i> sp.

TABLE 2. Distribution of dinosaurian ichnotaxa in Apachean strata of the Chinle Group (Branson & Mehl 1932; Lockley 1986; Conrad et al. 1987; Lockley et al. 1992, 1993; Hunt et al. 1993; Lockley & Hunt 1993, 1995). Note that the only other dinosaurian ichnofossils are putative ornithischian tracks from the Adamanian of New Mexico (Hasiostis et al. 1994). Abbreviations refer to states: AZ, Arizona; CO, Colorado; NM, New Mexico; OK, Oklahoma; TX, Texas; UT, Utah; WY, Wyoming. *Répartition des ichnotaxons dans les niveaux apacheans du Groupe de Chinle. Remarque que les autres ichnofossiles de dinosauriens ne sont qu'hypothétiquement des traces d'ornithischiens dans l'Adamanién du Nouveau-Mexique (Hasiostis et al. 1994).*

Late Tuvolian dinosaur body-fossils are also rare outside western North America. Notable exceptions are the ornithischians *Pekinosaurus olseni* and *Galtonia gibbidens* from the Conewagan of the Newark Supergroup of eastern North America (Huber et al. 1993; Hunt & Lucas 1994).

Dinosaurs are numerically more common in the Norian of the Chinle Group than in the Carnian, although this may be biased by the fact that early Revueltian strata are particularly rich in terrestrial reptiles (Hunt & Lucas 1993b). There are at least 12 species of Revueltian dinosaurs known from the Chinle Group, and fragmentary specimens suggest the presence of several more. The best dated and best studied Norian dinosaur faunas outside North America are from the Stubensandstein of Germany, where prosauropod specimens are the most common, but each prosauropod fauna is monogeneric (*Sellosaurus* in Stubensandstein; *Plateosaurus* in Knollenmergel). Theropods also occur in the Stubensandstein (e.g., *Halticosaurus*), but ornithischians are absent or very rare (New Mexico, Morocco) in all prosauropod-bearing faunas in the Triassic.

It is difficult to gauge how common or diverse Rhaetian dinosaurs are in the Chinle Group because of facies problems. Rhaetian tetrapod faunas are depauperate in dinosaurs in east-central and northeastern New Mexico, but at the Ghost Ranch quarry over 95% of the specimens pertain to theropods, probably reflecting the sampling of semiaquatic as opposed to terrestrial communities respectively. The track record seems to indicate that dino-

sauurs were much more common in the Rhaetian of the western United States than in the Norian. Tracks that we interpret to have been made by prosauropods (*Tetrasauropus*, *Pseudotetrasauropus*) are notably common at Apachean tracksites relative to the poor record from older portions of the Chinle Group (Lockley & Hunt 1995).

Outside North America, herrerasaurid theropods are restricted to the late Carnian. However, in the Chinle Group there are at least three Norian herrerasaurids. There are no herrerasaurids from other well-dated Norian units, such as those in Europe. Indeed, theropod dinosaurs discriminate three biogeographic provinces in the Late Triassic (Fig. 9). A northern province (e.g. Western Europe) contains only ceratosaurs, whereas a southern province (South America, South Africa, India) yields only herrerasaurids. A central province, which includes the United States, contains both ceratosaurs (e.g., *Coelophysis*) and herrerasaurids. Prosauropod distributions provide some support for the recognition of three provinces, with plateosaurids and thecodontosaurids being most common in the northern province, melanosaurids and blikanasaurids in the south, with prosauropods being rare in the central province. Ornithischians are poorly known worldwide from the Late Triassic, but *Pisanosaurus* is restricted to the southern province and *Revueltosaurus*-like forms are currently only known from the central province (eastern and western North America, Morocco). No ornithischian specimens have been collected from the northern province.

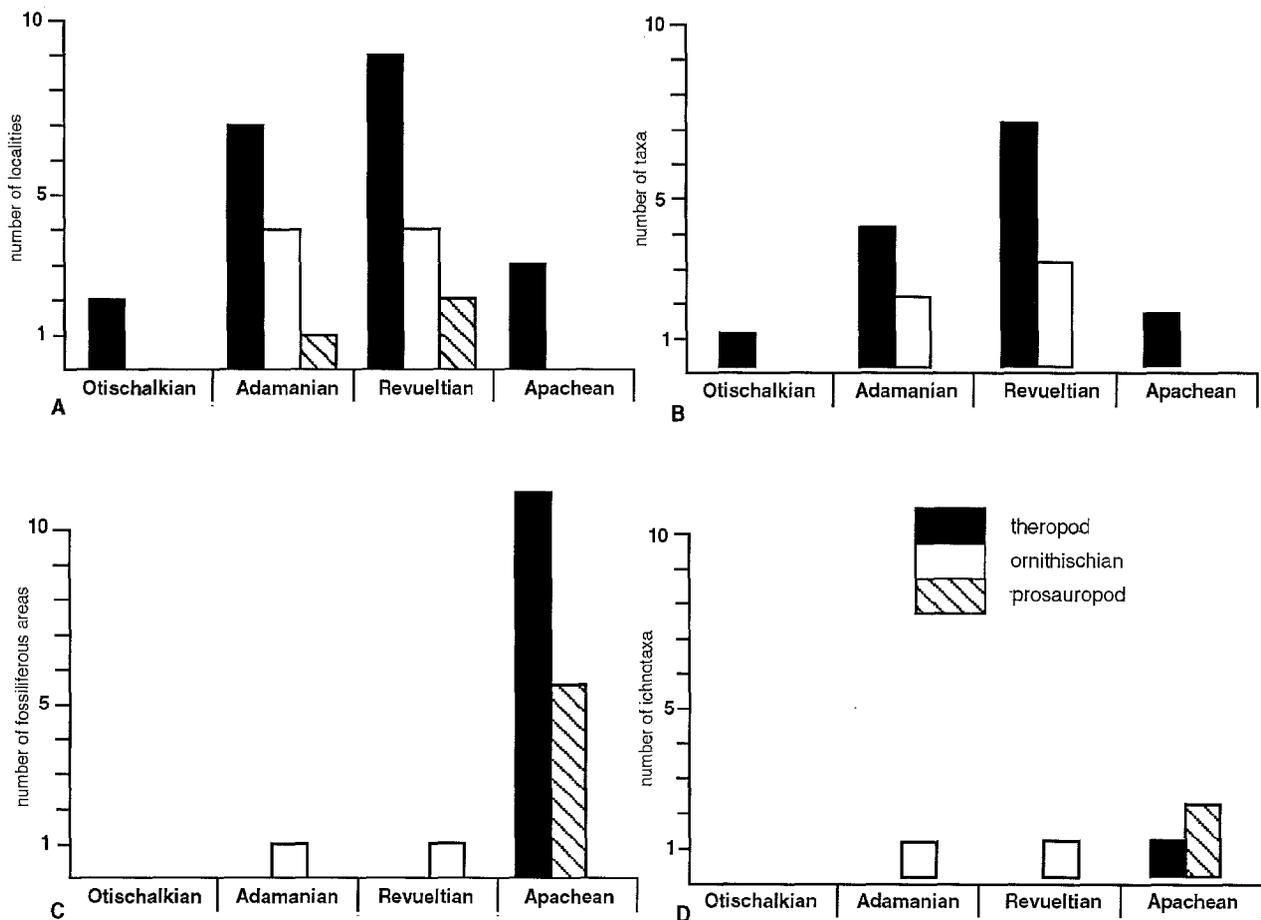


FIGURE 8 - Histogram of dinosaur taxa (and ichnotaxa) through time in the Late Triassic of western North America. **A-B.** Dinosaurs known from body fossils. **C-D.** Dinosaurs known from footprints. **A.** Localities yielding dinosaur body fossils. **B.** Number of taxa of dinosaurs apparent from body fossils. **C.** Number of fossiliferous areas that yield vertebrate tracks. **D.** Number of dinosaurian ichnotaxa. *Histogramme des taxons de dinosaures (et ichnotaxons) dans le Trias supérieur de l'Ouest de l'Amérique du Nord. A-B. Dinosaures connus d'après des restes osseux. C-D. Dinosaures connus d'après des empreintes de pied. A. Sites ayant fourni des restes osseux de dinosaures. B. Nombre de taxons d'après des restes osseux. C. Nombre de sites fossilifères ayant fourni des pistes de vertébrés. D. Nombre d'ichnotaxons de dinosaures.*

Ornithischians are rare throughout the Chinle Group, and most occurrences are isolated teeth. No ornithischians are present in Otischalkian-age strata. They are present in Adamanian faunas, but only in the Revuelitian (Norian) is more than one species known. Apachean ornithischians are unknown. Ornithischians such as *Revueltosaurus* and *Tecovasaurus* are widespread taxa that have biochronological utility.

The Prosauropoda are the rarest clade of dinosaurs present in the Chinle. These large herbivorous dinosaurs apparently only flourished in drier conditions than most of those represented by Chinle rocks (Hunt 1991). Footprint evidence suggests that prosauropods became more common in the Rhaetian because of the abundance of *Pseudotetrasauropus* and *Tetrasauropus* relative to other kinds of tracks. The only well dated Norian-

Rhaetian sequence of vertebrate faunas outside North America are in Germany (Benton, 1986, 1993) and Greenland (Jenkins et al 1994; Kent & Clemmensen 1996), and here, also, prosauropods become very numerous in the Rhaetian (and late Norian).

In the Chinle Group, vertebrate tracks are stratigraphically restricted, with a few exceptions, to Apachean-age units. This is obviously a taphonomic artifact, but a similar distribution occurs in South Africa, where vertebrate tracks become very common in the latest Triassic (Olsen & Galton 1984). No species of dinosaur body fossils found in the Chinle Group are clearly known from other areas, except the possible occurrence of *Syntarsus* at Ghost Ranch. However, the Apachean ichnotaxa *Tetrasauropus* and *Pseudotetrasauropus* also occur in South Africa and Europe. This is tenuous evi-

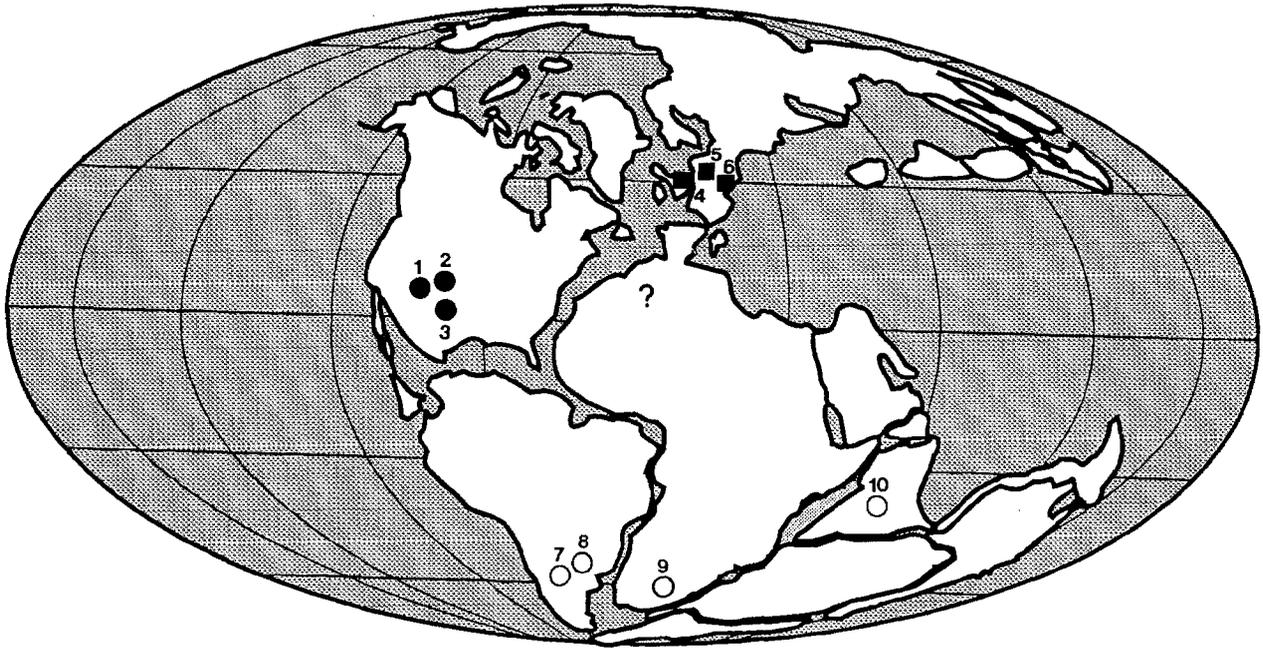


FIGURE 9 - Principal Late Triassic dinosaur localities and biogeographic provinces. Solid circles are localities with ceratosaurs and herrerasaurids: 1, Arizona, USA; 2, New Mexico, USA; 3, Texas, USA. Solid squares are localities with ceratosaurs and no herrerasaurids: 4, United Kingdom; 5, Belgium; 6, Germany. Open circles have herrerasaurids and no ceratosaurs; 7, Argentina; 8, Brazil; 9, South Africa; 10, India. Question mark (?) indicates the ornithischian and prosauropod fauna of Morocco that not yet produced fossil bones of theropods. Basemap from Lucas & Morales (1993). *Principaux sites de dinosaures du Trias supérieur et provinces biogéographiques. Les cercles pleins représentent les sites avec des cératosaures et des herrerasauridés. Les cercles vides représentent les localités qui ont des herrerasauridés et pas de cératosaures. Les points d'interrogation indiquent les faunes d'ornithischiens et prosauropodes du Maroc qui n'ont pas encore fourni d'os de théropodes (d'après la carte de Lucas & Morales 1993).*

dence to suggest that dinosaur faunas were becoming slightly more cosmopolitan in the latest Triassic, foreshadowing the intercontinental distribution of many Liassic dinosaur taxa (e.g. *Massospondylus*, *Dilophosaurus*, *Syntarsus*, *Scelidosaurus*).

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APPENDIX

SYSTEMATIC PALAEOLOGY

SAURISCHIA, Seeley, 1871
 THEROPODA Marsh, 1881
 HERRERASAURIDAE Benedetto, 1973

Genus *Caseosaurus* nov. gen.

Type Species - *Caseosaurus crosbyensis* nov. sp.

Etymology - In recognition of E.C. Case who discovered the holotype and made substantial contributions to our knowledge of Late Triassic tetrapods.

Diagnosis - *Herrerasaurus* whose ilium differs from *Staurikosaurus* and *Herrerasaurus* in possessing: (1) an elongate and dorsoventrally narrow posterior blade; (2) a narrow ridge on the lateral margin that extends from the anterodorsal margin of the acetabulum to the anterodorsal anterior spine (sensu Novas, 1993); (3) a highly reduced brevis fossa; and (4) a semicircular margin dorsal to the acetabulum; differs from *Chindesaurus bryansmalli* in possessing a less deep brevis shelf which does not extend to the posterior margin, a lateral longitudinal ridge (for sacral rib articulation) which is placed more ventrally and a much thinner (less than half) posterior blade in dorsal view.

Caseosaurus crosbyensis nov. sp.

Coelophysis sp. - Case, 1927, p. 221, fig. 7.

Chindesaurus bryansmalli - Long & Murry, 1995, p. 174, figs 180-181.

Diagnosis - As for genus.

Holotype - UMMP 8870, right ilium.

Type horizon - Tecovas Member of the Dockum Formation (Upper Triassic: late Tuvolian).

Type locality - Crosby County, Texas - exact location unknown.

Etymology - Named for Crosby County, Texas, which yielded the holotype.

CERATOSAURIA Marsh, 1884

Genus *Camposaurus* nov. gen.

Type species - *Camposaurus arizonensis* nov. sp.

Diagnosis - Theropod that differs from all ceratosaurs except *Rioarribasaurus* and *Syntarsus* in possessing tarsals fused to the tibia and fibula and differs from *Rioarribasaurus* and *Syntarsus* in that the ventral margin of the astragalus in anterior/posterior view is horizontal rather than deeply concave (Long & Murry 1995) and further differs from *Coelophysis* in that the fibula was in contact with the tibia in anterior view for a distance equal to at least one and a half times the width of the astragalus plus calcaneum (compare Colbert 1989, fig. 87A).

Etymology - Honors Charles Camp, who excavated the *Placerias* quarry and all specimens of this new genus.

Discussion - The paratypes of *Camposaurus* provide additional characters that distinguish this taxon from *Coelophysis* and *Syntarsus*, including femoral head more rectangular and dorsal centra more waisted in ventral view.

Camposaurus arizonensis nov. sp.

Theropod - Lucas et al. 1992, p. 172, fig 1.

Ceratosauria undet. - Long & Murry, 1995, figs 191-192.

Diagnosis - As for genus

Type specimens - Associated right and left distal hindlimbs and fused astragali and calcanea (UCMP 34498).

Paratypes - UCMP uncatalogued, proximal right femur (Long & Murry 1995, figs 191, 192A-E), partial sacrum (Lucas et al. 1992, fig. 1d; Long & Murry 1995, fig. 192Y), dorsal centrum (Long & Murry 1995, fig. 192Q-T), 3 incomplete sacra; MNA Pl. 2777, dorsal centrum (Long & Murry 1995, fig. 192M-P).

Tentatively referred specimen - A proximal left pubis (Long & Murry 1995, fig. 192K-L).

Type horizon - Bluewater Creek Formation of Chinle Group (Upper Triassic, late Carnian).

Type locality - *Placerias* quarry, Apache County, Arizona (UCMP locality A269).

Etymology - Alludes to the state of Arizona, which yielded the holotype.

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