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Tetrapod biostratigraphy and biochronology of the Triassic–Jurassic transition on the southern Colorado Plateau, USA

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Abstract

Nonmarine fluvial, eolian and lacustrine strata of the Chinle and Glen Canyon groups on the southern Colorado Plateau preserve tetrapod body fossils and footprints that are one of the world's most extensive tetrapod fossil records across the Triassic–Jurassic boundary. We organize these tetrapod fossils into five, time-successive biostratigraphic assemblages (in ascending order, Owl Rock, Rock Point, Dinosaur Canyon, Whitmore Point and Kayenta) that we assign to the (ascending order) Revueltian, Apachean, Wassonian and Dawan land-vertebrate faunachrons (LVF). In doing so, we redefine the Wassonian and the Dawan LVFs. The Apachean–Wassonian boundary approximates the Triassic–Jurassic boundary. This tetrapod biostratigraphy and biochronology of the Triassic–Jurassic transition on the southern Colorado Plateau confirms that crurotarsan extinction closely corresponds to the end of the Triassic, and that a dramatic increase in dinosaur diversity, abundance and body size preceded the end of the Triassic.

Keywords: Triassic–Jurassic boundary; Colorado Plateau; Chinle Group; Glen Canyon Group; Tetrapod

1. Introduction

The Four Corners (common boundary of Utah, Colorado, Arizona and New Mexico) sit in the southern portion of the Colorado Plateau (Fig. 1), a relatively stable piece of the Earth's crust that is mostly covered by flat-lying sedimentary rocks of Mesozoic age. A portion of these Mesozoic strata, rocks of Late Triassic and Early Jurassic age, represent one of the most significant records of the Triassic–Jurassic transition on land, which took place over an interval of about 20 Ma, between 210 and 190 Ma. On the southern Colorado Plateau, the Triassic–Jurassic transition was a time of significant changes in the composition of the terrestrial vertebrate (tetrapod) fauna. Here, we place the tetrapod fossils of the Triassic–Jurassic transition on the southern Colorado Plateau into a detailed biostratigraphic and biochronologic framework based on a synthesis of old and newly collected data. We then discuss the implications of this framework for mapping some of the major events in tetrapod evolution across the Triassic–Jurassic boundary.

2. Geography and lithostratigraphy

Strata that document the Triassic–Jurassic transition on the southern Colorado Plateau (Fig. 2) are best

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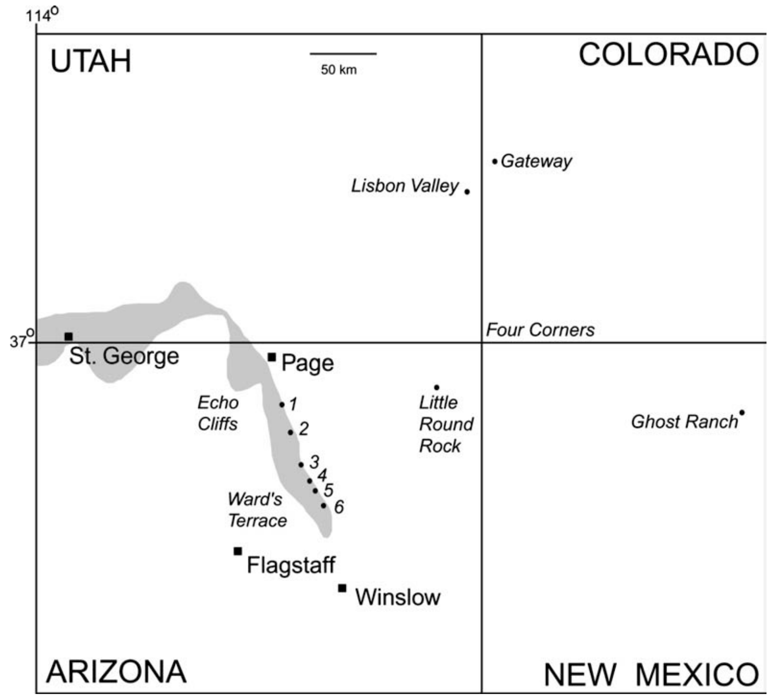


Fig. 1. Index map of southern Colorado Plateau showing place names mentioned in text. The gray area is the outcrop belt of the Moenave Formation and the numbered points are the measured sections in Fig. 4.

exposed in parts of southern Utah, northern Arizona and western Colorado. Three principal areas preserve the most extensive and fossiliferous outcrops, and have been recently studied by us in some detail: (1) St. George–Kanab area in southwestern Utah; (2) Echo Cliffs–Ward's Terrace area of northern Arizona; and (3) Gateway area of southwestern Colorado (Fig. 1). Other areas (for example, Lisbon Valley in southeastern Utah and Ghost Ranch area of northern New Mexico: Fig. 1) encompass much less extensive outcrop areas relevant to the Triassic–Jurassic transition, but they also contribute important information to our understanding of this time interval.

2.1. Chinle Group

The majority of the Upper Triassic strata on the southern Colorado Plateau are assigned to the Chinle Group (formerly formation) (Gregory, 1917; Stewart et al., 1972; Lucas, 1993; Lucas et al., 1997). Critical strata to understanding the Triassic–Jurassic transition on the southern Colorado Plateau are the two uppermost formations of the Chinle Group, the Owl Rock and Rock Point formations (Figs. 2 and 3).

The Owl Rock Formation is about 70 to 150 m thick and consists of interbedded limestone, and pale red/brown siltstone, sandstone and mudstone (Fig. 3A). Originally interpreted as a vast lake deposit (e.g., Blakey and Gubitosa, 1983; Dubiel, 1989, 1993, 1994), recent analysis (Tanner, 2000) indicates otherwise. The Owl Rock sediments accumulated in a palustrine system–a mosaic of small ponds, swamps, river courses and stable floodplain surfaces–and was deposited in a low gradient flood basin during a time of increasing aridity. Critical to this interpretation is recognition that most of the Owl Rock limestone beds are not lake deposits, but instead are mature calcrete palaeosols (Lucas and Anderson, 1993; Tanner, 2000). Owl Rock strata are confined to the southern Colorado Plateau, cropping out primarily in southern Utah, northeastern Arizona and west-central New Mexico (Stewart et al., 1972; Lucas and Hayden, 1989; Lucas et al., 1997; Heckert and Lucas, 2003).

The overlying, youngest (stratigraphically highest) portion of the Chinle Group is the Rock Point Formation (Figs. 2 and 3). Rock Point strata on the southern Colorado Plateau consist mostly of reddish brown and pale red, non-bentonitic siltstone and laminated or ripple-laminated sandstones that are very fine to fine-grained micaceous quartzarenites. These beds typically are laterally continuous and give the impression of cyclical deposition (Fig. 3A). A few beds of limestone–siltstone–quartzite–pebble conglomerate and trough-

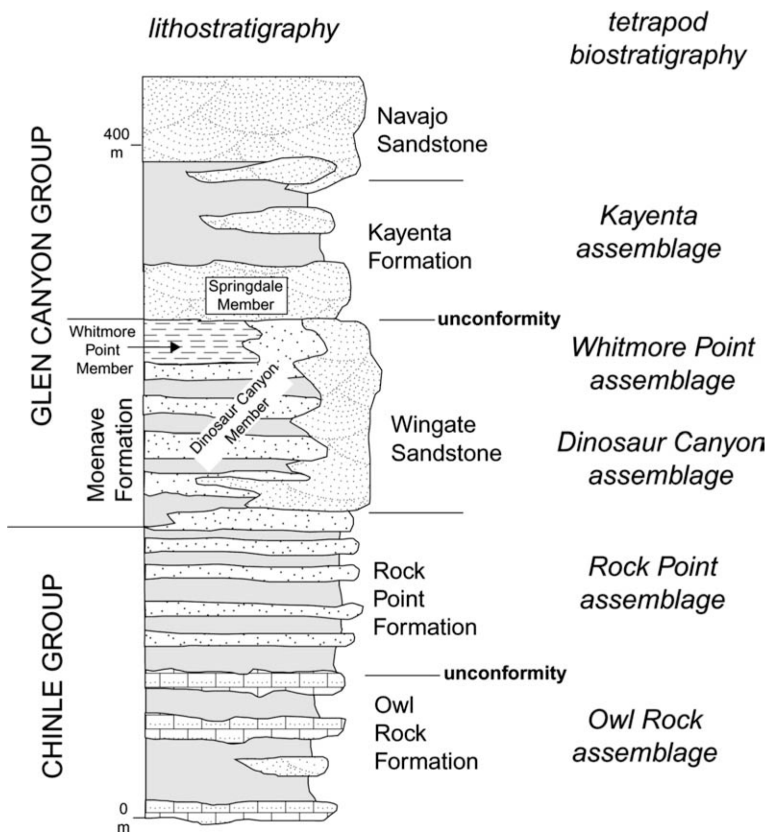


Fig. 2. Summary of lithostratigraphy across the Triassic–Jurassic transition on the southern Colorado Plateau and the distribution of the biostratigraphic assemblages of tetrapod fossils discussed in the text.

cross-bedded sandstone are locally present in the Rock Point Formation. The Rock Point–Owl Rock contact is a distinct unconformity (Stewart et al., 1972; Lucas, 1993; Lucas et al., 1997). Maximum Rock Point thickness is about 300 m, but its typical thickness is about 50 to 100 m. Rock Point deposition took place in a more arid setting than did the deposition of underlying Chinle Group rocks, in a mosaic of eolian dunes and sheet sands, river channels, floodplains and playa lakes (Dubiel, 1989, 1994; Tanner, 2003).

2.2. Glen Canyon Group

Strata that generally overlie the Chinle Group on the southern Colorado Plateau have long been assigned to the Glen Canyon Group (Fig. 2) and thought to be of Early Jurassic age (Averitt et al., 1955; Harshbarger et al., 1957; Pipiringos and O'Sullivan, 1978; Peterson, 1994; Blakey, 1994). These are the (in ascending order) Moenave, Wingate, Kayenta and Navajo formations (Fig. 2). Recent study (e.g., Lucas et al., 1997; Lucas and Heckert, 2001; Tanner et al., 2002; Molina-Garza et al., 2003; Lockley et al., 2004) confirms two important points advocated by some early students of the Glen Canyon Group: (1) the Chinle and Glen Canyon Groups have an interfingering and transitional (not unconformable) contact; and (2) the lower part of the Glen Canyon Group is of latest Triassic age. Current data thus indicate the Triassic–Jurassic boundary is in a relatively conformable ("continuously" deposited) rock succession within the Moenave and Wingate formations, not at an unconformity at the base of the Glen Canyon Group, as advocated by some workers (e.g., Pipiringos and O'Sullivan, 1978). Our work also confirms the proposal of Marzolf (1994) that the Rock Point, Moenave and Wingate formations constitute a single, unconformity-bounded tectonosequence.

The Moenave Formation is generally about 100-m thick and is mostly fine-grained sandstone, siltstone and shale (Harshbarger et al., 1957; Wilson, 1967; Irby, 1996). Most of the formation is the Dinosaur Canyon Member, a succession of brightly colored, reddish orange to light brown eolian and fluvial sandstone and siltstone (Figs. 2 and 3B). In the Moenave type section, near Tuba City, Arizona, all of the Moenave section is

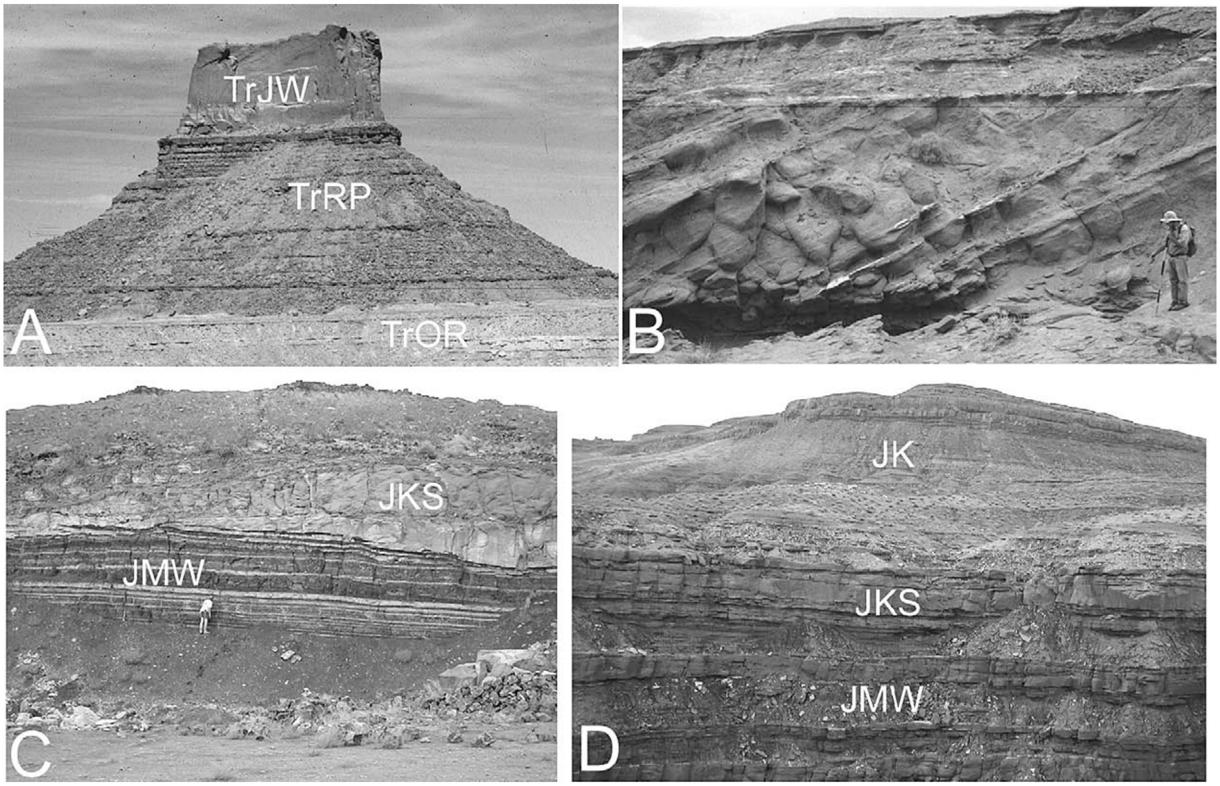
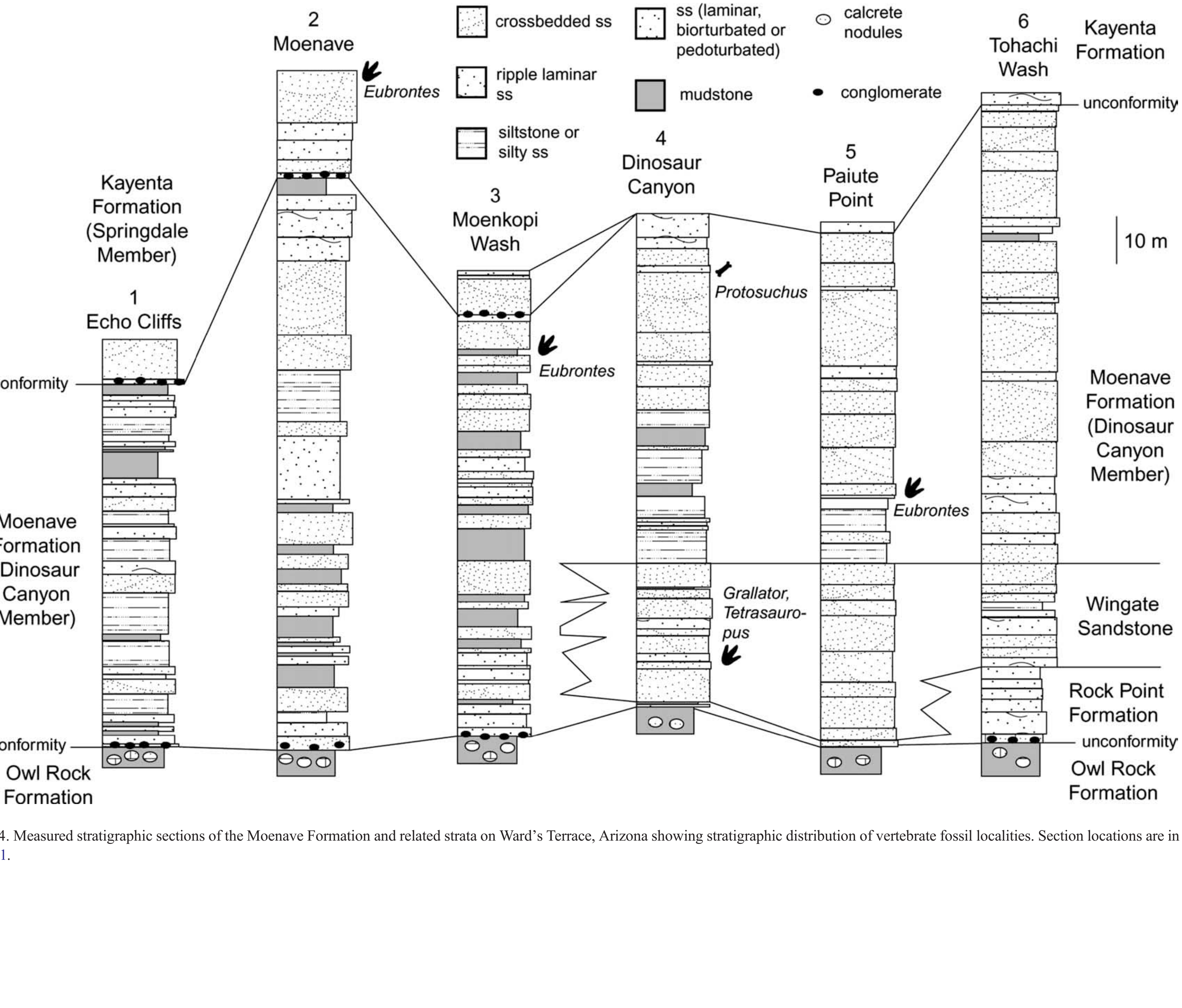


Fig. 3. Photographs of selected outcrops of the Triassic–Jurassic transition on the southern Colorado Plateau. A, Little Round Rock in northeastern Arizona is the type section of the Rock Point Formation (TrRP), which disconformably overlies the Owl Rock Formation (TrOR) and is conformably overlain by the Wingate Sandstone (TrJW). B, Characteristic outcrop of the Dinosaur Canyon Member of the Moenave Formation on Ward's Terrace Arizona shows steeply dipping foresets of an eolian sandstone. C, At St. George Utah, cyclically bedded lacustrine strata of the Whitmore Point Member of the Moenave Formation (JMW) are overlain disconformably by sandstone of the Springdale Member of the Kayenta Formation (JKS). D, In the Warner Valley near St. George, Utah, the Whitmore Point Member of the Moenave Formation (JMW) is overlain disconformably by the Springdale Member of the Kayenta Formation (JKS), which grades upward to similar sandstones and siltstones of the remainder of the Kayenta Formation (JK).

Dinosaur Canyon Member, as it is throughout the Moenave outcrop belt along the Echo Cliffs and Ward's Terrace of northern Arizona (Fig. 4). However, north of the Grand Canyon in Arizona and in southwestern Utah, the upper part of the Moenave Formation is lacustrine strata. These strata are the Whitmore Point Member (Wilson, 1967), gray to red shale and siltstone up to 25-m thick (Figs. 2 and 3C–D). The Whitmore Point lacustrine system has been called "Lake Dixie," but it is uncertain if one or more lakes were responsible for Whitmore Point deposition (Kirkland et al., 2002).

Across its outcrop belt, the Springdale Sandstone disconformably overlies the Moenave Formation (above the Whitmore Point Member north and west of the Grand Canyon, above the Dinosaur Canyon Member to the south and east) (Figs. 2 and 3C–D). Originally named as part of the Chinle Formation (Gregory, 1950), the Springdale Sandstone was later included in the Moenave Formation (Harshbarger et al., 1957). However, because of its lithologic similarity to overlying strata of the Kayenta Formation and basal unconformity it makes more sense to include the Springdale as the basal member of the Kayenta Formation (Olsen, 1989; Marzolf, 1994; Lucas and Heckert, 2001; Tanner et al., 2002). The Springdale Sandstone is as much as 32-m thick and consists of medium- to coarse-grained sandstone, conglomerate and minor mudstone lenses (Fig. 3C–D). Trough cross-beds and laminar beds are the common bedforms, and it is a fluvial deposit (e.g., Edwards, 1985; Luttrell and Morales, 1993).

In the Tuba City–St. George area, the overlying remainder of the Kayenta Formation is mostly fine-grained sandstone, siltstone and mudstone of smaller river systems and floodplains (Luttrell, 1987) (Fig. 3D). However, to the east, the Kayenta becomes more sandy, and the upper part of the formation is interbedded with



4. Measured stratigraphic sections of the Moenave Formation and related strata on Ward's Terrace, Arizona showing stratigraphic distribution of vertebrate fossil localities. Section locations are in 1.

eolian facies of the Navajo Sandstone (e.g., Harshbarger et al., 1957; Luttrell, 1996). Both the Kayenta and Navajo are Early Jurassic in age, and well postdate the Triassic–Jurassic boundary. Therefore, the complex details of their internal stratigraphy are not critical to further discussion here.

To the east of the Moenave outcrop belt, in the Four Corners and to the east and north, the Wingate Sandstone occupies essentially the same stratigraphic position as the Moenave Formation—the Wingate overlies the Rock Point Formation and is overlain by the Kayenta Formation or younger strata (Figs. 2 and 3A). This suggests some sort of lateral equivalence of the Moenave and Wingate (Harshbarger et al., 1957; Edwards, 1985; Clemmensen et al., 1989; Tanner and Lucas, this volume). The Wingate is usually about 100-m thick and consists almost exclusively of thick beds of eolian sandstone (Harshbarger et al., 1957; Clemmensen et al., 1989) (Fig. 3A). Similar beds of eolian sandstone are found in parts of the Moenave Formation to the west, supporting the concept of the dry eolian system of the Wingate (to the east) being laterally equivalent to the wet eolian system of the Moenave (to the west) (Edwards, 1985; Clemmensen et al., 1989; Blakey, 1994; Tanner and Lucas, this volume).

Detailed stratigraphic work by us on Ward's Terrace (Fig. 4) confirms most of the basic stratigraphic relationships between the Rock Point, Wingate and Moenave formations originally advocated by Harshbarger et al. (1957). Thus, the lower Moenave can be physically traced into the laterally equivalent upper Rock Point and part of the Wingate Sandstone.

Fossils and magnetostratigraphy indicate the Rock Point, lower Moenave and at least the lower Wingate are of Late Triassic age (see below). Fossils and magnetostratigraphy also indicate the upper Moenave and uppermost Wingate are of Early Jurassic age (see below). This means the Triassic–Jurassic boundary on the southern Colorado Plateau is in the Moenave–Wingate interval, which is a succession of wet eolian and dry eolian sedimentary deposits (Tanner and Lucas, this volume).

3. Tetrapod biostratigraphy and biochronology

The principles and practices of tetrapod biostratigraphy and biochronology employed here are those explained by Lucas (1998) when he created a global Triassic tetrapod biochronology. To summarize briefly, we identify tetrapod biostratigraphic assemblages as distinctive assemblages of tetrapod fossils from discrete stratigraphic intervals. Most vertebrate palaeontologists refer to such assemblages as "faunas." We fit these assemblages into a framework of Late Triassic–Early Jurassic tetrapod biochronology largely developed by Lucas and Hunt (1993), Lucas (1996, 1998) and Lucas and Huber (2003). This framework is a temporal succession of land-vertebrate faunachrons (LVF). A LVF is a biochronological unit with its beginning defined by the first appearance datum (FAD) of a tetrapod index genus. The end of a LVF is defined by the beginning of the succeeding LVF. Each LVF has a characteristic tetrapod assemblage, so, at a minimum, the LVF is the time interval equivalent to this assemblage; actually, each LVF is the time interval between two FADs, which is usually more time than is represented by the characteristic assemblage. For the Triassic–Jurassic transition, the already defined LVFs that we use are (in ascending order) the Revueltian, Apachean, Wassonian and Dawan. Here, we redefine the Wassonian and Dawan to make their boundaries more precise.

4. Tetrapod biostratigraphy

To develop a tetrapod biostratigraphy of the Triassic–Jurassic transition on the southern Colorado Plateau, we recognize five distinctive fossil assemblages from stratigraphically successive intervals (Fig. 2). The assemblages (lowest to highest) are referred to here as: (1) Owl Rock; (2) Rock Point; (3) Dinosaur Canyon; (4) Whitmore Point; and (5) Kayenta.

4.1. Owl Rock assemblage

No fossil plants or palynomorphs have been reported from the Owl Rock Formation of the Chinle Group. The invertebrate fauna consists only of unionid bivalves (freshwater clams) that are typical of upper Chinle Group strata, and thus are of little biostratigraphic significance (Good, 1998). Nevertheless, the Owl Rock Formation yields a substantial vertebrate fossil assemblage from localities on Ward's Terrace near Tuba City, Arizona (Kirby, 1989, 1991, 1993; Long and Murry, 1995; Murry and Kirby, 2002). This assemblage consists of hybodont, paleoniscoid, colobodontid, semionotid and coelacanthid fishes, the metoposaurid amphibians *Apachesaurus* and *Buettneria*, the phytosaur *Pseudopalatus*, the aetosaur *Typothorax coccinarum*, a rauisuchian (cf. *Postosuchus*) and indeterminate crocodylomorphs (sphenosuchians). No tetrapod footprints are known from the Owl Rock Formation. The Owl Rock assemblage is numerically and taxonomically dominated by phytosaurs, aetosaurs and metoposaurs, so it much resembles the vertebrate fossil assemblage of the underlying Painted Desert Member of the Petrified Forest Formation in northern Arizona (Lucas and Heckert, 1996; Heckert and Lucas, 2002).

4.2. Rock Point assemblage

Palynomorphs from the Rock Point Formation at Ghost Ranch indicate a Norian age (Litwin, 1986; Litwin et al., 1991), and nonmarine trace fossils from these strata indicate burrowing and feeding by terrestrial arthropods (Gillette et al., 2003), but are not age diagnostic. Tetrapod body fossils from the Rock Point Formation in Utah–Arizona are few and fragmentary. In the Eagle basin of Colorado, Rock Point strata yield a small body fossil assemblage that includes indeterminate phytosaurs, the crocodylomorph *Hesperosuchus* and the aetosaurs *Paratypothorax* and *Aetosaurus* (Small and Sedlmayr, 1995; Small, 1998). However, at Ghost Ranch in northwestern New Mexico, one of the world's great Triassic vertebrate fossil quarries is in Rock Point strata (Colbert, 1989; Lucas and Hunt, 1992; Lucas et al., 2003). This is the Whitaker quarry (also called the Ghost Ranch or *Coelophysis* quarry), known since its discovery in 1947 (Colbert, 1989). Recently discovered ostracods and conchostracans from the Whitaker quarry are not age diagnostic, though they do indicate the presence of a shallow pond prior to formation of the main bone bed (Rinehart et al., 2004).

The Whitaker quarry bone bed is dominated by skeletons of the theropod dinosaur *Coelophysis bauri* (Colbert, 1989) (Fig. 5A). Nevertheless, it also includes scales of redfieldiid and coelacanthid fishes, sphenodont jaw fragments, the sphenosuchian *Hesperosuchus*, a drepanosaur, a rauisuchian skeleton (cf. *Postosuchus*), a skeleton of the archosaur *Vancleavea* and skulls of the phytosaur *Redondasaurus* (Hunt and Lucas, 1993; Clark et al., 2000; Harris and Downs, 2002; Hungerbühler, 2002; Hunt et al., 2002; Lucas et al., 2003; Rinehart et al., 2004).

The Whitaker quarry is an unusual fossil assemblage—a mass kill of dinosaurs and a few other tetrapods. This may explain why no metoposaurs or aetosaurs are known from the quarry. The age equivalent vertebrate fossil assemblage of the Redonda Formation in east-central New Mexico includes numerous fossils of metoposaurid amphibians and aetosaurs (Lucas, 1997; Lucas et al., 2001a).

More prevalent than body fossils, the Rock Point Formation tetrapod fossil record is dominated by footprints. Indeed, most of the Chinle Group tetrapod footprint record is from the Rock Point and correlative (Apachean-age) units (e.g., Redonda and Sloan Canyon formations of eastern New Mexico) (e.g., Lockley and Hunt, 1994, 1995; Lucas, 1997; Lockley et al., 2001; Lucas et al., 2001b; Gaston et al., 2003). On the southern Colorado Plateau, tetrapod footprints are found in the Rock Point Formation in Arizona, Utah and especially in the Gateway, Colorado area of southwestern Colorado (Lockley et al., 1992; Gaston et al., 2003; Lockley et al., 2004). This track record is dominated by small theropod tracks (ichnogenus *Grallator*) but also includes the track ichnogenera *Brachychirotherium*, *Rhynchosauroides*, *Gwyneddichnium*, *Pseudotetrasauropus* and *Tetrasauropus*. These are the tracks of crurotarsans (aetosaurs, phytosaurs and/or rauisuchians: *Brachychirotherium*), sphenodonts (*Rhynchosauroides*), tanystropheids (*Gwyneddichnium*) and sauropodomorph dinosaurs (*Pseudotetrasauropus* and *Tetrasauropus*) (Lockley et al., 1992; Lockley and Hunt, 1995; Lockley et al., 2001; Nicosia and Loi, 2003; Lockley et al., 2004; but see Rainforth, 2003 for a different interpretation of the track makers of *Pseudotetrasauropus* and *Tetrasauropus*). They augment the body fossil record of the Rock Point interval, which has failed to produce bones or teeth of tanystropheids or sauropodomorphs.

The Rock Point interval thus yields a Late Triassic tetrapod assemblage in some ways (e.g., crurotarsans present) similar to the Late Triassic tetrapod faunas of older parts of the Chinle Group. What sets the Rock Point fauna apart, though, is the relative abundance of theropod and sauropodomorph dinosaurs, known mostly from footprints; relatively few dinosaurs are known from older Chinle Group strata (Hunt et al., 1998; Heckert et al., 2000; Heckert, 2001).

4.3. Dinosaur Canyon assemblage

The Dinosaur Canyon assemblage encompasses tetrapod fossils from strata of the lower to middle part of the Dinosaur Canyon Member of the Moenave Formation and laterally equivalent strata of the Wingate Sandstone. These strata have no fossil record of plants, palynomorphs or invertebrates. They yield only a sparse tetrapod bone record (one phytosaur skull: Fig. 5B), but contain numerous tetrapod footprints (Lockley and Hunt, 1994, 1995; Lockley et al., 2004). The phytosaur skull, from the lower part of the Wingate Sandstone in the Lisbon Valley of southeastern Utah, belongs to the Apachean index taxon *Redondasaurus* (Lucas et al., 1997). The footprints are of small theropods (*Grallator*), crurotarsans (*Brachychirotherium*), sauropodomorphs (*Tetrasauropus*) and synapsids (including numerous small cynodont and/or mammal tracks, though the track makers of some of the "synapsid" tracks remain uncertain) (Fig. 5E). Other than the synapsid tracks, which are numerous and diverse in the Wingate Sandstone in the Gateway area (Schultz-Pittman et al., 1996; Lockley et al., 2004), the tetrapod footprints of most of the

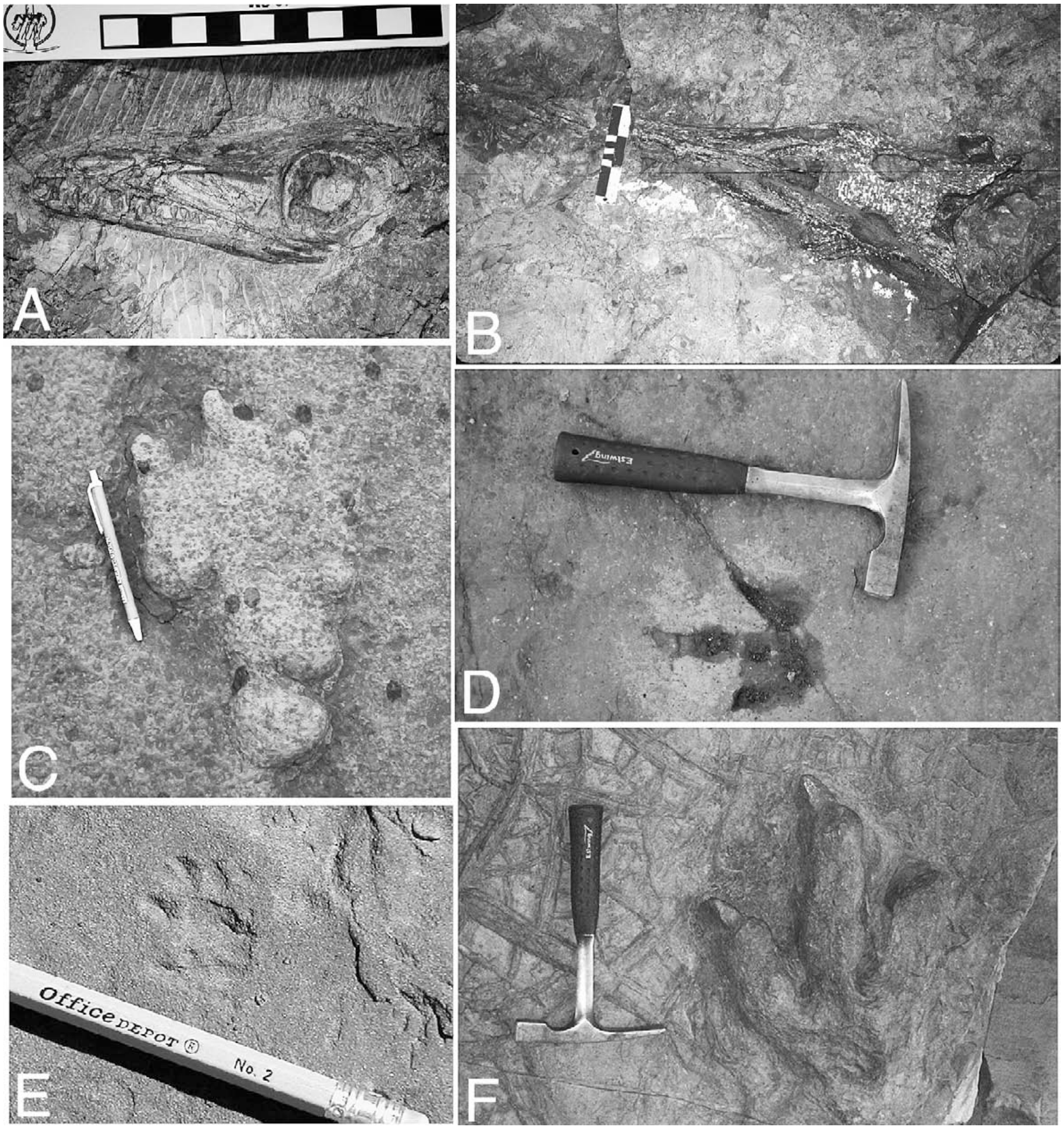


Fig. 5. Selected tetrapod fossils and tetrapod footprints of the Rock Point, Dinosaur Canyon and Whitmore Point assemblages. A, Skull of the theropod dinosaur *Coelophysis bauri* from the Rock Point Formation at the Ghost Ranch dinosaur quarry, New Mexico; scale in cm. B, Skull of the phytosaur *Redondasaurus* in the lower part of the Wingate Sandstone at Lisbon Valley, Utah; small bars on scale are cm. C, Track of prosauropod dinosaur (*Otozoum*) in upper part of Wingate Sandstone at Gateway, Colorado. D, Footprint of small theropod dinosaur (*Grallator*) in Kayenta Formation near St. George, Utah. E, Synapsid (or mammal?) footprint in lower part of Wingate Sandstone at Gateway, Colorado. F, Footprint of large theropod dinosaur (*Eubrontes*) in upper part of Dinosaur Canyon Member of Moenave Formation at St. George, Utah.

Dinosaur Canyon assemblage are similar to those of the Rock Point assemblage.

4.4. Whitmore Point assemblage

The tetrapod fossil assemblage of the uppermost Dinosaur Canyon Member, the entire Whitmore Point Member of the Moenave Formation and the uppermost Wingate Sandstone is referred to here as the Whitmore Point assemblage. We conceive of the strata that yield this assemblage as sedimentary rocks deposited in “Lake Dixie” (Whitmore Point Member), in shoreline, fluvial and wet eolian facies generally to the east and southeast of “Lake Dixie” (upper Dinosaur Canyon

Member) and in the laterally equivalent end phase of the Wingate erg to the east.

Body fossils were sparse in this interval until the discovery in 2000 of the remarkable bone and track sites in the upper Dinosaur Canyon and Whitmore Point members at St. George and vicinity (Kirkland et al., 2002; Chin et al., 2003; Milner et al., 2004). These localities yield plant, invertebrate and vertebrate body fossils, especially of conchostracans, semionotid fishes, and theropod dinosaurs that are currently under study. Also significant are skeletons of the small terrestrial crocodylomorph *Protosuchus* from the upper part of the Dinosaur Canyon Member in Arizona (Colbert and Mook, 1951; Crompton and Smith, 1980).

The tetrapod footprint record of this interval is dominated by tracks of large theropods (ichnogenus *Eubrontes*) but also includes many small theropod tracks (*Grallator*) and sauropodomorph tracks (including a remarkable trackway of *Otozoum* from the upper Wingate near Gateway, Colorado: Fig. 5C) (e.g., Olsen and Galton, 1977; Olsen and Sues, 1986; Irby, 1993; Lockley and Hunt, 1994, 1995; Irby, 1996; Lockley et al., 2004; Milner et al., 2004).The most striking difference between the Dinosaur Canyon and Whitmore Point tetrapod assemblages is the absence of crurotarsans, either as body fossils or footprints, in the Whitmore Point assemblage.

4.5. Kayenta assemblage

A significant unconformity separates the Kayenta assemblage (from the Kayenta Formation) from the underlying Whitmore Point assemblage. No palynomorphs or fossil plants and only a few invertebrates (mostly ostracods) are known from the Kayenta Formation (Kietzke and Lucas, 1995), but it does yield numerous tetrapod footprints and body fossils (e.g., Sues et al., 1994; Lockley and Hunt, 1994, 1995; Curtis and Padian, 1999). Kayenta footprints are mostly of large (*Eubrontes*) and small (*Grallator*: Fig. 5D) theropods. The stratigraphically equivalent dune and inter-dune deposits of the Navajo Sandstone have a more diverse track assemblage that includes footprints of crocodilians (*Batrachopus*), ornithischian dinosaurs (*Anomoepus*), prosauropod dinosaurs (*Otozoum*) and synapsids (*Brasilichnium*) (e.g., Lockley and Hunt, 1994, 1995; Rainforth and Lockley, 1996). This is a characteristic, dinosaur-dominated Early Jurassic footprint assemblage.

The Kayenta tetrapod body fossil assemblage (Sues et al., 1994; Curtis and Padian, 1999) includes a frog (*Prosalirus*), caecilian (*Eocaecilia*), turtle (*Kayentachelys*), sphenodonts, crocodylomorphs (*Eopneumatosuchus* and unnamed taxa), a pterosaur (*Rhamphinion*), thyreophoran dinosaurs (*Scutellosaurus* and *Scelidosaurus*), a heterodontosaurid dinosaur, theropod dinosaurs (*Megapnosaurus* [better known by the invalid homonym "*Syntarsus*"] and *Dilophosaurus*), a prosauropod dinosaur ("*Massospondylus*"), tritylodontid therapsids (*Oligokyphus*, *Kayentatherium*, *Dinnebiton*) and mammals (*Dinnetherium* and haramyids) (see Curtis and Padian, 1999 and references cited therein).

5. Tetrapod biochronology

5.1. Revueltian

The Revueltian LVF is the time between the FAD of the aetosaur *T. coccinarum* and the beginning of the Apachean (Lucas, 1998; Lucas et al., 2002). The Owl Rock assemblage includes the Revueltian index taxa *Pseudopalatus* and *T. coccinarum*, and this indicates the Owl Rock Formation is of Revueltian age (Lucas and Heckert, 1996; Lucas, 1998) (Fig. 6). The Owl Rock assemblage is the stratigraphically highest Revueltian assemblage in northern Arizona; it is stratigraphically above the characteristic assemblage of the Revueltian LVF, which is from the Painted Desert Member of the Petrified Forest Formation (Lucas, 1993; Heckert and Lucas, 2002). However, these two assemblages are very similar in composition and cannot be separated biochronologically.

5.2. Apachean

The Apachean LVF is the time interval between the FAD of the phytosaur *Redondasaurus* and the beginning of the Wassonian LVF (Lucas, 1998; Lucas and Huber, 2003). The Rock Point and Dinosaur Canyon assemblages both contain *Redondasaurus*, the principal index taxon of the Apachean, so we assign them an Apachean age (Lucas et al., 1997) (Fig. 6).

5.3. Wassonian

Lucas and Huber (2003: 158) introduced the Wassonian LVF as follows:

> We introduce here the Wassonian LVF for the time equivalent to the vertebrate fossil assemblage from the McCoy Brook Formation at Wasson Bluff, Nova Scotia. The combined vertebrate fossil assemblages from NEZ [Newark extrusive zone] and post-NEZ strata are of Wassonian age, which is part of Early Jurassic (Hettangian to ?Pliensbachian) time. The principal Wassonian guide fossil is the prosauropod *Ammosaurus*, which is known from fragmentary

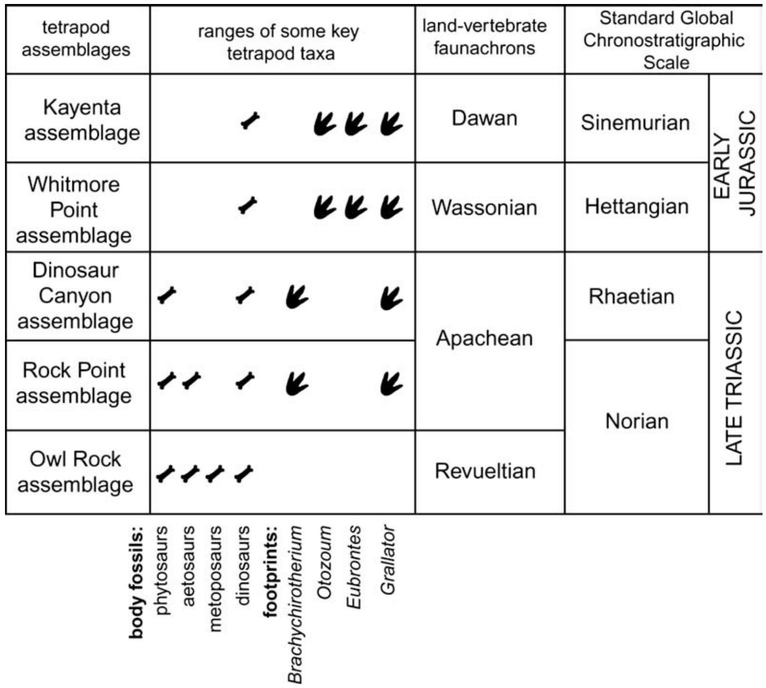


Fig. 6. Stratigraphic distribution of principal tetrapod taxa across the Triassic–Jurassic transition on the southern Colorado Plateau.

skeletons from the McCoy Brook Formation and from the holotype and other specimens from the middle and upper Portland Formation. The sphenodontid *Clevosaurus*, the crocodylomorph *Protosuchus*, and trithelodontids are other biochronologically useful Wassonian taxa.

We redefine the Wassonian to make its boundaries more precise, though the redefinition does not substantially change the time interval Wassonian as Lucas and Huber (2003) defined it. Thus, we define the Wassonian as the time between the FAD of the crocodylomorph *Protosuchus* and the beginning of the Dawan LVF. The "*Ammosaurus*" from the McCoy Brook Formation is not that genus, but instead a new taxon (T. Fedak, personal commun., 2004). We advocate *Protosuchus* (known from Arizona, Nova Scotia and South Africa) as the principal index fossil of the Wassonian LVF. Its presence in the Whitmore Point assemblage identifies it as of Wassonian age (Fig. 6).

5.4. Dawan

Lucas (1996) introduced the Dawan LVF as the time equivalent to the vertebrate fossil assemblage of the Lufeng Formation in southern China. We redefine the Dawan LVF here to make its boundaries more precise. Thus, the beginning of the Dawan is the FAD of the theropod dinosaur *Megapnosaurus* ("*Syntarsus*") (known from Arizona and southern Africa with certainty, and less certainly from China and Europe). The end of the Dawan LVF is the beginning of the next LVF introduced by Lucas (1996), the Dashanpuan. We define the beginning of the Dashanpuan as the FAD of the sauropod dinosaur *Shunosaurus*.

Index taxa of the Dawan include *Megapnosaurus*, *Dilophosaurus*, *Massospondylus* and *Oligokyphus*, all taxa that are part of the Kayenta assemblage. The Kayenta assemblage thus is of Dawan age (Fig. 6). The few body fossils and more extensive footprint assemblages of the Navajo Sandstone also are at least in part of Dawan age. However, the end of the Dawan is difficult to place on the southern Colorado Plateau because of the general lack of biostratigraphically useful tetrapod fossils between the Kayenta assemblage and the Upper Jurassic dinosaur-dominated assemblage of the Morrison Formation. Probably the Dawan–Dashanpuan boundary is close to the contact between the Navajo Sandstone and overlying Carmel Formation, but this is not certain for lack of data.

6. Correlation to the global timescale

Correlation of the tetrapod assemblages just discussed to the standard global chronostratigraphic timescale (Fig. 6) is somewhat imprecise and uncertain, as is typical when totally nonmarine Mesozoic fossils and strata are being correlated to a timescale rooted in marine biostratigraphy and biochronology. Magnetostratigraphy, palynostratigraphy and cross correlation of terrestrial tetrapods in marine strata (for example, the Revueltian aetosaur *Aetosaurus* is found in Norian marine strata in Italy: Wild, 1989) indicate the Revueltian is of Norian (approximately early or middle Norian) age (e.g., Lucas, 1998; Lucas et al., 1998).

The Late Triassic vertebrate faunachrons recognized in the American Southwest can be correlated to the German Keuper, which helps to establish the early–middle Norian age of the Revueltian and the Norian–Rhaetian age of the Apachean. Thus, the lower and middle Stubensandstein of the Keuper yield tetrapods of Revueltian age, whereas the upper Stubensandstein and Knollenmergel yield Apachean-age tetrapods (Lucas, 1999). Nevertheless, the lowermost Jurassic tetrapod record in Europe is mostly from fissure fills of uncertain age in terms of marine biostratigraphy. Therefore, correlation of the Lower Jurassic tetrapods (especially the Wassonian LVF) to the marine timescale must be based primarily on their correlation to the Newark Supergroup in eastern North America, relying on the correlation of the Newark by magnetostratigraphy and radioisotopic ages to the marine timescale (Olsen et al., 2002b).

Earlier arguments that the Apachean is equivalent to the Rhaetian (Lucas, 1993, 1998) are difficult to sustain in the light of new data. These arguments were largely based on a stage-of-evolution assessment of the Apachean phytosaur *Redondasaurus*. This phytosaur is more derived than the Knollenmergel (late Norian) phytosaurs of the German Keuper, so *Redondasaurus* was therefore assigned a Rhaetian age. However, the Norian aetosaur *Aetosaurus* occurs in Rock Point strata in Colorado (Small, 1998), and the Rock Point palynomorphs suggest a Norian age (Litwin, 1986). Clearly, the Apachean is younger than the Revueltian (which is approximately early to middle Norian), so we tentatively regard it as late Norian in age.

There are several compelling reasons to assign a Late Triassic age to the Apachean Dinosaur Canyon assemblage: (1) the Apachean phytosaur *Redondasaurus* is present, and no phytosaur is known from Jurassic strata; (2) the footprint ichnogenus *Brachychirotherium* is not known anywhere from Jurassic strata; (3) the lower Dinosaur Canyon Member is laterally equivalent to strata of well established Late Triassic age (upper Rock Point Formation); (4) the Wingate Formation basal contact is gradational with underlying Upper Triassic strata of the Rock Point Formation; and (5) magnetostratigraphy of the Dinosaur Canyon interval is reasonably correlated to the magnetostratigraphy of uppermost Triassic strata of the Newark Supergroup in eastern North America (Molina-Garza et al., 2003).

Although it is possible to assign the Dinosaur Canyon assemblage to the Late Triassic, its precise correlation to the marine timescale is uncertain. Probably it equates to part or all of Rhaetian time, simply because the Dinosaur Canyon interval is the youngest Triassic interval on the Colorado Plateau and is conformably overlain by strata that apparently correlate to the earliest part of the Early Jurassic (Hettangian).

Also, note that the middle parts of the Dinosaur Canyon Member of the Moenave Formation and of the Wingate Sandstone lack age-diagnostic fossils (Figs. 2 and 4). This means that the top of the Triassic cannot be placed exactly in the nonmarine strata on the southern Colorado Plateau, but instead falls in a stratigraphic interval about 30 to 50 m thick. More fossil collecting with detailed stratigraphic data is needed to provide a more precise placement of the top of the Triassic on the southern Colorado Plateau.

There are several compelling reasons to assign an earliest Jurassic age to the Whitmore Point assemblage (and the Wassonian LVF): (1) no *bona fide* Triassic index fossils are known from the Whitmore Point assemblage; (2) *Protosuchus* records elsewhere (McCoy Brook Formation in Nova Scotia, upper Elliott Formation in South Africa) are in strata of earliest Jurassic age (Shubin et al., 1994; Lucas and Hancox, 2001); (3) no *bona fide Otozoum* are known from Triassic strata (Rainforth, 2003); (4) not all *Eubrontes* tracks are Early Jurassic, but most North American occurrences are (Lucas and Tanner, 2004); (5) the palynomorph sample from the Whitmore Point Member is dominated by the conifer pollen taxon *Corollina meyeriana* (Peterson and Pipiringos, 1979; Litwin, 1986), a common occurrence in earliest Jurassic strata (though this sometimes happens in Upper Triassic strata as well); and (6) magnetostratigraphy of the Whitmore Point interval has been readily correlated to the magnetostratigraphy of the earliest Jurassic (Hettangian) interval of the Newark Supergroup in eastern North America (Molina-Garza et al., 2003).

There is no doubt that the Dawan Kayenta tetrapod assemblage is of Early Jurassic age, as it well represents a cosmopolitan Early Jurassic tetrapod fauna with genera such as *Megapnosaurus*, *Dilophosaurus*, *Massospondylus* and an abundance of tritylodontids (Lufeng Formation of southern China, La Boca Formation of northern Mexico, upper Elliott Formation of the South African Karoo and Early Jurassic fissure fills of Western Europe) (e.g., Olsen and Galton, 1977, 1984; Luo and Wu, 1994; Lucas, 1994, 1996; Irmis, 2004). Furthermore, the type material of the dinosaur *Scelidosaurus* is known from lower Sinemurian marine strata in the United Kingdom, which suggests that the Kayenta assemblage is early Sinemurian in age (Padian, 1989; Lucas, 1996). If so, the hiatus between the Kayenta and Whitmore Point intervals represents part of Hettangian time.

7. Implications for tetrapod evolution

The five biostratigraphic assemblages of tetrapod fossils on the southern Colorado Plateau discussed here bracket the Triassic–Jurassic boundary (T–J boundary). The four biochronological units they are assigned to are of Late Triassic (Revueltian, Apachean) and Early Jurassic (Wassonian, Dawan) age. We thus discuss here the implications of this biostratigraphy and biochronology (Fig. 6) for understanding tetrapod evolution across the T–J boundary.

Such a discussion, nevertheless, needs to identify the obvious taphonomic and palaeoenvironmental biases inherent to the tetrapod fossil record across the T–J boundary on the southern Colorado Plateau. Viewed broadly, the five biostratigraphic assemblages we identify encompass body fossils and footprints from a variety of lithofacies that represent different depositional systems. This makes it difficult to simply compare each assemblage to the other because the differences between the assemblages in large part arose from taphonomic and palaeoenvironmental factors and are not simply the result of temporal succession and evolution. For example, the Owl Rock assemblage is strictly a body fossil assemblage from fluvial lithofacies of a palustrine depositional system. In contrast, the overlying Rock Point assemblage is both body fossils (mostly from a single mass death assemblage) and footprints from a range of fluvial, lacustrine and eolian lithofacies. The two assemblages thus differ in large part because of the different kinds of fossils being examined, the different lithofacies and other taphonomic controls.

Despite these differences, two clear events in tetrapod evolution across the T–J boundary are documented on the southern Colorado Plateau. The first is the extinction of the crurotarsans. This extinction, usually referred to as the extinction of “thecodonts,” was identified half a century ago by Colbert (1958) as the principal tetrapod extinction at the end of the Triassic (also see Olsen et al., 2002a). Crurotarsan footprints are present in the lower-middle Wingate Sandstone but absent in the upper Wingate and laterally equivalent upper Dinosaur Canyon Member of the Moenave Formation. A phytosaur skull is present at the base of the Wingate Sandstone, but no stratigraphically higher crurotarsan body fossils are known on the southern Colorado Plateau. We take this to indicate crurotarsan extinction between the Dinosaur Canyon and Whitmore Point assemblages, which is at the Apachean–Wassonian boundary and thus very close to the T–J boundary. Given the patchy stratigraphic distribution of the crurotarsan fossils in these assemblages, we make no quantitative claims about diminishing taxonomic diversity or abundance prior to the extinction. We can only say that the tetrapod record on the southern Colorado Plateau has a tetrapod assemblage with crurotarsans followed by an assemblage without crurotarsans, and that the assemblages closely bracket the T–J boundary. This suggests crurotarsan extinction took place approximately at the T–J boundary, as others have inferred from more global data (e.g., Benton, 1986).

The second trend in tetrapod evolution across the T–J boundary worth commenting on is the dramatic latest Triassic change in dinosaurs. The assemblages from the southern Colorado Plateau show that a sudden increase in numbers, diversity and body sizes of dinosaurs took place during the Apachean, before the T–J boundary (Hunt, 1991; Hunt et al., 1998; Heckert, 2001). Thus, Apachean body fossil and footprint assemblages on the southern Colorado Plateau are dinosaur dominated. They also include the footprints of truly large (estimated 10 m or more body length) sauropodomorph dinosaurs, which is the first evidence of truly large dinosaurs during the Late Triassic on the southern Colorado Plateau.

Several workers (e.g., Benton, 1986; Hunt, 1991; Heckert, 2001; Olsen et al., 2002a) have drawn attention to a relatively sudden increase in dinosaur abundance, diversity and body size during the latest Triassic, well documented in Germany, South Africa, Argentina and in the American Southwest. This change is geographically widespread and not lithofacies correlated, so we believe it is a real evolutionary event. The southern Colorado Plateau record thus supports the conclusion that the dinosaur rise to dominance began before the end of the Triassic and just before the extinction of crurotarsans (“thecodonts”), which coincided with the Triassic–Jurassic boundary.

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