Anatomy of the Late Triassic Dinosauromorphs from the Dockum Group of Texas: Their Biostratigraphic, Paleobiogeographic and Evolutionary Significance

by

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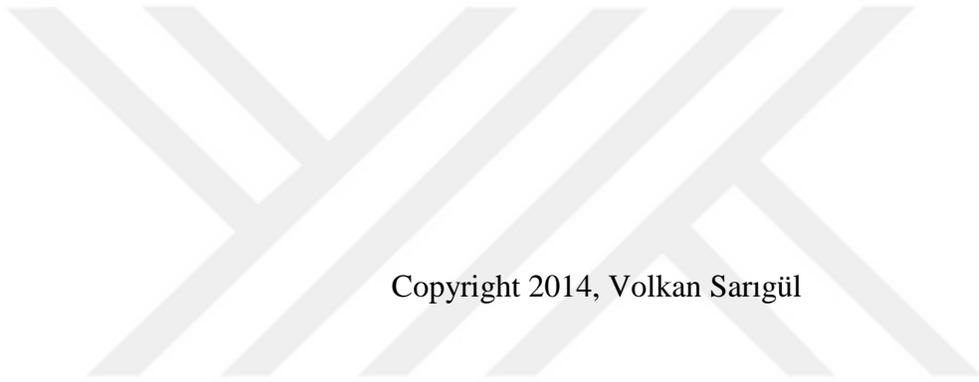
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# Abstract

The richer and taxonomically more diverse dinosauromorph fauna of the Dockum Group, as comprehensively documented for the first time in the present work, provided new insights on the Late Triassic land vertebrate biochronology and paleobiogeography, especially for the late Carnian-early Norian interval. Although the most recent geochronologic works now enables for a recalibration of the Late Triassic phytosaur biochronology relative to the marine sequence, a direct correlation with South America is still lacking. In this context, the dinosauromorphs are proposed here as a prospecting biostratigraphic tool to correlate North America with South America. Especially, the first appearance of dinosaurs and their early global radiation at the late Carnian-early Norian interval provides a direct correlation with the *Paleorhinus* Fauna in northern continents (and India) and the *Hyperodapedon* Acme Zone in southern continents. Conclusive evidences in both northern and southern continents manifest that the occurrence of earliest dinosaurs was global even from the beginning. Ischigualasto and Tecovas formations are the primary candidates to pinpoint the center of origin for dinosaurs by keeping each step of the dinosauromorph evolution, in accord with the new alignment which considers the lagerpetids as the basal taxon of the dinosauromorph clade and the silesaurids as the sister group of dinosaurs.

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# Chapter 1

# Introduction

Triassic Period is important moment in the history of life, at least for the terrestrial vertebrates. During this time, many vertebrate groups first appeared in the fossil record including lissamphibians, turtles, squamates, dinosaurs and the precursors of crocodiles and mammals while aerial vertebrates such as kuehneosaurs, pterosaurs and possibly birds also originated at the time to conquer the sky (Chatterjee 1997). The Triassic Period was also the time when highly specialized marine reptiles such as ichthyosaurs, placodonts and nothosaurs invaded the oceans.

Terrestrial biota quickly recovered their diversity after the catastrophic Permian-Triassic mass extinction. In Gondwana continents, Permian Ottokariales (e.g. *Glossopteris*) flora is replaced by Umkomasiales (e.g. *Dicroidium*) flora, where the pteridophytes (lycophytes and sphenophytes) had also reflourished rapidly (Anderson et al. 1999). Therapsids rebounded from their severe losses to dominate the Pangaean landscape in Early Triassic (Parrish et al. 1986), but their sizes were generally small, except dicynodonts. Consequently, larger proterosuchids and erythrosuchids ruled Early Triassic terrestrial ecosystem as the top predators. Temnospondyli amphibians were also quite diverse in Early Triassic and often used as index taxa to establish non-marine tetrapod biostratigraphy of Lower and Middle Triassic, especially in Russia and Eastern Europe (e.g. Ochev and Shishkin 1989). Together with dicynodonts, the diversity archosauromorphs (predominantly rhynchosaurs and other *incertae sedis* groups) increased during Middle Triassic, but it is the Late Triassic period that we see the real

worldwide dominance of archosaurs. The Carnian is marked by the appearance of pphytosaurs, aetosaurs and other crurotarsans that dominated the tetrapod faunas, especially in North America, until the end of the period.

The oldest definitive records of basal dinosauromorphs are documented from the Anisian strata of southern Africa with the body fossils of *Asilisaurus kongwe* (Nesbitt et al. 2010) and *Lutungutali sitwensis* (Peecook et al. 2011; 2013); whereas some footprint evidence from Poland might move back the origin of basal dinosauromorphs to the Olenekian (Brusatte et al. 2010c). It is traditionally accepted that dinosaurs (*sensu* Padian and May 1993) first appeared in the latest Carnian, around 230 million years ago. A series of discoveries which predominantly occurred in the 21st century clearly manifested that a large array of dinosauromorphs had existed especially during Late Triassic and they had lived in close association with crurotarsan archosaurs and other land tetrapod elements (e.g. Irmis et al. 2007a). Unlike the classical theories which championed a dinosaur take over during the Late Triassic based on physiological superiority (e.g. Bakker 1968, 1971, 1972) or as a consequence of an environmental perturbation (e.g. Benton 1983a, 1986, 1991, 1994, 2006) the early dinosaur diversity was relatively low both in diversity and abundance compared to crurotarsans. Thus, the prevalence of dinosaurs did only happened after the end-Triassic extinction where most of the crurotarsans went extinct (Brusatte et al. 2008a, 2008b, 2010b, 2011; Langer et al. 2010). Nevertheless, the origin and early evolution of dinosaurs still receives much attention, especially in terms of understanding the evolutionary background (i.e. the phylogenetic fuse), revealing the trends in Late Triassic paleobiogeography and improving the terrestrial biostratigraphy.

Besides the first two summarizing chapters about the general geology and taphonomy of the Dockum Group sediments, the main scope of this work is to provide an extensive documentation of Dockum dinosauromorphs of Texas for the first time and to display their biostratigraphic, paleobiogeographic and evolutionary significance. The Dockum Group dinosauromorphs are widely distributed, from the lower levels of the Tecovas Formation and to the upper levels of the Bull Canyon Formation. Together with the comparative anatomy section of the vertebrate paleontology, the dinosauromorphs of Dockum will contribute to improve two aspects of the Upper Triassic land tetrapod biostratigraphy: (1) provision of an intercontinental biocorrelation, especially with South America, in corroboration with the phytosaur biostratigraphy and the marine-correlated chronostratigraphy, and (2) evaluation of the dinosaur fossils in context of the evolution and radiation of early dinosaurs.

All of the dinosauromorph fossils presented in this work are present in the repository of the Museum of Texas Tech University, except a set of specimens which are on loan from the West Texas A&M University (i.e. WTAMU specimens). Necessary preparations were performed by using air-scribe, dental tools and pin vices; whereas various glues (Parloid B-72, Vinac B-15, Butvar, cellulose sculpting medium) were used to repair broken fragments. All the specimen photographs are taken by a professional photographer (Bill Mueller) and edited by the author. An Olympus SZH Stereo-microscope system with camera adapter attached to a TV monitor was used for viewing small sized specimens at higher magnification.

# Chapter 2

# Geological Setting

The Triassic Period was a time of transition, particularly in global tectonics and the evolution of vertebrates. All the landmasses were still coalesced into a one supercontinent called Pangea, which means all-land in ancient Greek. Pangea was the last configuration of supercontinent in geologic history. It was surrounded by the Panthalassa Ocean, the ancestral Pacific Ocean, and was subdivided into two main landmasses Laurasia in the north and Gondwana continents in the south. Those two supercontinents were separated by the Tethys Ocean (Paleo- and Neo-) to the east (Figure 2.1).
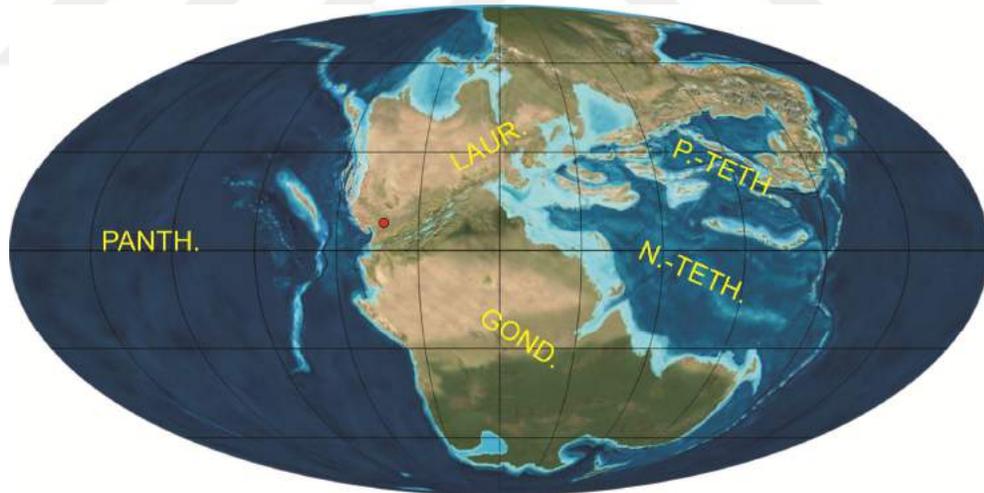


Figure 2.1 The Late Triassic Pangea (modified after Blakey 2011). Abbreviations: Panth., Panthalassa Ocean; Laur., Laurasia landmass; Gond., Gondwana continents; P.-Teth., Paleo-Tethys Ocean; N.-Teth., Neo-Tethys Ocean. Location of the Dockum Group is roughly marked by the dot.

## Pangea

Pangea began to coalesce in the Mid-Carboniferous (Pennsylvanian) by the collision of Gondwana continents with Laurentia/Baltica (Veevers and Powell 1987;

Veevers 1989) and was finalized in the Mid-Late Triassic to Early Jurassic (Şengör 1984; Zunyi et al. 1986) by the accretions of other landmasses such as South China (Şengör and Hsü 1984; Lin et al. 1985; Xiong and Coney 1985) and Cimmeria (Şengör 1984) to the northern Paleo-Tetyhan margin.

As the initial phase of major intra-Pangean rifting, east coast of North America and the northwest coast of Africa began to pull apart in Late Triassic (Manspeizer 1982). Those rift basins are correlated by the palynomorphs gathered from non-marine sequences the High Atlas Mountains at south of Marrakech and North American Triassic groups of Newark (Virginia, North Carolina, Pennsylvania and New Jersey), Chinle (Arizona and New Mexico) and Dockum (New Mexico and Texas); the shared biozone demonstrated that rifting began no later than middle Carnian time (Cousminer and Manspezier 1976). Moroccan and North American palynostratigraphy is also in direct correlation with Swiss and English Middle Keuper, the type Carnian of Austria and Keuper of Switzerland and North Sea (Cousminer and Manspezier 1976 and references therein).

Although the initial rifting of the Pangea in Late Triassic produced extensional basins around the future Atlantic Ocean, no oceanic lithosphere was generated until Early Jurassic, when the opening of the Central Atlantic Ocean had started. The age of the oldest basalts from the entire Central Atlantic Magmatic Province (CAMP) is dated circa 200 million years (Ma) ago with a maximum activity of 2 Ma (Deckart et al. 1997; Marzoli et al. 1999, 2004; Hames et al. 2000; Knight et al. 2004) in accord with the radiometric date of the base of Jurassic (Pálfy et al. 2000b).

## The Dockum Basin and the History of Dockum Group

Most early workers believed that the Dockum Basin strata were entirely of fluvial origin. Riggs et al. (1996) reconstructed a huge Late Triassic river system, the Chinle-Dockum Paleoriver, which ran northwesterly from the Texas Panhandle to New Mexico, Arizona, Utah, Wyoming and parts of Nevada and Idaho; then poured into the ancient shoreline of a back-arc basin (Figure 2.2). There are two main depocenters within this fluvial deposition, one is the Dockum Basin which is exposed at the western part of Texas and the eastern New Mexico; the other is the Chinle Basin which is located in the states further west in the Four Corners region (Figure 2.2). The main sequences of these basins, the Dockum Group and the Chinle Formation, are in direct correlation with each other, as recognized by the second half of the 20th century (Reeside et al. 1957, p. 1464) despite different nomenclature and diverse lithostratigraphic subdivisions. The Dockum Basin is a broad alluvial-lacustrine depositional basin about 400 km in width and 800 km in length; where the total sediment thickness varies from 70 to 700 meters (Chatterjee 1986a). There are two main exposures of the Dockum Group; one is located through the Canadian River Valley in northeastern corner of New Mexico and the northwestern corner of the Texas Panhandle; and the other lies in the western part of the Panhandle along the eastern and southeastern margins of the Llano Estacado and Southern High Plains (Figure 2.3). There are also some western outcrops along the Pecos River valley. The escarpments on the eastern side of the Llano Estacado are the scope area of this work (Figure 2.3).
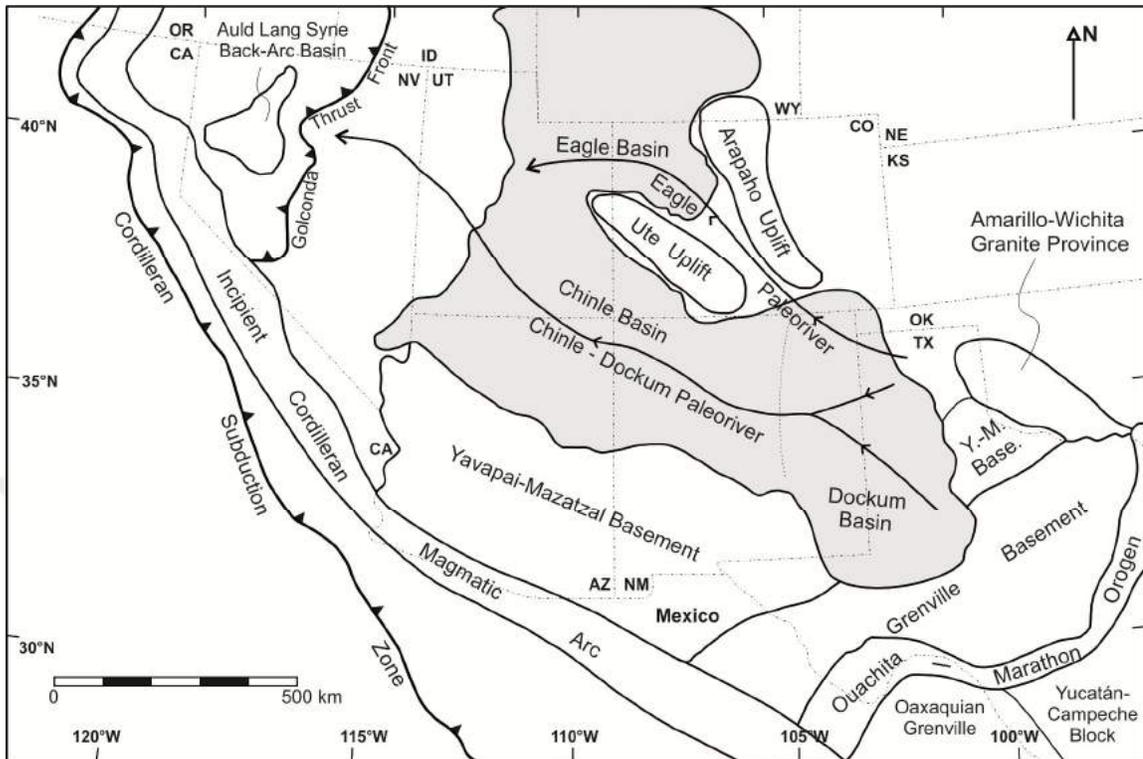
Figure 2.2 The drainage area of the Chinle-Dockum Paleoriver and surrounding paleogeography in the Late Triassic (simplified after Riggs et al. 1996; Dickinson and Gehrels 2008, 2010; Dickinson et al. 2010).
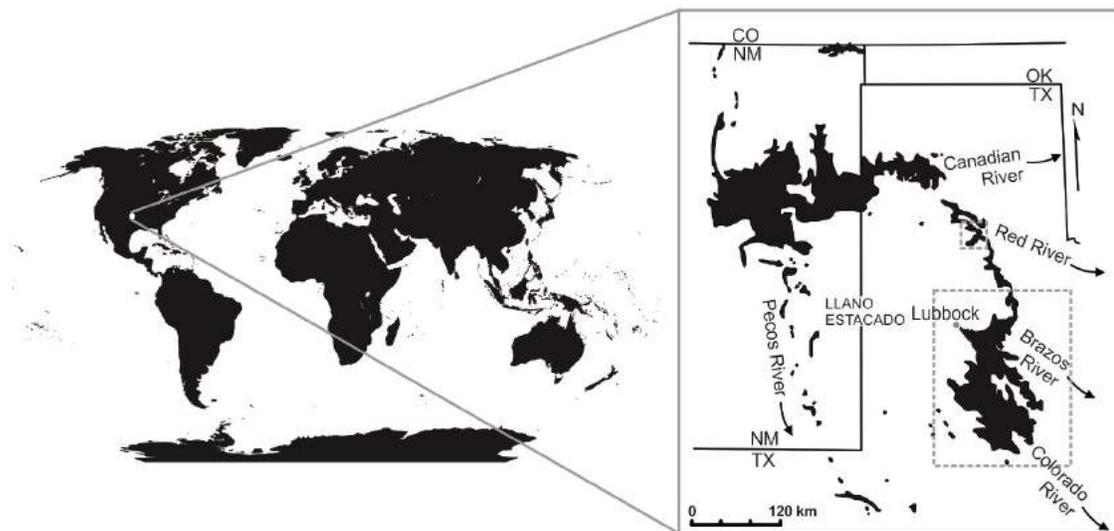


Figure 2.3 The locality map of the Dockum Group exposures (based on Lehman 1994a; Lehman and Chatterjee 2005). The scope areas of this study are indicated with the dashed rectangles.

The history of the Dockum Group extends back to 1830's. Distinctive Triassic red beds composed of clay, sandstone and conglomerates which are covering vast areas in western Texas are first recognized by Jules Marcou in 1835; however an official nomenclature applied much later in 1889 by Cummins (1890, 1891, 1892) in his survey reports about the Permian of Texas. Cummins identified these sediments as Dockum Beds, after a small town in Dickens County, Texas. Drake (1892), who was Cummins' assistant at the time (Lehman 1994a), used a tripartite subdivision: a lower sandy clay unit at the bottom, a mid sandstone/conglomerate unit above it and another sandy clay unit with some sandstones on top. Gould (1906, 1907) elevated Dockum beds to Dockum Group, and he was first to formally subdivide Dockum into two formations. These are the Tecovas Formation which is composed of shale and siltstone at the bottom and the overlying Trujillo Formation which is made of sandstone and conglomerate. Gould's nomenclature, nevertheless, is in correlation with Drake's subdivision where the Tecovas Formation corresponds to the lower shale unit whereas the Trujillo Formation covers the latter two levels (Lehman 1994a). Gould, and also Patton (1923), mapped the two formations exposed along the Canadian River valley.

By 1920's, geologists realized that all the Triassic rocks around the caprock escarpment (i.e. Llano Estacado) belong to the same geologic unit. Darton (1922, 1928) marked a basal sandstone unit, the Santa Rosa Sandstone, out of the coarse clastics at the base of the Tecovas Formation in Pecos River valley of New Mexico. This sandstone unit is traceable around the caprock with the previously identified quartoze conglomerates and sandstones (e.g. by Gould and Patton). Subsequently, the Redonda Member (later raised to formation by Griggs and Read [1959]) is recognized in New Mexico as a distinct

sandstone unit on the top of Dockum sequence (Dobrovoly and Summerson 1946, in Lehman 1994a). The last lithostratigraphic unit of the Dockum Group was recognized towards the end of the century. Chatterjee (1986a) preferred to rank the Dockum Group as a formation and distinguished the Cooper Member; which is composed of "upper" shales and a peculiar "upper" fauna, by modifying Drake's upper unit.

Although it was studied since the late 19th century, a decent and consistent lithostratigraphic nomenclature for the Dockum Group was proposed quite recently. Accordingly, the Dockum Group consists of five formations, namely Santa Rosa Formation, Tecovas Formation, Trujillo Formation, Cooper Canyon Formation and Redonda Formation (Lehman and Schnabel 1992; Lehman 1994a, 1994b). The Cooper Canyon Formation (Lehman et al. 1992) was the formal substitute for the previous Cooper Member/Formation (see Chatterjee 1986a) which was preoccupied for a Tertiary marl unit (e.g. Cooke and MacNeil 1952). During the interval between naming the Cooper Formation and re-naming the Cooper Canyon Formation, the Bull Canyon Formation was described (Lucas and Hunt 1989a), giving the Bull Canyon Formation priority (*contra* Lehman 1994b).

## Depositional Setting and Lithostratigraphy of the Dockum Group

Although it is now accepted as a Late Triassic fluvial-lacustrine sequence of red beds around the Southern High Plains of western Texas and eastern New Mexico, the depositional setting for the Dockum Group was debated in previous works. A lacustrine model for Dockum was mainly proposed by McGowen et al. (1979, 1983) but also by Johns and Granata (1987). They speculated there was a huge lake in the area and it was

fed by large rivers, originating in the surrounding highlands with large deltas and river mouths pouring into this lake. This assumption was based in the sandstone isopach mapping where it shows thick sandstone bodies covered the periphery and the lithology grades into mudstones towards the center of the basin. This endorheic accumulation with a fining upwards trend was indicating an alternation of gently dipping delta foresets and river channel deposits of the whole Dockum sequence.

On the other hand, concurring with earlier studies, it is suggested that the Dockum Group is predominantly made of fluvial deposits (e.g. Murry 1989a; Lehman and Schnabel 1992; Lehman 1994a, 1994b; Lehman and Chatterjee 2005). Based on the reinterpretation of the outcrops, Lehman pointed out the true nature of paleocurrents which were not draining into a single basin but they were dispersing in different directions. Moreover, the thick sandstone and mudstone depositions were separated into two main sequences (which does not correspond to the "lower" and "upper" sequence subdivisions of the previous lacustrine scheme) by a major disconformity (i.e. Tr-4 in Figure 2.4); therefore the isopach data is impracticable now since the sequence is not continuous. The provenance rocks of the Dockum sediments are another paleocurrent indicator, where the sediments were mainly coming from the eastern and southern metamorphic basements, therefore the paleocurrent direction was towards west-northwest (e.g. Riggs et al. 1996; Dickinson and Gehrels 2008, see below). The lacustrine deposition was indeed present in the Dockum Group, but it is mainly restricted to lower part of the Tecovas Formation rather than dominating the whole sequence.

The lower boundary of the Dockum Group is unconformable with the fluvial Middle Triassic Anton Chico Formation (Figure 2.4). The Anton Chico Formation predominantly consists of dark red and gray colored litharenites with conglomerate and mudstone interbeddings (Lucas and Hunt 1987). It was originally included in the lower part of the Santa Rosa Sandstone of Darton (1922, see above) and remained associated until the discovery of Anisian vertebrates within (Lucas and Hunt 1987). The vertebrate biostratigraphy indicates a direct correlation between Moenkopi and Anton Chico formations, and therefore, manifest the presence of the same unconformity (Tr-3, Pipiringos and O'Sullivan 1978) which separates these Middle Triassic units from the Upper Triassic sequences (i.e. Chinle Formation and Dockum Group) (Figure 2.4). Anton Chico Formation is restricted to the New Mexico sections; therefore it is not included in the present study.

The Palo Duro Geosol was former prior to the deposition of the Dockum Group, either on top of the Anton Chico Formation or directly on the underlying Permian strata (Kanhalangsy 1997; Lehman and Chatterjee 2005). Previously recognized as the "mottled unit/strata" (Steward et al. 1972; Dubiel 1987), this is a multicolored paleosol horizon which can be up to 5 meters in thickness and it is composed of a siltstone with early diagenetic carbonate (calcrete/caliche) and silicified carbonate (silcrete) alongside of mottling iron-oxide mineral formations and biogenic reworking (lungfish burrows).
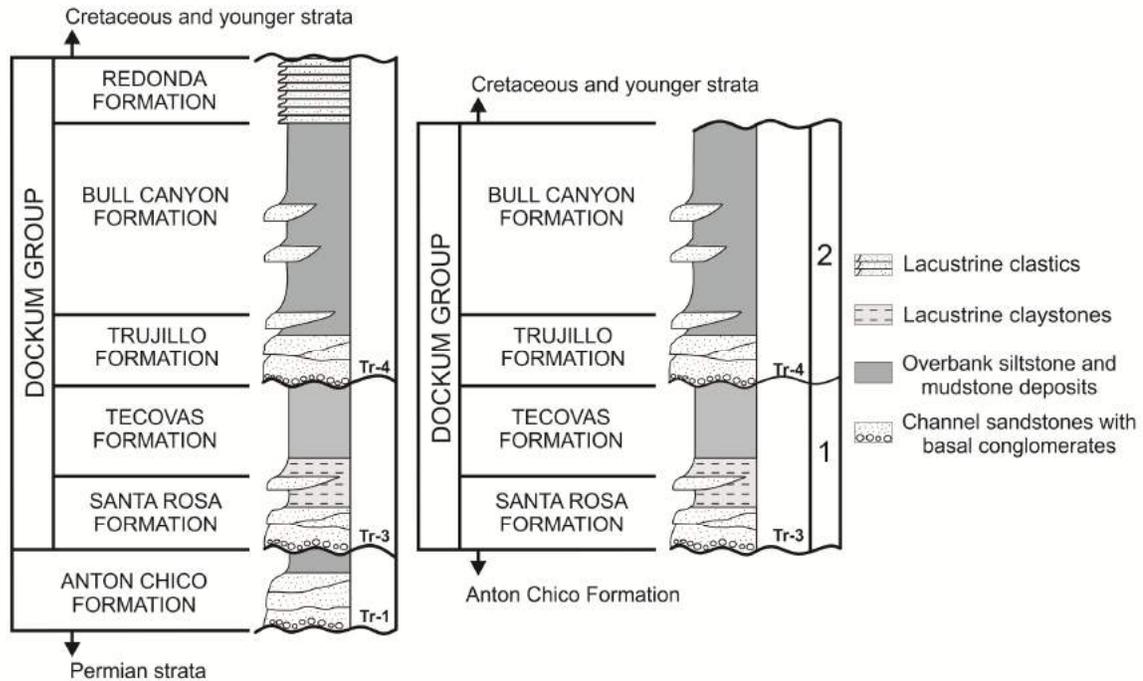
Figure 2.4 Generalized sequence of the Upper Triassic Dockum Group and the Anisian Anton Chico Formation (left) and the exposed portion in Texas area (right) (redrawn after Lehman and Chatterjee 2005). The two unconformable fluvial sequences are labeled as 1 and 2. Sequence boundaries after Pipiringos and O'Sullivan (1978) and Lucas (1991).

There are two unconformable fluvial sequences within the Dockum Group, both grading from channel sandstones to floodplain mudstones (Figure 2.4). The lower one is a thinner (less than 80 m., Lehman and Chatterjee 2005) sequence and consists of the Santa Rosa and Tecovas formations. The basal Santa Rosa Formation is a conspicuous sandstone unit within the Dockum Group with exceptionally high quartz content (Lehman and Chatterjee 2005). The vertical section displays a typical fining upward sequence of a river channel deposit; it starts with basal conglomerates and proceeds to trough and tabular cross-bedded sandstone, followed by parallel-laminated sandstone and ripple-laminated sandstone, and finally siltstone on top. The scarcity of mudstones and carbonized wood fragments indicate a braided river facies (Lehman and Chatterjee, op. cit.). The Santa Rosa Formation gradually passes to the Tecovas Formation, which is a

claystone-mudstone unit with intertonguing fine sandstone layers in the lower part (Lehman and Chatterjee 2005). Lower part the Tecovas Formation is characterized by significant lacustrine deposits which consist of green/yellow colored claystone beds composed largely of smectite (Na-smectite) with lesser amounts of illite and kaolinite and also with some scattered nodules of mainly carbonate (Fritz 1991; Lehman and Chatterjee 2005), whereas the upper part displays floodplain clayey and micaceous mudstone facies with minor channel deposits (May 1988; Lehman and Chatterjee 2005). This highly aquatic environment had a very rich fresh water fauna, including unionid bivalves (e.g. Elder 1987), ostracods (e.g. Kietzke and Lucas 1991), sharks (e.g. Johnson 1980; Murry 1981) and various bony fishes (e.g. Warthin 1928; Murry 1986, 1987b, 1989a, 1989b, 1989c). The Tecovas Formation is equivalent to the Los Estros Member of the Santa Rosa Formation (Lucas and Hunt 1987), the Garita Creek Formation (Lucas and Hunt 1989a) and the Colorado City Formation (Lucas 1993).

The overlying fluvial sequence is much thicker (over 150 m, Lehman and Chatterjee 2005) and it consists of the Trujillo and Bull Canyon formations (Figure 2.4). It is separated from the lower sequence by the Tr-4 unconformity, that resulted after subaerial erosion and reworking phase (Lucas 1991). The Trujillo Formation typically consists of micaceous litharenitic sandstones, which were eroded from a high grade metamorphic rock provenance (Long and Lehman 1993, 1994, 2009). It represents a typical fining upwards sequence of a meandering river facies, that starts with basal conglomerates, fines into massive or parallel-laminated sandstones, then passes to trough and tabular cross-bedded sandstones and finishes with red siltstone and mudstones (Lehman and Chatterjee 2005). The upper boundary with the Bull Canyon Formation is

very smooth since the upper mudstones are laterally equivalent. The Bull Canyon Formation is predominantly made of reddish siltstone and mudstones with local sandstone lenses and distinctly high mica content with abundant metamorphic fragments (Long and Lehman op. cit.; Lehman and Chatterjee 2005, p. 329). It is a clear example of a floodplain facies with steeply dipping mud layers into the gullies in various angles, accompanied with abundant unionid bivalve fossils (Freiler 1987; Lehman and Chatterjee 2005).

The Redonda Formation is the uppermost unit of the Dockum Group sequence. It is a lacustrine unit with both clastic and carbonate input that crops out only in northeastern New Mexico (Hester and Lucas 2001), and therefore will be excluded in this study. The Redonda Formation displays an alternation of sandstones and mudstones of fluvial/deltaic facies with minor micritic limestone interbeds. The lack of aridity features (e.g. evaporites), abundant bioturbation and absence of organic rich layers indicate that the Redonda Lake was a perennial, shallow but well oxygenated lake (Hester 1988; Hester and Lucas 2001).

In addition to the formal lithologic subdivisions, three main facies are recognized within the Dockum Group (Lehman and Chatterjee 2005). The channel-related facies comprised of sandstone and conglomerate accumulations in a fining upward sequence; the overbank floodplain facies is predominantly made of clayey and micaceous mudstones (predominantly for the Bull Canyon Formation) intercalated with thin, local sandstone lenses; and the lacustrine facies mainly consisted of claystones with occasional caliche and clastic layers. Those three facies correspond to Santa Rosa and Trujillo

formations; upper part of the Tecovas Formation and Bull Canyon Formation; and the lower part of the Tecovas Formation, respectively (Figure 2.4).

## The Tectonic Evolution of the Chinle-Dockum Paleoriver Basin

Tectonic evolution of the Chinle-Dockum Paleoriver Basin has a long geologic history. The initial phase of the basin formation began in the Late Proterozoic-Middle Cambrian interval with the opening of the Southern Oklahoma Aulacogene (Shatski 1946, in Hoffman et al. 1974), or the Arbuckle-Wichita-Amarillo fault system (see Thomas 1983, figure 1). The embedded mafic intrusions that followed this tectonic event created an excessively sunken slab on the continental crust into the mantle. This uncompensated basin was filled by a thick marine sedimentation during whole Paleozoic Era, especially during Carboniferous and Permian epochs. Subsidence of the basin was reactivated (DeRito et al. 1983) by the initial rifting of the Pangea in the Late Triassic. The rifting caused uplift around the future Gulf of Mexico; thus regenerated the sediment sources from the Late Paleozoic Ouachita-Marathon orogenic belt and triggered the westward accumulation of Dockum and Chinle fluvial sequences into the previously formed Permian basins (Johns and Granata 1987). The Permian units are unconformably overlain by the Middle Triassic fluvial units of the Moenkopi Formation (Tr-1 unconformity, Pipiringos and O'Sullivan 1978) and the equivalent Anton Chico Formation (Dickinson and Gehrels 2008) (Figure 2.4).

Additionally, detrital zircon analysis pointed out multiple provenance areas for the Chinle-Dockum Paleoriver deposits (Dickinson et al. 2007; Dickinson and Gehrels 2008, 2010). The Cambrian granite floor of the Amarillo-Wichita Uplift supplied the

Texas exposures of the Santa Rosa Formation and the coeval basal sandstones of the

Eagle Basin in Utah and Colorado (Figure 2.2), whereas the recycled grains of the Late

Proterozoic Grenville Orogeny and the Neoproterozoic-Paleozoic basement of the Late

Paleozoic Ouachita Orogeny supplied the rest of the basal sandstones of the Chinle-

Dockum deposition (Figure 2.2), including New Mexico exposures of the Santa Rosa

Formation (Dickinson and Gehrels 2008, figure 4). Following sequences (i.e. Trujillo and

Bull Canyon formations and the coeval strata of the Chinle Formation) were continued to

be supplied by the Grenville Province and also by the Ouachita Mountains in a lesser

extent (Dickinson and Gehrels 2008, figure 5). Another major contributor was the

Mesoproterozoic Yavapai-Mazatzal Basement (Figure 2.2), or the Mogollon Highlands.

The Yavapai-Mazatzal basement had a greater influence in grain composition of the

Moenkopi Formation and the basal sandstone units (equivalents of the Shinarump

Member) of the lower sequence of the Chinle Formation in Arizona and Utah. The

influence of grain accumulation from the Yavapai-Mazatzal basement was diminished in

the upper parts of the Chinle-Dockum deposits, but still traceable in the Sonsela Member

of the Chinle Formation in Arizona and New Mexico.

Considering the Dockum Group sediments in Texas, the Santa Rosa Formation

differs from the overlying units by having a different source area (Amarillo-Wichita

granite, see above), whereas the rest of the sequence was mainly supplied by the

Grenville and Ouachita orogenic provinces with gradually increased influence of the

former province, especially in the upper sequence (i.e. Tecovas and Bull Canyon

formations). This situation concurs with the previous interpretations (Long and Lehman

1993, 1994, 2009; Lehman and Chatterjee 2005, p. 329 and references therein). On the

other hand, the lower sequence (i.e. Santa Rosa and Tecovas formations) includes

significant amount of grains from the Yavapai-Mazatzal basement, compared to the upper

sequence.

# Chapter 3

# Dockum Tetrapod Fauna

The Dockum Group represents one of the finest and most diverse Late Triassic land tetrapod assemblages in the world (e.g. Chatterjee 1986; Murry 1986, 1987b, 1989c; Parrish and Carpenter 1986; Long and Murry 1995; Lehman and Chatterjee 2005). The first discovery of tetrapod fossils was made by W. F. Cummins in 1890 northwest of Spur, Dickens County, Texas. These bones were identified by the famous paleontologist Edward Drinker Cope in 1891-92 (Cope 1893). In the early 20th century, E. C. Case of the University of Michigan began systematically collecting the Dockum fossils, especially from Crosby, Dickens, Garza, and Howard counties of Texas and he made major contributions to the understanding of the Dockum fauna (Gregory 1972). By the early 1980s, the current phase of Dockum vertebrate exploration has been carried out by Sankar Chatterjee of the Museum of Texas Tech University (MoTTU) and his students with a significant collection of various temnospondyli, therapsids, procolophonids, sphenodontians, and a rich assemblage of archosauromorph fauna (e.g. Lehman and Chatterjee 2005) (Figure 3.1). This entire vertebrate assemblage was collected from the overbank flood plain facies (i.e. Tecovas and Bull Canyon formations) of the Dockum, but the intervening channel facies of Trujillo Formation is virtually sterile and contain few bone fragments. Similarly, the basal Santa Rosa Formation is equally poor in fossil content.
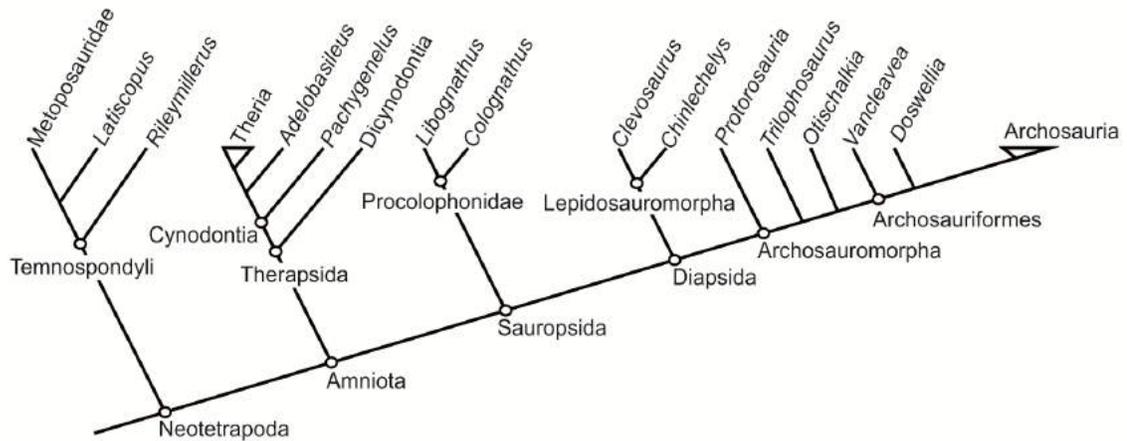
Figure 3.1 Cladogram for the non-archosaurian tetrapods of Dockum (phylogenies of temnospondylians after Schoch [2008]; cynodonts after Luo [2002] and Lui and Olsen [2010]; procolophonids and lepidosauromorphs after DeBraga and Rieppel [1997]; archosauromorphs after Dilkes [1998], Modesto and Sues [2004], Dilkes and Sues [2009], Nesbitt et al. [2009a]). Taxon name definitions are neglected in the cladogram.

## Non-Archosaurian Tetrapod Fauna of Dockum

### Basal Tetrapods

Temnospondyli tetrapods represent the anamniote (i.e. non-amniotic) tetrapods of the Dockum Group (Figure 3.2). Temnospondyli are mainly represented by metoposaurids from various horizons of Tecovas and Bull Canyon formations, including *Koskinonodon* (replacement name for *Buettneria*, Mueller 2007) and *Apachesaurus* (Hunt 1993). Metoposaurids or metoposaurs were generally large, semi-aquatic animals about 2 to 5 meters in length and widely documented in the Upper Triassic strata (Hunt 1993; Schoch and Milner 2000; Schoch 2008), however *Apachesaurus* was a very small member with a length of 50 cm. Metoposaurs have distinct parabolic and flat skulls on which the orbits are dorsally placed on the rostral portion, and they contain a large pineal opening on the posterior portion of the skull. The skull is heavily ornamented with distinctive lateral lines on each side. The other members of the Dockum temnospondyli are *Latiscopus disjunctus* (Wilson 1948) and *Rileymillerus cosgriffi* (Bolt and Chatterjee

2000). Both taxa are collected from the Tecovas Formation; the former one from the Otis Chalk Quarry and latter one from the Post Quarry. *Rileymillerus*, though superficially resembles *Latiscopus*, is a much smaller animal; the skull is only a couple centimeters long and possesses quite different cranial morphology than other temnospondyli by having a cylindrical skull and orbits on the side of the skull (Bolt and Chatterjee 2000). Both *Latiscopus* (together with almasaurids) and *Rileymillerus* are placed closely to the Metoposauridae (see Schoch 2008, figure 10) (Figure 3.1).
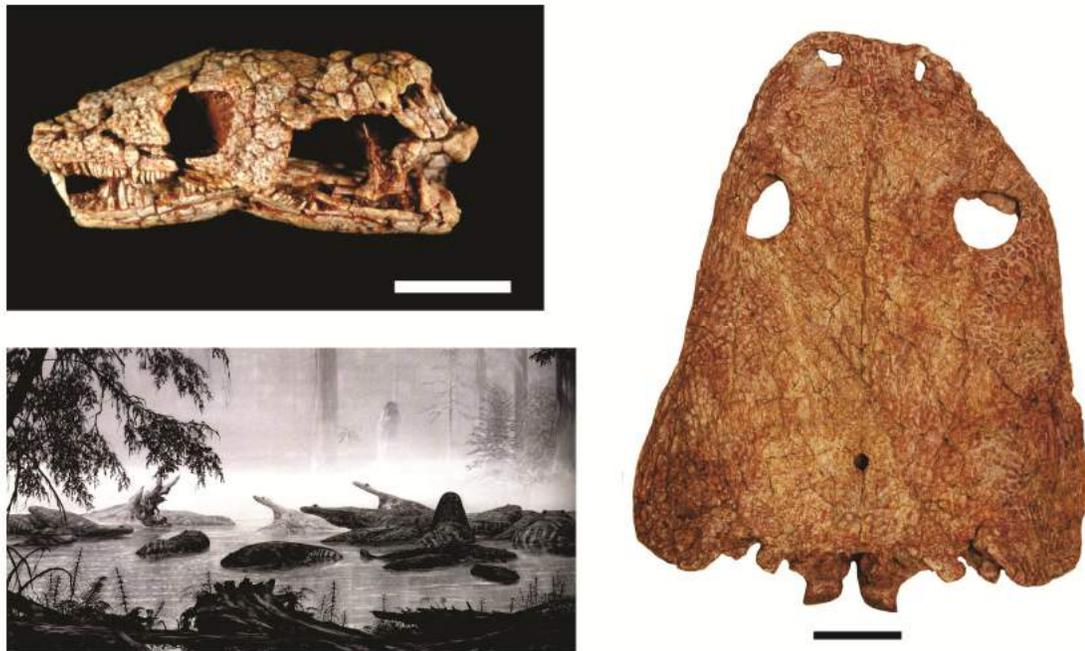


Figure 3.2 Late Triassic temnospondyls of Dockum. *Rileymillerus* (upper left, scale bar = 1 cm) and *Koskinonodon* (right, scale bar = 10 cm) skulls (photo credits: Bill Mueller). An illustration for a group of metoposaurs in a Late Triassic morning (lower left, image credit: Douglas Henderson in Fraser [2006]).

**Therapsids**

Therapsids were one of the first land tetrapods that flourished after the great Permian-Triassic extinction; however their diversity gradually decreased during the Triassic and only few cynodonts survived to the Early Jurassic including the precursors

of mammals, whereas some researchers claim that dicynodonts also survived to the

Cretaceous Period (Thulborn and Turner 2003). Dicynodonts of the Late Triassic were

about 3-4 meters in length, as large as a cow, and they had edentulous jaws with no or

tiny tusks. North American dicynodonts were somewhat smaller than their South

American relatives. Dicynodonts are rarely collected from the North American Triassic;

they were previously known from few localities of the Chinle Formation, including the

famous *Placerias* Quarry of Arizona (e.g. Lucas and Heckert 2002a). Additionally, their

presence has also been reported recently from various localities in the Tecovas Formation

(Mueller and Chatterjee 2007). The Dockum dicynodonts may represent several new taxa

but the material is yet to be formally described (Figure 3.3).
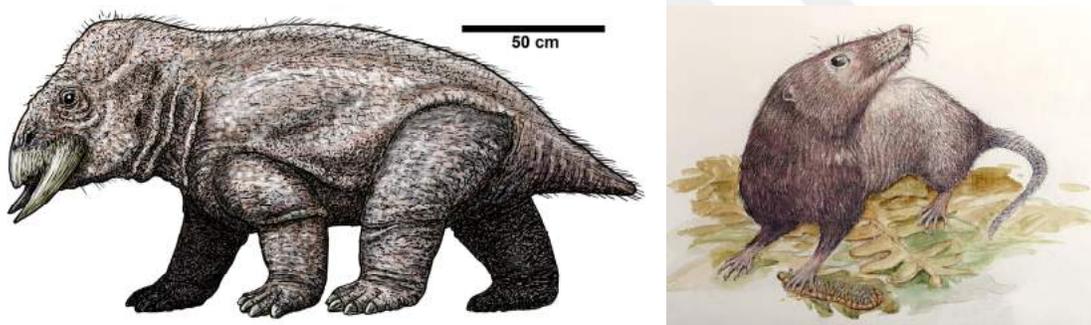


Figure 3.3 Late Triassic therapsids of North America. Artist's impression of the dicynodont *Placerias* with unusually large tusks (left) from the Chinle Formation, a taxon which is possibly related to the undiagnosed dicynodonts from Dockum (image credit: Jeffrey W. Martz). Life restoration of *Adelobasileus* (right), which was a rat-sized animal (image credit: Mary Sundstrom for the New Mexico Museum of Natural History and Science, http://www.nmnaturalhistory.org/adelobasileus-cromptoni.html).

Cynodonts of Dockum included a small, rat-sized tritheledontid *Pachygenelus*

*milleri* (Chatterjee 1983) and a stem mammalian *Adelobasileus cromptoni* (Lucas and

Hunt 1990; Lucas and Luo 1993) (Figure 3.3). Both taxa were collected from the Tecovas

Fomation; *P. milleri* from the Post Quarry whereas *A. cromptoni* from the

stratigraphically lower Kalgary Locality. *Pachygenelus* is represented by a partial dentary

with distinctly serrated teeth, whereas *Adelobasileus* is diagnosed on a partial endocranium. Phylogenetic analyses indicate that they are closely related to mammals (e.g. Luo 2002; Lui and Olsen 2010).

**Non-Archosauromorph Sauropsids**

A variety of parareptiles, stem-turtles and lepidosaurians were also presented in the Dockum Group, including some poorly diagnosed or uncertainly placed taxa. *Libognathus sheddi* (Small 1997) was discovered on the Double U Ranch locality (formally UU Sand Creek locality, MOTT 3882) in the Bull Canyon Formation. Although it is diagnosed solely on the lower jaw fragments, another well preserved skull leaves little doubt about its procolophonid affinity (Mueller and Chatterjee 2003). The other procolophonid collected from the Dockum Group is *Colognathus obscurus* (Murry 1986, redefined *Xenognathus obscurus* of Case [1928]) from the Kalgary Locality, located in the Tecovas Formation, is known only from jaw fragments. An ancestor of the turtles, *Chinlechelys tenertesta* from the New Mexican outcrops of the Bull Canyon Formation is mainly recognized by the highly fragmentary remnants of the carapace (Joyce et al. 2009). Rhynchocephalian *Clevosaurus* (Lehman and Chatterjee 2005) and various fragments of other sphenodontids and diphydontosaurids are also present in the Dockum collection, but the material awaits detailed diagnosis and description.

**Archosauromorphs**

The Dockum Group has yielded a great diversity of archosauromorphs, including the three main groups: Prolacertiformes, Rhynchosauria and Archosauriformes.

Prolacertiformes are probably paraphlyletic; most members have a mosaic of ancestral and derived characters, making their affinity uncertain. Recent cladistic analysis showed the genus *Prolacerta* is closer to Archosauriformes (e.g. Dilkes 1998; Modesto and Sues 2004; Gottmann-Quesada and Sander 2009). The rest of the prolacertiforms are now clustered in Protorosauria (e.g. Rieppel et al. 2003; Renesto et al. 2010), which appeared in the Late Permian (i.e. *Protorosaurus*) and radiated especially during the Middle and Late Triassic. In this realignment, *Drepanosaurus* sp. and *Malerisaurus langstoni* are the protorosaurian representatives in the Dockum Group. The half-meter long *Drepanosaurus* and related forms are grouped in a new clade Simiosauria and they are hypothesized to be arboreal/scansorial forms with a long and strong prehensile tail and bears a huge claw on the second manual phalange (Senter 2004; Renesto et al. 2010) (Figure 3.4). *Malerisaurus langstoni* of the Dockum represents the Late Triassic equivalent of modern-day basilisk lizard in size, proportions and behavior (Chatterjee 1986b; Figure 3.5).

*Trilophosaurus* is an archosauromorph from the Late Triassic of the southwestern North America (Figure 3.6). *Trilophosaurus buettneri* (Case 1928; Gregory 1945) possessed a somewhat high skull with secondarily closed lower temporal fenestra and peculiar mediolaterally elongated teeth (or dental plates) with multiple cusps for grinding vegetation. *Trilophosaurus* was originally recognized as a cotylosaur (Case 1928), then a protorosaur (Gregory 1945), an euryapsid (Romer 1966), and finally as an archosauromorph (Gauthier 1984; Benton 1985). Two more species of *Trilophosaurus* are identified so far, *T. jacobsi* (Murry 1987a) and *T. dornorum* (Mueller and Parker 2006). All three species of *Trilophosaurus* are present in Dockum sediments,

predominantly in the Tecovas formation but few remnants are also reported from the Bull

Canyon Formation.
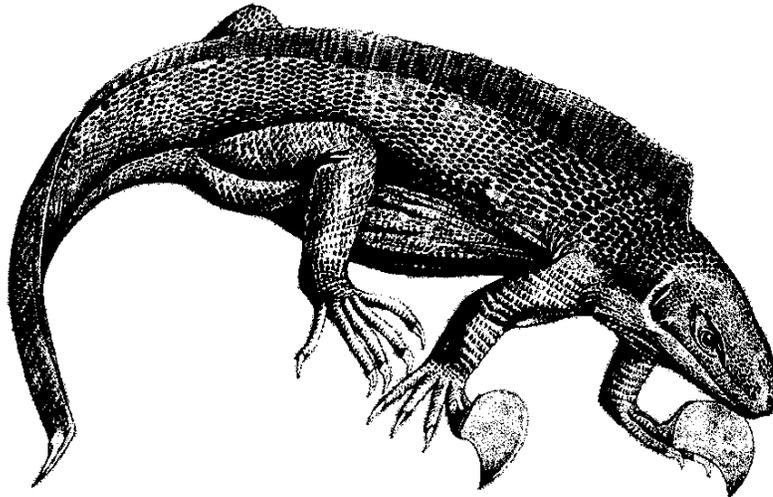
Figure 3.4 A sketch for *Drepanosaurus unguicaudatus* (after Pinna 1984, drawing by M. Demma). The size of this animal is around 40-50 cm in length.

Figure 3.5 Life restoration for *Malerisaurus langstoni* (after Chatterjee 1986b).
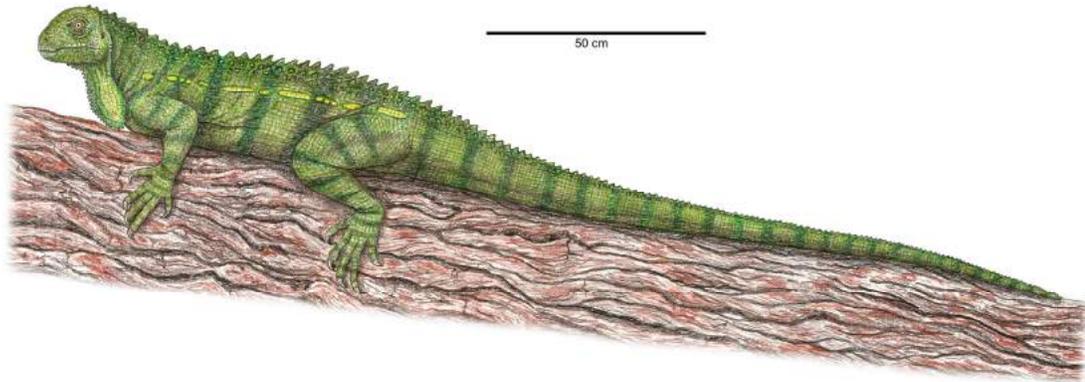
Figure 3.6 Artist's impression for *Trilophosaurus* (image credit: Jeffrey W. Martz).

Rhynchosaurs were the dominant herbivores in the Late Triassic Maleri Formation of India, Ischigualasto Formation of Argentina, Santa Maria Formation of Brazil and the Lossiemouth Sandstone of Scotland. They are characterized by specialized dentition with three peculiarities. First, the anterior part of the jaws is edentulous, with the development of beak-like premaxilla and anterior end of the dentary. Second, the ventral part of the maxilla bears multiple rows of tiny teeth running subparallel to the jaw margin. Third, the dentary has a sharp tooth bearing edge that fits into the groove of the maxillary plate (Chatterjee 1974). Rhynchosaurs are poorly represented in the Dockum based on some unpublished jaw fragments, mostly from the lower portion of the Tecovas Formation (e.g. McCarty Ranch, MOTT 0690). *Otischalkia elderae* (Hunt and Lucas 1991c) which is known from few isolated limb elements from the Otis Chalk Quarry is now regarded as an invalid taxon (e.g. Mukherjee and Ray 2014) and the true affinity of the skeletal parts is still in study (Bill Mueller, pers. comm. 2014).
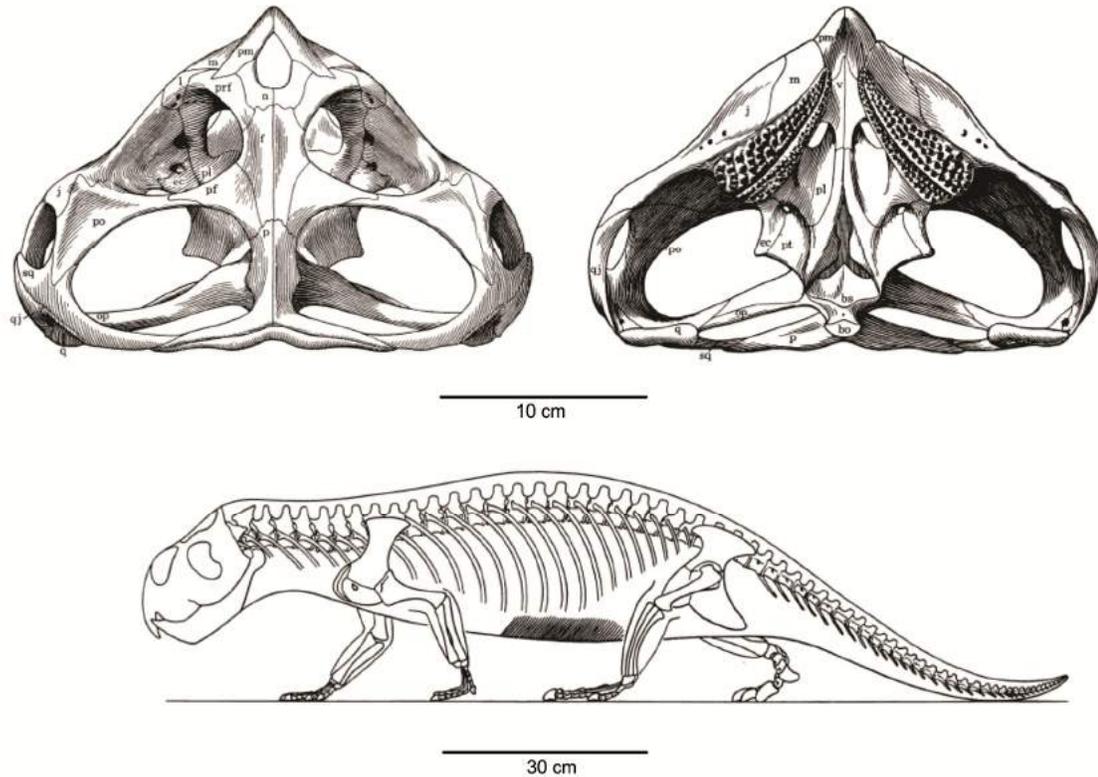
Figure 3.7 Reconstructions for Indian rhynchosaur "*Paradapedon*". Dorsal and palatal views of the skull (upper); and mounted skeleton (lower) (After Chatterjee 1974).

**Archosauriformes**

The archosauriforms of the Dockum Group had the highest diversity compared to other tetrapods. There are two stem archosauriform taxa collected from the lower part of the Tecovas Formation: *Vancleavea campi* and *Doswellia kaltenbachi*. *Vancleavea campi* is diagnosed based on fragmentary postcranial elements and distinct dermal armor from the lower Petrified Forest Member (now the Blue Mesa Member) of the Chinle Formation (Long and Murry 1995). A nearly complete skeleton of *V. campi* from the Whitaker Quarry of the Chinle Formation revealed its affinity as a stem archosauriform (Nesbitt et al. 2009a). Unique morphologies of *V. campi* includes imbricated osteoderms covering the entire body; a short, highly ossified skull and relatively small limbs and special adaptations such as dorsally oriented nares, indicate a semi-aquatic lifestyle which

is consistent with previous assumptions (see Small and Downs 2002) (Figure 3.8).

Despite the wide stratigraphic occurrence of in the Chinle Formation (Long and Murry

1995; Hunt et al. 2002), *V. campi* is reported only from the Tecovas Formation in

Dockum.
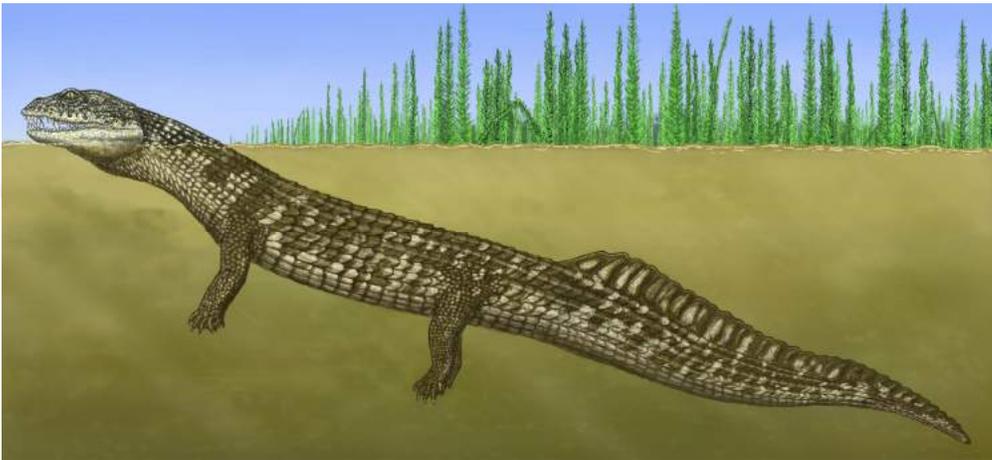


Figure 3.8 Life restoration of *Vancleavea* (image credit: Jeffrey W. Martz).

*Doswellia kaltenbachi* is originally discovered in the Newark Supergroup of

Virginia (Weems 1980) (Figure 3.9). Nevertheless, several vertebrae and osteoderm

fragments of *D. kaltenbachi* are collected from the lower part of Tecovas Formation (e.g.

Long and Murry 1995). This animal exhibits similar morphology to proterochamsids by

having an elongated skull with narrow snout, alongside a number of aetosaurian

characters in dermal scute patterns which had independently evolved, thus it is

traditionally placed together with Proterochampsia (Olsen 1989, pp. 54-55, in Long and

Murry op. cit.). Recent phylogenetic studies place *Doswellia kaltenbachi* as the sister

group of Proterochampsia (Dilkes and Sues 2009). The distribution of doswellids seems

to be global in the Late Triassic with two South American genera (Arcucci and

Marsicano 1998; Desojo et al. 2011) and a most recent European genus (Schoch and Sues

2014), in addition to the North American *Doswellia*.
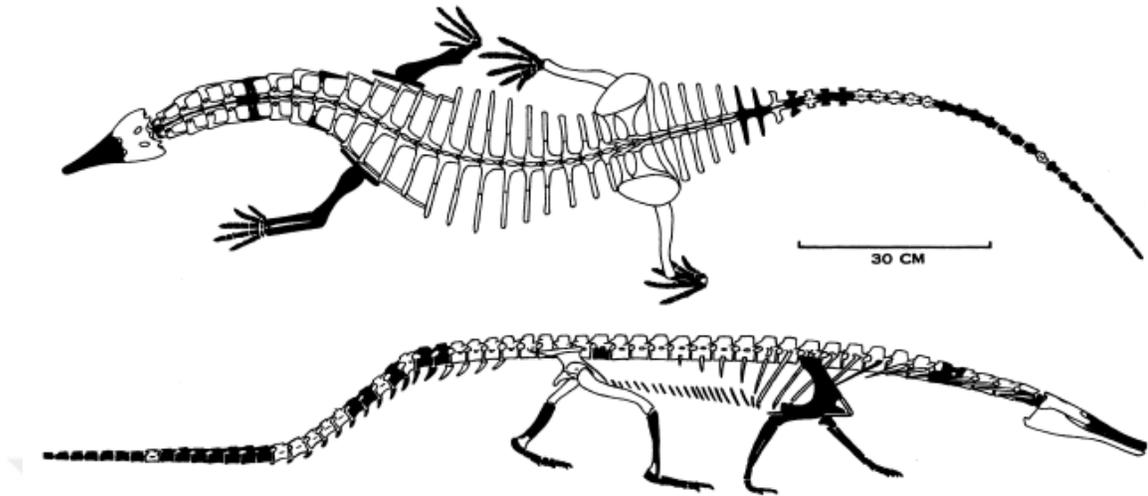
Figure 3.9 Skeletal reconstruction of *Doswellia kaltenbachi* (modified after Weems 1980, black areas are inferred by the author).

There are also some problematic non-archosaurian archosauriforms from the Dockum Group, such as *Tecovasaurus murryi* (Hunt and Lucas 1994), *Protecovasaurus lucasi* and *Crosbysaurus harrisae* (Heckert 2004) which were collected from the Tecovas Formation, while *Lucianosaurus wildi* is described from the Bull Canyon Formation (Hunt and Lucas 1994). *T. murryi* and *P. lucasi* are also reported from the Chinle Formation. All four taxa are diagnosed solely on isolated teeth which are reminiscent of the ones of ornithischians by having an asymmetrical morphology with sub-triangular cusps and distinct carinae and denticles of various shapes. However, these features appeared to be plesiomorphic among archosauriforms (also see below for *Revueltosaurus* spp. and *Technosaurus smalli*), therefore the phylogenetic placement for these taxa on the basis of tooth morphology remains uncertain (i.e. incertae sedis, Irmis et al. 2007b).

*Spinosuchus caseanus* (von Huene 1932) is another problematic taxon from the Dockum Group, documented only from the Tecovas Formation so far. Some cervical and anterior dorsal vertebrae together with a basicranium were originally identified as

*Coelophysis* (Case 1922, 1927), and then they are designated as a new taxon *S. caseanus* by von Huene (1932). However, the referred braincase is later affined with rauischians or poposaurids and the referred vertebrae may not belong to a saurischian (Chatterjee 1985; Gauthier 1986; Murry 1986; Murry and Long 1997). The vertebrae probably represent an undetermined neodiapsid with possible archosauromorph affinities (Long and Murry 1995, p. 198). It was also proposed a link between *S. caseanus* and ctenosaurids (Krebs 1969; Fa-Kui 1975, in Murry and Long 1997). More recently, the suggested relation of *S. caseanus* with *Trilophosaurus* based on zygopophyseal characters of the cervical vertebrae (Richards 1999a, 1999b; Spielmann et al. 2009) is rejected due to plesiomorphic distribution of such traits and considered as an indetermined archosauriform (Nesbitt et al. 2007).

## Dockum Archosaurs

Archosaurs were the ruling reptiles of the Mesozoic Era and the dominant vertebrates of the Dockum. The clade Archosauria includes the most recent common ancestor of crocodiles and birds and all of its descendants (Gauthier 1986). Classically, it is split into two major clades on the basis of ankle structure: Crurotarsi and Ornithodira (Sereno 1991a) (Figure 3.10). The clade Crurotarsi gave rise to crocodilian lineage and it is distinguished by the crurotarsal ankle structure with a peg-and-socket joint between the astragalus and calcaneum, giving them a plantigrade foot stance. The clade Ornithodira consists of pterosaurs and dinosauromorphs (including birds) and it is characterized by a mesotarsal ankle joint, where the hinge lies between the proximal and distal tarsal rows and accompanied by a digitigrade stance in dinosauromorphs (Figure 3.11).
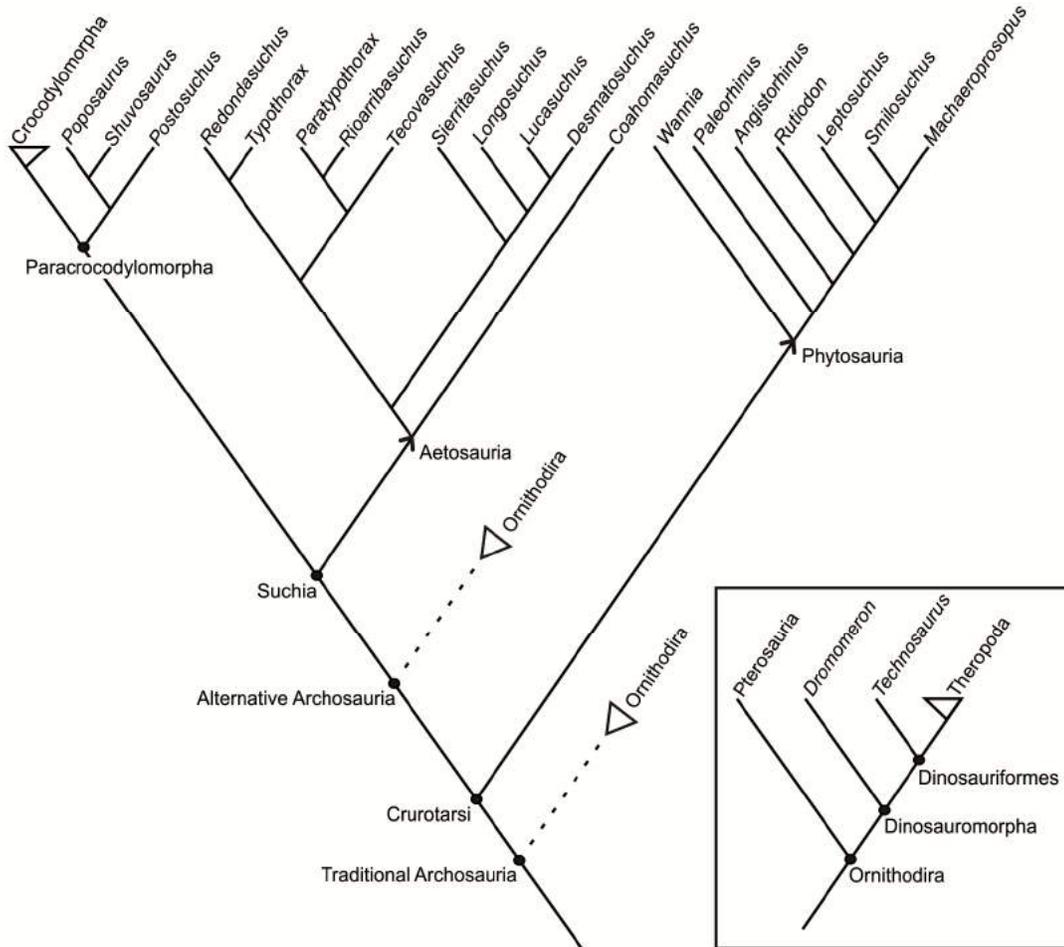
Figure 3.10 Cladogram comprised of Dockum archosaurs only, except Pterosauria (phylogenies compiled after Sereno 1991a; Parker 2007; Brusatte et al. 2010a; Stocker 2010, 2012b; Nesbitt 2011; Desojo et al 2012). For unrepresented taxa, see text. Filled circles are for node-based taxa, arrows are for stem-based taxa. The alternatively placement of the clade Archosauria excludes phytosaurs (e.g. Nesbitt 2011).

The Dockum ornithodirans are represented solely by the dinosauromorphs; no pterosaurs have been discovered as yet (Figure 3.10). The early records of pterosaurs are restricted to shallow marine environments (e.g. Dalla Vecchia 2013). Archosaur specimens/taxa which are poorly diagnosed or still in preparation are not included to the following section.
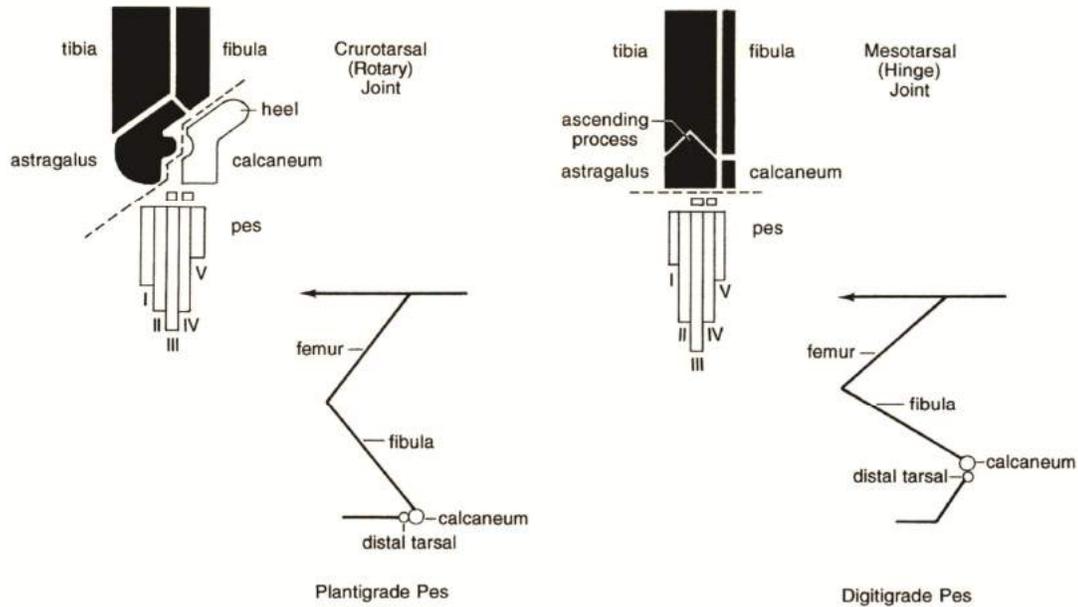
Figure 3.11 Ankle joints and stances. Left, the generalized crurotarsal ankle joint with the characteristic plantigrade stance; right, the mesotarsal ankle joint with the characteristic digitigrade stance in dinosauromorphs (after Chatterjee 1997).

**Crurotarsans**

Phytosauria, Aetosauria and Rauisuchia are the three groups of the Crurotarsi which are dominant in the Dockum Group (Figure 3.10). Phytosaurs have a crocodilian body shape, but easily recognizable with receded external nares on the skull roof that sit above the antorbital area and the body length may exceed 7 meters in length (Figure 3.12). Phytosaurs are ubiquitous in the Upper Triassic deposits of North America and Europe. The clade Phytosauria is traditionally considered as basal group of the Crurotarsi, however some recent cladistic analysis place them as a sister group to Archosauria due to homoplasic distribution of the traditional phytosaurian characters among pseudosuchians (Nesbitt 2011; Stocker and Butler 2013) (Figure 3.10). Phytosaur fossils are widely distributed throughout the Dockum Group. Several taxa of phytosaurs are known from the Dockum Group, including *Wannia scurriensis* (new senior synonym for *Paleorhinus scurriensis*, Stocker 2012b), *Promystriosuchus ehlersi*, *Paleorhinus* spp., *Leptosuchus*

spp., *Rutiodon* spp. and *Machaeroprosopus* spp. (Figure 3.10). *W. scurriensis* is recently

placed as the basal member of the clade Phytosauria (Stocker 2012b), whereas the

placement of *P. ehresi* is considered uncertain (Stocker and Butler 2013).

*Machaeroprosopus* is now considered as the new senior synonym for *Pseudopalatus*

(Parker et al. 2013) and *Redondasaurus* (Hungerbühler et al. 2013) (Figure 3.12).
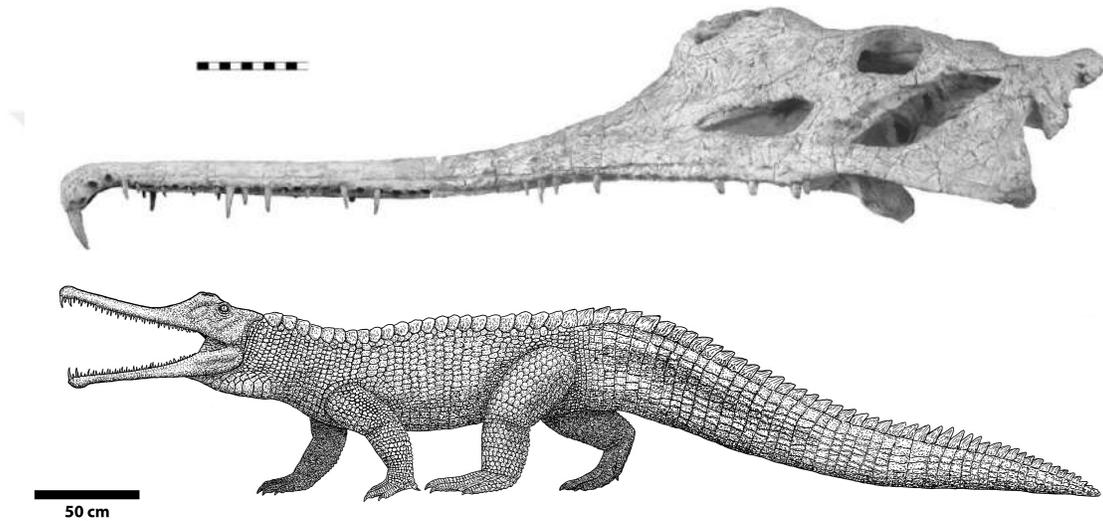


Figure 3.12 The holotype skull (TTU-P10076) for *Machaeroprosopus lottorum* (scale bar = 10 cm, after Hungerbühler 2013) and the artist's impression for the same genus (image credit: Jeffrey W. Martz).

Members of the clade Aetosauria are characterized with a distinctive morphology,

including a bony dermal armor composed of discrete osteoderms or scutes with large

spikes in some taxa. They have a toothless, upturned beak with specialized posterior

dentition for herbivory. The fossil record indicates that they might have been the earliest

worldwide radiation of herbivorous/omnivorous archosaurs (Harris et al. 2003). The

aetosaur genera from the Dockum Group represent several taxa including *Stegomus*

*arcuatus*, *Coahomasuchus kahleorum*, *Calyptosuchus wellesi*, *Adamanasuchus*

*eisenhardtae*, *Typothorax* spp., *Redondasuchus* spp., *Tecovasuchus chatterjeei*,

*Rioarribasuchus chamaensis*, *Paratypothorax andressorum*, *Apachesuchus heckerti*,

*Sierritasuchus macalpini*, *Longosuchus meadi*, *Lucasuchus hunti*, *Desmatosuchus* spp. (Figure 3.10). The 4.5 meters long *Desmatosuchus* holds the title of being the largest aetosaur discovered so far (Figure 3.13). Fragments of *Stegomus arcuatus*, which were originally discovered in the Newark Supergroup, are present in the collection of the Texas Tech Museum but this taxon was recently regarded as invalid (Desojo et al. 2013). *Apachesuchus heckerti* is a new taxon erected on previously known fragments of an neoaetosauroid from the Redonda Formation, probably a basal form (Spielmann and Lucas 2012, pp. 84-86) just like *Coahomasuchus*.
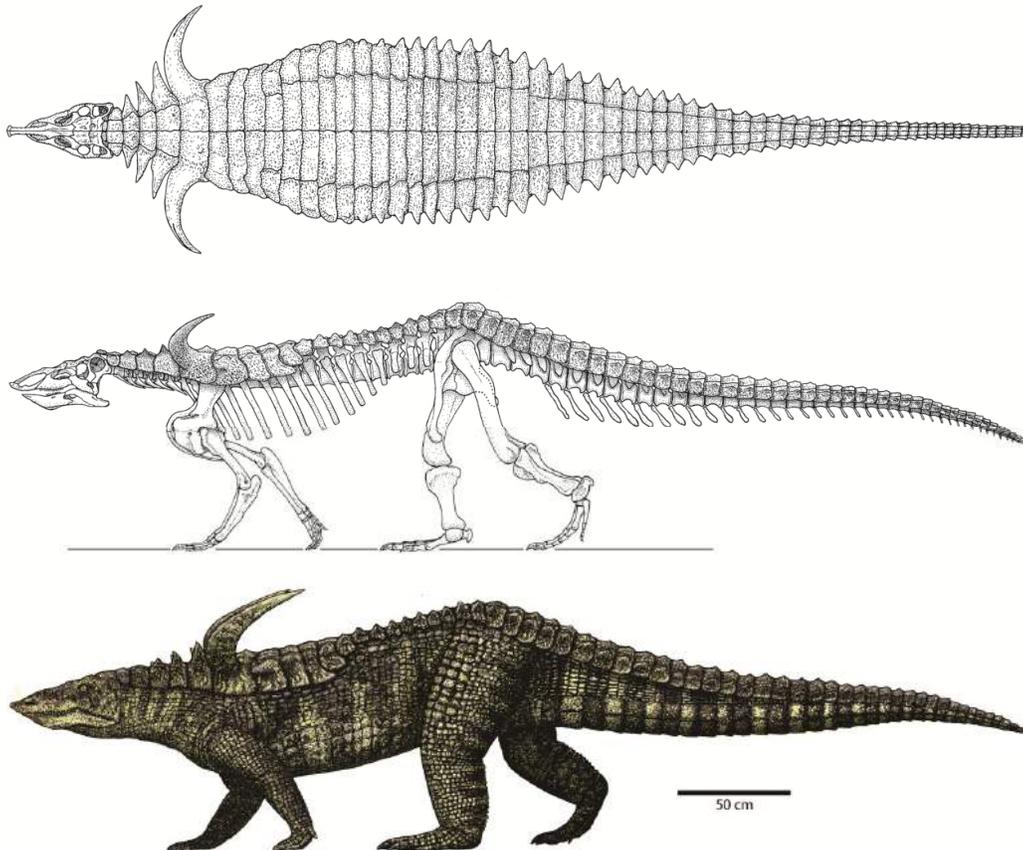


Figure 3.13 Skeletal drawings from dorsal (upper) and side (middle) views and life restoration (lower) of *Desmatosuchus*, the largest aetosaur so far (modified from drawings of Jeffrey W. Martz).

*Revueltosaurus callenderi* (Hunt 1989b), collected from the Bull Canyon Formation as well as from the Petrified Forest Member of the Chinle Formation (Padian 1990), was initially associated to an ornithischian on the basis of asymmetrical and subtriangular isolated teeth which are well separated from the alveolar portion with a neck. The holotype consisted solely of isolated teeth, however, the subsequent discovery of the related jaw fragments with preserved teeth, alongside of various cranial and postcranial elements provided more details about the affinity of this animal. Presence of a postfrontal, a calcaneum fits into the crocodile-normal ankle joint and paramedian osteoderms with anterior bars have suggested that *R. callenderi* is a crurotarsan or a closely related form (Parker et al. 2005), possibly close to aetosaurs (Irmis et al. 2007b; also see Desojo et al. 2012, figure 20).

Rauisuchians are derived crurotarsans that superficially resemble theropod dinosaurs in body plan, especially in skull and bipedal posture, but they lack the traditional dinosaurian hallmarks such as a perforated acetabulum or a mesotarsal ankle joint. Rauisuchians are now considered as a sister taxon to Crocodylomorpha (e.g. Wu and Chatterjee 1993; Long and Murry 1995; Nesbitt and Norell 2006; Nesbitt 2007; Nesbitt et al. 2013). Members of this group display two main types of morphology; they are either large sized formidable carnivores like *Poposaurus* and *Postosuchus* or gracile, ostrich-like omnivores like *Shuvosaurus* (Figure 3.10). Over 9-meters-long *Postosuchus kirkpatricki* which was the largest carnivore of the Triassic hitherto discovered, belongs to the first group (Figure 3.14). It has a massive head with serrated teeth, relatively short limbs and hands with erect and powerful hind limbs show uncanny resemblance to theropods (Chatterjee 1985). On the other hand, *Shuvosaurus inexpectatus* is a gracile,

ostrich-like animal with toothless beak and bipedal posture (Chatterjee 1993) (Figure 3.15). *Shuvosaurus* was originally diagnosed based on a solitary cranium. Nonetheless, further analysis of an associated a postcranial skeleton named *Chatterjeea elegans* (Long and Murry 1995, pp. 161-162) clarified its identity, where *C. elegans* became a junior synonym for *Shuvosaurus inexpectatus* (Nesbitt and Norell 2006; Nesbitt 2007). Both aetosaurians and rauisuchians had independently achieved erect gait by modification of the ilium and dorsally shifted acetabulum, so that the femur could align to a vertical position. In spite of their erect posture, aetosaurians are obligate quadrupeds whereas rauisuchians are facultative bipeds.

50 cm
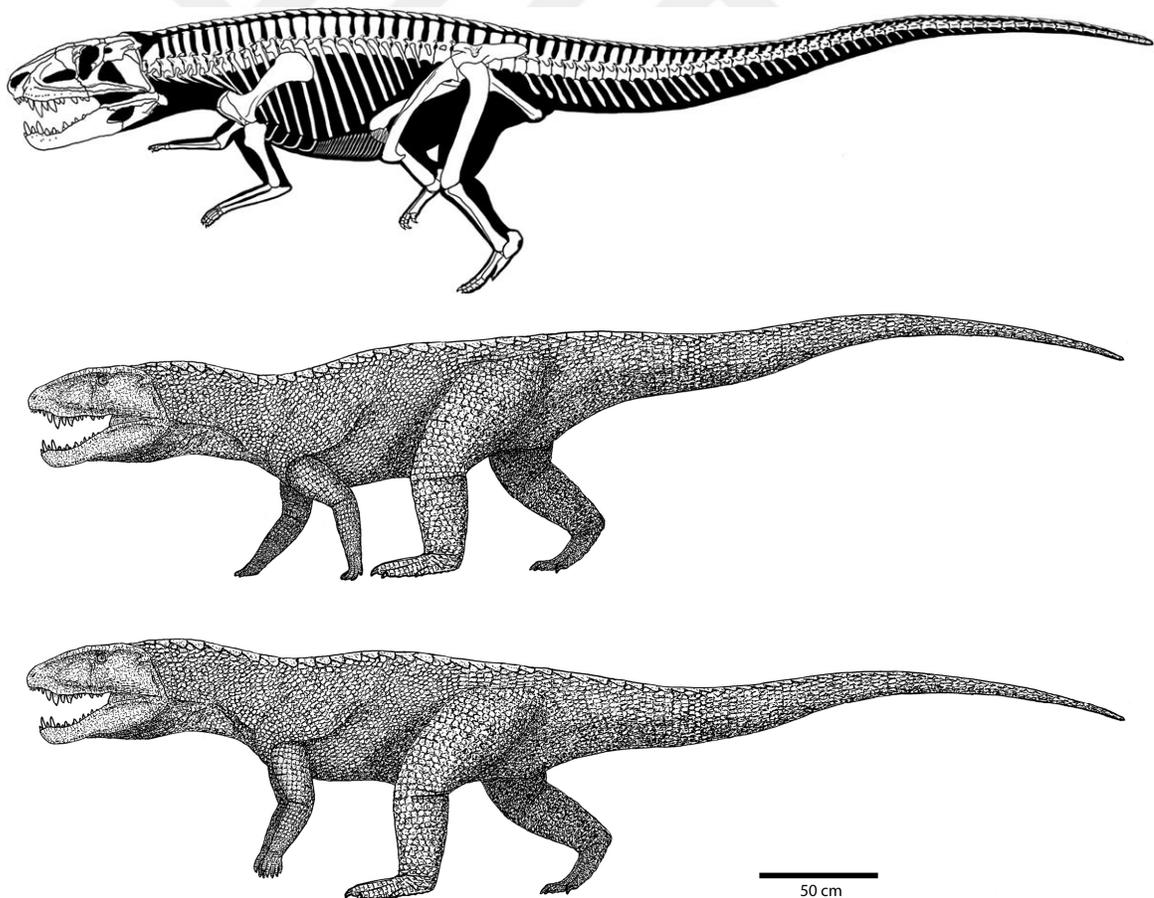
Figure 3.14 Skeletal restoration of *Postosuchus kirkpatricki* (after Weinbaum 2013) with quadrupedal and bipedal stances respectively (image credit: Jeffrey W. Martz).
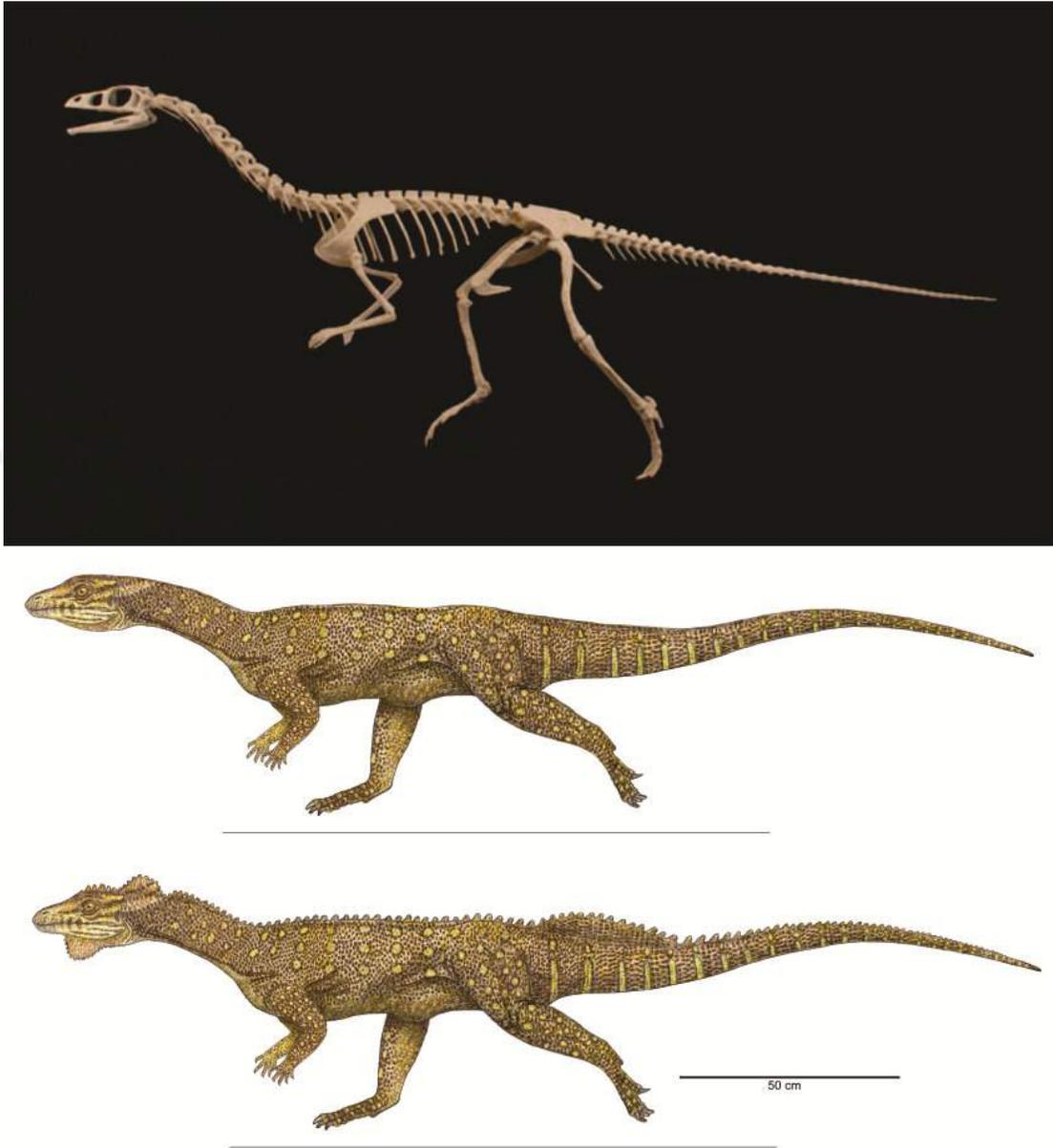
Figure 3.15 Mounted skeleton cast of *Shuvosaurus inexpectatus* (photo credit: Bill Mueller) with two different impression for the same taxon (image credit: Jeffrey W. Martz).

The remaining crurotarsan clade Crocodylomorpha is also represented in the Dockum Group (Figure 3.11). Three crocodylomorph taxa from the Dockum Group were erected so far: *Parrishia mccreai* and *Hesperosuchus agilis*, both from the Tecovas Formation (Long and Murry 1995) and *Redondavenator quayensis* from the Redonda

Formation (Nesbitt et al. 2005). Unfortunately, crocodylomorph fossils in the Museum of Texas Tech collection occur mostly by isolated elements, such as the preserved complete femur from the Post Quarry (i.e. TTU-P11443, Martz et al. 2013). The rest of the crocodylomorph specimens are still in preparation and they will not be discussed in this section.

**Ornithodirans**

Ornithodirans of the Dockum are represented only by dinosauromorphs (Figures 10 and 11), as no pterosaurs have been discovered as of yet, and the putative basal forms are excluded in this study (i.e. Atanassov 2002; the procoelous taxa in Martz et al. 2013). In contrast to the crurotarsan material, the dinosauromorph material of the Dockum is incomplete, often represented by isolated elements. So far, there have been three taxa described: *Dromomeron*, *Technosaurus* and *Protoavis*, all unearthed from the Post Quarry near Post, Texas.

*Dromomeron* was a small, around a meter in length and bipedal dinosauromorph which contains two species, *D. romeri* and *D. gregorii*. *Dromomeron romeri* was discovered in the Norian Petrified Forest Member of Chinle Formation, New Mexico based on hind limb elements (Irmis et al. 2007a), whereas *Dromomeron gregorii* is diagnosed based on a complete femur and associated many other hind limb elements from the Otis Chalk Quarry, Texas (Nesbitt et al. 2009b). *D. gregorii* was also collected from the *Placerias* Quarry in Arizona (ibid.), which lies within the lower part of Chinle Formation (Heckert 1997; Parker and Martz 2011). An isolated left femur of *D. gregorii* (TTU-P11282) was published for the first time in a work about the Post Quarry vertebrate

assemblage (i.e. Martz et al. 2013), alongside with an unspecified dinosauriform tibia (TTU-P11127). *Dromomeron* is now clustered together with *Lagerpeton chanarensis* (Romer 1971; Sereno and Arcucci 1993) and both genera are classified under the clade Lagerpetidae (Nesbitt et al. 2009b) (Figure 3.10).

 *Technosaurus smalli* is estimated to be about 1.8 meters long and is known from jaw fragments with triangular teeth with a well developed neck and denticular edges, a vertebra and an astragalus in mesotarsal pattern with an ascending ramus (Chatterjee 1984). However, following reexaminations of the holotype (Sereno 1991b; Irmis et al. 2007b; Nesbitt et al. 2007) only the premaxilla and the dentary can be assigned to *Technosaurus*. *T. smalli* was originally allied with Fabrosauridae (Chatterjee 1986; Murry 1986) on the basis of tooth morphology which resembles basal ornithischians such as *Pisanosaurus* (Norman et al. 2004); however such similarity may be the result of convergent evolution. Based on highly similar jaw morphology, *Technosaurus* is currently allied with silesaurids which is considered to be the sister group of Dinosauria, (Brusatte et al. 2010a; Langer et al. 2010, 2013; Nesbitt et al. 2010) (Figure 3.10).

 *Protoavis texensis* (Chatterjee 1991, 1997, 1999) is probably the most noteworthy and most controversial discovery from the Dockum Group (see Ostrom 1991; Chiappe 1995; Padian and Chiappe 1998; Nesbitt et al. 2007). It is considered to be the earliest bird based on the confluence of the upper and lower temporal fenestrae and the orbit as in extant birds (see Goodrich 1958), along with a highly derived braincase and flight apparatus. It is regarded as a member of the avialan clade and more derived than *Archaeopteryx* (Chatterjee 1997).

No sauropodomorph fossils are hitherto reported from the Dockum Group or from the Triassic of North America, whereas the alleged ornithischians were previously discarded by the subsequent discoveries and phylogenetic analyses (see above, also Irmis et al. 2007b; Nesbitt et al. 2007). However, there are some unequivocal basal theropod fragments from the Dockum Group (Figure 3.10) and few preliminary papers about this theropod material (TTU-P10071, 10072, 10082, 10534 and 11044) has been published (Lehman and Chatterjee 2005; Nesbitt et al. 2007; Nesbitt and Chatterjee 2008; Martz et al. 2013). These theropods are reported to be *Coelophysis* or at least close to coelophysoid group. On the other hand, *Caseosaurus crosbyensis* (Hunt et al. 1998) was described for an isolated ilium from the Tecovas Formation (see Case 1927) and is considered a junior synonym for *Chindesaurus bryansmalli* from the Petrified Forest Member (*sensu* Parker 2005) of Chinle Formation (Long and Murry 1995). Some other skeletal fragments of *C. bryansmalli* are also reported from the New Mexican outcrops of the Bull Canyon Formation in (Long and Murry, op. cit., p. 174). Another described theropod from the Bull Canyon Formation in New Mexico is the *Gojirasaurus quayi* (Carpenter 1997) that is considered as a putative coelophysoid (Nesbitt et al. 2007). Together with the unpublished fossils, the affinity of these theropods and other dinosauromorphs from Dockum will be evaluated in following chapters.

## Taphonomy of the Land Tetrapods in Southwestern North America

The term taphonomy was coined by Russian paleontologist Ivan Antonovich Efremov (1908-1972), which corresponds to the study of conditions and processes by which organisms become fossils. It appears that there are two main components of land

tetrapod taphonomy: Death and burial. The process of taphonomy initiates with death, where an organism is either killed by the environment (flooding, mass movement, volcanic effects etc...) or it dies by natural causes (predation, disease, drowning etc...). Environmental perturbations in large scale creates a mass mortality which involves multiple species; whereas perturbations in smaller degrees only reflects a death assemblage of a single species, as exemplified by the occasional mass mortalities in various tetrapod taxa (e.g. birds) due to a sudden change in their habitat (Figure 3.16).

| | Magnitude | Implications |
|---|---|---|
| Natural Causes | Individual fossils | Occasional deaths of individuals |
| Environmental Perturbations | Mass mortality (Single or few taxa) | Local disturbance |
| | Mass mortality (Multiple taxa) | Global/Regional catastrophe |

Figure 3.16 Summarizing table for the mortality phase in taphonomy

Being covered by sediment very quickly or preserved in a quiet medium significantly increases the chances for a dead body to become a fossil, where in both cases it is crucial to get minimally exposed to the physical and chemical agents, especially to oxygen. It is not surprising to observe intact preservations in autochthonous burials (Figure 3.17 and 3.18). Autochthonous burial indicates that the animal is preserved at the death site or where the parts are discarded (Behrensmeyer and Hook 1992, page 19). An autochthonous burial generally produces intact preservation in two main patterns. One is the instant burial (e.g. turbidities, mudflows, debris flows, lahars etc.); including a thick sediment cover after a catastrophic event which accumulates to a particular area in a very short time, as documented in the Late Cambrian Burgess Shale

biota in Canada and in the Early Cretaceous Jehol biota in China. The other can be

termed as calm burial, indicating an undisturbed settling area due to properties of the

aqueous medium (stratification, anoxia, depth etc...). These quiet environments are

perfect for an intact preservation of fossils which are typically exemplified by huge

permanent lakes as the Green River Formation in Wyoming and the Messel Shale biota in

Germany, both from the Eocene Epoch. Quaternary tar pits of La Brea in California can

also be counted as another type of conservative medium. All these fossil sites represent

mass mortality of whole community in exquisite detail, a snapshot of ecological

interaction with intact fossil preservations (Konservat-Lagerstätten). However, not all

autochthonous burials produce intact preservation. In ephemeral lakes, carcasses of the

riparian animals which have died around the lake are seasonally revealed. Thus, those

carcasses become exposed for further degradation, scavenging and trampling and finalize

with an attritional preservation due to loss of the skeletal elements in high numbers.
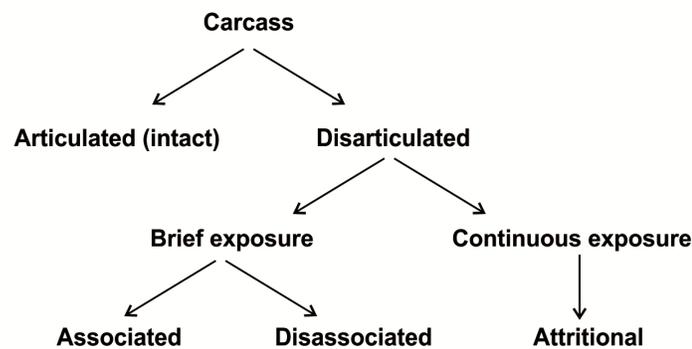
Figure 3.17 Summarizing diagram for the preservation types of a tetrapod carcass.

| | | Regime | Mechanism | Preservation | Examples from Chinle and Dockum |
|---|---|---|---|---|---|
| Burial | Autochthonous | High energy (e.g. turbidites, mudflows, volcanic activities) | Covered by sediment | Intact | N/A |
| | | Low energy (e.g. quiet lakes, tar pits) | Preserved by the properities of the medium | Intact | N/A |
| | | Low energy (e.g. ephemeral lakes, sabkhas) | Revealed for further degradation | Attritional | - Boren Quarry<br>- Kirkpatrick Quarry |
| | Parautochthonous | Low energy (e.g. seasonal flooding) | Covered by sediment | Associated | - Whitaker Quarry<br>- *Trilophosaurus* assemblage (Otis Chalk Quarry)<br>- Abandoned channels (Macy Ranch and Patricia Quarry) |
| | | | | Disassociated | - *Placerias* Quarry<br>- Lamy Quarry<br>- Post Quarry |
| | | High energy (e.g. flash floods, active river channels) | Scattering by current | Attritional (sorted) | - Many of the floodplain fossil localities |

Figure 3.18 Summarizing table for the burial phase in taphonomy for tetrapods in a fluvial environment, including the examples from Chinle and Dockum.

On the other hand, disarticulation of a skeleton initiates when a preserving medium is absent (Figure 3.17 and 3.18). A riparian tetrapod carcass lying on a river bank or floating in a river channel is commonly exposed long enough for disarticulation, as experienced ordinarily in nature, whereas physical abrasion, trampling and chemical oxidation is directly related to the disassociation of disarticulated skeletal elements. In a long-term exposure to those external factors will take part in attrition and scattering which corresponds to the loss of skeletal elements. In other words, the association and attrition of skeletal elements depends on how long the carcass is exposed to the external agents. Besides the environment, extensive scavenging or degradation might take part in disassociation and attrition; however modern case studies indicate that this type of consumption and decay won't let the carcass preserved in the geologic record in most

cases (Behrensmeyer 1975, pages 476-479 and references therein). Only the skull might be an exception due to the excessive ossification and possession of the least flesh and viscera in quantity.

Therefore, disarticulating carcasses could only become a fossil if they are transported into a preserving environment. In fluvial environments, carcasses of the riparian tetrapods generally transported within the same fluvial habitat, if not carried away to paralic settings, and buried in close vicinity which is termed as parautochthonous. Unlike allochthonous burial which reflects that the body is transported both from the original site of death and out of the original habitat; parautochthonous burial refers to the transportation of the body from the original site of death but still preserved in the original habitat (Behrensmeyer and Hook, op. cit.). The dominant regime in fluvial environments which influences parautochthonous burial is flooding. There are two types of flooding: seasonal flooding and flash flooding. Seasonal floods occur in annual cycles, as the inundations of the River Nile in Egypt or the Ganges-Padma River in India and Bangladesh. Seasonal floods do not play a considerable part in killing organisms but they rather are important in burial (e.g. floodplain sedimentation, crevasse-splay deposits). Low energetic seasonal floods keep disarticulated skeletons either associated or disassociated but always protect the carcass from further attrition (Figure 3.18). On the other hand, a flash flood fits to the definition of a catastrophic mortality which might cause a mass mortality for the riparian tetrapods. Especially in arid and desert regions like modern day Arabia and North Africa, heavy rains usually create flash floods. As well as mass movements which create autochthonous preservations with instant burial, flash floods are also originated from heavy rains. Therefore, only

sediments that a flash flood can carry are the ones on its pathway. Although flash floods carry much coarser grains compared to the seasonal floods due to their higher current velocity, they are more of an erosional agent rather than a sedimentary in larger scale (e.g. Channeled Scablands in Washington State). In terms of taphonomy, flash floods mainly contribute to the dispersal and scattering of the disassociated body parts to a larger area (Figure 3.18). As another high energetic medium in fluvial environments, the active river current will also scatter the skeletal parts if the disarticulated body parts fall into the river channel (Figure 3.18). Thus, attrition for the riparian tetrapods in fluvial environments is related to the current velocity of the medium (i.e. water); but it is also proportional to the surface area and volume of the skeletal parts (Voorhies 1966; Behrensmeyer 1975, 1988). Lighter particles such as vertebra and ribs (Group I of Voorhies) are transported further away relative to more robust parts like limb elements and pelvis (Group II of Voorhies) and skull and jaw as the most durable parts (Group III of Voorhies).

## Taphonomy of the Chinle Tetrapods: a Prelude to Dockum Taphonomy

The taphonomy of the Chinle Formation is better known and more extensively worked relative to the Dockum Group, where both deposits are rich in occasional fossil findings of individual deaths. No catastrophic mass mortality events are recorded in any Chinle or Dockum sites; however, there are various monotaxic mass mortality sites, especially within the Chinle Formation, where there are three main sites of these unusual preservation sites: Whittaker (*Coelophysis*) Quarry, *Placerias* Quarry and Lamy Quarry.
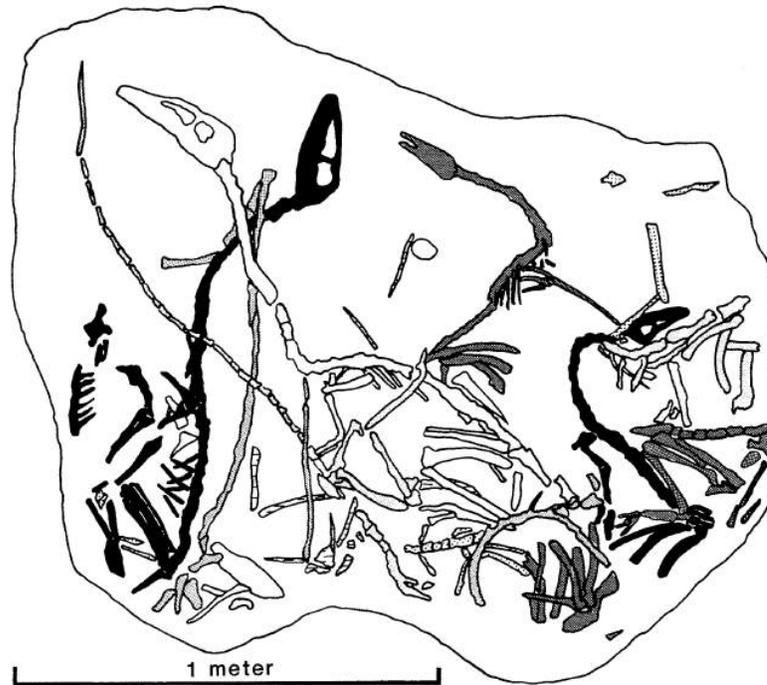
Figure 3.19 Taphonomy of the *Coelophysis* individuals of the Whitaker Quarry (after Schwartz and Gillette 1994). This slab is redrawn by the cited authors based on the block no. IX in the American Museum of Natural History, including the highlights by Edwin H. Colbert.

The Whitaker Quarry (or the Ghost Ranch *Coelophysis* Quarry of Colbert) is a fossil locality situated in Rio Arriba County, New Mexico, and belongs to the uppermost portion of the Upper Triassic Chinle Formation. This quarry is the most famous fossil site in the Chinle-Dockum Basin which produced exceptional preservations of the theropod *Coelophysis*. This quarry includes a concentration of numerous adult and juvenile *Coelophysis* individuals, even with stomach contents in some which are recently reevaluated (Nesbitt et al. 2006). Although it is generally suspected from an asphyxiation/heat during a volcanic eruption or any sort of poisoning/disease for this mass mortality, it is proposed that those animals are most likely perished during a drought and their carcasses were washed downstream in a short distance during a seasonal flooding and accumulated in a small crevasse channel (Schwartz and Gillette

1986, 1994; Hunt and Lucas 1989). It is also assumed that the recurved necks and tails of *Coelophysis* individuals and the presences of aridity structures such as caliche layers and mud cracks indicate that their demise preceded the burial. Although *Coelophysis* individuals were buried relatively soon after the death before any serious scavenging or disarticulation, this type of preservation points to a parautochthonous burial where 70 to 75 per cent of the remnants are disarticulated to some extent (Figure 3.19).

  *Placerias* Quarry is discovered by Charles Camp and Samuel Welles in 1930's and it is located in lower part of the Chinle Formation near St. Johns, Apache County, Arizona. Alongside of various other taxa like aetosaurs, rauisuchians and various microvertebrates (e.g. Kaye and Padian 1994; Long and Murry 1995; Lucas et al. 1997a; Irmis 2005; Parker 2005), this site is particularly important by the discovery of dicynodont *Placerias hesternus* (or *P. gigas* of Camp and Welles 1956). This quarry reflects another mass mortality probably due to an intense drought, similar to the Whitaker Quarry (Fiorillo et al. 2000). Current sedimentologic evidence supports this theory against the marsh/pond assumption of Camp and Welles (1965; Jacobs and Murry 1980) where those animals typically congregate, by the presences of typical aridity structures such as pedogenic (secondary) carbonate nodules, root casts and mottled strata, together with the absences of coal or organic matter-rich horizon, and of the aquatic and amphibian fossils. This dead assemblage was carried away by the low energetic seasonal floods to a short distance and parautochthonously buried. Although the bones stand disarticulated and unassociated, they also display a narrow range of bone weathering (i.e. little post-mortem damage) which indicates a relatively slower burial with more exposure to decay but not enough to get introduced to physical scavenging or trampling. The

relative abundances of skeletal elements mostly favor epipodial elements such as humerus and femur (Voorhies Group II), suggesting a mild sorting by the seasonal flooding. Skulls and mandibles are often crushed and collected in pieces of individual elements.

Lamy Quarry is another case study to evidence a mass mortality (Romer, 1939; Colbert and Imbrie, 1956). This quarry is located in the lower part of the Garita Creek Formation (Lucas and Hunt 1989a) in Santa Fe County, New Mexico. The death assemblage in the Lamy quarry is actually paucitaxic, including few taxa as evidenced by isolated phytosaur teeth, an archosaur sacrum and various microvertebrate remains. But the fossil record in dominated by the *Koskinonodon perfectus* (new senior synonym for *Buettneria perfecta*, see Mueller [2007]) mass mortality (Figure 3.20). Originally, the cause for this mortality is also tied to a serious drought, where those amphibians were assembled together in a drying pond and died all together, *in situ* (Romer 1939; also Gregory 1980). However, reexaminations on this quarry which provided disarticulated and mixed skeletal elements revealed a fluvial sorting on a floodplain, executed by a seasonal flooding event (Hunt and Lucas 1989, 1995). Although the carbonate nodules; rhizoliths etc. are found widespread within the pedogenically modified floodplain mudstones, absences of such direct evidences of aridity in the fossiliferous layer of the Lamy Quarry are argued to question the real effect of aridity in this mass mortality (Lucas et al. 2010, *contra* Fiorillo et al. 2000).

Figure 3.20 A large slab from the Lamy Quarry which contains both cranial and postcranial elements of *Koskinonodon perfectus*, situated in the Museum of Comparative Zoology, Harvard University (after Colbert and Imbrie 1956; Lucas et al. 2010).

Unlike Whitaker and *Placerias* quarries, transportation and sorting might have played a more important part in the Lamy Quarry, especially creating a peculiar situation for robust skulls and mandibles. In Lamy Quarry, both delicate (vertebral and shoulder girdle elements) and robust (skull and mandible) elements of the *Koskinonodon* are preserved together. This represents a contrast in fluvial sorting (see Voorhies 1969) which might explained in two different models: either these elements were accumulated in two different regimes or highly flattened metoposaur skulls acted as a rib or a girdle element which had a higher surface area proportioned to the volume unlike any other tetrapod skull (Zeigler et al. 2002). However, it is reported that numerous limb bones were also collected from the Lamy Quarry, which signifies a main enrichment of Group II elements alongside of Group III elements of Voorhies (1969) (Lucas et al. 2010).

All three forecited Chinle quarries reflect different stages of parautochthonous burial after a mass mortality (see Figures 3.16 and 3.18). *Coelophysis* skeletons of the Whitaker quarry are disarticulated to some point but still found associated. On the other hand, both *Placerias* and *Koskinonodon* skeletal elements show complete disarticulation and disassociation, predominantly due to hydraulic sorting with slight wearing due to chemical corrosion in the former one. All three quarries are located in floodplain deposits, where it is assumed that those mass mortalities probably occurred due to intense drought periods, and the carcasses are covered by the following seasonal flooding before any serious physical disturbance.

## Dockum Taphonomy and Fossil Localities

As already discussed above, three main facies are recognized in the Dockum Group as the channel-related facies, the overbank floodplain facies and the lacustrine facies, predominantly made of sandstones, mudstones and claystones respectively (see Lehman and Chatterjee 2005). All three facies and corresponding formations host various fossil sites (Figures 3.21 and 3.22), but they also display different taphonomic patterns. The taphonomy of the Dockum Group is very much alike to the one of the Chinle Formation (see Figures 3.16, 3.17 and 3.18). There are several fossil localities with occasional deaths, as well as some important mass mortality sites. The riparian tetrapod fossils of Dockum and Chinle are buried either autochthonously or parautochthonously. All the tetrapod fossils are collected within their original habitat of fluvial deposits, and they show all three types of preservation patterns — associated, disassociated and attritional.
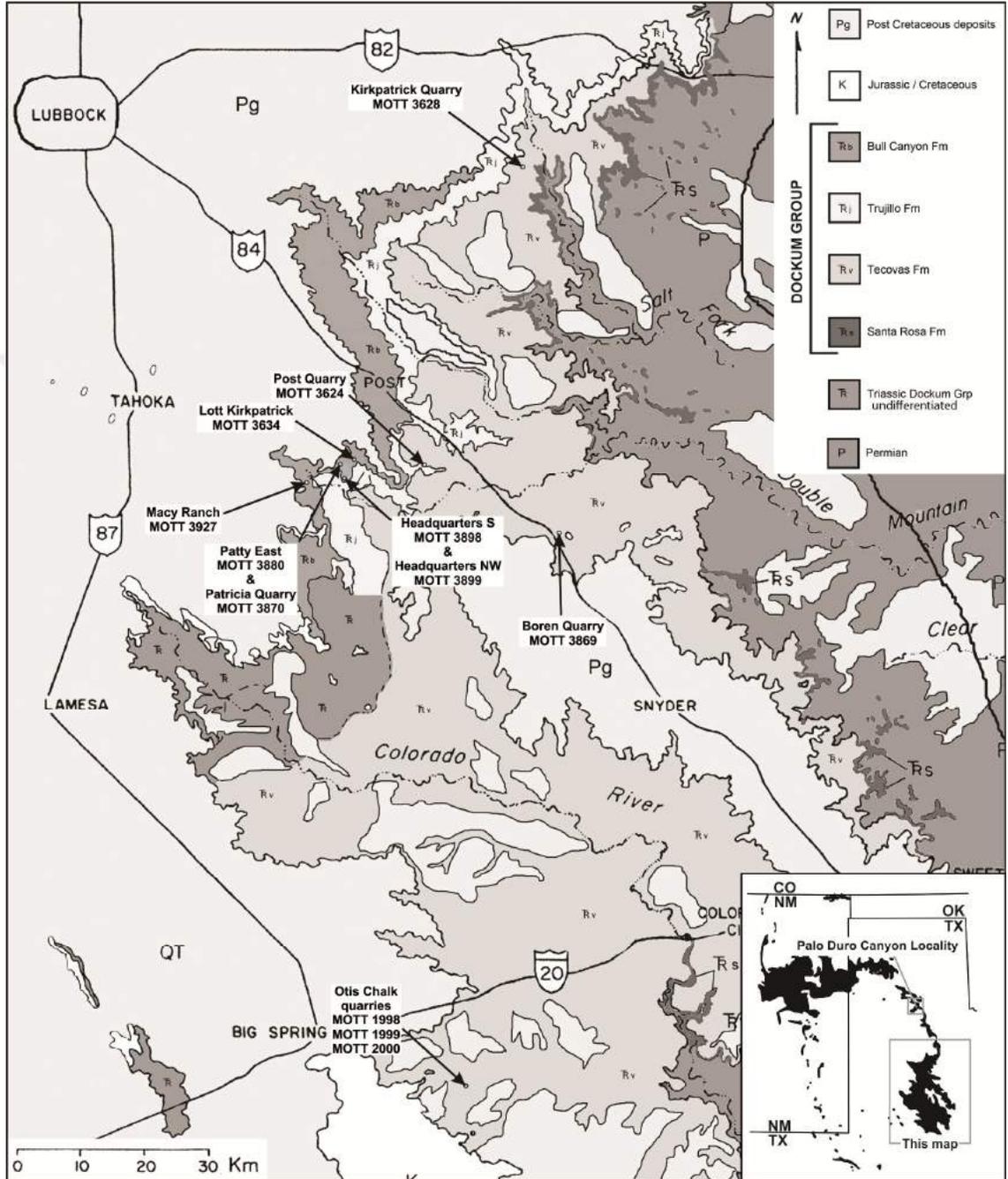
Figure 3.21 Lithostratigraphic map of the study area with the dinosauromorph bearing quarries (adopted and modified from Lehman and Chatterjee 2005; Martz 2008; Mueller 2014, dissertation in progress).
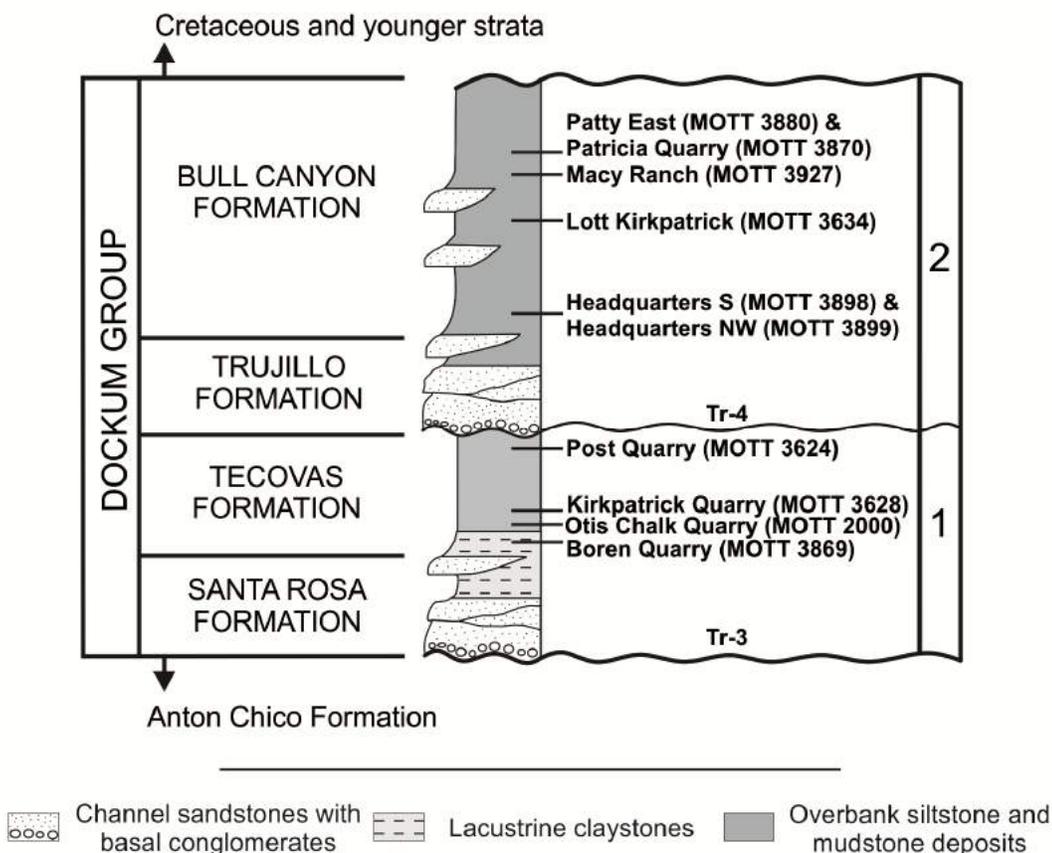
Figure 3.22 Columnar section of the Dockum Group in Texas, including the generalized lithostratigraphy, sequences (1 and 2) and the stratigraphic positions of the dinosauromorph bearing quarries (modified after Lehman and Chatterjee 2005; Martz et al. 2013 and Bill Mueller, pers. comm. 2014). Palo Duro Canyon Locality is within the Tecovas Formation; however its stratigraphic position is unknown.

**The Channel Facies**

The Santa Rosa and Trujillo formations which represent the main channel facies are not fossiliferous due to the high environmental energy. So far, only a couple of metoposaur bone fragments and a phytosaur skull (*Wannia scurriensis*, Stocker 2012b) were collected from the Santa Rosa Formation. Similarly in Trujillo Formation, only one osteoderm of the aetosaur *Longosuchus meadi* was reported. There are no quarries within this study from any of the two formations (see Figures 3.21 and 3.22). The channel facies represents the active river channel with massive, cross bedded sandstones; the

abandoned, crevasse or other passive channels with predominant mudstone lithology are included in the floodplain facies.

**The Floodplain Facies**

The floodplain deposits, especially the proximal facies, are generally the richest in fossil content but the tetrapod fossils are rarely articulated (e.g. Smith 1993). Dockum deposits display quite a variety of floodplain taphofacies, including the remnant channels of the main river channel which are highly fossiliferous. These abandoned river channels, including oxbow lakes, display beautiful examples of autochthonous preservation pattern (Lehman and Chatterjee 2005). Accordingly, this type of depositional structures correspond to the channel-fill taphofacies (Behrensmeyer 1988) with fine grained sediments which contains relatively more associated skeletons, in contrast to the channel-lag taphofacies which represents the active river channel itself with coarser sediments, high flow and active reworking (see Behrensmeyer op. cit., table 1). The main separation of the channel-lag and channel-fill taphofacies of Behrensmeyer (1988) also explains the lack of fossil material in the Santa Rosa and Trujillo formations (see Figure 3.22). The tetrapod fossil content in those abandoned channel deposits is mainly dominated by the aquatic or semi-aquatic animals (Lehman and Chatterjee 2005), as exemplified in Macy Ranch (MOTT 3927) and Patricia Quarry (MOTT 3870) localities in the upper part of the Bull Canyon Formation (Figure 3.23). In both quarries, it is documented associated skeletons of the phytosaur *Machaeroprosopus* within the "abandoned channel facies" (Lehman and Chatterjee 2005; Hungerbühler et al. 2013) (Figure 3.23). This type of burial probably occurred in a quiet oxbow lake where the carcass exposed to a low pace

seasonal flood which have gently carried the semi-articulated and associated skeleton into a depression in a short distance.



Figure 3.23 The associated *Machaeroprosopus* skeleton in the Museum of Texas Tech University gallery from the Macy Ranch (MOTT 3927) locality, together with the holotype skull of *M. lottorum* (lower right) from the Patricia Quarry (MOTT 3870) (Photo credit: Bill Mueller).

However, both Macy Ranch (MOTT 3927) and Patricia Quarry (MOTT 3870) localities produced only a few well preserved individuals. Channel-fill deposits show noteworthy preservations in some cases, as in the *Trilophosaurus* assemblage of the Otis Chalk Quarry. It is argued that the taphonomy of the Otis Chalk tetrapods, at least partially, affected by the flash floods (Elder 1978, 1987). Tetrapod fossils of the Otis Chalk are found in two different preservation patterns. Quarry 1 (TMM 31025; MOTT 1998) displays an accumulation of mostly associated *Trilophosaurus* skeletons, together with abundant freshwater bivalves (*Unio*) and coprolites. A mixture of delicate and robust bones of this quarry shows no signs of abrasion. On the other hand, Quarry 3 (TMM 31100; MOTT 2000) although it also comprises well preserved delicate bones,

dense bones are abraded and display biologic reworking. Accompanying *Unio* shells and coprolites are also fragmented. Quarry 2 (TMM 31099; MOTT 1999) and Quarry 3a (TMM 31185) are similar to quarries 1 and 3 respectively. This contrast between two taphonomies is interpreted by different energy regimes; a quick deposition after a catastrophic flooding (quarries 1 and 2); and a large scale transportation with gradual deposition after a low pace flooding (e.g. crevasse splay model) which is responsible for the attrition of the elements (quarries 3 and 3a).

However, there are some discrepancies in Elder's thesis. Even if a flash flood is considered as the cause for the *Trilophosaurus* thanatocoenose in Quarry 1, flash floods do not carry enough sediments in order to provide an instant burial (see above), and also, the preservation of both delicate and dense bones of disarticulated skeletons directly eliminates the presence of a high energy environment during the burial phase (Behrensmeyer 1975, 1988). As happened in the Whitaker Quarry, mass accumulation of *Trilophosaurus* (also see Gregory 1945) is similar to the one of *Coelophysis* by means of gentle sediment covering which succeeds the mass mortality. In this context, the *Trilophosaurus* assemblage of the Otis Chalk Quarry is considered here as the taphonomic equivalent of the Whitaker Quarry (see Figure 3.18). Most likely, the biogenic material would affect minimum damage in a gradual flooding, thus for the Quarry 3 (and 3a), worn bones and broken shells are possibly related to *post-mortem* corrosion, scavenging and trampling, rather than *in-situ* fluvial abrasion.

In addition to the Elder's observations, many faunal members of the Otis Chalk quarries are represented mostly by skull, limbs or carapace (e.g. Lucas et al. 1993) which indeed points out a dominant parautochthonous burial with attritional preservation (see

Figure 3.18). However, it seems that those particular quarries of Otis Chalk cannot be characterized by any exclusive preservation type. The two other important elements of the Otis Chalk fauna, the problematic *Otischalkia* (Hunt and Lucas 1991c, see Chapter 2) and *Dromomeron gregorii* (Nesbitt et al. 2009b) are represented predominantly by the limb bones (i.e. Group II of Voorhies) which are collected from Quarry 1 and Quarry 3, respectively. This situation clearly represents an occasional sorting by the medium (i.e. water) in each quarry, where the bones were widely scattered.

An exceptional preservation area with lots of disassociated skeletons is also present in the Dockum sequence. This area is the Post Quarry, perhaps the most productive and the most famous quarry among all Dockum localities, which is located to the upper part of the Tecovas Formation. The Post Quarry (MOTT 3624, formerly known as Miller Quarry) was regarded as a type section of the Cooper Canyon Formation. However, recent mapping suggests that it belongs to the Tecovas Formation (Martz 2008; Martz et al. 2013). Post Quarry has yielded the holotypes of the iconic genera *Rileymillerus*, *Pachygenelus*, *Technosaurus*, *Postosuchus*, *Protoavis* and *Shuvosaurus* as well as many complete crurotarsan skeletons such as *Desmatosuchus*, the largest aetosaur hitherto discovered, and many other tetrapods including *Apachesaurus*. Post Quarry has also produced other dinosauromorphs including *Dromomeron* and *Chindesaurus* which will be discussed in the present work.
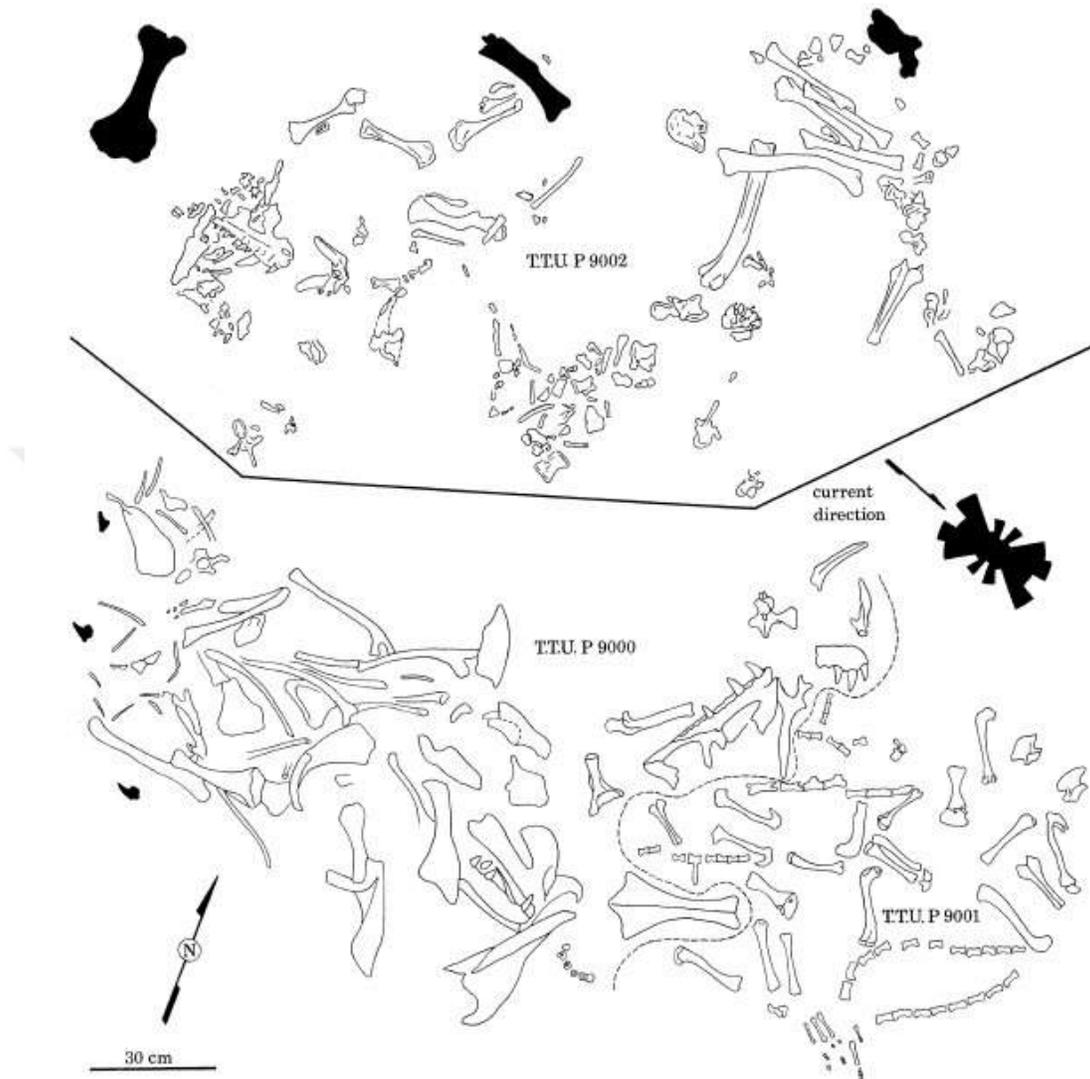
Figure 3.24 Taphonomy of the *Postosuchus kirkpatricki* specimens in the Post Quarry (after Chatterjee 1985).

The taphonomy of the Post Quarry is complex. Initially, it was interpreted as a flash flood event for the concentration of this multitaxic bone bed in very small area, both juveniles and adults (Chatterjee 1985). However, some long term process of bone concentration is suggested for the later dispersal of the disarticulated skeletons with both delicate and robust pieces, of which the long axis of bones are found aligned (Lehman and Chatterjee 2005). No matter what is the cause of this mass mortality, it strongly

signifies a low energetic seasonal flooding which covered the decaying and

disarticulating carcasses. In this context, the taphonomy of the Post Quarry displays high

similarities with the *Placerias* Quarry with the parautochthonous and somewhat delayed

burial (see Figure 3.18). One significant difference in Post Quarry is that the

disarticulated fossil parts are found clustered in large chunks of mudstones, as seen in the

holotype of *Postosuchus kirkpatricki* (Figure 3.24), however the scattered nature of the

bones falls into the disassociated preservation rather than associated preservation (*contra*

Lehman and Chatterjee 2005).

On the other hand, the main depositional pattern is parautochthonous for the rest

of the Dockum floodplain facies localities including the remaining localities of Macy

Ranch, Patricia Quarry, Otis Chalk quarries (see above) and the Palo Duro Canyon

Locality (Figures 3.21 and 3.22). The tetrapod remains are often isolated and scattered

bones with occasional damage and distortion, signifying an attritional burial (Figure

3.18). Similarly, the Dockum dinosauromorphs are mostly represented only by a single

bone, mostly by a femur or tibia. They do not possess obvious bite marks or any other

traces of scavenging but diagenetic distortions in some. Both femur and tibia belong to

Group II of Voorhies (1966) which has a medium resistance to dispersal and

transportation (see above), signify a small scale transportation for these limb bones and

therefore more powerful flood currents than usual (Behrensmeyer 1975, figure 5).


**The Lacustrine Facies**

The lacustrine facies of Dockum contains various fossil sites, where the bones are

largely disassociated with calcareous coating. However, unlike the regular lacustrine

facies which are generally characterized by relatively deep and permanent lakes with exquisite preservation, the Dockum settling was closer to sabkha/playa lakes which are ephemeral with a very shallow water level (see Figure 3.18). This is a peculiar lacustrine facies which had accumulated in local floodplain depressions, probably formed by dissolution of the Permian salt layer beneath and accompanied subsidence (Lehman and Chatterjee 2005). The vertebrate fossil assemblages are dominated by occasional deaths of aquatic and semi-aquatic animals which were all autochthonously buried. The bones are found in the coarse carbonate granule layers, as well as within the lacustrine mudstone. Many of these elements are delicate and beautifully preserved. The burial phase includes re-exposition of the fossils for further degradation due to the total evaporation of these peculiar lakes; which brings an attritional preservation. This lacustrine facies is mainly restricted to the lower part of the Tecovas Formation, as documented in Boren and Kirkpatrick quarries (Figures 3.22 and 3.23).

The Boren Quarry (MOTT 3869, formerly known as Neyland Quarry) situated at the lowermost part of the Tecovas Formation and it is the lowermost quarry in this study. It is associated with few sandstone and siltstone beds of channel and over-bank deposits. Although only one associated skeleton which belongs to *Paleorhinus* is preserved in Boren Quarry, most of the faunal elements are composed of disassociated parts of both aquatic and terrestrial tetrapods. An attritional trend also appears for the dinosauromorph remains from these sites. Above it, the Kirkpatrick Quarry (MOTT 3828, the "Kirkpatrick Sites" of Lehman and Chatterjee [2005]) is rich in disarticulated but well-preserved microvertebrates in carbonate fine conglomerate infillings with unionid bivalves. This

composition indicates also a high non-vertebrate biologic activity was also present in

these freshwater systems (Figure 3.25).
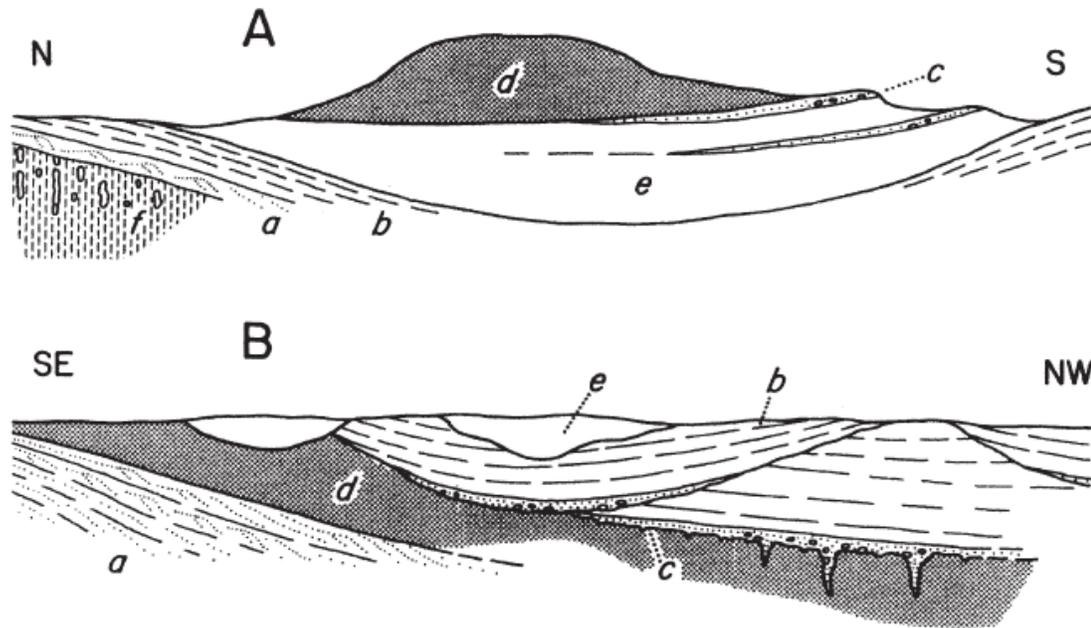
Figure 3.25 Characteristic structure and facies of Dockum ephemeral lakes in the
Kirkpatrick Quarry (modified after Lehman and Chatterjee 2005). Tetrapod bones are
found within the carbonate granule conglomerate with unionid bivalves (c) in a typical
Dockum lacustrine sequence of very fine ripple cross-laminated and parallel-laminated
sandstone (a); thinly bedded red siltstone (b); massive dark red mudstone (d); green-gray
claystone with coprolites (e); and tan-yellow mudstone with carbonate filled burrows.

In summary, we have two main fossiliferous facies in Dockum: the floodplain

facies and the lacustrine facies. The floodplain quarries provide beautiful examples of

parautochthonous burial, where the skeletal elements are mostly found attritional under

high environmental energy. The *Trilophosaurus* assemblage of the Otis Chalk Quarry and

the Post Quarry assemblage represent the two mass mortality sites in the Dockum

floodplain facies. The former one consists of many individuals of the cited taxon with

associated preservation, whereas the latter yields many different taxa in close temporal

sequence but the skeletal elements are dispersed. The taphonomy of lacustrine facies in

Dockum is attritional, possibly due to the occasional exposition of the carcass for further scavenging, trampling or physicochemical degradation.

# Chapter 4

# Descriptions of the Dockum Dinosauromorphs of Texas

The clade Dinosauromorpha (Benton 1985) was erected as one of the first clades after the cladistic tradition had entered the fossil archosaur studies (Figure 4.1). The definition for Dinosauromorpha is a node-based and expressed as *Lagerpeton chanarensis*, *Marasuchus lilloensis* (n. comb. *Lagosuchus lilloensis*, Sereno and Arcucci 1994), *Pseudolagosuchus major*, Dinosauria (including Aves) and all descendants of their most recent common ancestor (after Sereno 1991a).

## Stance and Locomotion of Archosaurs

The locomotor module is one of the main distinguishing parameters of dinosauromorphs (e.g. Bakker 1968; Charig 1972), probably the most important one. In lepidosaurs and stem archosauromorphs, the articulation surfaces of the femur lie on counter sides where the capitulum faces dorsally and the condyli lie ventrally, regarding the articulation *in vivo*. Such configuration and related features on femur definitely mandates a sprawling posture (e.g. Romer 1956; Hutchinson 2001b) (Figure 4.2). *Trilophosaurus* is a good example for sprawling archosauromorphs where the femoral head is very faint and positioned closely to a relatively large internal trochanter. On the countering posterolateral side, protraction/leg swing muscles are attached to the posterior ridge which is separated from the femoral head by the intertrochanteric (adductor) fossa (e.g. TTU-P18247).
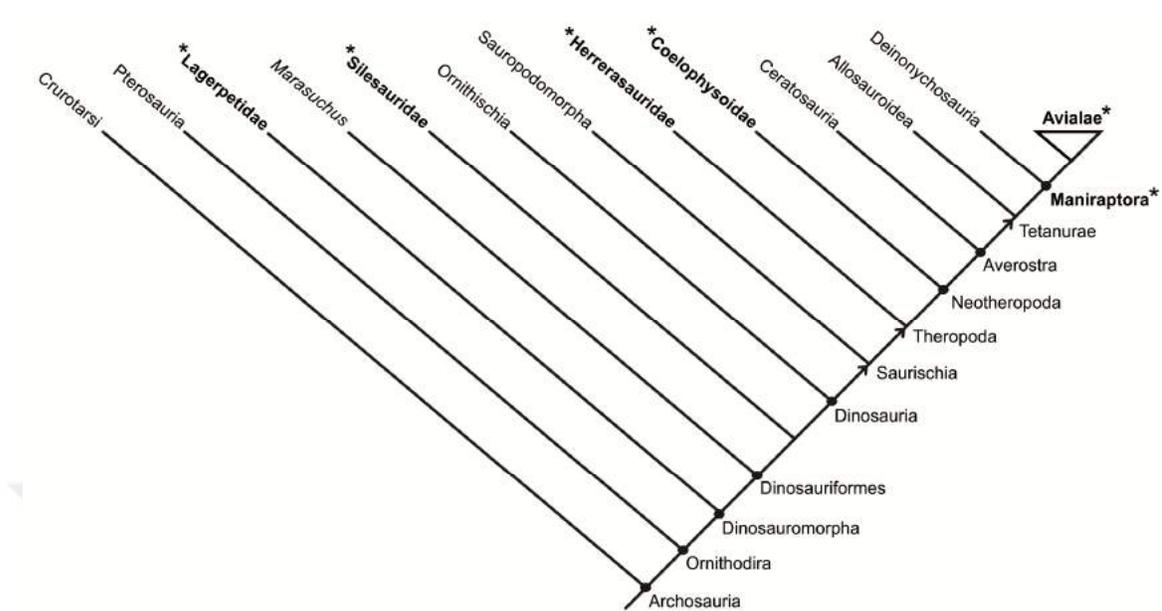
Figure 4.1 Simplified cladogram showing the phylogenetic relationships of the Dockum archosaurs (Points for node-based clades, arrows for stem-based clades). **Archosauria**: no teeth present on vomer, palatine and pterygoid, calcaneal tuber directed more than 45° posterolaterally, calcaneum with contiguous articular surfaces for fibula and distal tarsal 4; **Crurotarsi**: Crurotarsal peg-and-socket ankle joint; **Ornithodira**: Mesotarsal (hinge-like) ankle joint; **Dinosauromorpha:** ventrally descending articular surface on proximal femur for pelvic antitrochanter, prominent cnemial crest on tibia, ascending process on astragalus; metatarsal V unhooked; **Dinosauriformes:** proximal femur with trochanteric shelf and protruding lesser trochanter (also in "robust" *D. gregorii*), posterior process on distal tibia, anterolaterally placed ascending process on astragalus; **Dinosauria:** iliac acetabular wall concave, reduced IV. and V. manal digits (manal records are very poor in non-dinosaurian dinosauromorphs); **Saurischia:** propubic pelvic pattern; **Theropoda:** Intramandibular joint well developed, hollow long bones, aligned posterior condyli on tibia; **Neotheropoda**: furcula (no preservation in herrerasaurids), derived brevis fossa on ilium, concave surface between cnemial crest and posterior condyli on the proximal surface of tibia, fibular crest on tibia, deeper reception of the ascending process of astragalus; **Averostra:** Promaxillary fenestra on snout; advanced astragalotibial joint; **Tetanurae:** Derived maxillary and humeral features, modified manus with three digits, more robust pelvic and hind limb features in most; **Maniraptora:** Vertical quadrate, interdental plates absent on dentaries, epipophyses placed proximally to postzygapophyseal facets on cervical vertebrae (Selected synapomorphies after Marsh 1881, 1884; Seeley 1887; Chatterjee 1982; Gauthier 1986; Novas 1989, 1996; Sereno and Arcucci 1990; Sereno 1991a; Sereno and Novas 1993; Currie 1997; Padian and Chiappe 1998; Paul 2002; Kellner 2004; Langer and Benton 2006; Turner et al. 2007; Nesbitt et al. 2009d; Nesbitt 2011; Carrano et al. 2012; Langer et al. 2013). In the Dockum Group, six successive taxa of Lagerpetidae, Silesauridae, Herrerasauridae, Coelophysoidea, Maniraptora and Avialae are represented (bold fonts with asterisks), thus filling the major gaps in the early evolutionary history of dinosaurs.

The femur of *Proterosuchus* is also very similar to primitive archosauromorphs and the same plesiomorphic configuration is observed also in *Erythrosuchus* (Parrish 1992; Gower 2003) whereas *Erythrosuchus* differs from the ancestral forms by having both intertrochanteric fossa and a fourth trochanter (Parrish, op. cit.), which receives the main hip retraction muscle (Figure 4.3). The homology of the fourth trochanter is still unresolved; however its prominence is in direct correlation with the diminishing internal trochanter (Hutchinson 2001b).
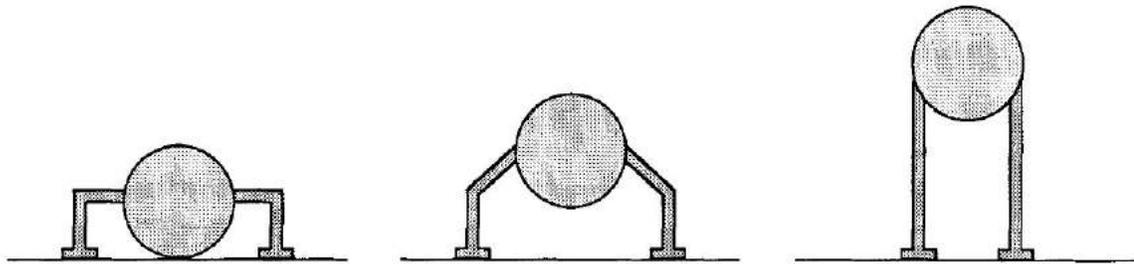


Figure 4.2 Posture sketches for sprawling (left), semi-erect (middle) and erect (right) poses (Gatesy 1991, modified after Charig 1972).
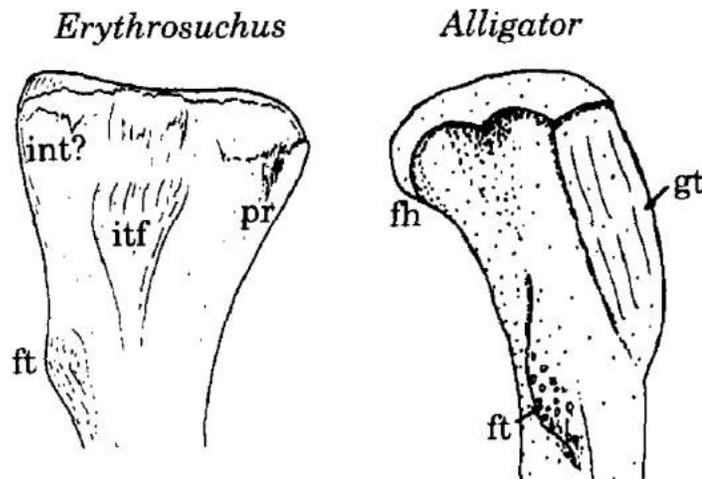


Figure 4.3 Sketches showing the flexor sides of the right femora of *Erythrosuchus* (after Parrish 1992) and *Alligator* (Hutchinson 2001b). Abbreviations: **fh**, femoral head; **ft**, fourth trochanter; **gt**, greater trochanter; **i**, internal trochanter; **itf**, intertrochanteric fossa; **pr**, posterior ridge.

The switch in hind limb positioning under the body leads to a semi-erect or an erect gait that is a shared trait for the out-group of Proterosuchidae and Eryhtrosuchidae (Benton and Clark 1988; also see Kubo and Benton 2007). The orientation and kinematics of femur affects posture dramatically; where in non-sprawling posture the intertrochanteric fossa gets less pronounced, internal trochanter and adductor ridge fade away (Figure 4.3). In modern crocodiles (e.g. *Alligator*), the sigmoid or "S-shaped" femur positioned the projected femoral head dorsomedially which enables a semi-erect posture termed as "high walk" (Gatesy 1991). Similar type of twist in the femur of *Euparkeria* (Ewer 1965), and of the members of Proterochampsidae (e.g. Trotteyn et al. 2012) and Phytosauria (e.g. TTU-P14330) strongly indicates a semi-erect gait. The study of the pelvic girdle and hind limbs indicate that *Euparkeria* was a facultative biped where it mostly stands on four limbs, where the members of the latter two groups are presumably obligate quadrupeds, like modern crocodiles. In the rest of suchians, despite the sigmoid femoral pattern, an erect gait is gained due to the evolution of the supraacetabular crest, a laterally prolonged process of the ilium which covers the proximal end surface of the femur and possibly helps the vertical alignment with trochanteric ligaments (Figure 4.4). This posture is informally called "pillar-erect" in literature (Bonaparte 1984; Benton and Clark 1988).

Erect crocodilian kin such as rauisuchians and aetosaurs solved this problem by re-positioning the hip articulation towards dorsal side, whereas dinosauromorphs also independently achieved an erect gait. Despite the sigmoidal shape of the femur in non-dinosaurian dinosauromorphs and also in basal dinosaurs (as well as many crurotarsans, Nesbitt 2011), erect gait in dinosauromorphs is established by (1) an expanded

trochanteric fossa (facies articularis antitrochanterica) that articulates to the corresponding antitrochanteric facet of the pelvis and positions the long axis of the femur closer to the sagittal axis; (2) a prominent cnemial crest on proximal tibia that receives the iliotibial musculature; and (3) an ascending process on astragalus which braces the distal tibia and forms a more compact ankle structure (see Figure 4.1). In dinosaurs, the femoral head articulates into the hollow hip socket with a right angle (i.e. straight "dinosaurian" femur) that assures the erect stance ("buttress-erect" *sensu* Schachner et al. 2011, Figure 4.4); together with a derived greater trochanter that receives the hip stabilizer muscle, M. iliofemoralis (Welles 1986). The great trochanter seems to be evolved from the ancestral posterior ridge (Hutchinson 2001b, also see Figure 4.3) that is further accompanied by other derived characters on the pelvis and hind limbs in higher theropods. Ultimately towards modern birds, in concert with the reduction of the tail, the ilium gets enlarged anteriorly and attains larger surface area from where the hip stabilizer muscles originate, whereas the femur gets smaller compared to the tibia and the femoral shaft is positioned more horizontally, thus retracts in lesser degrees during locomotion (e.g. Hutchinson and Gatesy 2000; Hutchinson 2001a, 2001b).

As a consequence of this hind limb configuration in erect archosaurs, it only allows parasagittal movement with the notable exception of pterosaurs. Pterosaurs probably had an erect gait too, although their acetabulum is not perforated. The femoral head is dramatically projected dorsomedially from the shaft in pterosaurs, analogous to the human femur. Such extension creates a very dynamic femur, with a ball-and-socket joint movable in all 3 spatial axes.
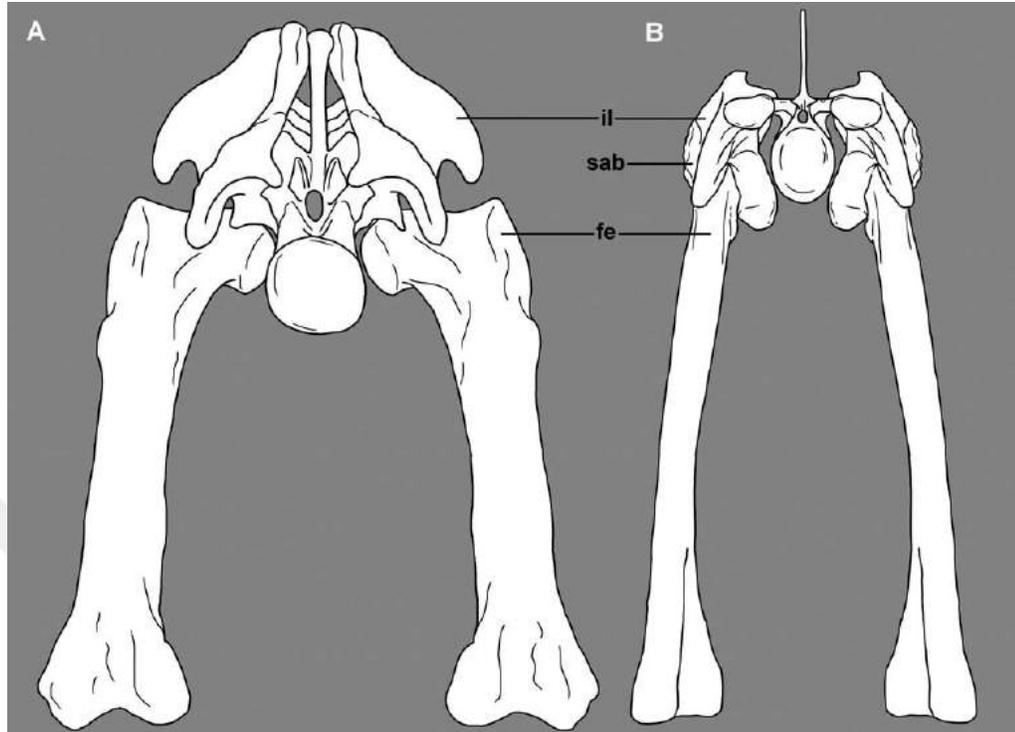
Figure 4.4 Sketches showing A, the "buttress-erect" posture of *Tyrannosaurus rex* (after Brochu 2003) and B, the "pillar-erect" posture of *Poposaurus gracilis* (Schachner et al. 2011). Note the projected femoral head penetrates into the perforated acetabulum in *T. rex*, whereas the dorsally pronounced femoral head is embraced by the iliac supraacetabular crest in *P. gracilis*, both resulting in an erect stance. Abbreviations: **fe**, femur; **il**, ilium; **sab**, supraacetabular buttress/crest.

## Phylogenetic Relationships of Dockum Dinosauromorphs

In this section, all the dinosauromorph specimens in the repository of the Museum of Texas Tech University (TTU-P) are described and discussed in details. It is followed the dinosauromorph phylogeny given above (Figure 4.1) to describe these specimens from basal groups to the most derived forms represented in the Dockum Group of Texas. These include several major clades as Lagerpetidae, Silesauridae, Herrerasauridae, Coelophysoidea, Maniraptora and Avialae. They provide critical insights on the origin and early evolution of theropod dinosaurs.

**Lagerpetidae**

ARCHOSAURIA Cope 1869 *sensu* Gauthier 1986

DINOSAUROMORPHA Benton 1985

LAGERPETIDAE Arcucci 1986 *sensu* Nesbitt et al. 2009b

<u>Brief description</u> **-** Lagerpetidae is currently the basal group of the clade

Dinosauromorpha. *Lagerpeton chanarensis* (Romer 1971; Bonaparte 1984; Arcucci

1986; Sereno and Arcucci 1993), *Dromomeron romeri* (Irmis et al. 2007a) and

*Dromomeron gregorii* (Nesbitt et al. 2009b) are the only representatives of this group.

Lagerpetids are small sized, about a meter long basal dinosauromorphs and they are

known mainly by their pelvis and hind limbs (Figure 4.5). Alongside the sacral vertebrae,

some adjacent dorsal and caudal vertebrae were also preserved for *Lagerpeton*

*chanarensis*. Lagerpetids have a typical archosaurian pelvis as seen in basal

dinosauromorphs with relatively small preacetabular and postacetabular processes which

are demarcated by a narrow central portion of ilium. Tibia is slightly longer than femur,

indicating cursorial adaptation. Although no metatarsal or tarsal elements are preserved in

*Dromomeron*, a didactyly pes in *Lagerpeton* was linked to a possible saltatory habit

(Sereno and Arcucci, op. cit.). Despite the limited nature of the referred skeletal elements,

*Lagerpeton* was previously assumed as an insectivore (Bonaparte 1982), whereas

*Dromomeron* is considered as a small carnivore (Irmis et al. 2007a; Nesbitt et al. 2009b).
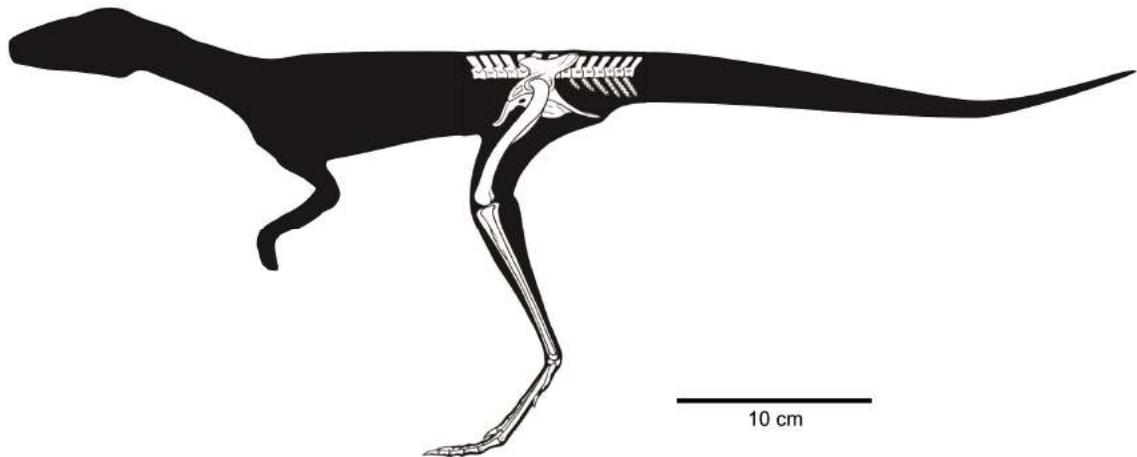
Figure 4.5 The possible reconstruction of a lagerpetid. Skeletal portion belongs to *Lagerpeton chanarensis* (after Sereno and Arcucci 1993). Scale is 10 cm.

Revised diagnosis **-** (1) a hook-shaped femoral head; (2) lack of the anterolateral tuber; (3) enlarged posteromedial tuber on proximal femur, which now becomes the largest tuber on the proximal femur; (4) anteromedially placed emarginated surface below the femoral head; (5) enlarged fibular condyle (crista tibiofibularis) on the distal end of the femur which is now larger than medial condyle; (6) anteromedial corner of the distal femur is squared or makes an acute angle; (7) a posteriorly situated ascending process on the astragalus (Sereno and Arcucci 1993; Irmis et al. 2007a; Nesbitt et al. 2009b; Nesbitt 2011).

*Dromomeron* Irmis et al. 2007a

Revised diagnosis **-** (1) a fibular condyle (crista tibiofibularis) with a concave posterolateral surface; (2) a distinct depression or scar on the anterior side of the distal femur; and (3) a ventrally deflected lateral condyle of tibia, distinguishes the genus *Dromomeron* from *Lagerpeton* and other dinosauromorphs (Irmis et al. 2007a; Nesbitt et

al. 2009b; Nesbitt 2011). There are several aspects to distinguish the two *Dromomeron* species known so far, *D. romeri* and *D. gregorii* (Nesbitt et al. 2009b; Nesbitt 2011). The proximal portion of the femur of *D. gregorii* differs from the one of *D. romeri* by having a fourth trochanter and an anterior trochanter with a related trochanteric shelf. Moreover, the femur of *D. gregorii* is more robust in both ends, especially the distal condyli are relatively enlarged which reduced the intercondylar groove into a slit in larger forms. On the other hand, *D. romeri* carries a sharp ridge on the anteromedial edge of the distal femur (if not as prominent as in *D. romeri*, an anteromedial ridge is also described in some *D. gregorii* specimens by Nesbitt and colleagues [2009b, p. 510]). Tibiae of both species are similar except the distal configuration where distal tibial surface of *D. romeri* is elongated mediolaterally with a concave surface on the anteromedial side and a tuberosity on the lateral side. The concave surface on the anteromedial side receives an anteromedial process of the astragalus (not to be confused with the anterior or posterior processes of the astragalus).

<center>*Dromomeron romeri* Irmis et al. 2007a</center>

Type specimen **-** GR 218 complete left femur (holotype) and associated paratypes (Irmis et al. 2007a).

Horizon and locality **-** Hayden and Snyder quarries, Petrified Forest Member of Chinle Formation, Ghost Ranch, New Mexico (Irmis et al. 2007a).

**Dockum Lagerpetids**

The Dockum Group of Texas has yielded a variety of lagerpetids (specimens TTU-P11282, TTU-P12537, TTU-P12539, TTU-P18331, TTU-P20046 and TMM 31100-1306 [holotype of *Dromomeron gregorii*], WTAMU-X1, WTAMU-X2, WTAMU-X3) as described below.

TTU-P12537

(Figure 4.6)

Referred specimen - Proximal tibia, right

Horizon and locality - Headquarters South locality (MOTT 3898), Bull Canyon Formation, Garza County, Texas

Collector - Doug Cunningham

Description and remarks **-** Proximal surface is triangularly shaped and almost equilateral in border length. Cnemial crest is prominent and tip of the crest slightly kinked laterally, as well as rest of the lateral surface, and produces a sharp anterior edge. Posterior condyli are aligned, not pronounced and separated by a very shallow cleft. Lateral condyle is ventrally deflected as diagnostic of *Dromomeron* (Nesbitt et al. 2009b) whereas the medial condyle is mostly obliterated. Even though the medial condyle is obliterated, posterior condyli seem to be aligned and sub-equal in size, a situation which is more comparable to *D. romeri* (see Irmis et al. 2007a, figure 2; Nesbitt et al. 2009b, figure 4).
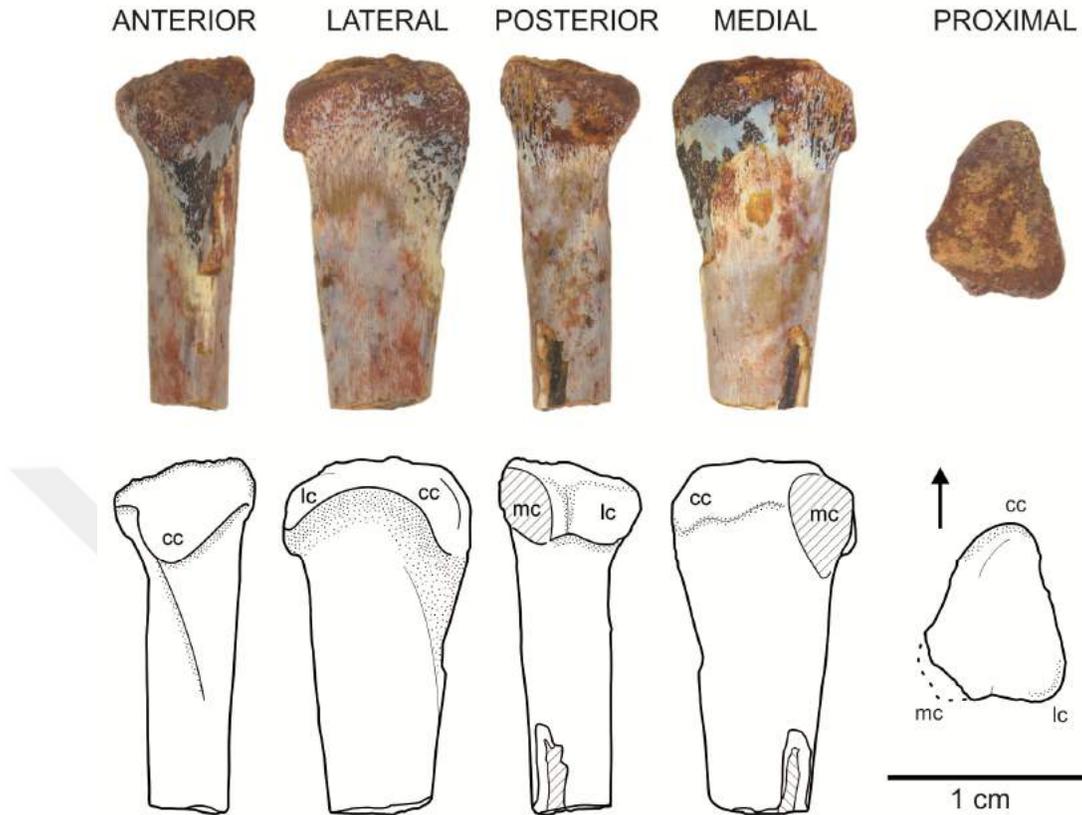
Figure 4.6 *Dromomeron romeri* (TTU-P12537), right proximal tibia. Abbreviations: **cc**, cnemial crest; **lc**, lateral crest; **mc**, medial crest. Hatches signify the damaged parts. Arrow points the anterior side.

TTU-P12539

(Figure 4.7)

Referred specimen **-** Proximal femur, right

Horizon and locality **-** Headquarters South locality (MOTT 3898), Bull Canyon

Formation, Garza County, Texas

Collector **-** Doug Cunningham

Description and remarks **-** The femoral head is broken but its hooked morphology

is still traceable. On the proximal end, the posteromedial tuber and adjacent trochanteric

fossa (facies articularis antitrochanterica) are distinct. Right below the broken capitulum,

a very faint emargination is present on the anterolateral side. Despite the inadequate

preservation, the smooth and gracile femoral shaft indicates the affinity to *D. romeri*.
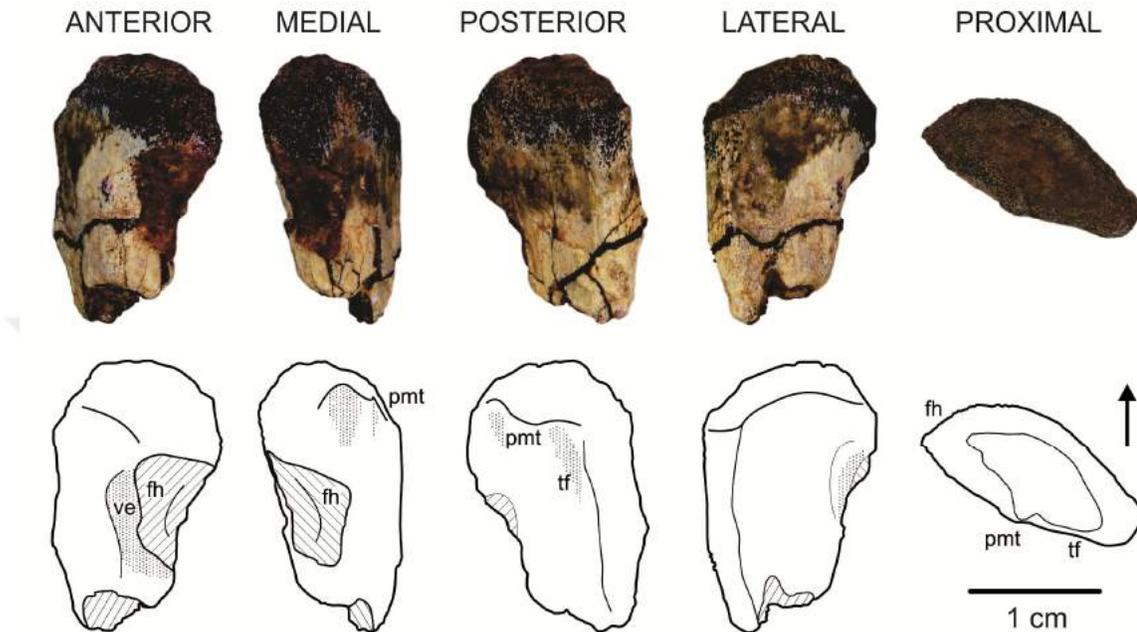


Figure 4.7 *Dromomeron romeri* (TTU-P12539), right proximal femur. Abbreviations: **fh**, femoral head (note that the femoral is broken); **pmt**, posteromedial tuber; **tf**, trochanteric fossa; **ve**, ventral emargination. Hatches signify the damaged parts. Arrow points the anterior side.

WTAMU-X1 (Specimen lacks catalog number)

(Figure 4.8)

Referred specimen **-** Distal femur, right

Horizon and locality **-** Palo Duro Canyon, Tecovas Formation, Briscoe County,

Texas

Collector **-** Gerald Schultz, West Texas A&M University (WTAMU)

Description and remarks **-** Slender shaft of the distal femur significantly widens

distally with a distinct ridge on the anteromedial side, which establishes its affinity (Irmis

et al. 2007a). Distal end is much larger mediolaterally than anteroposteriorly. Condyli are

small and do not projecting beyond the shaft. Medial and lateral condyli are well

separated by the intercondylar groove.
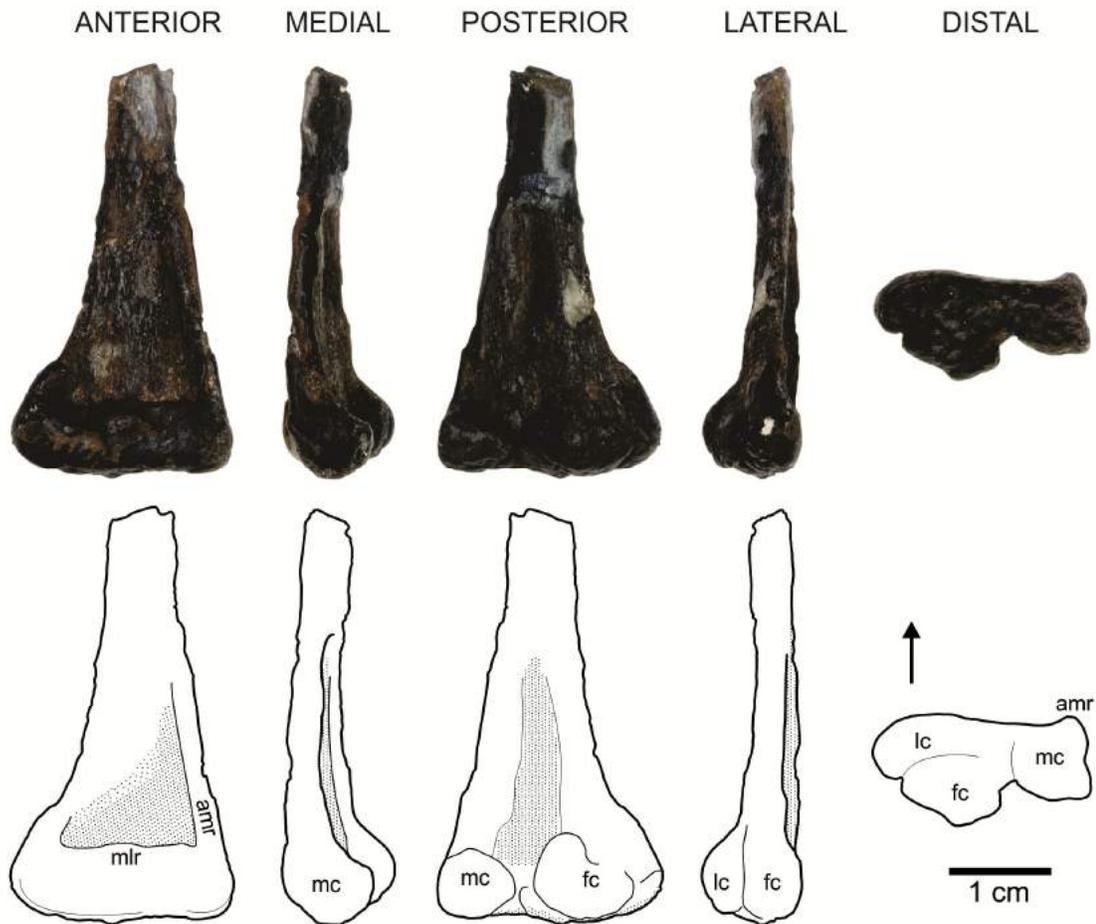


Figure 4.8 *Dromomeron romeri* (WTAMU-X1), right distal femur. Abbreviations: **amr**, anteromedial ridge (*sensu* Irmis et al. 2007a); **fc**, fibular condyle; **lc**, lateral condyle; **mc**, medial condyle; **mlr**, mediolateral ridge. Arrow points the anterior side.

*Dromomeron gregorii* Nesbitt et al. 2009b

TMM 31100-1306

Holotype - Complete left femur

Paratypes - Right femora (TMM 31100-464, TMM 31100-1308, TMM 31100-1234, TMM 31100-764); right tibia (TMM 31100-278); left tibia (TMM 31100-1314)

from the Otis Chalk Quarry 3 (see below), and also a distal portion of a left femur is referred (UCMP 25815) from the *Placerias* Quarry of the Chinle Formation.

Horizon and locality **-** Otis Chalk Quarry 3 (TMM 31100 = MOTT 2000), Tecovas Formation (Colorado City Formation *sensu* Lucas et al. 1993), Garza County, Texas.

Other referred sections **-** *Placerias* Quarry (UCMP locality A269) near St. Johns, Arizona which lies within the lower part of Chinle Formation (Heckert 1997 and Parker and Martz 2011).

Remarks **-** Despite any of the specimens stated above are evaluated within this study, the holotype of *D. gregorii* is collected from the Otis Chalk Quarry 3 (Nesbitt et al. 2009b) which is located at the lower portion of the Tecovas Formation.

TTU-P11282

(Figure 4.9)

Referred specimen **-** Complete left femur

Horizon and locality **-** Post Quarry (MOTT 3624), Tecovas Formation, Garza County, Texas.

Collector **-** Sankar Chatterjee

Description and remarks **-** Femoral head is rounded due to extensive ventral curvature and thus became hook shaped. Anterior margin of the proximal surface is smoothly curved and possesses the anteromedial tuber but lacks the anterolateral tuber, whereas the posterior margin possesses the characteristically large posteromedial tuber. The trochanteric fossa (facies articularis antitrochanterica) stands posterolaterally on the

proximal surface. Right below the proximal surface on the anterolateral side, it stands the anterior trochanter with a rugose trochanteric shelf. The fourth trochanter on the posteromedial side is relatively distinct. A depression/scar on the anterior surface of the distal femur that might have served an origin for M. femorotibialis externus (Nesbitt et al. 2009b, p. 502 and references therein) is bordered by a distinct anteromedial ridge. Distal end is distinctive with an enlarged fibular crest (crista tibiofibularis) which is larger than the lateral condyle and reduces the intercondylar groove. Medial condyle is well expanded posteriorly and it has straight anterior and medial borders. This specimen was previously assigned as *D. gregorii* (Martz et al. 2013), a diagnosis that is agreed with in this work.

TTU-P18331

(Figure 4.10)

Referred specimen **-** Proximal femur, left

Horizon and locality **-** Post Quarry (MOTT 3624), Tecovas Formation, Garza County, Texas

Collector **-** Sankar Chatterjee et al.

Description and remarks **-** Although the damaged tip of the femoral head obliterates the anteromedial tuber, the posteromedial tuber is beautifully preserved. The anterior trochanter with a trochanteric shelf is distinct as a rugose ridge on the anterolateral side. The trochanteric fossa is situated posteriorly, where the fourth trochanter bulges out more distally on the posteroventral side.
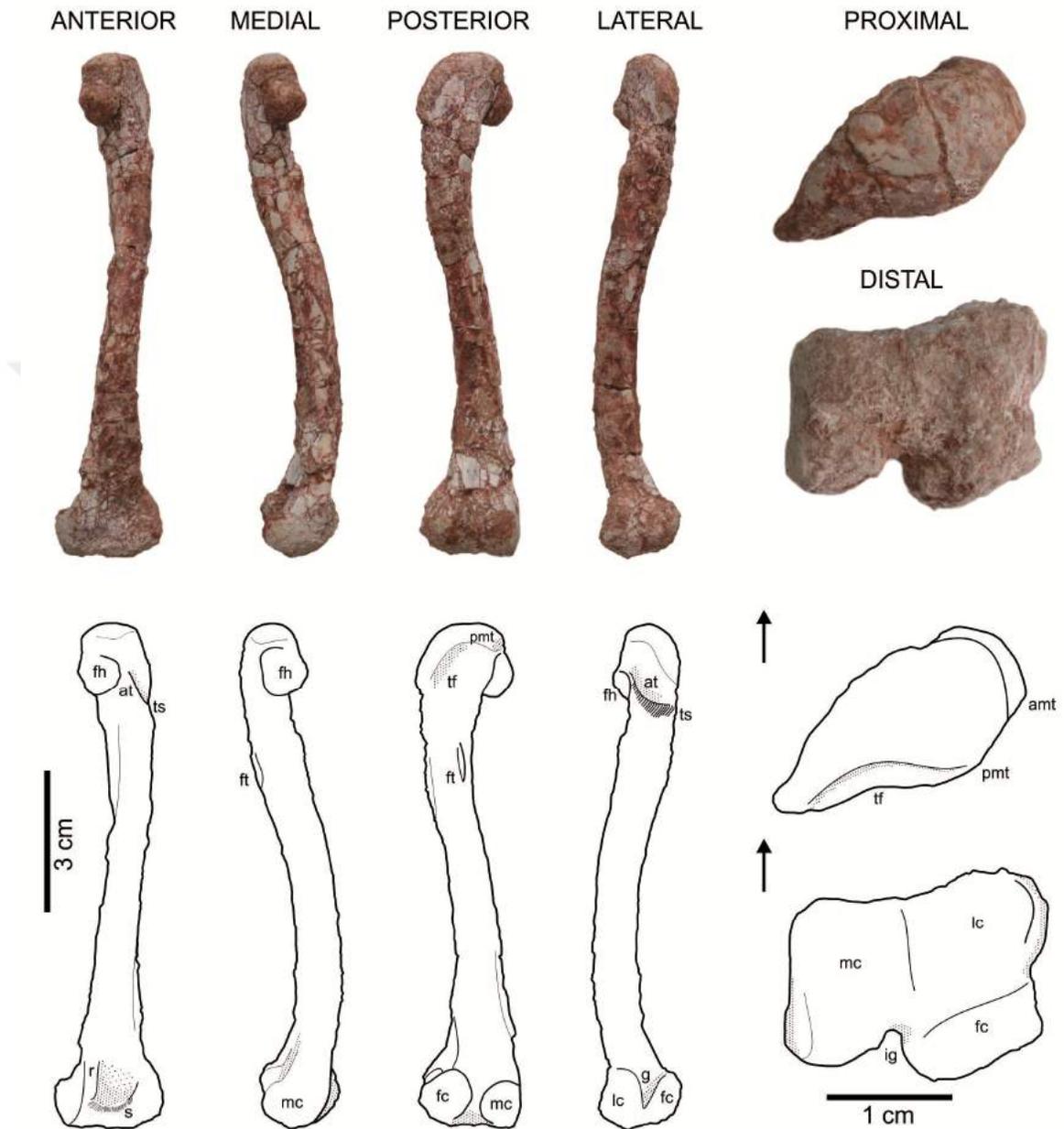
Figure 4.9 *Dromomeron gregorii* (TTU-P11282), left femur. Abbreviations: **amt**, anteromedial tuber; **at**, anterior trochanter; **fc**, fibular condyle; **fh**, femoral head; **ft**, fourth trochanter; **g**, groove; **ig**, intercondylar groove; **lc**, lateral condyle; **mc**, medial condyle; **pmt**, posteromedial tuber; **r**, ridge; **s**, scar; **tf**, trochanteric fossa; **ts**, trochanteric shelf. Proximal and distal views share the 1 cm. scale bar. Arrows point the anterior side.
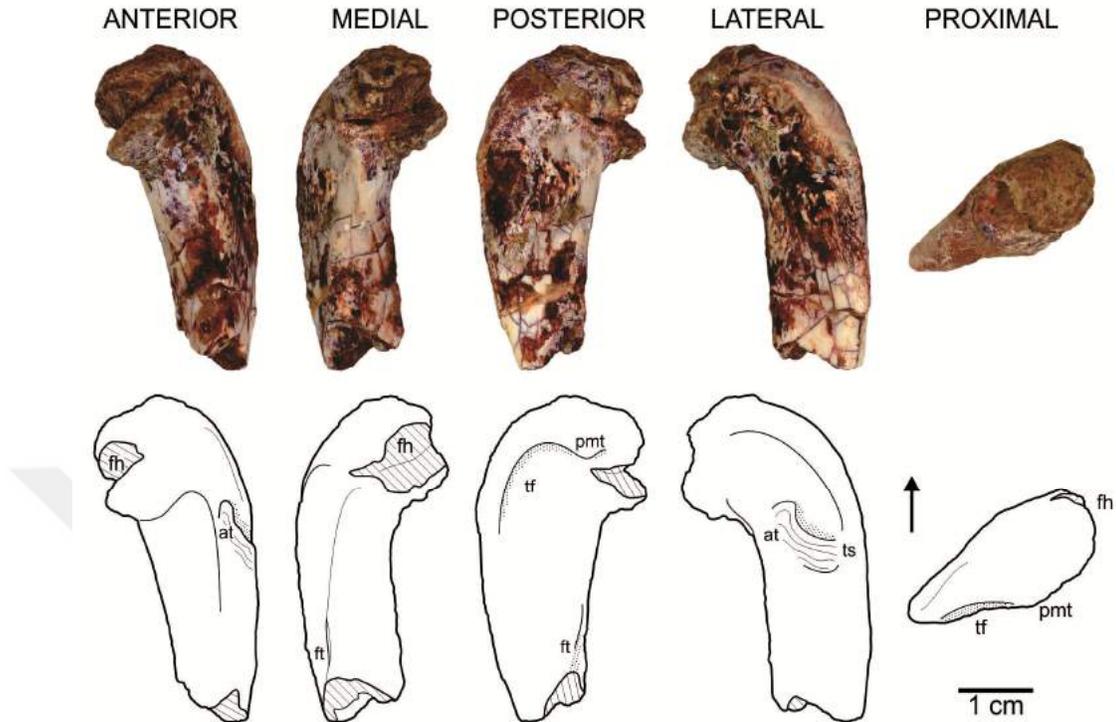
Figure 4.10 *Dromomeron gregorii* (TTU-P18331), left proximal femur. Abbreviations: **at**, anterior trochanter; **fh**, femoral head (note that the femoral is broken); **ft**, fourth trochanter; **pmt**, posteromedial tuber; **tf**, trochanteric fossa; **ts**, trochanteric shelf. Hatches signify the damaged parts. Arrow points the anterior side.

TTU-P20046

(Figure 4.11)

Referred specimen **-** Distal femur, left

Horizon and locality **-** Post Quarry (MOTT 3624), Tecovas Formation, Garza County, Texas

Collector **-** Sankar Chatterjee et al.

Description and remarks **-** As TTU-P11282, sizes and proportions of the distal condyli indicate a fully adult *D. gregorii* in the ontogenic scale (Nesbitt et al. 2009b). The muscle scar for M. femorotibialis externus is expressed as a slightly damaged rounder

77

fossa. The characteristic groove between the lateral and the fibular condyle is also highly reduced due to the relative enlargement of the latter.
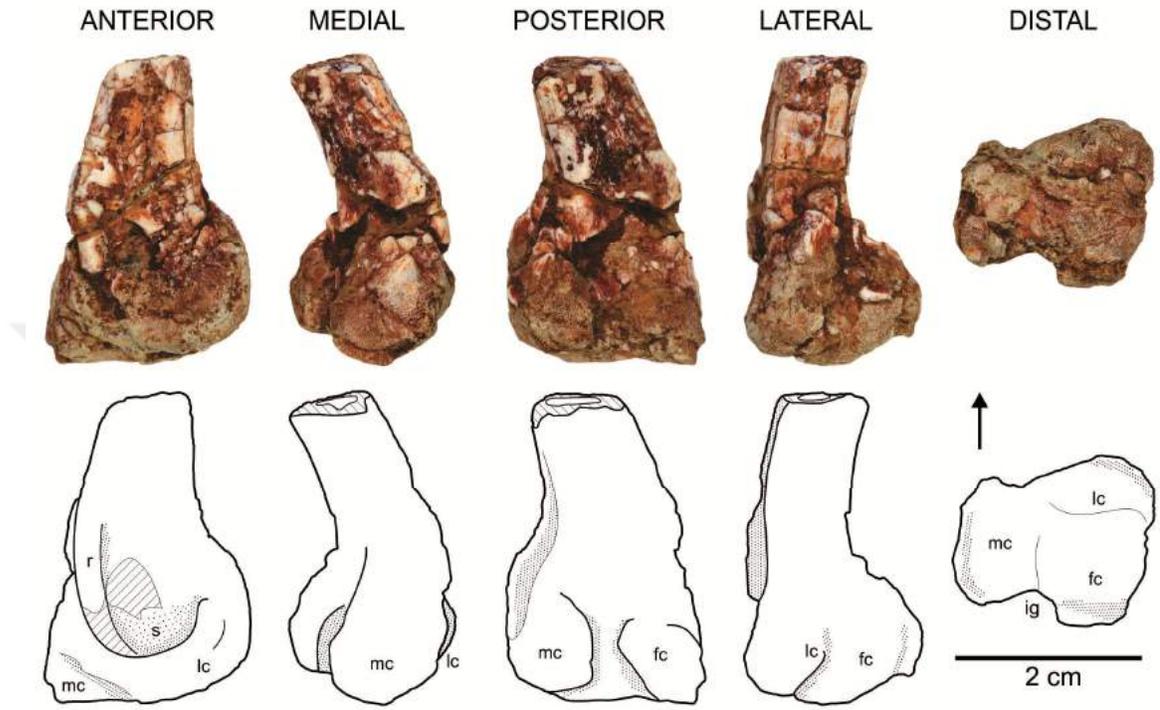


Figure 4.11 *Dromomeron gregorii* (TTU-P20046), right distal femur. Abbreviations: **fc**, fibular condyle; **ig**, intercondylar groove; **lc**, lateral condyle; **mc**, medial condyle; **r**, ridge; **s**, scar. Hatches signify the damaged parts. Arrow points the anterior side.

WTAMU-X2 (Specimen lacks catalog number)

(Figure 4.12)

Referred specimen **-** Proximal femur, right

Horizon and locality **-** Palo Duro Canyon, Tecovas Formation, Briscoe County, Texas

Collector **-** Gerald Schultz, West Texas A&M University (WTAMU)

Description and remarks **-** The anteromedial tuber of the femoral head is obliterated but the posteromedial tuber is quite visible. The ventral emargination is located on the anteromedial side. Anterior trochanter and the trochanteric shelf are

prominent with a rugose attachment surface. Only the top part of the fourth trochanter has survived.
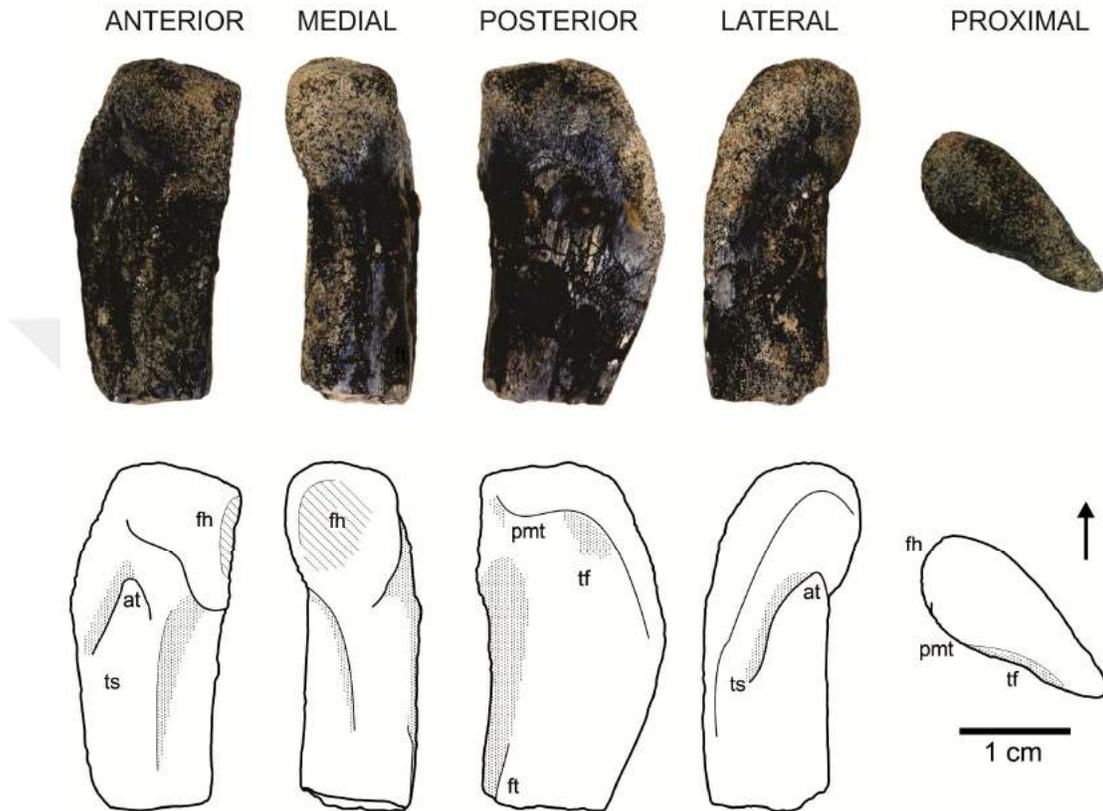


Figure 4.12 *Dromomeron gregorii* (WTAMU-X2), right proximal femur. Abbreviations: **at**, anterior trochanter; **fh**, femoral head (note that the femoral is broken); **ft**, fourth trochanter; **pmt**, posteromedial tuber; **tf**, trochanteric fossa; **ts**, trochanteric shelf. Hatches signify the damaged parts. Arrow points the anterior side.

WTAMU-X3 (Specimen lacks catalog number)

(Figure 4.13)

Referred specimen **-** Proximal tibia, right

Horizon and locality **-** Palo Duro Canyon, Tecovas Formation, Briscoe County, Texas

Collector **-** Gerald Schultz, West Texas A&M University (WTAMU)

Description and remarks **-** Proximal surface of the tibia is triangular in shape which is significantly longer in anteroposterior direction. Cnemial crest is prominent with a small ridge on the tip. The tip of the cnemial crest is slightly kinked laterally which produces a sharp anterior edge. A small lateral depression which stands posterior to the cnemial crest does not produce a strict sense tibial notch, since it does not extend down along the shaft. Posterior condyli are aligned posteriorly but the medial condyle stands higher. Lateral condyle is ventrally deflected and smaller than the medial one which is well expanded posteriorly. Shaft is mediolaterally compressed.
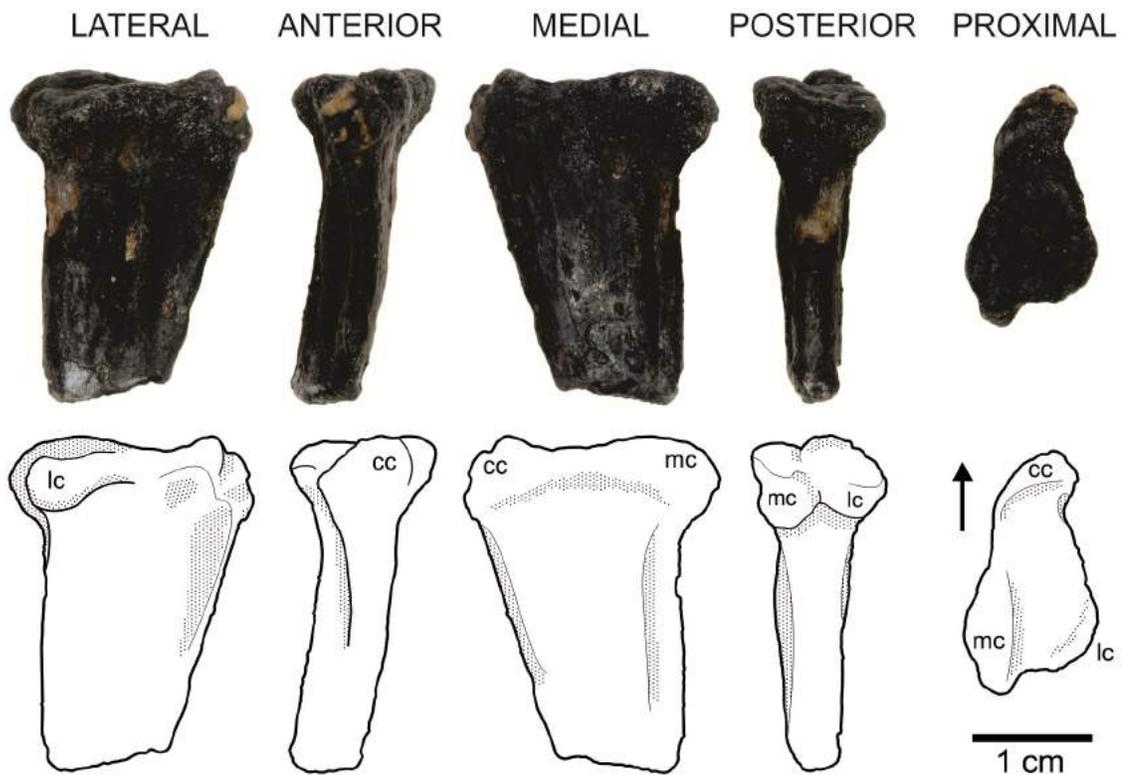
Figure 4.13 *Dromomeron gregorii* (WTAMU-X3), right proximal tibia. Abbreviations: **cc**, cnemial crest; **lc**, lateral crest; **mc**, medial crest. Arrow points the anterior side.

**A New Basal Dinosauromorph from Dockum**

A new taxon of basal dinosauromorph (TTU-P10546, TTU-P19803) from the Boren Quarry of the Tecovas formation is described below.

DINOSAUROMORPHA Benton 1985

Dinosauromorph gen. nov., sp. nov.

TTU-P10546; TTU-P19803

(Figures 4.14 and 4.15)

Referred specimens - Complete tibia, right (TTU-P10546); distal tibia, right (TTU-P19803)

Horizon and locality - Boren Quarry (MOTT 3869), Tecovas Formation, Garza County, Texas

Collector - Bill Mueller

Description and remarks - Proximal side of the tibia is somewhat altered, especially around the edges, and the tip of the anteriorly straight cnemial crest is missing. Lateral condyle is positioned anteriorly compared to the medial one, as documented in many non-theropod dinosauromorphs. There is no intercondylar cleft to separate the condyli. The shaft is slender; compressed mediolaterally and damaged in some parts. Distal potion is better preserved which is very diagnostic. Both the anterior and medial borders of the distal surface are rounded but the posterior corner is distally projected as a posteriorly tapering process which is expressed as a tuber on the distal surface. On the distal surface, a helical groove runs from the posterior side towards the lateral side where the bone is beveled proximally at the end of this groove.
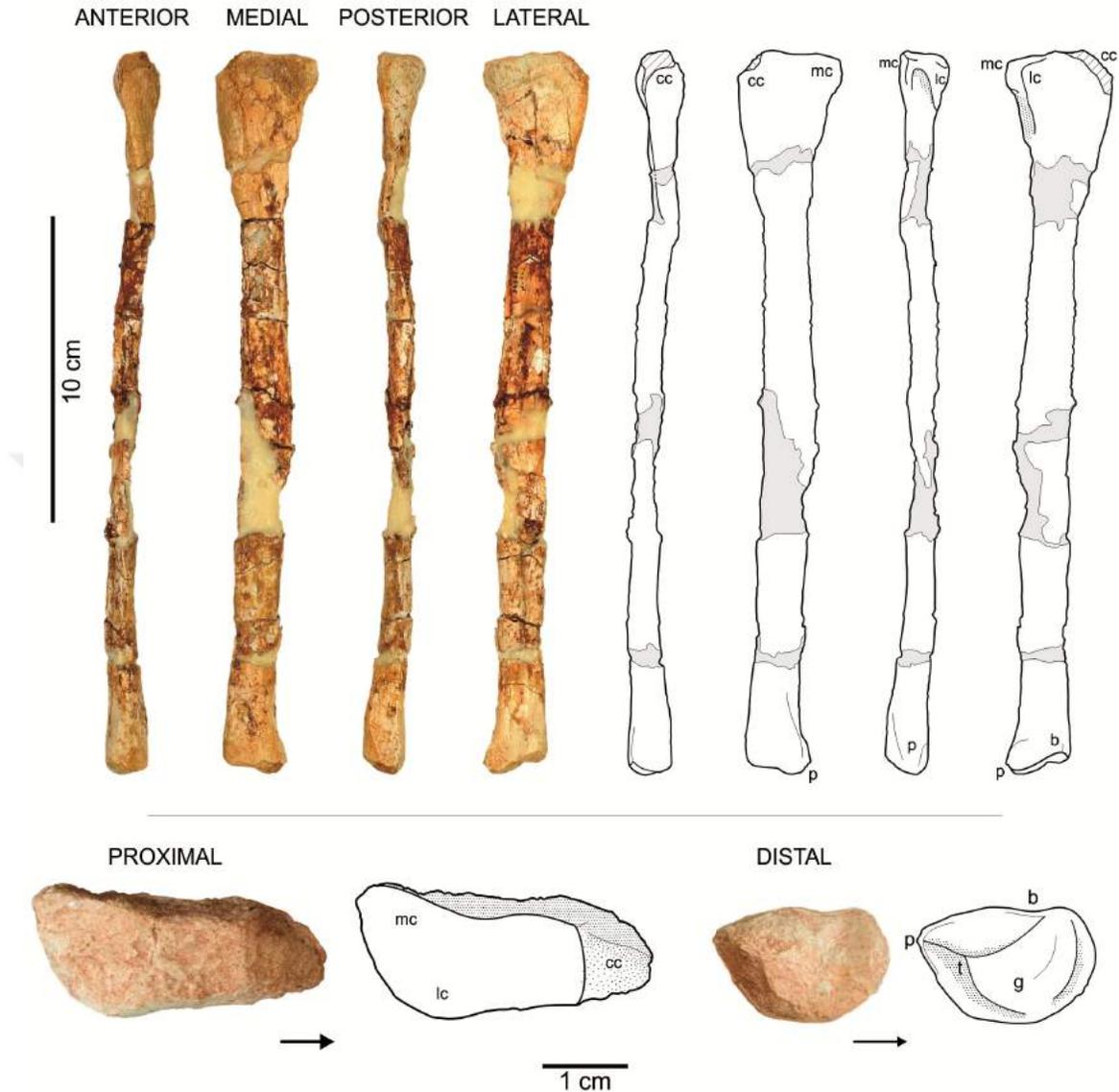
Figure 4.14 New dinosauromorph (TTU-P10546), right tibia. Abbreviations: **b**, beveled surface; **cc**, cnemial crest; **g**, groove; **lc**, lateral crest; **mc**, medial crest; **p**, distal process; **t**, tuber. Arrow points the anterior side.

Despite the similarity at the proximal portion, this specimen differs from both *Lagerpeton* and *Dromomeron* by the anteroposteriorly elongated distal end, therefore it lacks the reception of the posterior ascending process and other features of the typical lagerpetid astragalus (Sereno and Arcucci 1993; Nesbitt et al. 2009b; Nesbitt 2011, characters 355, 356, 366 and references therein). Although the distal portion of TTU-

P10546 is similar to dinosauriforms by having a lateral reception of the ascending process of the astragalus, it also lacks the posterior process on the lateral side (*sensu* Novas 1989) of the distal tibia with a proximodistally oriented groove which is synapomorphic for all dinosauriforms (Langer et al. 2013). Nevertheless, TTU-P10546 appears more derived than hitherto known lagerpetids and stands closer to dinosauriforms. TTU-P19803 is only represented by the distal part of tibia which is identical to TTU-P10546, only more compressed mediolaterally.
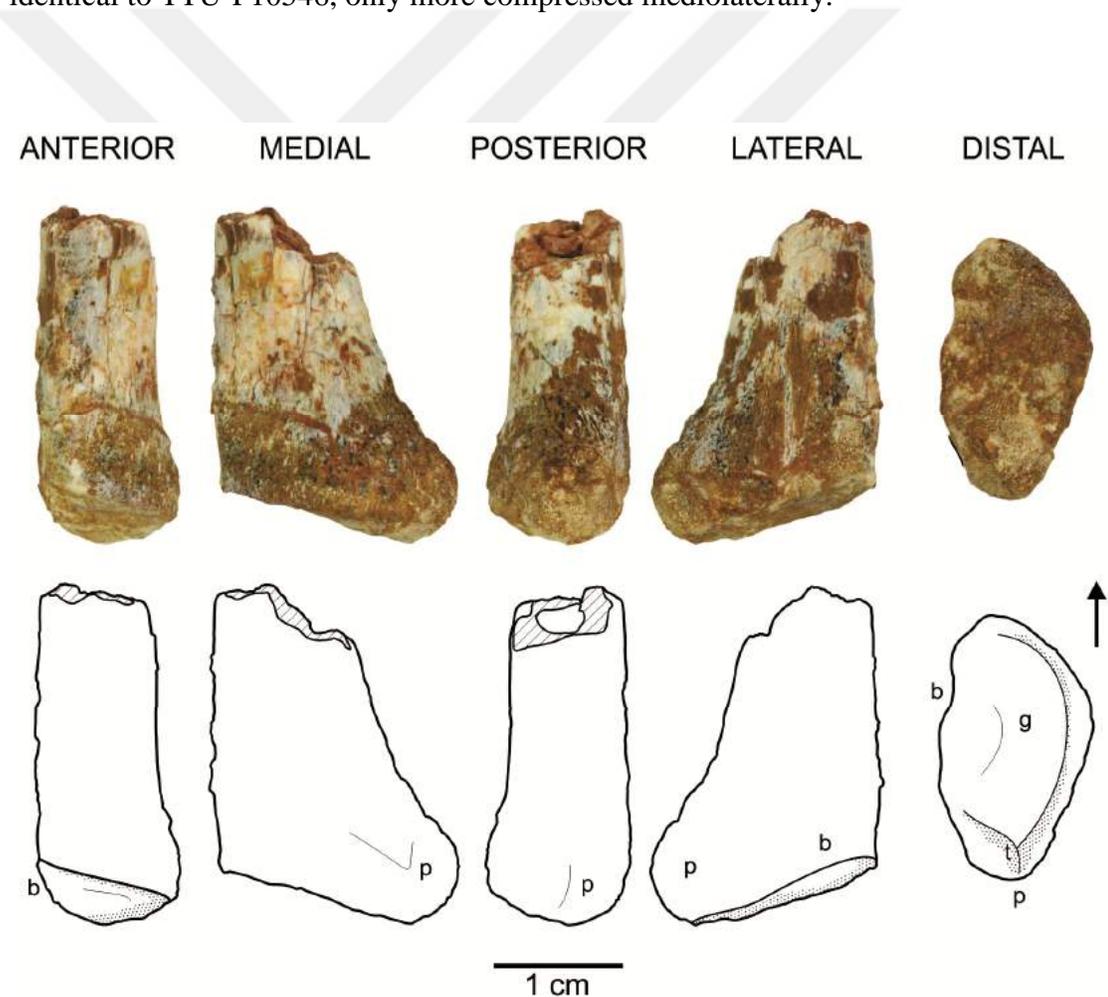


Figure 4.15 New dinosauromorph (TTU-P19803), right distal tibia. Abbreviations: **b**, beveled surface; **g**, groove; **p**, distal process; **t**, tuber. Arrow points the anterior side.

**Silesauridae**

DINOSAURIFORMES Novas 1992

SILESAURIDAE Langer et al. 2010

Brief description **-** Silesaurids are herbivorous quadrupeds which had a worldwide distribution during Middle and Late Triassic. Although most of the silesaurids like *Technosaurus smalli* (Chatterjee 1984) and *Pseudolagosuchus major* (Arcucci 1987) are diagnosed based on fragmentary material, fairly complete skeletons of *Silesaurus opolensis* (Dzik 2003) and *Asilisaurus kongwe* (Nesbitt et al. 2010) displayed a better picture about the nature of this group (Figure 4.16). Jaws are known for many silesaurids, which are equipped with generally leaf shaped teeth with occasional longitudinal striations and denticles in various sizes on the tooth keel (Langer et al., op. cit.). In most silesaurid taxa, the teeth are ankylosed (i.e. fused) to the alveolus (Nesbitt et al. 2010; Kammerer et al. 2013). The other part of the body that is mostly preserved in silesaurids is the pelvis and hind limbs. The femoral head is more pronounced and ventrally demarcated from the shaft by a notch which gets deepened in dinosaurs (Nesbitt et al. 2010; Nesbitt 2011, p. 147), whereas the acetabular portion even gets perforated in some (e.g. *Agnosphitys cromhallensis*, Fraser et al. 2002). Such derived feeding and locomotor modules raise the questions about whether the dinosaur ancestors were herbivore or carnivore or whether they were bipedal or quadrupedal (e.g. Langer et al. 2010; Barrett et al. 2011; Kubo 2011). Although it is a recently erected clade, Silesauridae is important for dinosaur ancestry; recent phylogenetic analyses placed them as the sister group of Dinosauria (Brusatte et al. 2010a; Langer et al. 2010, 2013; Nesbitt et al. 2010), replacing

the iconic position of *Marasuchus lilloensis* and other South American basal

dinosauromorphs (see Figure 4.1).



Figure 4.16 Skeletal reconstruction of the silesaurid *Silesaurus opolensis* (after Dzik 2003; Langer et al. 2013). Missing parts are omitted in the figure.

Revised diagnosis **-** (1) anterolateral edges of the supraoccipital possess rugose

ridge; (2) acetabulum with a straight ventral margin; (3) distinct notch located ventral to

the femoral head; (4) proximal surface of the femur bears a straight transverse groove

(Nesbitt et al. 2010). Other potential synapomorphies of silesaurids include a tapering

dentary with an edentulous tip and short crowned teeth that are fused (ankylosed) to the

alveoli (for the full list, see Nesbitt et al. 2010; Langer et al. 2013).

**Dockum Silesaurids**

Silesaurids are known from a single holotype specimen (TTU-P9021) in Dockum

Group of Texas. Chatterjee (1984) described an assorted series of material from the Post

Quarry as a primitive ornithischian, similar to the poorly known *Pisanosaurus* of

Ischigualasto Formation. The material consists of premaxilla, dentary, posterior part of

the lower jaw, an isolated vertebra, an astragalus and three claws. The most diagnostic

feature of *Technosaurus* was leaf shaped cheek teeth which are symmetrical in cross

section, as seen in basal ornithischians. Sereno (1991b) evaluated the material and

concurred with Chatterjee that the dentary belong to a basal ornithischian but the premaxilla may belong to a prosauropod. The other referred material of *Technosaurus*, according to Sereno, is not diagnostic for ornithischian affiliation. Only after the discovery of *Silesaurus* from the Late Triassic of Poland (Dzik 2003), did the true identity of *Technosaurus* becomes apparent. Nesbitt et al. (2007) and Irmis et al. (2007b) allied the premaxilla and dentary *Technosaurus* with those of *Silesaurus* on the basis of dental morphology, but the rest of the material may belong to other taxa. Therefore, only the premaxilla and dentary are described here.

<div style="text-align:center">

*Technosaurus smalli* Chatterjee 1984

TTU-P9021

(Figure 4.17)

</div>

Holotype **-** Incomplete dentary, right side and premaxilla, left side

Horizon and locality **-** Post Quarry (MOTT 3624), Tecovas Formation, Garza County, Texas

Collector **-** Sankar Chatterjee

Description and remarks **-** The description of *Technosaurus smalli* holotype originally includes a premaxilla, the posterior portion of a right side dentary, a dorsal vertebra, an astragalus and three ungulae (Chatterjee 1984). Following the original description of Chatterjee (1984), both the morphology and classification of *Technosaurus smalli* has been evaluated in great detail (Sereno 1991b; Irmis et al. 2007b; Nesbitt et al. 2007), changing from basal ornithischians to silesaurids. Only the premaxilla and dentary are included here as the diagnostic elements of the skull.
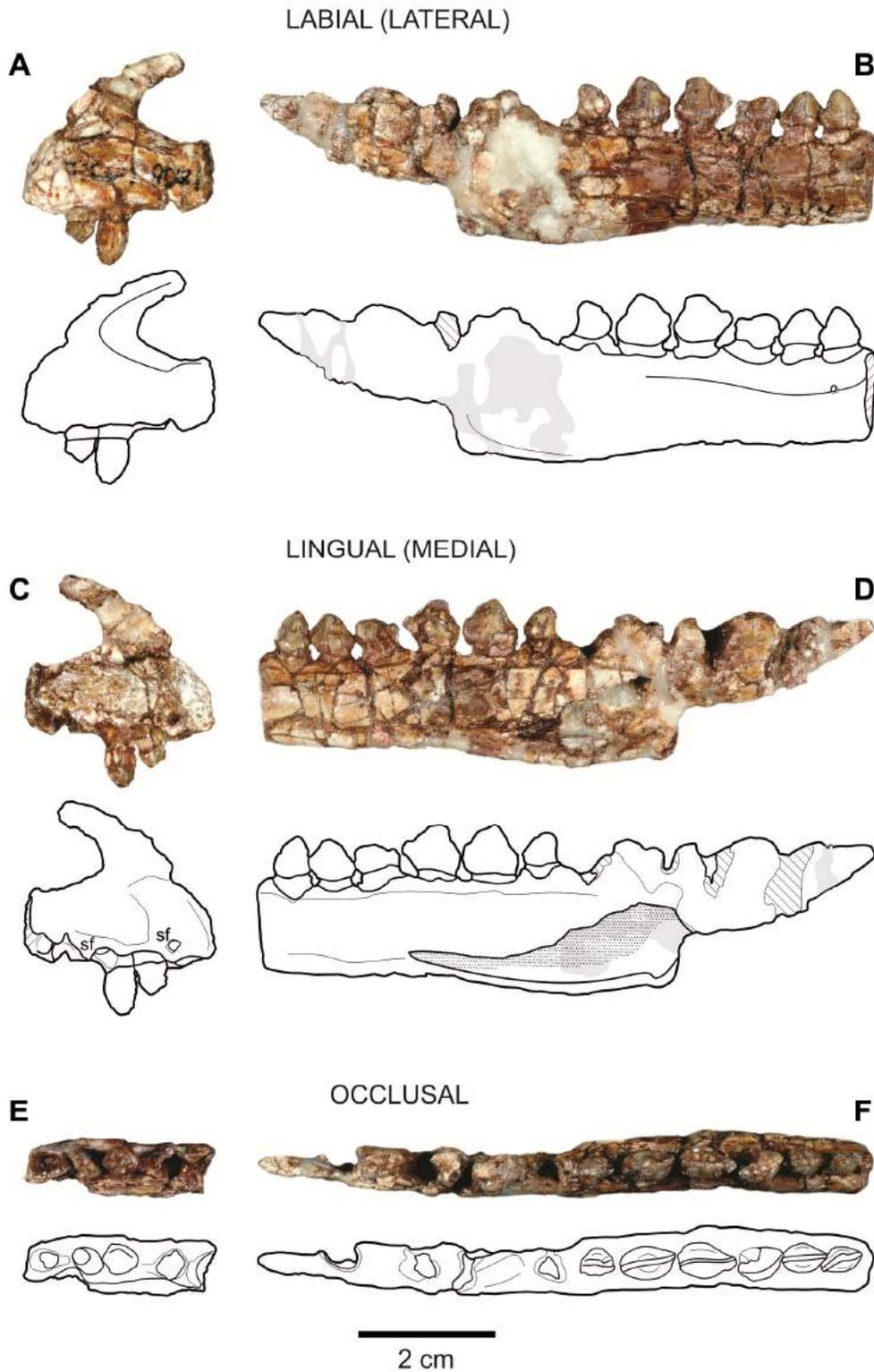
Figure 4.17 *Technosaurus smalli* holotype (TTU-P9021), left premaxilla (A, C, and E) and right dentary (B, D and F). Abbreviations: **sf**, special foramina (or window). Hatches signify the damaged parts.

Premaxilla bears three empty alveoli and two teeth on the occlusal surface and a distinct nasal process on dorsal side. In medial view, alveolar portion contains shallow pits. These pits are termed as "special foramina" (Edmund 1957, 1960) or "window" (Chatterjee 1978b) where the upcoming tooth germinates to replace the former one. The dentary lacks the anterior side, but the remaining portion is nicely preserved. Six teeth are preserved with at least four empty alveoli. Teeth are ankylosed to the alveolar portion, as diagnosed in many silesaurids (Nesbitt et al. 2010; Nesbitt 2011, character 174; Langer et al. 2013). This type of dental pattern was previously termed as ankylosed thecodonty (Edmund 1960) or ankylothecodonty (Chatterjee 1974). Meckelian groove restricted to ventral side, which posteriorly opens to a wider fossa for the articulation of splenial. Lateral side featureless except a large nutrient foramen on the anterior portion, which is recognized here in first time. In comparison with jaw morphology of other silesaurids, it is concluded that premaxilla and dentary do not belong to the same individual (Nesbitt et al. 2007). Teeth are placed marginally on the dentary; they are leaf shaped with cusps and rotated diagonally to each other, whereas teeth on premaxilla are more conical in shape. The surviving teeth are symmetrical in shape without any curvature. Faint striations/ribs are present in both premaxillary and dentary teeth.

**Other Basal Dinosauriforms of Dockum**

The only other non-dinosaurian dinosauriform specimen from the Dockum Group of Texas (TTU-P11127) cannot be placed definitely in the phylogeny due to the insufficient preservation of skeletal elements.

DINOSAURIFORMES Novas 1992

INCERTAE SEDIS

TTU-P11127

(Figure 4.18)

Referred specimen **-** Complete tibia, left

Horizon and locality **-** Post Quarry (MOTT 3624), Tecovas Formation, Garza County, Texas

Collector **-** Sankar Chatterjee et al.

Description and remarks **-** The specimen is severely crushed however features on the both ends are still recognizable. Proximal end is triangular in shape which is longer in anteroposterior direction. Cnemial crest is straight, pronounced and oriented anterolaterally. Lateral posterior condyle stands anteriorly to the medial condyle and smaller in size, despite the broken medial edge of the medial condyle. Despite being seriously damaged, the shaft seems to be smooth where no fibular crest is diagnosed. Distal end possess the helical (or step-wise) pattern where the anterior edge is beveled parallel to the ascending process of the astragalus. The longitudinal groove (*sensu* Novas 1996) is restricted on the lateral side without a deep penetration into the distal surface and to a small posterior process stands adjacently as typical in non-dinosaurian dinosauriforms (Novas 1989, 1996; Langer et al. 2013). Although the morphology is highly comparable to a typical silesaurid tibia, recent works couldn't pinpoint any exclusive silesaurid character for TTU-P11127 (Martz et al. 2013).
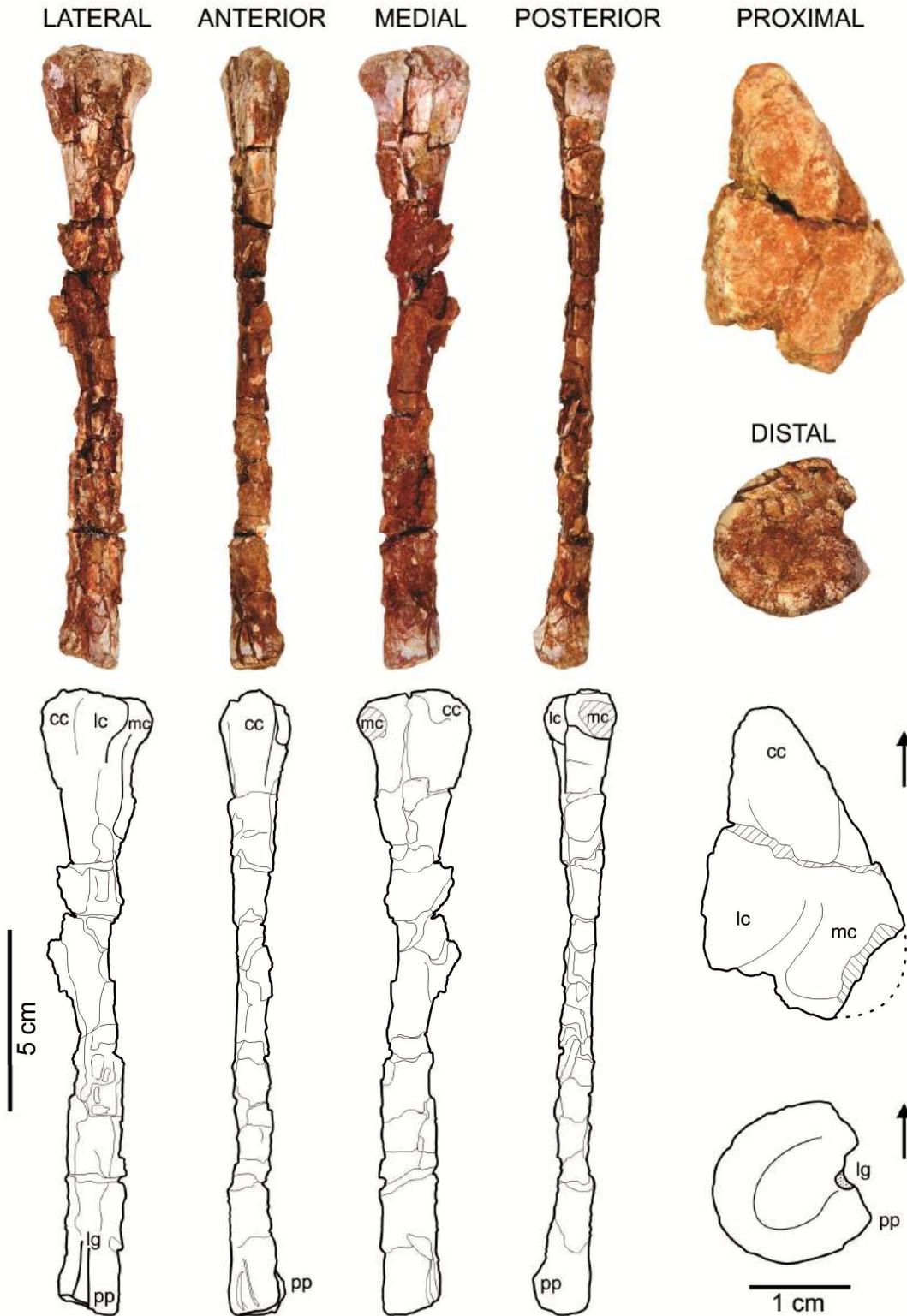
Figure 4.18 Dockum dinosauriform (TTU-P11127), left tibia. Abbreviations: **cc**, cnemial crest; **lc**, lateral condyle; **lg**, longitudinal groove; **mc**, medial condyle; **pp**, posterior process. Hatches signify the damaged parts. Proximal and distal views share the 1 cm. scale bar. Arrows point the anterior side.

**Herrerasauridae**

SAURISCHIA Seeley 1887 *sensu* Gauthier 1986

THEROPODA Marsh 1881 *sensu* Gauthier 1986

HERRERASAURIDAE Benedetto 1973

<u>Brief description</u> **-** Herrerasaurids are medium sized theropods; their length is about 3 meters, but they can grow up to 6 meters (Sereno and Novas 1992) (Figure 4.19). They represent the typical Late Triassic carnivorous dinosaurs of South America with three genera so far discovered: *Herrerasaurus ischigualensis* (Reig 1963; Benedetto 1973; Sereno and Novas 1992), *Staurikosaurus pricei* (Colbert 1970; Galton 1977) and *Sanjuansaurus gordilloi* (Alcober and Martinez 2010). The distribution of *Chindesaurus bryansmalli* (Long and Murry 1995), the only herrerasaurid discovered out of South America as yet (see below), is restricted to southwestern North America. Although they possess a perforated acetabulum, herrerasaurids were once recognized as a dinosaur ancestor based on several features such as the possession of only two sacral vertebrae and the absence of a brevis fossa on ilium (e.g. Padian and Gauthier 1985; Gauthier 1986; Padian and May 1993). However, various dinosaurian characters identified based on the new *Herrerasaurus* specimens which suggest theropod affinities for herrerasaurids, on both cranial and postcranial portions (e.g. Sereno et al. 1988; Novas 1993; Sereno and Novas 1992, 1993; Sereno 1993, 1999; Rauhut 2003; Nesbitt et al. 2009c; Martinez et al. 2011a; Nesbitt 2011). A third point of view about the herrerasaurids is that they constitute the basal stage of Saurischia, since some cladistic works showed closer relations between theropods and sauropodomorphs than herrerasaurids (e.g. Holtz and Padian 1995; Holtz 2000; Langer 2004; Langer and Benton 2006; Ezcurra 2010).

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A series of new discoveries of the non-dinosaurian dinosauromorphs (e.g. lagerpetids and silesaurids, see above) and of the basal saurischians (e.g. Sereno et al. 1993; Bonaparte et al. 1999; Langer et al. 1999; Martinez and Alcober 2009; Ezcurra 2010) quite expanded the array of characters that are used in the cladistic works. The current cladistic picture indicates that the early evolution of dinosaurs is more complicated than previously thought, where it is observed as a mosaic of traditional "dinosaurian" and "non-dinosaurian" characters in many stages. The ongoing debate about the phylogenetic placement of herrerasaurids is out of the scope of this study, nevertheless, herrerasaurs are considered here as the basal group of theropods.



Figure 4.19 Skeletal reconstruction of *Herrerasaurus ischigualensis* (Langer 2004, after Sereno and Novas 1992) Missing parts are omitted in the figure.

Revised diagnosis - (1) anteroposteriorly compressed "spool-shaped" posterior dorsal vertebrae; (2) axially shortened and robust neural spines which become squared in dorsal view on posterior dorsal and sacral vertebrae; (3) deep and expanded sacral ribs on the medial surface of ilium, especially the second one; (4) proximal caudal vertebrae possess vertical neural spines; (5) distal caudal prezygapophyses are elongated up to the 50% of the preceding vertebra; (6) acromial process extends distally compared to the scapular glenoid lip and forms almost a right angle with the scapular blade; (7) distal end

of the scapular blade is highly shortened (i.e. highly reduced expansion); (8) distal half of the pubis is anteroposteriorly expanded; (9) distal process of pubis (i.e. pubic boot) is axially broadened (thus the pubic pair display a U-shaped section, Benton and Langer 2006) and elongated more than 25% of the pubic length (Novas 1992); (10) absence of a brevis shelf (lateral shelf *sensu* Hutchinson 2001a) on the lateral side of ilium (Novas 1993; see Hutchinson 2001a for the evolution of the brevis shelf and fossa). Another synapomorphy of herrerasaurids is the possession of two sacral vertebrae (Novas 1992, 1993) which is still controversial. Different descriptions of *Herrerasaurus* and *Staurikosaurus* revealed a third sacral vertebra which is converted from the dorsal vertebra in the former one (Sereno 2007) and from the caudal vertebra in the latter one (Colbert 1970; Langer 2004; Bittencourt and Kellner 2009). In *Chindesaurus*, which is grouped within the Herrerasauridae, presence of only two sacral vertebrae is hypothesized based on the iliac morphology despite no sacral vertebra were found attached (Long and Murray 1995, but see below).

**Dockum Herrerasaurids**

The Dockum Group of Texas has yielded a variety of herrerasaurids (specimens UMMP 8870, TMM 31100-523, TTU-P10072, TTU-P10082, TTU-P11175, TTU-P12531, TTU-P12587, TTU-P12790, TTU-P16789) as described below.

*Chindesaurus* Long and Murry 1995

Revised diagnosis **-** (1) a prominent cleft is present on the anterior side of the astragalus which continues posteriorly across the distal astragalar surface as a groove; (2)

outline of distal astragalar surface glutealform; (3) anterior margin of the distal astragalar surface is much wider than the posterior one; (4) astragalus possesses a prominent posteroproximal projection beyond the proximal articular surface (Long and Murry 1995, page 173).

*Chindesaurus bryansmalli* Long and Murry 1995

(=*Caseosaurus crosbyensis* Hunt et al. 1998)

UMMP 8870; TMM 31100-523; NMMNH P-4415; NMMNH P-16656; NMMNH P-17325

Type specimen **-** PEFO 10395 partial skeleton, including an incomplete cervical centrum, posterior dorsal vertebrae, two sacral vertebrae, caudal vertebrae, in addition to numerous rib fragments and one chevron for the axial skeleton; fragments for the left and right side of the ilium, proximal portion of right pubis and most of the left pubic shaft, a complete but crushed right femur and the proximal portion of a left femur, fragmentary right femur and a complete astragalus for the appendicular skeleton.

Horizon and locality **-** Upper Petrified Forest Member, Petrified Forest National Park, Arizona.

Other referred sections **-** In Arizona, *Placerias* Quarry (UCMP locality A269) in the lower part of Chinle Formation (the Bluewater Creek Formation *sensu* Heckert 1997, or the Blue Mesa Member *sensu* Parker and Martz 2011); Dinosaur Hollow (PF 20) and Chinde Point N2 (PF 18) in the Petrified Forest Member of the Chinle Formation; in New Mexico, Bull Canyon Locality (NMMNH L00134), Revuelto Creek Locality (NMMNH L00176) and Barranca Locality (NMMNH L00073) of the Bull Canyon Formation, and

the Hayden Quarry in the Petrified Forest Member of the Chinle Formation (Irmis et al. 2007a); in Texas, Otis Chalk Quarry 3 (TMM 31100 = MOTT 2000), Tecovas Formation (Colorado City Formation *sensu* Lucas et al. 1993), Garza County and an unknown locality in Tecovas Formation, Crosby County.

<u>Remarks</u> **-** The holotype of *C. bryansmalli* is collected from the Chinle Formation in Arizona, where some additional vertebrae collected from *Placerias* Quarry, Dinosaur Hollow and Chinde Point N2 localities are also referred to this taxon. Nevertheless, the proximal portion of a left femur (NMMNH P-4415), various vertebra centra (NMMNH P-16656) and a complete centrum of a dorsal vertebra (NMMNH P-17325) are documented from Bull Canyon, Revuelto Creek and Barranca localities of the Bull Canyon Formation in eastern New Mexico, as well as a complete femur is documented from the Petrified Forest Member in Hayden Quarry, New Mexico (Irmis et al. 2007a). In Texas, proximal extremity of a left femur (TMM 31100-523) is reported from the Otis Chalk Quarry 3 (Long and Murry 1995, p. 174) and an isolated ilium from the Tecovas Formation (exact locality is unknown) that was first described by Case (1927), is referred to *Chindesaurus bryansmalli* considering its identicalness to the iliac fragments of the holotype (Long and Murry 1995). Despite the erection of a new taxon, *Caseosaurus crosbyensis*, for this particular ilium based on differences on the postacetabular portion (UMMP 8870, Hunt et al. 1998), new analyses cannot confirm a clear-cut distinction between *Chindesaurus bryansmalli* and *Caseosaurus crosbyensis* (Langer 2004; Nesbitt et al. 2007). Therefore in this work, *C. crosbyensis* is considered as a junior synoymn for *C. bryansmalli*, as previously suggested (Langer, op. cit.).

cf. *Chindesaurus bryansmalli* Long and Murry 1995

TTU-P10082

(Figures 4.20 and 4.21)

Referred specimen **-** Disarticulated pubis and postacetabular process of ilium with the proximal portion of the ischium attached, both left side

Horizon and locality **-** Tecovas Formation, Post Quarry (MOTT 3624), Garza County, Texas

Collector **-** Sankar Chatterjee

Description and remarks **-** Previous works correctly identified TTU-P10082 as an unequivocal theropod, based on the traditional definition of having an open acetabulum (Bakker and Galton 1974) and the morphology of the pelvis bone. The absence of a pubic fenestra disproves the coelophysoid affinity of this animal (Nesbitt and Chatterjee 2008, *contra* Lehman and Chatterjee 2005), which normally has to stand ventromedial to obturator fenestra (Tykoski and Rowe 2004). Moreover, the lack of a brevis fossa on the posteroventral corner excludes TTU-P10082 also from the clade Neotheropoda. The anatomy of this specimen is resembles to herrerasaurids rather to any other saurischian group (Nesbitt and Chatterjee 2008; Martz et al. 2013), however the affinity of this specimen at the generic level is hard to determine due to its mosaic of traits and also due to lack of other diagnostic elements.

The postacetabular (posterior) process of the ilium is a rectangular, low and robust piece which contains anteroposteriorly oriented muscle scars on the lateral surface, especially on the posterior part. Those muscle scars on the distinct rugose surface on the posterodorsal margin represent the origin for the tibial flexor muscles in propubic

theropods, whereas the ventrolateral side housed a portion of the hind limb-tail muscles (i.e. M. caudifemoralis brevis) in absence of a brevis fossa (e.g. Perle 1985; Carrano and Hutchinson 2002; Grillo and Azevedo 2011). Two sacral ribs are found attached to the medial side and both ribs are overlain by the medial shelf (*sensu* Hutchinson 2001a). The ischial peduncle is a short and sharp process which is found attached to the proximal tip of the ischium. Ischium is not fused to the ischial peduncle, but it partially contributes to the antitrochanter which posteriorly frames an open acetabulum. The preserved part of the ischium is mediolaterally compressed where the articulation surface between ischial peduncle and ischium is sub-triangular.
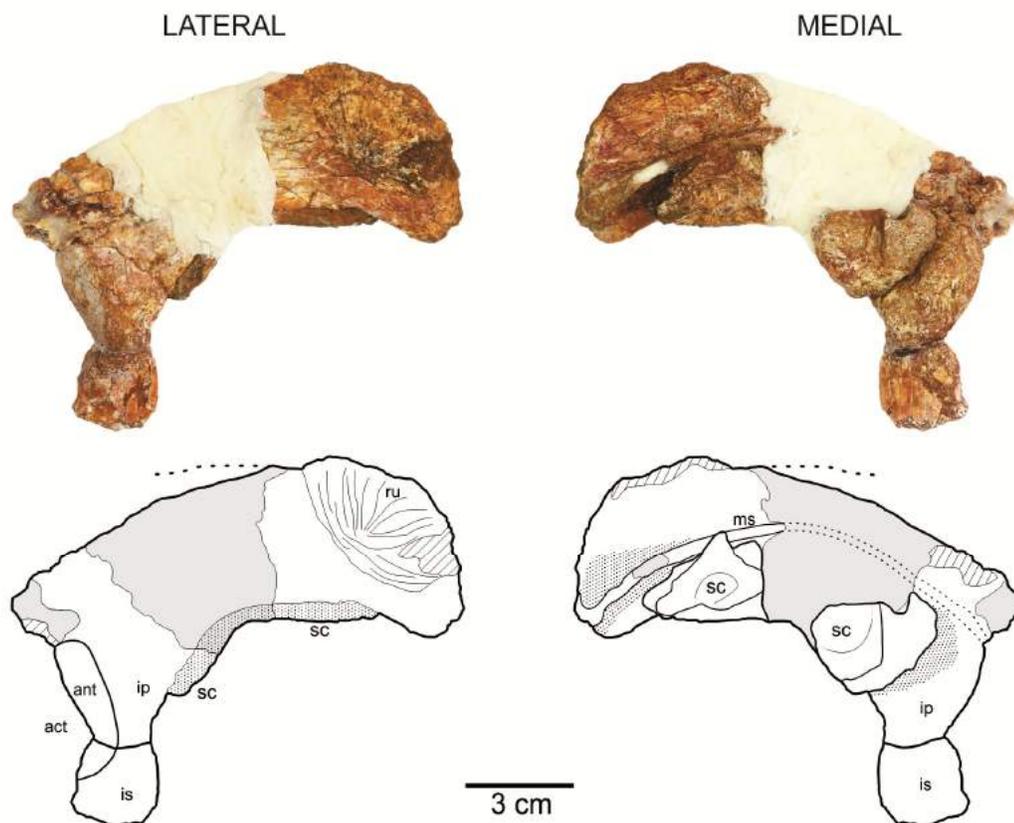


Figure 4.20 Dockum herrerasaurid (TTU-P10082), iliac postacetabular process. Abbreviations: **act**, acetabulum; **ant**, antitrochanter; **ip**, ischial peduncle; **is**, ischium; **ms**, medial shelf; **ru**, rugose surface; **sc**, sacral rib. Hatches signify the damaged parts.
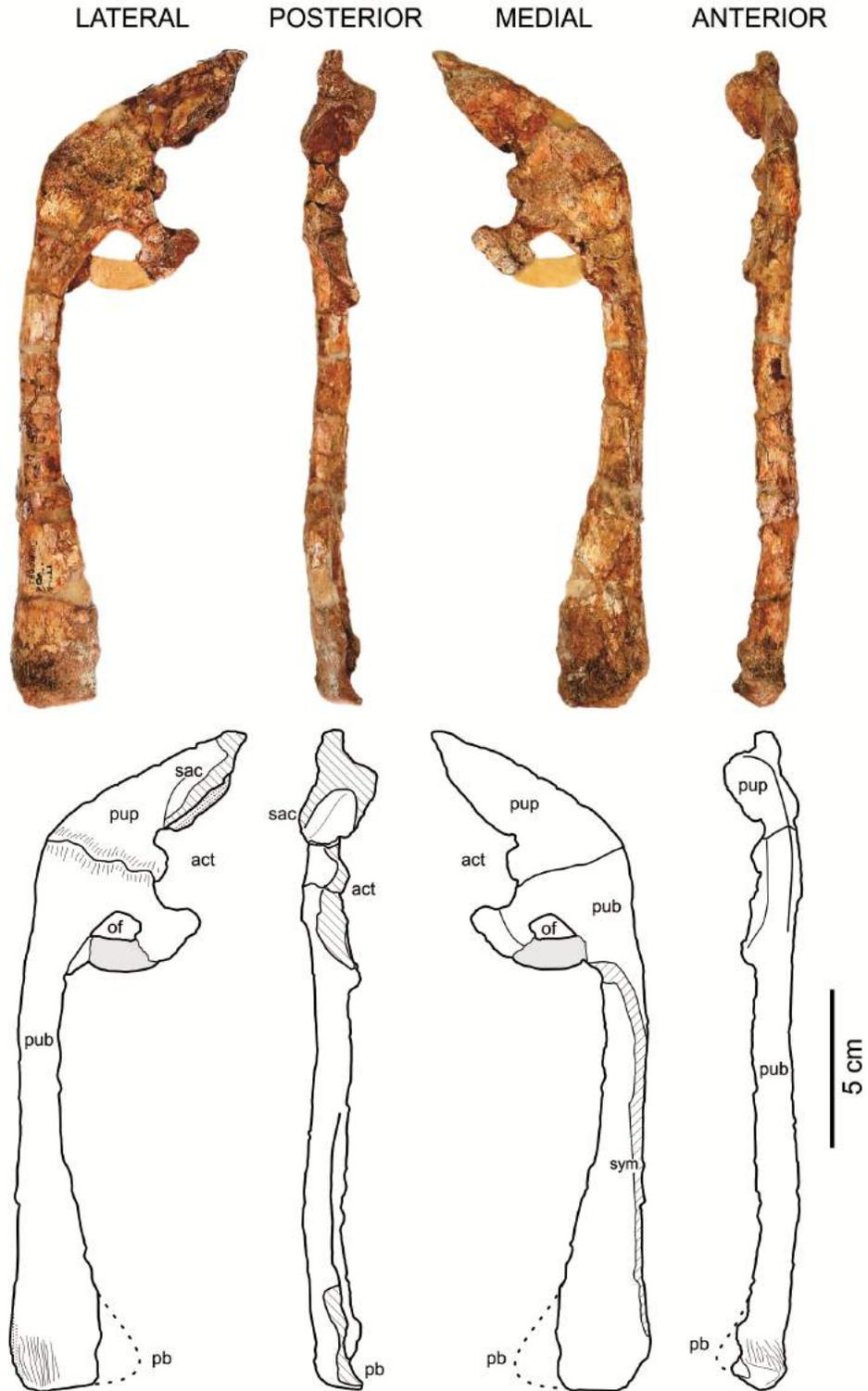
Figure 4.21 Dockum herrerasaurid (TTU-P10082), left pubis and pubic peduncle. Abbreviations: **act**, acetabulum; **of**, obturator fenestra; **pb**, pubic boot; **pub**, pubis; **pup**, pubic peduncle; **sac**, supraacetabular crest; **sym**, symphysis for pubic apron. Hatches signify the damaged parts.

The pubis is nearly complete. Posterior surface of the proximal pubis delimits the open acetabulum with the attached pubic peduncle. The pubic peduncle is mediolaterally compressed and it has a distinct supraacetabular crest on the lateral side. The iliopubic region possesses a distinct suture (i.e. no fusion) and slightly curved, where the pubis becomes ventrally oriented. This condition is comparable with the pubis of *Herrerasaurus*, however the proximal curvature of pubis is greater and extended more posteriorly in *Herrerasaurus* which is regarded as a unique feature of this animal (Novas 1993). The suture region has some rugosity on the lateral surface. The obturator foramen stands ventrally to the acetabulum with a restored ventral margin. A characteristic tuber for the attachment of M. ambiens cannot be identified on the anteroproximal area. The shaft is gradually compressed mediolaterally and expanded anteroposteriorly (*sensu* Novas 1992). The pubic apron is damaged but the median symphysis does not reach to the anterior tip. The anterolateral corner of the pubic tip is slightly rugose and there seems to be a slight bevel on the anteromedial side of the pubic tip, smaller than the one in *Staurikosaurus* which is autapomorphic to this taxon (Novas 1993). The pubic boot is missing on the posterior side that reveals a relatively large surface area. However, the exact dimensions of the pubic boot cannot be inferred.

The postacetabular process of ilium was originally collected as two fragments: one with the antitrochanter and the ischial pedunle, whereas the other representing the posterior blade, including the medial shelf (*sensu* Hutchinson 2001a). Those two fragments were glued together assuming that they were adjacent pieces, on which the pelvic reconstructions of TTU-P10082 are based (Nesbitt and Chatterjee 2008, figures 1c and 1d; Martz et al. 2013, figures 15a and 15b). However, the boundary of two fragments

was discontinuous at the ventral border which indicates that there is a missing portion in-between. The missing part between the two iliac fragments likely housed the origin for M. caudofemoralis brevis. Moreover, the assumed reconstruction creates an anatomically implausible position for the posterior portion of the bone, where the sacral ribs aligned in a posterodorsal-anteroventral axis.

The restored postacetabular process in this work might reveal the true affinity of this individual. In comparison with the only North American herrerasaurid *Chindesaurus bryansmalli* (Long and Murry 1995) it shows distinct similarities on the postacetabular ilium. Both share a long and low postacetabular process with the posterodorsal rugosity and also a pronounced medial shelf on the medial side of the bone. Although no attached sacral vertebrae were found, it is stated that *Chindesaurus* possess the ancestral state of having only two sacral vertebrae because of the small size of the postacetabular process (Long and Murry 1995), where the medial shelf serves a dorsal support only for the second sacral rib (Langer 2004). However, its size is comparable with the TTU-P10082 which possesses two sacral ribs attached on the postacetabular process clearly indicates that TTU-P10082 has a minimum three sacral vertebrae since the first primordial sacral rib is always placed anterior to the ischial peduncle, generally around the acetabular area (Novas 1996; Nesbitt and Chatterjee 2008). Unfortunately, the iliac blades in all ornithodirans found in southwestern North America are incomplete in different parts, thus it does not allow for a descent comparison (Nesbitt and Chatterjee 2008, pp. 145-6). Also the poor preservation of the pubis of *Chindesaurus* holotype does not provide any information for comparison. Nevertheless, concurring with the previous works, TTU-P10082 is a herrerasaurid which is comparable with *C. bryansmalli*.

cf. *Chindesaurus* sp.

TTU-P12531

(Figure 4.22)

Referred specimen **-** Proximal femur, right

Horizon and locality **-** Headquarters South locality (MOTT 3898), Bull Canyon Formation, Garza County, Texas

Collectors **-** Doug Cunningham and Bill Mueller

Description and remarks **-** Periphery of the proximal surface is slightly damaged. The capitulum is well rounded and medially offset with a swollen anteromedial corner. Proximal tubera of the femoral head (*sensu* Nesbitt 2011) and the femoral ligament (ligamentum capitis femoris) groove are absent, or at least very poorly developed on the anteromedial corner. Laterally, the helical trochanteric fossa is highly developed and expanded over the proximal surface, where it obliterates the typical longitudinal groove as documented in many dinosauriforms (fossa trochanterica *sensu* Langer [2004]).

This expanded morphology of the trochanteric fossa is previously diagnosed in *Chindesaurus* and in some specimens of *Herrerasaurus* (Langer, op. cit.). Absence of the femoral ligament groove demarcates TTU-P12531 from the neotheropods (Rowe 1989a), but also from *Herrerasaurus* (Novas 1993). Although no astragalus is preserved for diagnosis, the absence of the femoral ligament groove and the over-expanded trochanteric fossa indicate that TTU-P12531 might be related to *Chindesaurus bryansmalli* (Long and Murry 1995, page 180), but the smaller size and limited expansion of the femoral head clearly distinguishes it from *C. bryansmalli*. Therefore, no definitive diagnosis can be made since only the proximal portion of the femur is preserved.
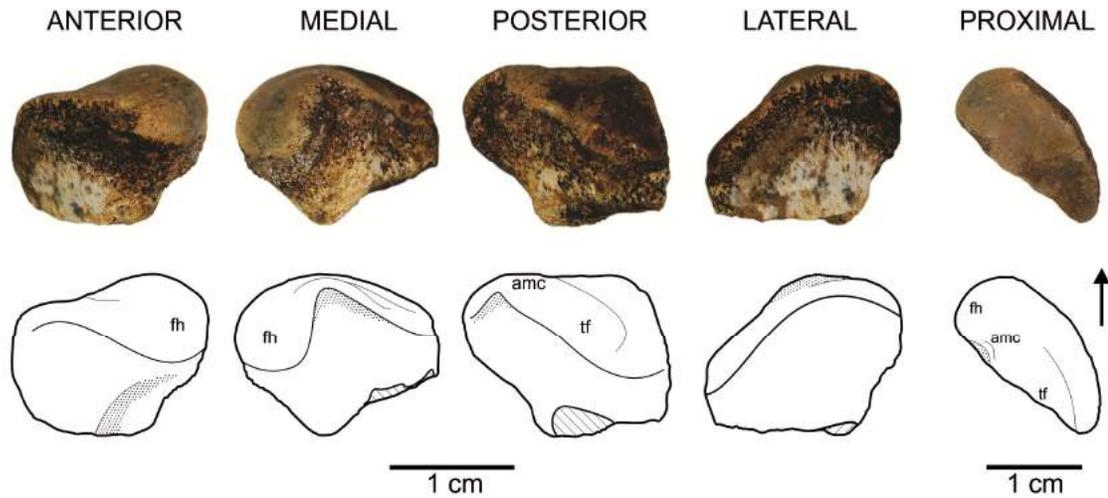
Figure 4.22 Dockum herrerasaurid (TTU- P12531), proximal right femur. Abbreviations: **amc**, anteromedial corner of the proximal femur; **fh**, femoral head; **tf**, trochanteric fossa. Hatches signify the damaged parts. Proximal view has its own scale. Arrow points the anterior side.

THEROPODA Marsh 1881 *sensu* Gauthier 1986

HERRERASAURIDAE Benedetto 1973

INCERTAE SEDIS

TTU-P10072

(Figures 4.23, 4.24, 4.25, 4.26, 4.27, 4.28)

Referred specimen **-** An associated skeleton of a theropod includes various

vertebrae and pelvic fragments, proximal end of left femur, distal end of left tibia and left

astragalus

Horizon and locality **-** Lott Kirkpatrick locality (MOTT 3634), Bull Canyon

Formation, Garza County, Texas

Collectors **-** Yiao-Chun Wu and Sankar Chatterjee

Revised description and remarks **-** The axial skeleton is represented by a series of

isolated vertebrae. Presacral vertebrae include three articulated but fragmented posterior

dorsal vertebrae. Only the anteriormost one of the dorsal vertebrae has a survived centrum which is partially damaged but well rounded and slightly waisted. The articular surfaces are amphiplatyan (*sensu* Romer 1956) with faint rims which possess small peripheral ridges. There is only one partially preserved neural spine and transverse process. The neural spine has a relatively large body but since it is crushed, the exact shape and dimensions are unknown. However the hypantrum is still diagnosable on the anterior side. The transverse process stands on the dextral side and elongated laterally with a diapophyseal facet at the tip. Ventrally to the transverse process, it bears characteristic diapophyseal laminae of all saurischian dinosaurs (Wilson 1999) and a distinct parapophysis. Caudal vertebrae include two fragmented anterior caudal vertebrae and a relatively robust articulated series of middle caudal vertebrae, all amphiplatyan/platycoelous (*sensu* Romer 1956). Anterior caudals possess distinct neural arches with short and posteriorly located neural spines. Posterior caudals consist of 4 articulated elements where the first and the last ones are represented only by their attached halves. Compared to the anterior ones, they are thinner and elongated. They also possess lower neural spines, triangular transverse processes and extended zygapophyses towards the adjacent unit. The remnant of a chevron is preserved between the middle two vertebrae. Chevron facets are not distinct on the ventral side. None of the preserved vertebrae possess any kind of lateral fossae/pleurocoels or ventral groove.
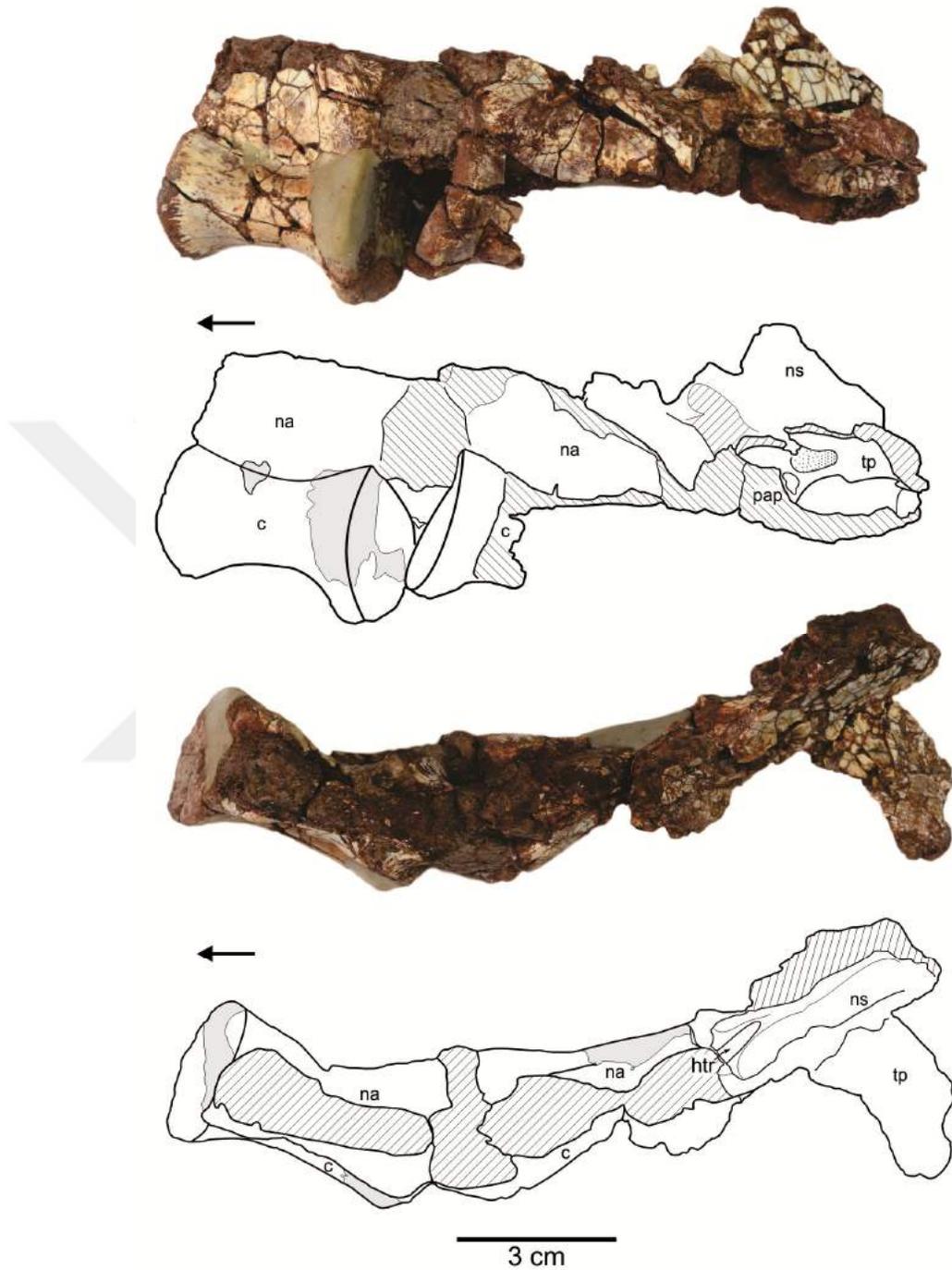
Figure 4.23 Dockum herrerasaurid (TTU-P10072), dorsal vertebral series. Abbreviations: **c**, vertebral centrum; **htr** hypantrum; **na**, neural arch; **ns**, neural spine; **pap**, parapophysis; **tp**, transverse process. Hatches signify the damaged parts. Arrows point the anterior side.
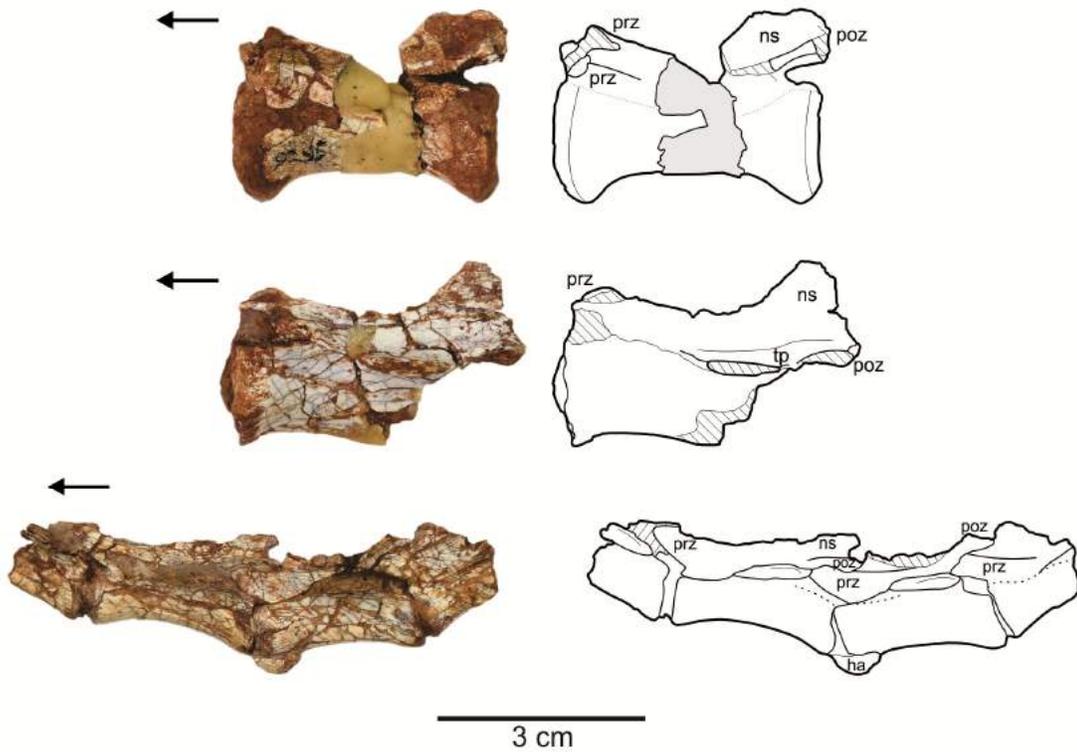
Figure 4.24 Dockum herrerasaurid (TTU-P10072), caudal vertebral series. Abbreviations: **ha**, haemal arch (remnant); **ns**, neural spine; **poz**, postzygapophysis; **prz**, prezygapophysis; **tp**, transverse process. Hatches signify the damaged parts. Arrows point the anterior side.
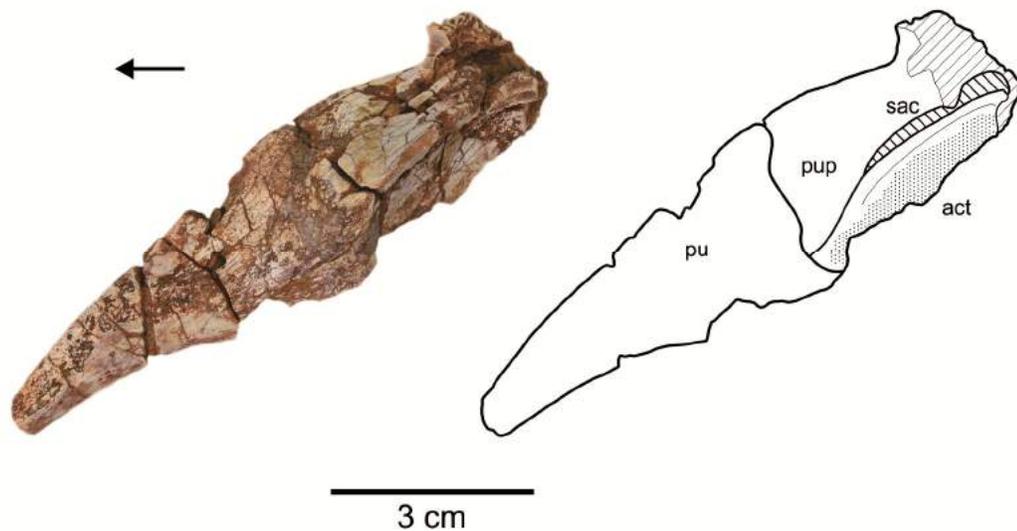


Figure 4.25 Dockum herrerasaurid (TTU-P10072), iliopubic portion. Abbreviations: **act**, acetabulum (the anterodorsal portion); **pu**, pubis; **pup**, pubic peduncle of ilium; **sac**, supraacetabular crest. Hatches signify the damaged parts. Arrow points the anterior side.

Pelvis is incomplete. The proximal part of the right pubis is a slender element without any diagnostic features, slightly crushed and attached to the pubic peduncle by a sigmoidal suture. The pubic peduncle of ilium has a concave posterior surface which constitutes a part of the acetabular border and a thin and worn supraacetabular crest above it which reaches to the iliopubic suture. Additionally, posterodorsal corners of both ilia are also collected. Each iliac fragment possesses a rugose area on the posterodorsal edge with a small process on the posteroventral corner as visible on the left half (*contra* Nesbitt and Chatterjee 2008), and a medial shelf (*sensu* Hutchinson 2001a) on the medial side which is first identified in this work. The medial shelf is more prominent on the sinistral element which projects over the edge of the flat posteroventral end of the ilium. This medial shelf dorsally bounds the sacral ribs, as seen in *Chindesaurus* (Long and Murry 1995), *Herrerasaurus* (Novas 1993; Galton 2000) and basal sauropodomorphs (Young 1942; Benton et al. 2000b). Below the medial shelf, there is a triangular facet with lateral striations which is demarcated from the rest of the ventral surface by a distinct ridge. This facet probably had received the last sacral rib.

## LATERAL



## MEDIAL



## POSTERIOR



3 cm
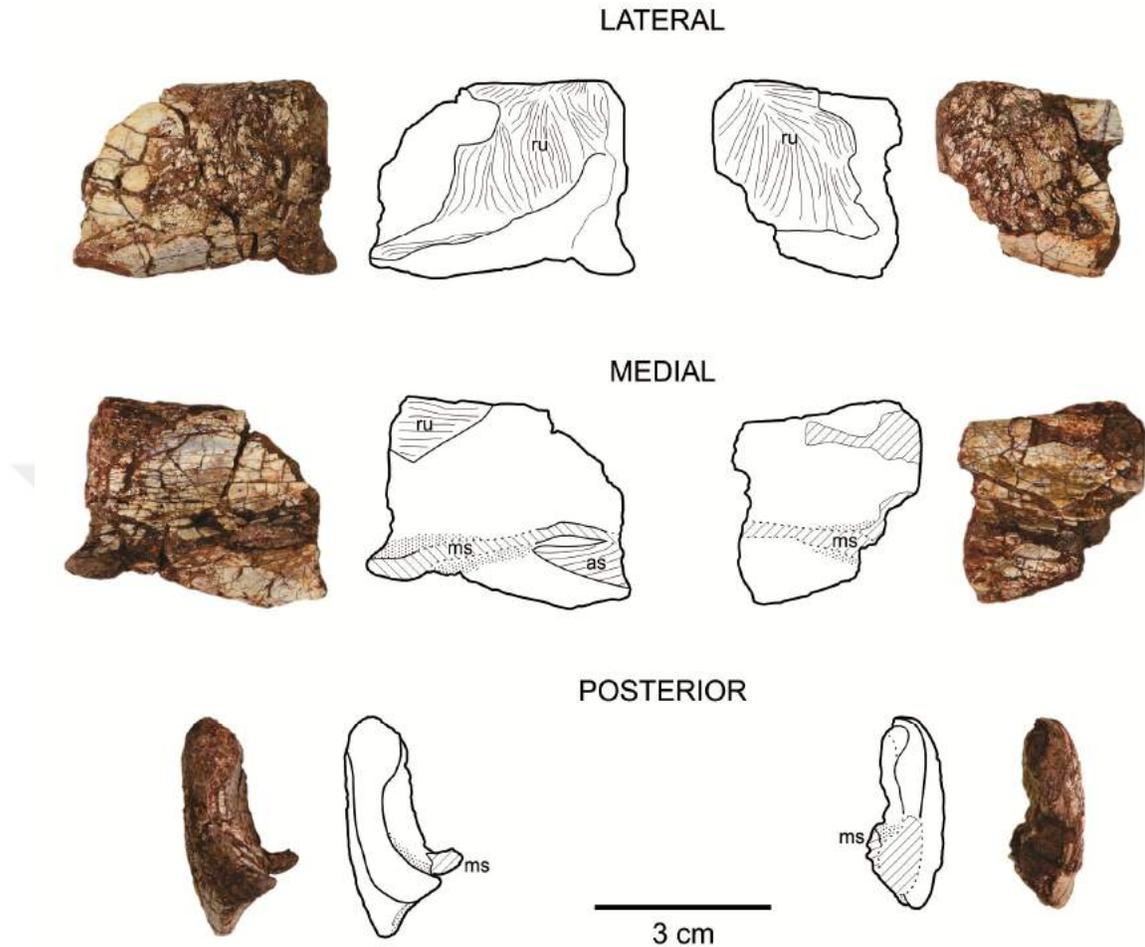
Figure 4.26 Dockum herrerasaurid (TTU-P10072), posterodorsal corners of left and right postacetabular processes. Abbreviations: **as**, articulation surface for the sacral rib; **ms**, medial shelf; **ru**, rugose surface. Hatches signify the damaged parts.

Head of the femur is rounded and possesses all three proximal tubera (*sensu* Nesbitt 2011). Anteromedial tuber is pronounced and curved posteriorly. As well as the groove for the ligament femoris capitis, both anterolateral and posteromedial tubera are well developed. In this context, TTU-P10072 stands more derived compared to the plesiomorphic condition in dinosauriforms, including other herrerasaurids (Nesbitt and Chatterjee 2008; Alcober and Martinez 2010, figure 7F). A distinct trochanteric fossa (facies articularis antitrochanterica) runs distally on the posterolateral margin of the proximal end which expands medially, however not completely as in *Chindesaurus* and

in some specimens of *Herrerasaurus* (Langer 2004) since the proximal groove is still present on the proximal surface. Greater trochanter (or dorsolateral trochanter) stands as a small ridge on the anterolateral margin, placed right below to the proximal end. The anterior trochanter is damaged and the actual shape is unknown. However, it appears that a bulbous ridge had been present there possibly with a trochanteric shelf (Nesbitt and Chatterjee 2008). The well-preserved fourth trochanter is missing the distal end, whereas the preserved portion of the proximal shaft is highly fractured which reveals the hollow nature.
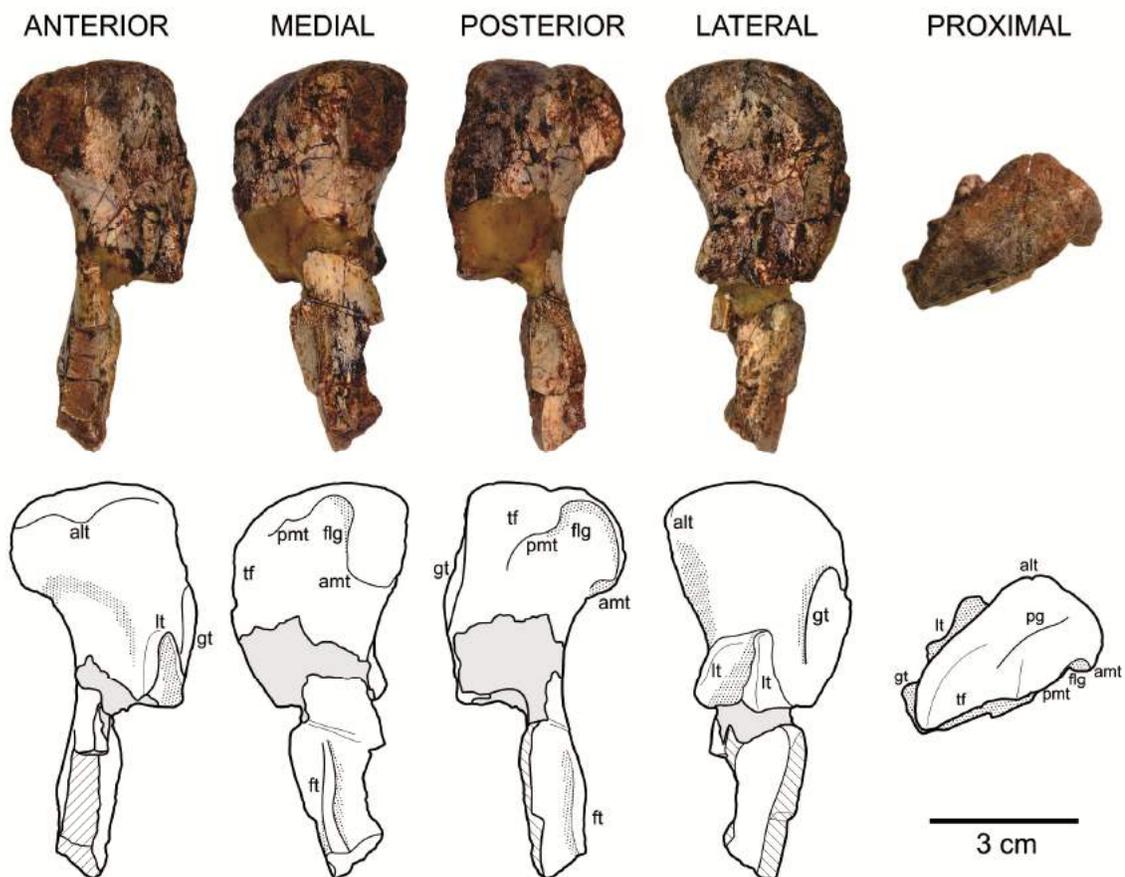


Figure 4.27 Dockum herrerasaurid (TTU-P10072), proximal left femur. Abbreviations: **alt**, anterolateral tuber; **amt**, anteromedial tuber; **flg**, femoral ligament (ligament femoris capitis) groove; **gt**, greater trochanter; **lt**, lesser trochanter; **tf**, trochanteric fossa; **pg**, proximal groove; **pmt**, posteromedial tuber. Hatches signify the damaged parts. Arrow points the anterior side.

Outer surface of the distal tibia is rugose; especially on the anterior and medial sides. The distal surface is sub-rounded, retains an enlarged posterior descending process (a post-fibular wing *sensu* Novas 1989) and a restricted ancestral longitudinal groove which turned into a deeply penetrated, U-shaped articulation facet for the ascending process of astragalus. The posterior process is flattened distally with a ventral notch which fits to corresponding raised process on the posterior border of the astragalus. This type of reception was previously noted for *Chindesaurus bryansmalli* (Long and Murry 1995) *Coelophysis bauri* (Nesbitt and Chatterjee 2008, p. 150). The corresponding left astragalus has a subcardiform or bean-shaped outline with an anterior groove and bears a foramen (extensor canal) on the anterior side of the ascending process. The ascending process is an anterolaterally positioned wedge-shaped structure with a steep lateral border which delimits the fibular facet. Posterior to the ascending process, a dorsal basin which receives the post-fibular wing is demarcated from the rest of the tibial facet by an anteroposteriorly oriented ridge. In this case, the tibial facet is now subdivided to an anteromedial and to a posterior basin, as documented in *Agnosphitys* (Fraser et al. 2002) and various basal saurischians (see Long and Murry 1995; Langer and Benton 2006, character 92 and references therein; Nesbitt et al. 2009a). The broken posteromedial corner of the astragalus is completed with cellulose sculpting medium to a rounded and raised one, concurrent with the rest of the posterior border. The raised process on the posterior border connects to the corresponding notch on the distal tibia (see above). Astragalus articulates laterally to the calcaneum unlike *Herrerasaurus*, *Saturnalia* and other sauropodomorphs where astragalus slightly overlaps with a ventrolateral

articulation the calcaneum (Novas 1993; Nesbitt and Chatterjee 2008). Distal surface is convex which had formed a hinge joint with distal tarsals.
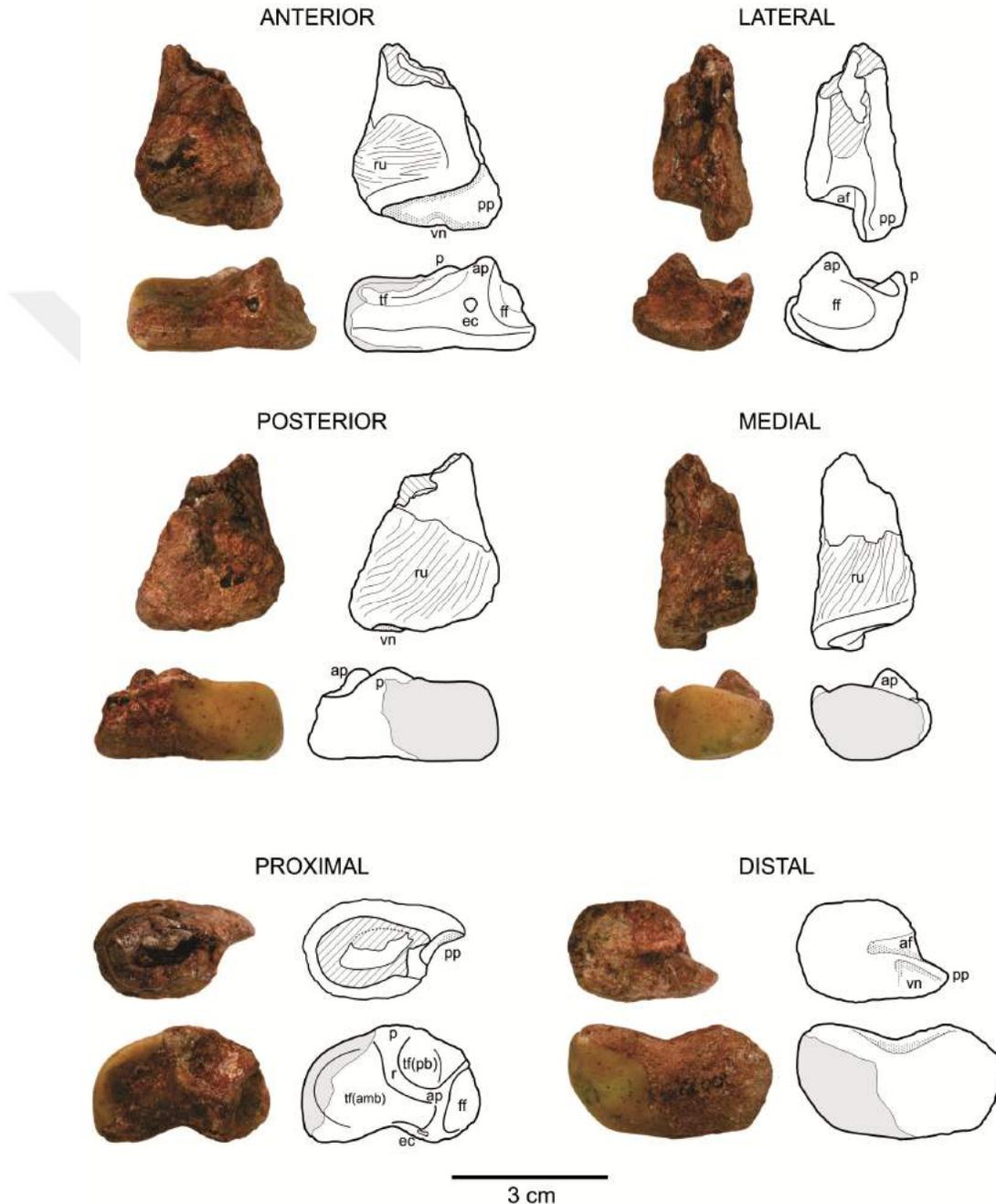


Figure 4.28 Dockum herrerasaurid (TTU-P10072), distal tibia and corresponding astragalus of the right hind limb. Abbreviations: **af**, articulation facet for astragalus; **ap**, ascending process of astragalus; **ec**, extensor canal/foramen; **ff**, fibular facet; **p**, dorsal process of the astragalus; **pp**, posterior process; **r**, ridge; **ru**, rugose surface; **tf**, tibial facet (**amb** for anteromedial basin, **pb** for posterior basin); **vn**, ventral notch. Hatches signify the damaged parts. Arrow points the anterior side.

Additionally, those elements are clustered together with the fragments of vertebrae, ribs and various undiagnosable flat bones. The affinity of TTU-P10072 is previously assigned to Theropoda (*sensu* Gauthier 1986) by Nesbitt and Chatterjee (2008), which now corresponds to Neotheropoda since herrerasaurids are here considered as the basal group of theropods (*sensu* Sereno and Novas 1992; Novas 1993). However, cumulative characters indicate a more ancestral place for TTU-P10072, probably closer to herrerasaurids *sensu* Novas (1992, 1993). The absence of a brevis shelf on the postacetabular ilium (Novas 1993) which concurs with the presence of a medial shelf (Hutchinson 2001a) is the most prominent herrerasaurid synapomorphy of TTU-P10072, whereas the absence of a longitudinal ridge on the posterior side of the distal tibia excludes it from the Neotheropoda (Nesbitt 2011). A derived proximal femur with various tubera and trochanters and an enlarged posterior process on the distal tibia were previously recorded in *Herrerasaurus* and *Chindesaurus*, respectively (Novas 1993; Long and Murry 1995; Langer 2004). On the other hand, the posterior dorsal vertebrae of TTU-P10072 are not peculiarly spool-shaped, but considerably waisted as in coelophysoids.

TTU-P11175

(Figure 4.29)

Referred specimen **-** Complete right tibia

Horizon and locality **-** Headquarters Northwest locality (MOTT 3899), Bull Canyon Formation, Garza County, Texas

Collector **-** Doug Cunningham
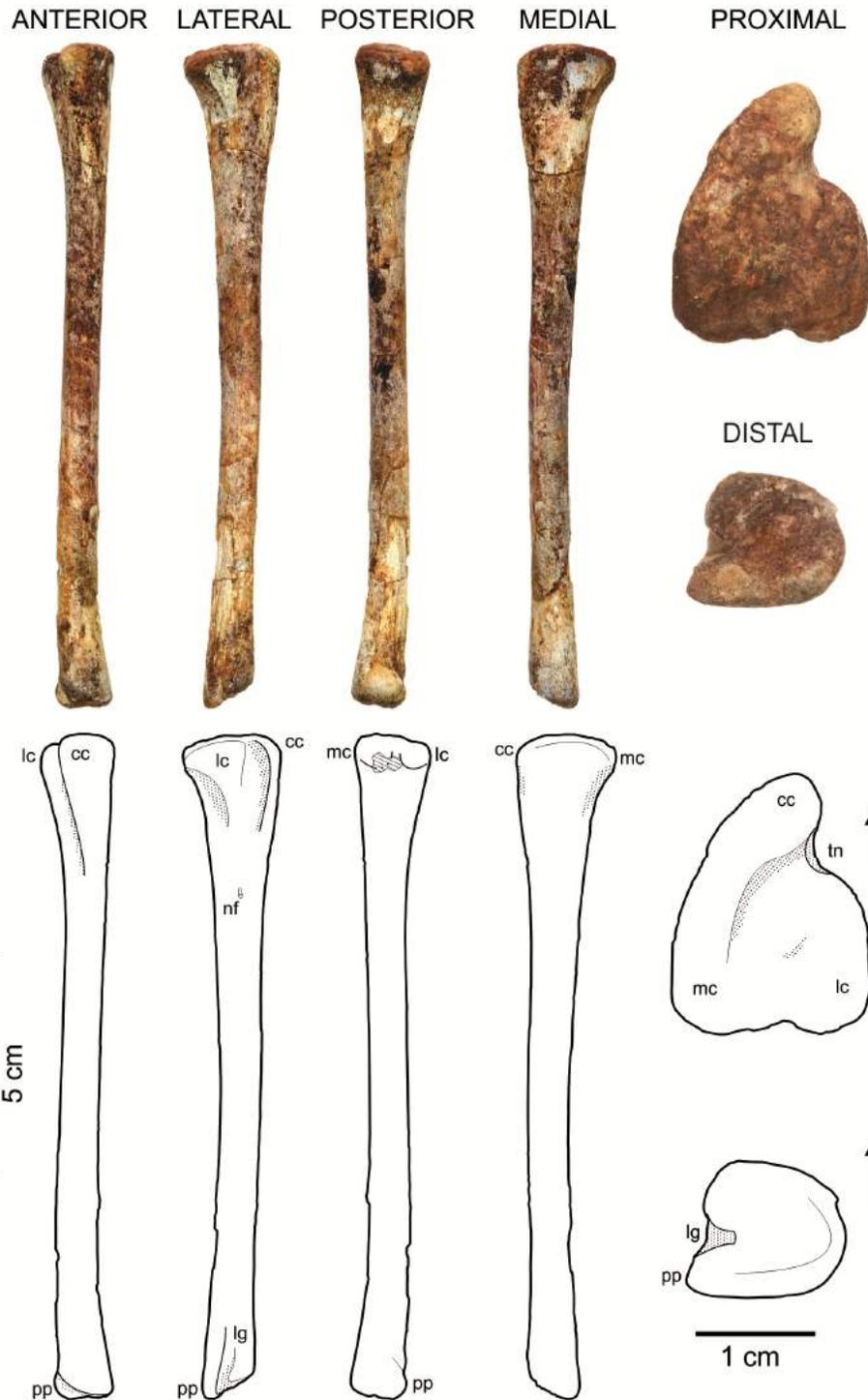
Figure 4.29 Dockum herrerasaurid (TTU-P11175), right tibia. Abbreviations: **cc**, cnemial crest; **lc**, lateral condyle; **lg**, longitudinal groove; **mc**, medial condyle; **nf**, nutrient foramen; **pp**, posterior process; **tn**, tibial notch. Hatches signify the damaged parts. Proximal and distal views share the 1 cm. scale bar. Arrow points the anterior side.

Description and remarks **-** The slender tibia has a sub-triangularly shaped proximal surface with a crescentic cnemial crest with a smooth tibial notch and distinct medial and lateral condyli. The medial border is slightly elevated; the rest of the proximal surface is mostly flat. The posterior condyli are leveled, aligned posteriorly and separated by a notch. The lateral (fibular) condyle has a flattened lateral surface, whereas the medial condyle and the intercondylar notch are slightly obliterated by tool marks. No fibular crest or any other neotheropod characters were present on the proximal side. The shaft is hollow and rounded in transverse section, gets somewhat waisted towards the distal end without any noticeable structure, except the nutrient foramen which stands below to the lateral condyle. The distal end bears a longitudinal groove, contiguous with the ventrolateral notch (*sensu* Novas 1989) on the distal surface for the reception the ascending process of the astragalus. The ventrolateral notch does not deeply penetrate into the distal surface, concurring with the herrerasaurid condition. The distal surface of the tibia is sub-rounded and possesses a small posterior process.

TTU-P12587

(Figure 4.30)

Referred specimen **-** Proximal femur, left

Horizon and locality **-** Macy Ranch (MOTT 3927), Bull Canyon Formation, Garza County, Texas

Collectors **-** Bill Mueller and Doug Cunningham

Description and remarks **-** The topmost portion of the femur is preserved, except the missing posterolateral portion including some of the trochanteric fossa (facies articularis antitrochanterica). TTU-P12587 is identical to the femur of TTU-P10072,

except the minute size and missing proximal groove; therefore the same diagnosis is

applicable.
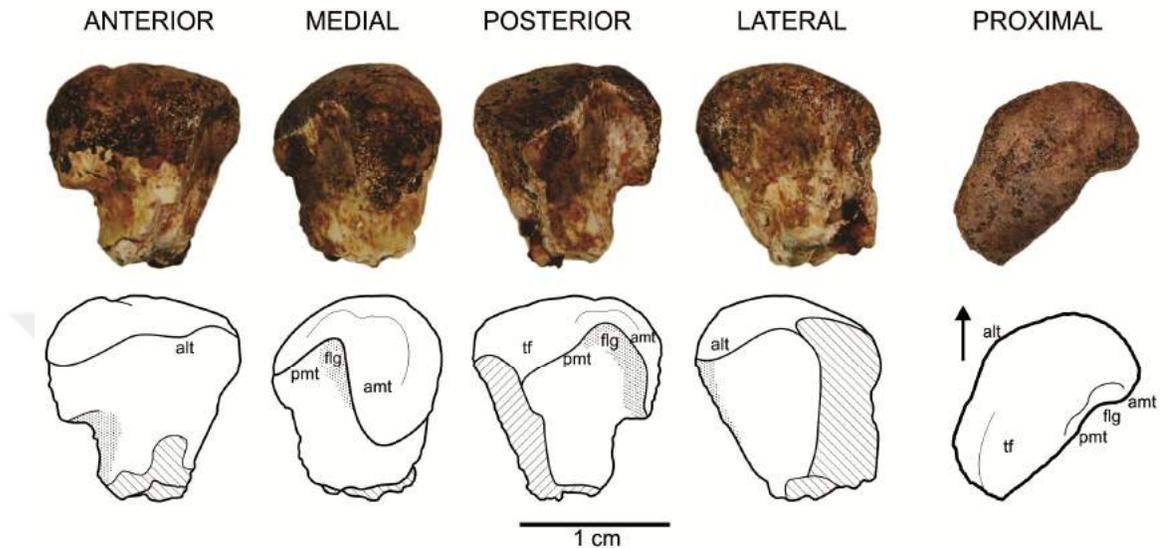


Figure 4.30 Dockum herrerasaurid (TTU-P12587), proximal left femur. Abbreviations: **alt**, anterolateral tuber; **amt**, anteromedial tuber; **flg**, femoral ligament (ligament femoris capitis) groove; **tf**, trochanteric fossa; **pmt**, posteromedial tuber. Hatches signify the damaged parts. Arrow points the anterior side.


TTU-P12790

(Figure 4.31)

Referred specimen **-** Vertebral fragments

Horizon and locality **-** Macy Ranch (MOTT 3927), Bull Canyon Formation,

Garza County, Texas

Collector **-** Bill Mueller

Description and remarks **-** Only a single vertebra is preserved in single piece

which is suitable for a decent description among other associated but highly fragmented

vertebrae. The vertebra is somewhat elongated and waisted; compressed dorsoventrally and

possesses enlarged articular ends and lateral fossae on sides. Both ends are severely damaged

and characteristic large rims around the articular surfaces are completely faded away. Neural

spine is totally obliterated where the neural canal is revealed. Comparative anatomy of TTU-P12790 matches with *Chindesaurus bryansmalli* (PF 10395; Long and Murry 1995), however it is not enough to pinpoint a taxon solely based on vertebral fragments.
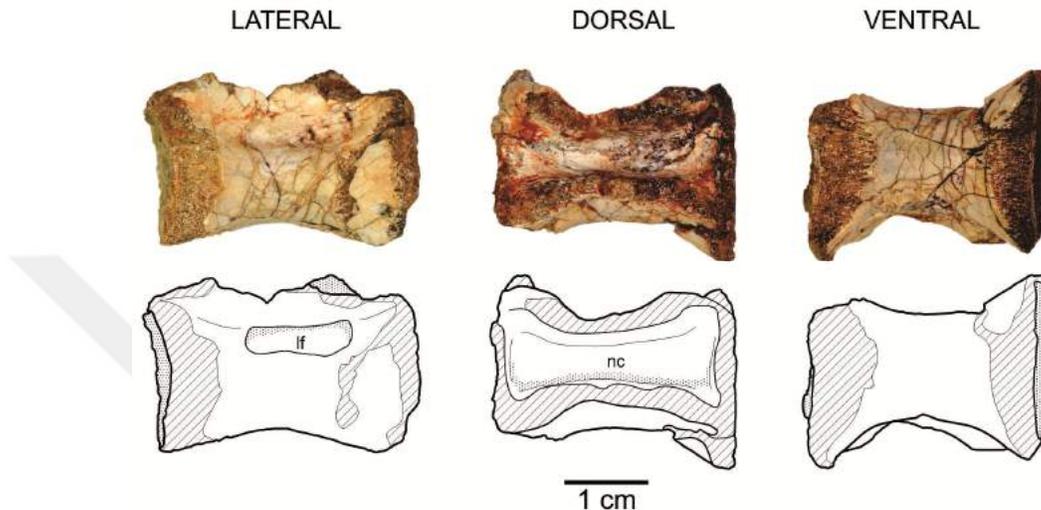


Figure 4.31 Dockum herrerasaurid (TTU-P12790), vertebra. Abbreviations: **lf**, lateral fossa; **nc**, neural canal. Hatches signify the damaged parts.

TTU-P16789

(Figure 4.32)

Referred specimen **-** Posterior dorsal vertebra

Horizon and locality **-** Patricia Quarry (MOTT 3870), Bull Canyon Formation, Garza County, Texas

Collector **-** Bill Mueller

Description and remarks **-** It is a fairly complete vertebra, except damaged anterior face and broken tips of the transverse processes and of the neural spine. The neural spine retains saurischian characters of a hyposphene-hypantrum accessory intervertebral articulation (Gauthier 1986) and principal diapophyseal laminae on the transverse processes as in all saurischian dinosaurs (Wilson 1999). The centrum is

anteroposteriorly short and spool shaped which is diagnostic in herrerasaurids (Novas 1992). Tiny ridges decorate the periphery of the posterior end. The parapophyseal facet is not present on the centrum, therefore indicating that TTU-P16789 belongs to the posterior series of the presacral column. Centrum also has blind fossae on sides. This type of shallow excavations is previously documented in *Herrerasaurus* (Novas 1993) and *Chindesaurus* (Long and Murry 1995) among herrerasaurids, but they are not considered as "true" piercing pleurocoels of derived saurischians (e.g. Wedel 2007).
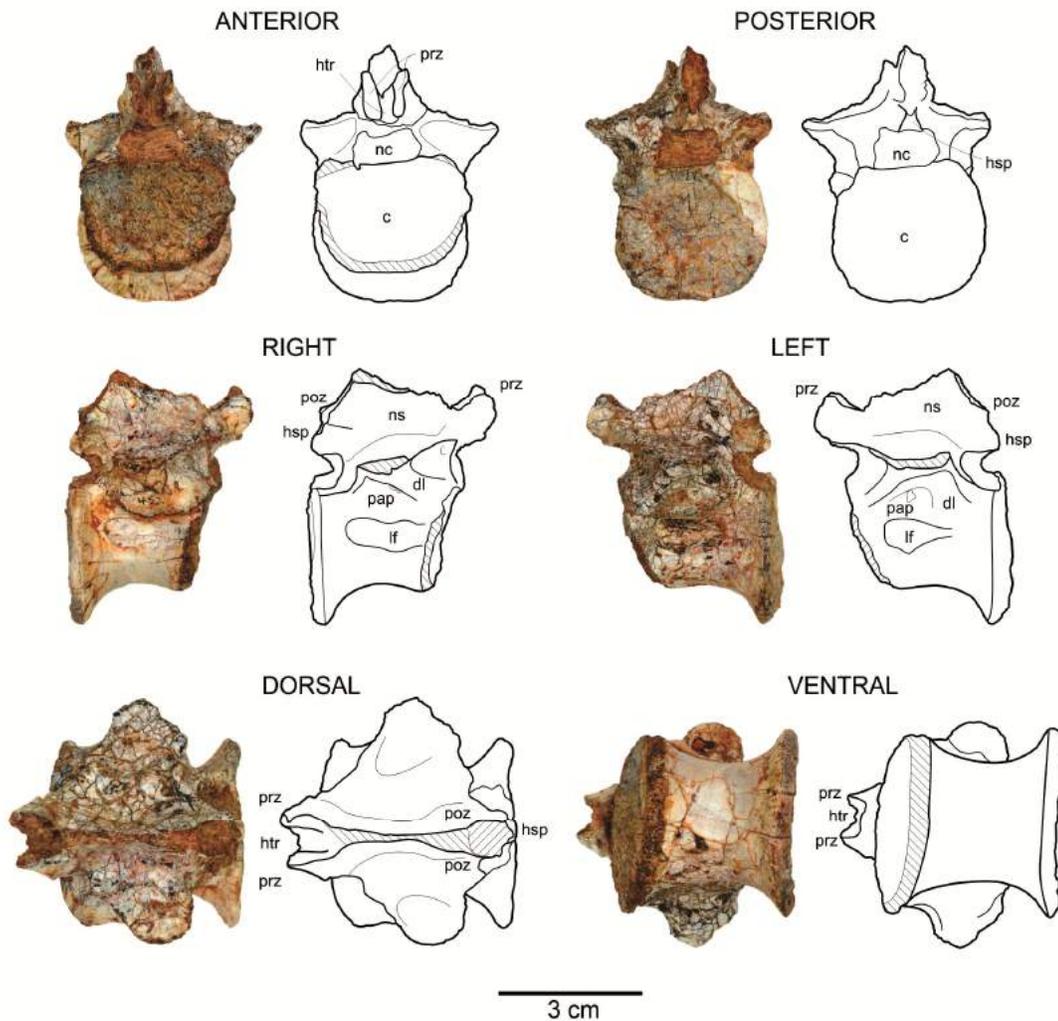


Figure 4.32 Dockum herrerasaurid (TTU-P16789), posterior dorsal vertebra. Abbreviations: **c**, vertebral centrum; **hsp**, hyposphene; **htr** hypantrum; **lf**, lateral fossa; **nc**, neural canal; **pap**, parapophysis; **poz**, postzygapophysis; **prz**, prezygapophysis. Hatches signify the damaged parts.

As a result of convergent evolution, both diapophyseal laminae and hyposphene-hypantrum articulation may occur in paracrocodylomorphs (Wilson 1999; Weinbaum 2013). However, the vertebral centra are relatively elongated in paracrocodylomorphs (*sensu* Nesbitt 2011) rather than being spool shaped (e.g. *Postosuchus kirkpatricki* [TTU-P9002]) and both zygapophyses and hyposphene-hypantrum articulations are relatively gracile in herrerasaurids.

**Coelophysoidea**

THEROPODA Marsh 1881 *sensu* Gauthier 1986

NEOTHEROPODA Bakker 1986 *sensu* Sereno 1998

COELOPHYSOIDEA Holtz 1994 *sensu* Nopcsa 1928

Brief description **-** Pioneering cladistic works (Gauthier 1986; Rowe 1989a, 1989b; Rowe and Gauthier 1990; Holtz 1994, 2000; Tykoski and Rowe 2004) have regarded the clade Ceratosaruia as the cumulative of classical coelophysoids and ceratosaurs, a view which is mostly abandoned today. Nevertheless, a stem-based definition is produced for the clade Coelophysoidea which covers all ceratosaurs closer to *Coelophysis* than to *Carnotaurus* (Sereno 1998), whereas it is also suggested that a similar type of grouping was previously used by Nopcsa (1928), under the suborder Coelurosauroidae. However, the recent attempts could not identify any clades within Coelophysoidea in all most parsimonious trees (Carrano and Sampson 1999, 2008; Carrano et al. 2005; Nesbitt et al. 2009). Therefore, Coelophysoidea serves as a "catch-all" clade that includes all the transitional forms between herrerasaurids and averostrans, in other words, the basal neotheropods (Figure 4.1).

*Coelophysis* is the best known taxon within this group with the beautiful preservations in Ghost Ranch Quarry of the Chinle Group, New Mexico (see Taphonomy section). *Coelophysis* is a slender-built theropod about 2.5 meters long (Figure 4.33) and it is one of the primordial Norian-Rhaetian dinosaurs that extends to the earliest Jurassic (see Rowe 1989a; Irmis 2004). The most complete specimen among three described genera (Cope 1887a, 1887b, 1889), *Coelophysis bauri* was selected as the lectotype by O. P. Hay in 1930 (Colbert 1989). In following decades, *Coelophysis* has become a subject of comparison with other similar type of theropods, such as *Syntarsus rhodesiensis* (Raath 1969, 1977). A remarkable similarity between *Coelophysis* and *Syntarsus* is also recognized by Colbert (1989) and he considered *Coelophysis* as the ancestral form of *Syntarsus*. Later on, *Coelophysis* is referred as the senior synonym for *Syntarsus* (Paul 1988, 1993; Bristowe and Raath 2004). The generic name *Syntarsus* is abandoned recently since it is turned out to be a homonym for a beetle in Colydiinae group (Ivie et al. 2001), and the proposed name *Megapnosaurus* is considered another junior synonym for *Coelophysis*. *Rioarribasaurus* (Hunt and Lucas 1991a) is an invalid attempt to set a new holotype for *Coelophysis* and it is also regarded as another junior synonym for *Coelophysis* (Paul 1993). *Coelophysis* is also regarded as a senior synonym for *Podokesaurus* Talbot 1911 and *Longosaurus* Welles 1984 (Colbert 1964, 1989). Species-level synonym of *Coelophysis bauri* and *Coelophysis rhodesiensis* are listed in taxonomy related publications (e.g. Carrano et al. 2012, p. 227). Documented bone fragments of a small crocodylomorph within the stomach contents of *Coelophysis*, which once interpreted as cannibalism, suggests that this animal was an active predator (Nesbitt et al. 2006).
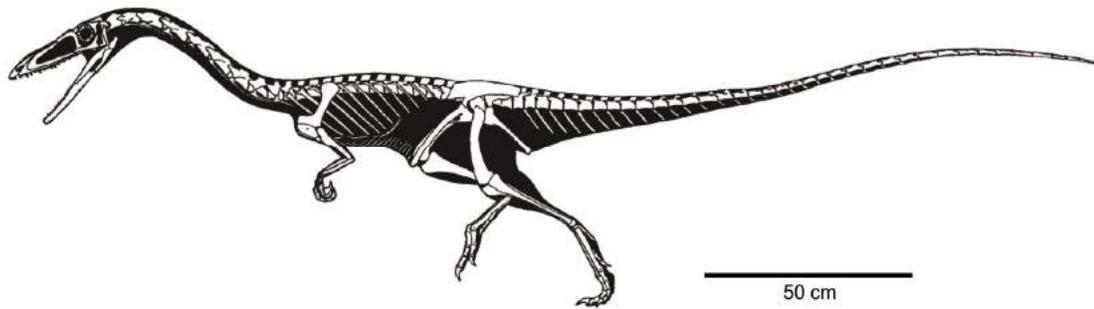
Figure 4.33 Skeletal reconstruction of *Coelophysis bauri* (after Paul 1993)

The rest of the unequivocal coelophysoids can be listed as:

- *Camposaurus arizonensis* (Hunt et al. 1998; Nesbitt et al. 2007; Ezcurra and Brusatte 2011) from the lower part of the Chinle Formation, Arizona (lower Norian).

- *Procompsognathus triassicus* (Frass 1913; Ostrom 1981; also see Sereno and Wild 1992 and Knoll 2008) from the middle Stubensandstein of Germany (upper Norian)

- *Liliensternus liliensterni* (Welles 1984, as the senior synonym for *Halticosaurus liliensterni* of von Huene 1934) from the Knollenmergel (Trossingen Formation, Germany) (upper Norian).

- *Lophostropheus airelensis* (Ezcurra and Cuny 2007, or the "Airel theropod" Cuny and Galton 1993) from the upper sections of French Keuper (upper Norian-Rhaetian).

- *Gojirasaurus quayi* (Carpenter 1997; also see Nesbitt et al. 2007) from the Bull Canyon Formation of New Mexico (upper Norian).

- *Dilophosaurus wetherilli* (Welles 1954, 1970, 1984) from the Kayenta Formation, Arizona (Lower Jurassic).

- *Coelophysis kayentakatae* (Rowe 1989a) from the Kayenta Formation, Arizona (Lower Jurassic).

- *Segisaurus halli* (Camp 1936; Carrano et al. 2005) Navajo Sandstone, Arizona (Lower Jurassic).

- *Coelophysis* sp. (Irmis 2004) and *Sinosaurus triassicus* (Xing et al. 2013, n. comb. for *Dilophosaurus sinensis* Hu 1993) from the Lower Lufeng Formation, China (Lower Jurassic).

- *Panguraptor lufengensis* (You et al. 2014) is the most recent coelophysoid discovery from the Lower Lufeng Formation, China (Lower Jurassic).

*Zupaysaurus rougieri* from the Los Colorados Formation of Argentina is pointed out as a putative Triassic coelophysoid which was originally described as a basal tetanuran (Arcucci and Coria 2003; Ezcurra and Novas 2007). *Sarcosaurus woodi* from the Lower Lias of England (Andrews 1921) might also belong to the coelophysoids as recently suggested (Carrano et al. 2005, but see Welles 1984; Gauthier 1986).

Diagnosis - No strict consensus is present on the monophyly of the clade Coelophysoidea as discussed before (see the description part above), nevertheless, some conditional synapomorphies (i.e. co-existence of multiple characters on the same element) of those coelophysoids or basal neotheropods are proposed here only for tibiae and ilia relevant to the Dockum specimens as: (1) derived ilium with sub-equal peduncle sizes which receives less than six sacral vertebrae (Tykoski and Rowe 2004; Carrano and Sampson 2008) and (2) although it is fused with proximal tarsals in some specimens (e.g. Raath 1969; Colbert 1989; Ezcurra and Brusatte 2011), a typical rhomboidal distal tibia

which is consisted of an expanded posterior descending process (or a post-fibular wing *sensu* Novas 1989) on the lateral side and a longitudinal ridge on the posterior side which is recently recognized as a synapomorphy of neotheropods, including a deeply penetrated diagonal articulation groove on the anterior side with the consequent reduction or loss of the lateral longitudinal groove (Novas 1989, 1996; Nesbitt 2011). In contrast, the astragalotibial articulation pattern of ceratosaurs (*sensu* Carrano and Sampson 2008) is closer to tetanurans, where the outline for the distal tibia is mediolaterally expanded and triangular (Rauhut 2008, character 208), which brings a looser bracing for the ascending process due to the vertical distortion of the step-like process on the anterior side of the distal tibia and the subsequent migration of the ascending process attachment more anteromedially. Additionally, the ascending process even gets more laminar in some ceratosaurs and fused to the anterior side of the distal tibia (e.g. Madsen and Welles 2000; Carrano et al. 2002; Wilson et al. 2003).

**Dockum Coelophysoids**

The Dockum Group of Texas has yielded a variety of coelophysoids (specimens TTU-P10071, TTU-P10534, TTU-P11044, TTU-P14786) as described below.

TTU-P10071

(Figure 4.34)

Referred specimen **-** Ilium with the missing preacetabular process, right

Horizon and locality **-** Tecovas Formation, Post Quarry (MOTT 3624), Garza County, Texas

Collector **-** Sankar Chatterjee

Revised description and remarks **-** The iliac squama is well extended posteriorly; mediolaterally compressed and relatively elevated dorsally. The postacetabular process is trapezoidal in shape, possesses a deep but narrow brevis fossa. The posterior tip of the postacetabularprocess is missing. On the lateral side, the supraacetabular crest is highly damaged but its extent on the pubic peduncle as a thinner crest is clearly traceable. Caudally, the supraacetabular crest doesn't seem to be contiguous with the lateral shelf of the brevis fossa (*sensu* Hutchinson 2001a) (*contra* Nesbitt and Chatterjee 2008; the "lateral brevis shelf" *sensu* Carrano and Sampson, character 118) and such discontinuity is distinguishes TTU-P10071 from *Coelophysis*, at least from *C. rhodesiensis* (Raath 1977, also see Ezcurra and Cuny 2007, figure 5). Medially, the exact number of attached sacral vertebrae is not clear (Nesbitt and Chatterjee 2008); however personal observation shows that there was probably five vertebral attachments *in vivo*, including the dorsosacral on the missing anterior process. In this context, a caudosacral and a dorsosacral joined to the first two primordial sacrals where a second caudosacral supported the ilium only by the transversal processes.  Since the ilium fossilized as an isolate element, it clearly lacks the fusion of the pelvic bones. Pubic peduncle is robust, has an oval and plano-concave articular surface on the ventral side and a concave posterior side. Ischiac peduncle is sub-triangular in shape, smaller than pubic peduncle and possesses an anterolaterally facing antitrochanter. The attachment surface on the ventral side of the ischiac peduncle displays anterolateral and posteromedial articulation facets.

This specimen is affined with the coelophysids in previous works (Lehman and Chatterjee 2005; Nesbitt and Chatterjee 2008), but most recently it is considered as neotheropod, *incertae sedis* (Martz et al. 2013). TTU-P10071 is closer to coelophysoids by the possession of 5 sacral vertebrae and the trapezoidal postacetabular process which is comparable to various coelophysoids (e.g. *Liliensternus*, *Coelophysis*) rather than ceratosaurs which possess minimum 6 sacral vertebrae, confluent lateral ridge and supraacetabular crest, and also very characteristic "peg-and-socket" style peduncle joints in most. Moreover, the relatively small size and less expanded attachment surface of the pubic peduncle clearly manifests that TTU-P10071 is not a tetanuran dinosaur.
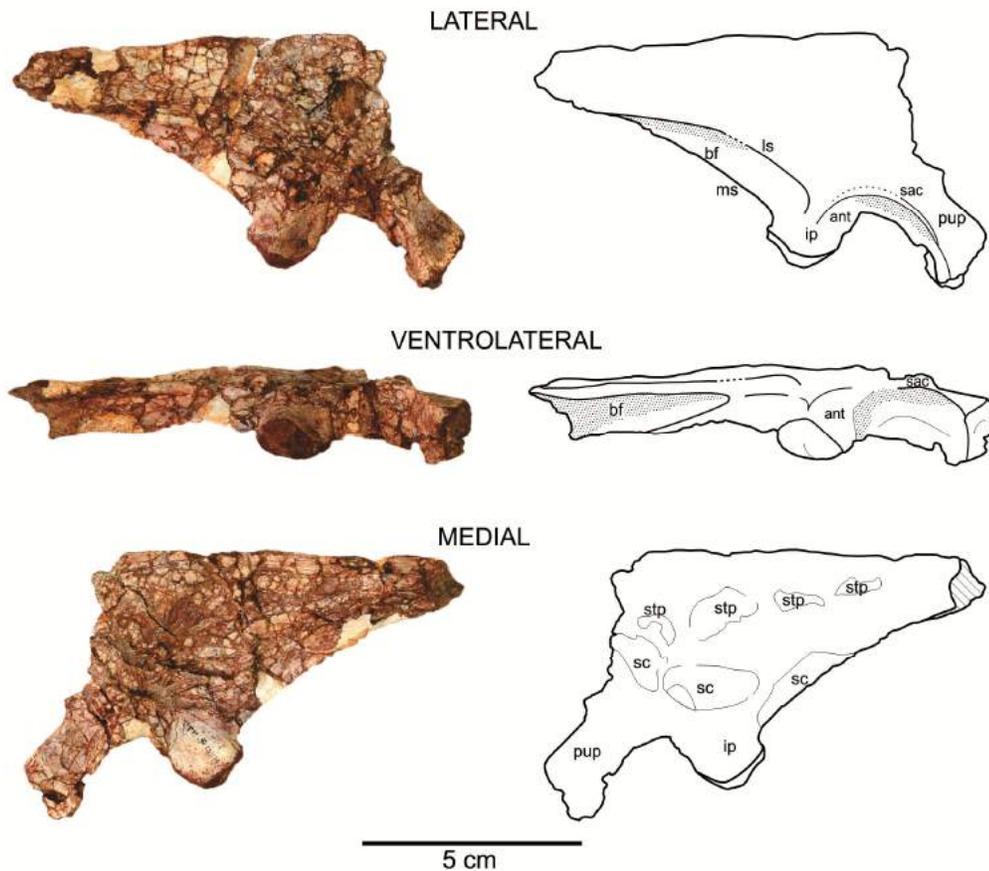


Figure 4.34 Dockum coelophysoid (TTU-P10071), right ilium. Abbreviations: **ant**, antitrochanter, **bf**, brevis fossa; **ls**, lateral shelf; **ms**, medial shelf; **pi**, ischial peduncle of ilium; **pup**, pubic peduncle of ilium; **sac**, supraacetabular crest; **sc**, sacral rib attachment; **stp**, sacral attachment of transverse process. Hatches signify the damaged parts.
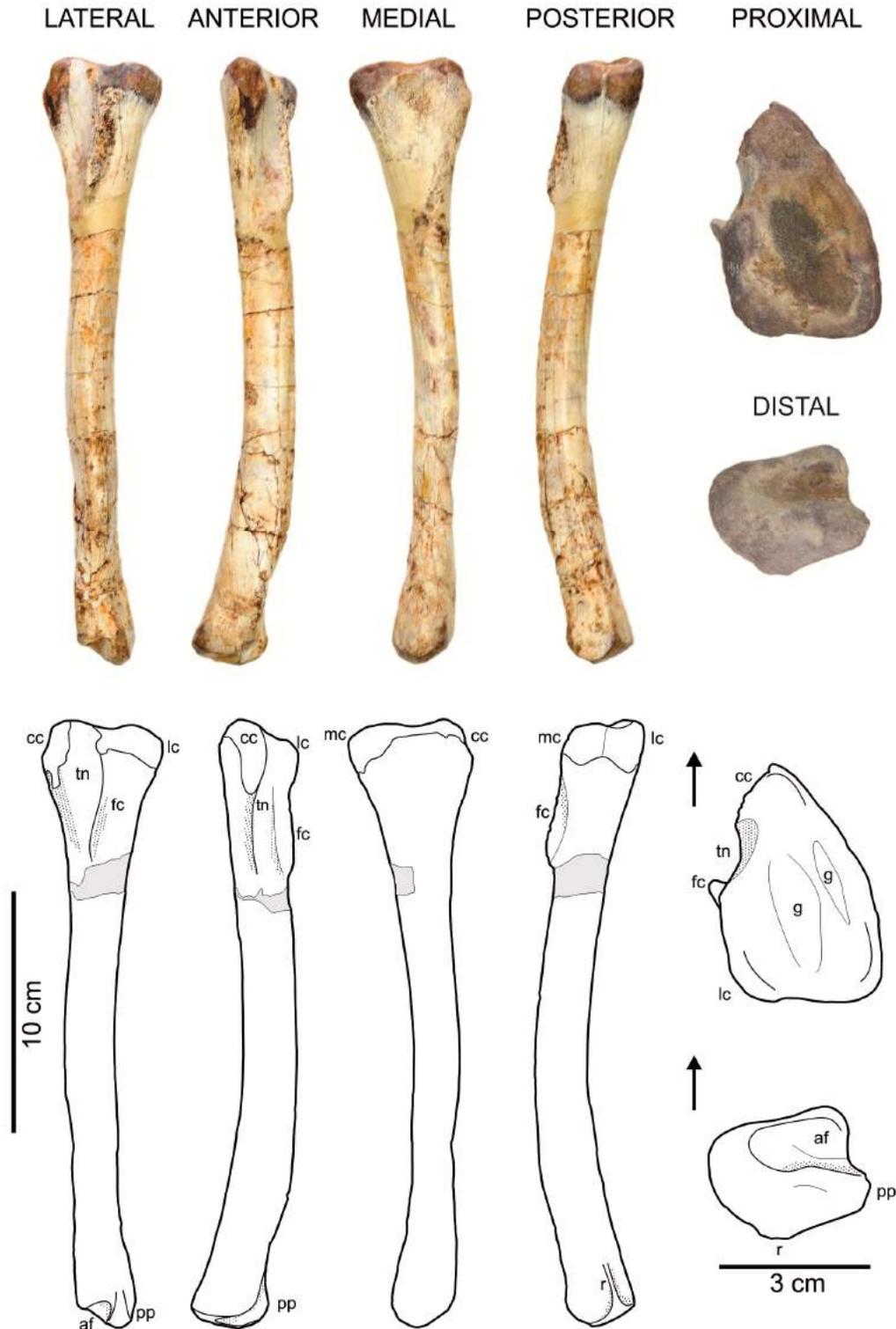
Figure 4.35 Dockum coelophysoid (TTU-P10534), right tibia. Abbreviations: **af**, articular facet for astragalus; **cc**, cnemial crest; **g**, groove; **lc**, lateral condyle; **mc**, medial condyle; **pp**, posterior process; **r**, posterior ridge; **tn**, tibial notch. Hatches signify the damaged parts. Proximal and distal views share the 3 cm. scale bar. Arrows point the anterior side.

TTU-P10534

(Figure 4.35)

Referred specimen **-** Complete left tibia

Horizon and locality **-** Patty East Site (MOTT 3880), Bull Canyon Formation, Garza County, Texas

Collector **-** Doug Cunningham

Revised description and remarks **-** The proximal surface of the tibia is slightly eroded, sub-triangularly shaped, anteroposteriorly longer than wide and the medial edge is somewhat higher than the lateral edge. There is a nicely preserved groove on the medial edge, probably served as an insertion point for some collateral ligament occurring between femur and tibia. Similarly, the central part of the proximal surface is also depressed where it probably housed some cruciate ligaments. Such depression demarcates the cnemial crest from the posterior condyli where it also extends between the two condyli. Both condyli are pronounced where the lateral (fibular) condyle is rounded and slightly smaller than the medial one. The posterior margin of the condyli is contiguous. Anterior part of the cnemial crest is missing but it still stands prominent in basal dinosaur range and it is somewhat bended towards the fibular side, covering a smooth-surfaced tibial notch. A well-developed fibular crest is present on the proximolateral side which gradually bulks distally. The bone was broken just below the proximal head and restored with cellulose sculpting medium from where the nutrient foramen has to be. The shaft is hollow, sub-circular and slightly bowed to the medial side presumably due to poor taphonomic conditions where some cracks and compression marks are visible especially at the distal part, displaying secondary damage. The distal

end is rhomboidal in distal view, possesses an enlarged posterior process (i.e. a post-fibular wing), a deeply penetrated articulation groove for the ascending process of astragalus and a robust longitudinal ridge on distal margin is also present on the posterior side.

Nesbitt et al. (2007) previously mentioned this specimen as the "unnumbered" and identified it as Theropoda *indet*. A robust fibular crest and the distal end pattern manifest the non-tetanuran neotheropod affinity of TTU-P10534 (Nesbitt 2011). Despite being almost at the half size, the tibial morphology is highly comparable to that of *Dilophosaurus* (see Welles 1984), including the robust and poorly flared cnemial crest, configuration and relative sizes of tibial condyli, triangular shape of the fibular crest and the distal tibial pattern with a relatively smaller post-fibular wing. Thus, TTU-P10534 might represent an ancestral form to the Early Jurassic dilophosaurids.

TTU-P11044

(Figure 4.36)

Referred specimen **-** Complete right tibia

Horizon and locality **-** Post Quarry (MOTT 3624), Tecovas Formation, Garza County, Texas

Collector **-** Sankar Chatterjee

Revised description and remarks **-** Proximal surface of the tibia is very well preserved; it is sub-triangularly shaped and anteroposteriorly longer than wide. The cnemial crest is flared in both proximal and lateral axes and it stands as the highest point of the proximal surface. A depression on the central part separates the cnemial crest from

the posterior condyli which probably accommodated some femorotibial cruciate ligaments. The posterior condyli are well pronounced and demarcated by a clear intercondylar cleft. The medial condyle is relatively larger and possesses a higher outer edge. The strong cnemial flare creates a distinct tibial notch, bordered with a small but well developed fibular crest. A fossa of unknown origin is noted on the tibial notch, right between the cnemial and fibular crests. The shaft is slightly worn but still in good shape. It is sub-rounded in transverse section and runs straight to the distal end without any noticeable structure. The distal part is also beautifully preserved and somewhat expanded mediolaterally. The distal end is rhomboidal in distal view, possesses an enlarged posterior process (i.e. a post-fibular wing), a deeply penetrated articulation groove for the ascending process of astragalus and a robust longitudinal ridge on distal margin is also present on the posterior side.

This element is previously mentioned in the 2008 article of Nesbitt and Chatterjee and assigned in the clade Theropoda (*sensu* Gauthier 1986) which recently reassessed as a neotheropod (Martz et al. 2013). In addition, the distal configuration of the bone indicates that this individual is a potential coelophysoid.

TTU-P14786

(Figure 4.37)

Referred specimen **-** Distal tibia, left

Horizon and locality **-** Headquarters South locality (MOTT 3898), Bull Canyon Formation, Garza County, Texas

Collector **-** Doug Cunningham
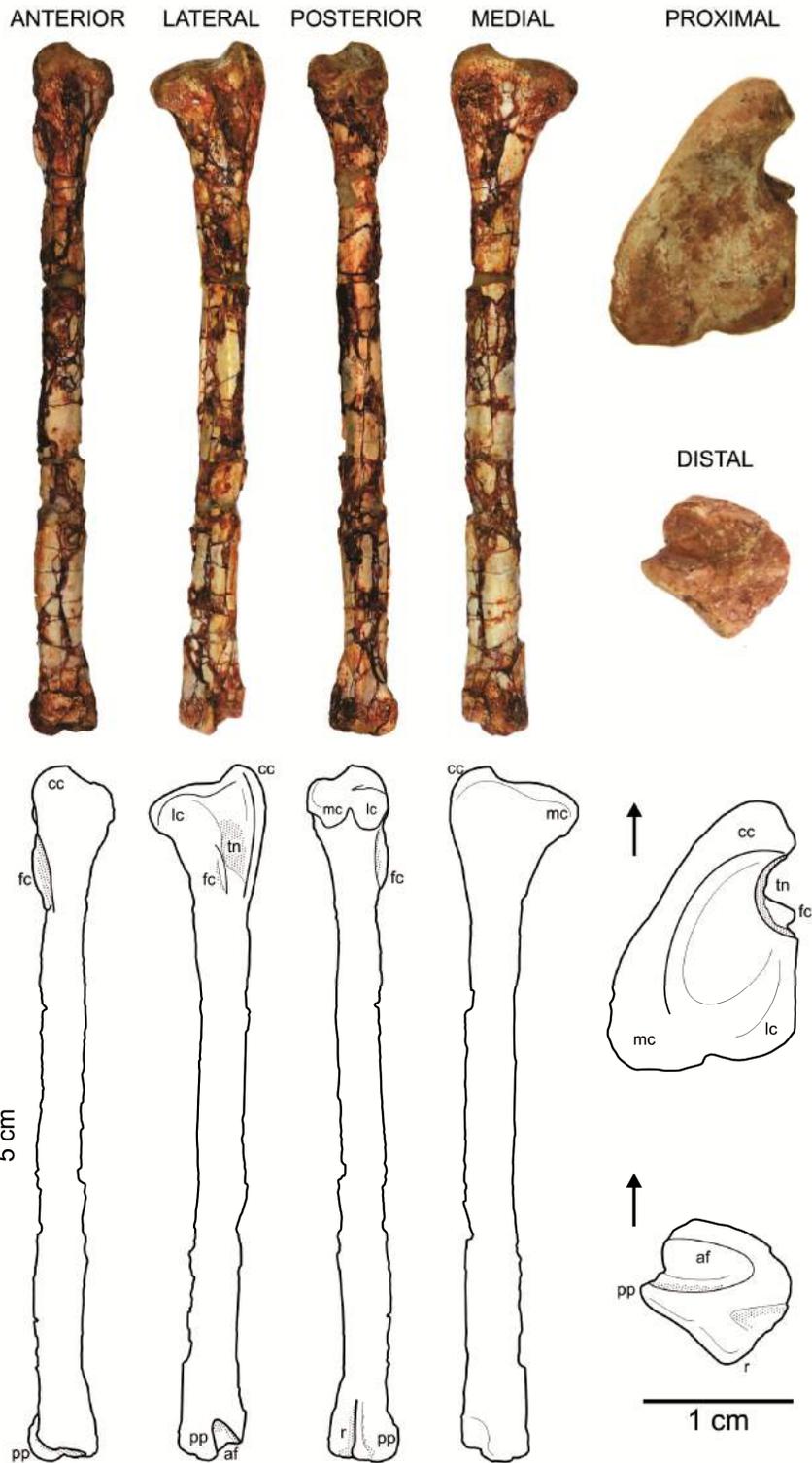
Figure 4.36 Dockum coelophysoid (TTU-P11044), right tibia. Abbreviations: **af**, articular facet for astragalus; **cc**, cnemial crest; **lc**, lateral condyle; **mc**, medial condyle; **pp**, posterior process; **r**, posterior ridge; **tn**, tibial notch. Proximal and distal views share the 1 cm. scale bar. Arrows point the anterior side.

Description and remarks **-** Although only the distal part of the tibia is preserved, presences of a deeply penetrated articulation facet for the ascending process of astragalus, an enlarged posterior process (i.e. a post-fibular wing) on the lateral side and a longitudinal ridge on the posterior side clearly manifests the neotheropod affinity with the rhomboidal distal surface of tibia.
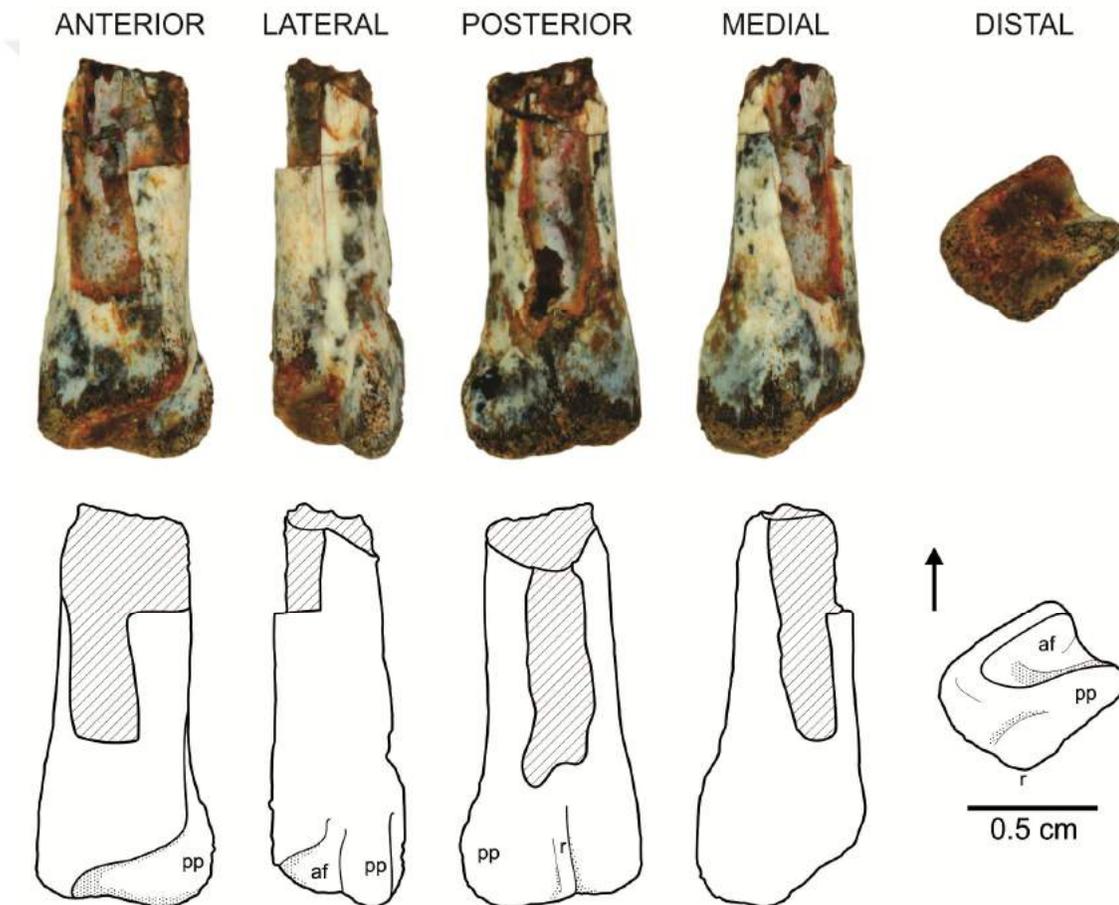


Figure 4.37 Dockum coelophysoid (TTU-P14786), left distal tibia. Abbreviations: **af**, articular facet; **pp**, posterior process; **r**, posterior ridge. Hatches signify the damaged parts. Proximal and distal views share the 1 cm. scale bar. Arrows point the anterior side.

## New Morphotypes of Dockum Theropods

In this section, three new taxa of theropods will be discussed separately from the rest of the dinosauromorph fossils. These new theropod morphotypes include three dentaries from the Boren Quarry (MOTT 3869) (TTU-P10514 and TTU-P10517 as Morphotype 1a and Morphotype 1b, respectively, and TTU-P10515 as Morphotype 2) and intermixed skeletal fragments from the Post Quarry (MOTT 3624) (TTU-P11254a and TTU-P11254b which are referred to Morphotype 3a and Morphotype 3b, respectively). All these new theropods are characterized by miniature and gracile forms, which is an unusual situation for the Triassic Period.

### Morphotypes 1a, 1b and 2

DINOSAURIA Owen 1842 *sensu* Padian and May 1993

SAURISCHIA Seeley 1887 *sensu* Gauthier 1986

THEROPODA Marsh 1881 *sensu* Gauthier 1986

Description - Three small, gracile, and enigmatic theropod dentaries have been recovered from the Boren Quarry (MOTT 3869) of Tecovas Formation. These three specimens were found in close proximity in a 10 cm diameter area. Based on the dental pattern, TTU-P10514 and TTU-P10517 are considered closer as morphotypes based on the similar leaf-shaped posterior dentition, whereas TTU-P10515 probably represents a different morphotype. In life, these early gracile theropods would be about the size of an adult *Archaeopteryx*. These specimens are incomplete and represented only by isolated dentaries. However, unique dental morphology and serration density help to diagnose their theropod affinity. Small size and dental innovation in these taxa provide some

critical insights about the miniaturization of early radiation of theropods. Because of the fragile nature of the specimen, only one side of each specimen was prepared and exposed.

Size, shape, and serration density of theropod teeth **-** In recent times, dental morphology and nature of serration have been used extensively in taxonomic identification of isolated teeth of theropods (Farlow et al. 1991; Ray and Chinsamy 2002; Smith et al. 2005; Larson and Curry 2013). Thus intact teeth within a jaw have a great degree of taxonomic utility. Theropod teeth are diagnosed based on several attributes: fore-aft (mesial-distal) basal length (FABL), tooth crown height, basal (labial-lingual) width, serration density, serration size and the curvature of the apex (e.g. Farlow and Brinkman 1987; Farlow et al. 1991; Smith et al. 2005; Larson and Curry 2013) (Figure 4.38). FABL is measured at or near the level of the proximal (basal) end of the distal tooth keel. Serration density is defined as the serration count per 5 millimeters of tooth keel, a parameter mainly used to classify small to medium sized theropods, where the tooth sizes range from less than a centimeter up to several centimeters. Usually, early theropod teeth are finely serrated. The coarse denticles are not common in Triassic theropods, but widespread in Cretaceous forms such as dromaeosaurids and troodontids (e.g. Currie et al. 1990; Fiorillo and Currie 1994; Sankey et al. 2002; Larson and Currie 2013). Although dental serration is plesiomorphic condition in carnivorous archosaurs, it shows a wide range of variations among different clades. Serration patterns on the TTU-P10514, TTU-P10515 and TTU-P10517 with an oval cross section indicate their theropod affinity. In phytosaurs or rauisuchians, teeth have a D-shaped cross section (Abler 1997). Dental morphology of basal ornithischians and basal sauropodomorphs are remarkably different than theropods e.g. by possessing triangular/spatulate crowns with a

basal constriction (e.g. Gauffre 1993; Chatterjee and Zheng 2002; Norman et al. 2004; Sereno et al. 2013).
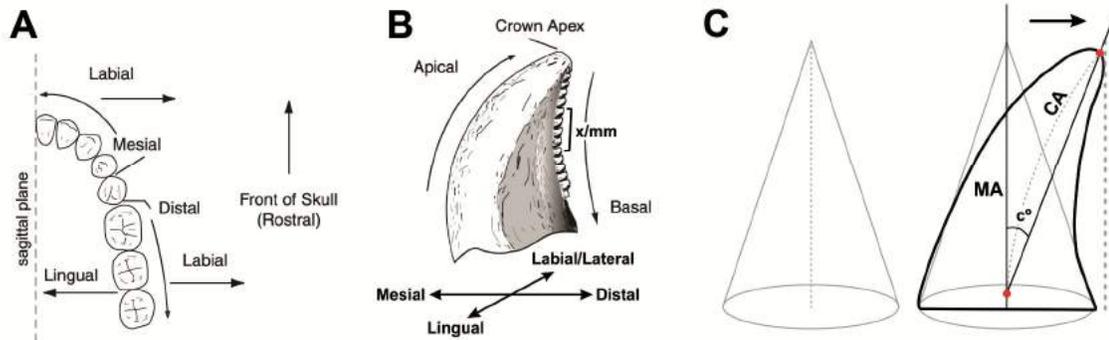


Figure 4.38 Explanatory figures for the dental patterns. (A) Schematic human dental arcade in palatal view showing mesial, distal, labial and lingual directions; (B) Maxillary tooth of theropod *Saurornitholestes* (modified after Currie et al. 1990; Smith and Dodson 2003) with primary directions and the serration density scale per millimeter (x/mm); (C) Apical displacement and crown curvature (modified after Smith et al. 2005), including the curvature angle (c°) added in this work which is defined as the angle between the midline axis (MA) and the segment line drawn from the point of intersection between the midline axis and the curvature axis (CA), to the tip of the tooth.

Diagnosis **-** Highly serrated carnivorous teeth; very slender jaw; median symphysis small, faint, and flexible, restricted to the tip, indicating kinetic jaw.

Morphotype 1a, gen. nov., sp. nov.

Diagnosis – Differs from all known theropods in that the dentary has strongly heterodont dentition; the rostral tooth is conical, unserrated and precumbent, followed by highly recurved, compressed and keeled dentition with relatively coarse denticles; the caudalmost tooth is large, subtriangular, symmetrical, and keeled; Meckelian fossa curved upward at the level of medial symphysis.

TTU-P10514

(Figures 4.39, 4.40, 4.41, 4.42)

<u>Referred specimen</u> **-** Dentary, right side, medial side exposed.

<u>Horizon and locality</u> **-** Boren Quarry (MOTT 3869) Tecovas Formation, Garza County, Texas

<u>Collector</u> **-** Sankar Chatterjee

<u>Description and remarks</u> **-** TTU-P10514 is embedded in the mudstone where only the medial side of the dentary is visible. The jaw ramus is around 2.4 centimeters long and slender, where the symphysis is small, loose, and restricted to the rostral tip, indicating a ligamentous, kinetic attachment. The alveolar margin runs parallel to the ventral margin of the jaw for most of its length, but curves upward rostrally to form a tapered tip. Below the alveolar margin, the Meckelian groove lies close to the ventral margin of the jaw ramus and runs parallel to the caudal end of the jaw. Such a ventral position of the Meckelian groove has been identified in several groups (Nesbitt 2011, p. 101) including dinosauriforms such as *Lewisuchus*, *Silesaurus* and *Sacisaurus* as well as in some basal ornithischians such *Lesothosaurus* (Sereno 1991a) and *Eocursor*.

The total dental count in the preserved section is 11; the first nine teeth are followed by an empty alveolus for the tenth tooth position. The first rostral tooth is slim, conical, long and precumbent without any serrations. The second tooth is transitional and more robust compared to the first one, and somewhat recurved. Teeth 3-9 are serrated, laterally compressed, caudally curved, and mesiolaterally expanded at the base. The fourth tooth stands somewhat larger compared to others. The eleventh, the caudal-most tooth is the most unusual in the series. It is highly expanded mesiodistally with coarse

serrations and becoming symmetrical and leaf-shaped. The nature of the serrations is obscured in many teeth, but they are inclined about 45º towards the apical side. The exact number of serrations is unknown because of poor preservation, but an average of 15 serrations on each keel is estimated in relation to the height of the tooth (~2.5 mm). On the distal side, the serrations are rounded in outline, whereas on the mesial side, they are somewhat pointed. The lingual alveolar margin is reinforced by small and rectangular interdental plates at the base of each tooth, associated with replacement pits, which are termed "special foramina" or "window" (Edmund 1957). In these pits, each replacement tooth germinates and grows in size, and eventually invades the corresponding position of the older tooth. Replacement activity is clear in the jaw, as evidenced by empty alveoli, different tooth sizes, special foramina, and the presence of small erupting teeth.
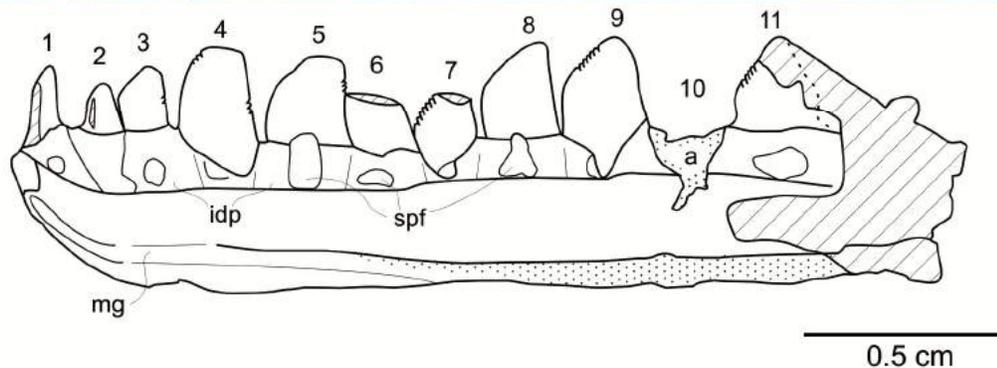


Figure 4.39 Theropoda (TTU-P10514) right side dentary. Abbreviations: **a**, empty alveolus; **idp**, interdentary plates; **mg**, Meckelian groove; **sm**, symphyseal area; **spf**, special foramen. Numbers represent total number of teeth, regardless of preservation.
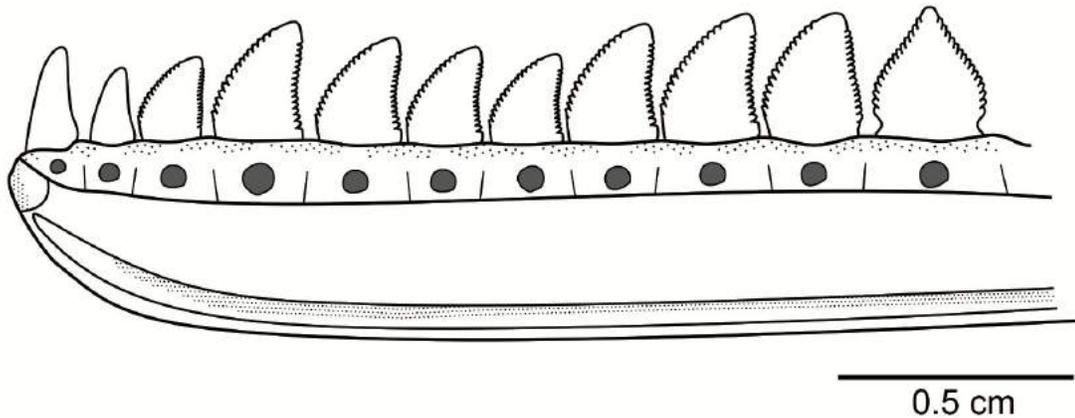
Figure 4.40 Restored right dentary of TTU-P10514.

In TTU-P10514, the crowns of the teeth taper apically but there are great variation of apex displacement and crown curvature along the tooth row from rostral to caudal region (Figure 4.41). The most unusual feature of the dentition is the development of strong heterodonty which is unusual among theropods. The only other theropod with heterodont dentition is known in *Masiakasaurus knopfleri*, a Late Cretaceous abelisaurid from Madagascar (Sampson et al. 2001), if *Eoraptor lunensis* is excluded from the Theropoda (e.g. Sereno et al. 2013). Even at *M. knopfleri*, heterodonty is not as strong as in Dockum specimens where the differentiation only occurred on the keel (Figure 4.42). Probably these heterodont teeth functioned as multipurpose implements for killing and capturing insects and other small animals.

Dental measurements of TTU-P10514

1. mesial-distal basal length (FABL) = ~1.5 mm

2. tooth crown height = ~3 mm

3. serration density = 8-10 per mm for central teeth

4. serration sizes = coarse

5. apical displacement and crown curvature =  ~7º for anterior teeth, ~23.5º for
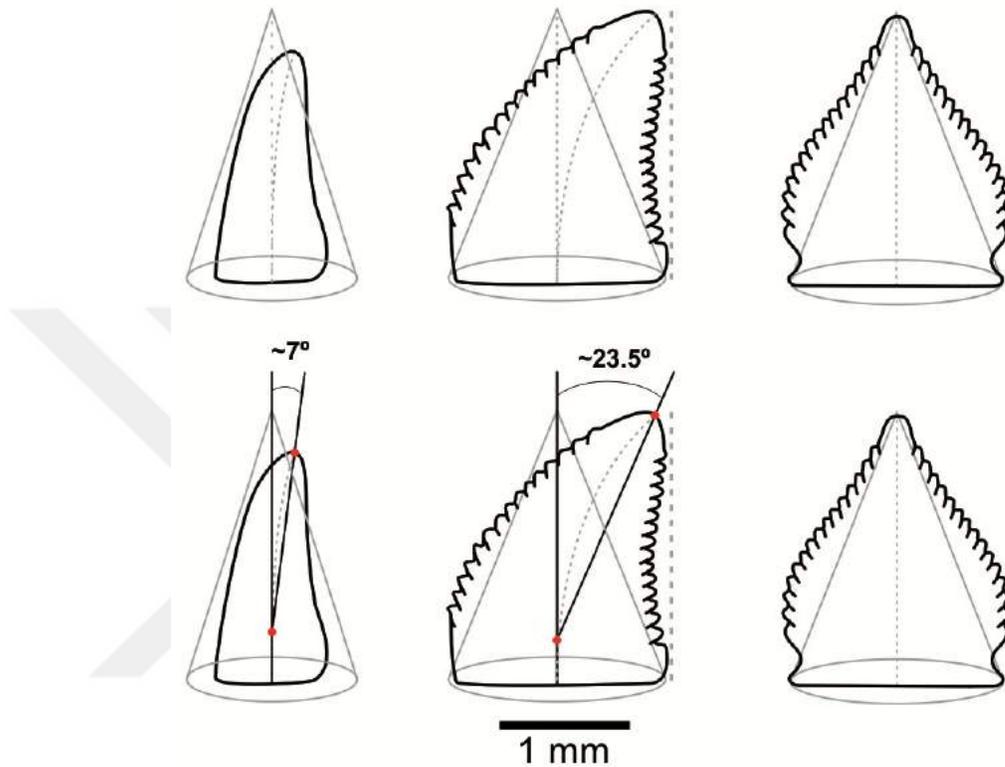
   central teeth



Figure 4.41 Heterodonty of TTU-P10514 with restored teeth: left, conical and caniniform first and second teeth; middle, recurved, laterally compressed and highly serrated central teeth; right, eleventh tooth assumes nearly symmetrical condition without much curvature.
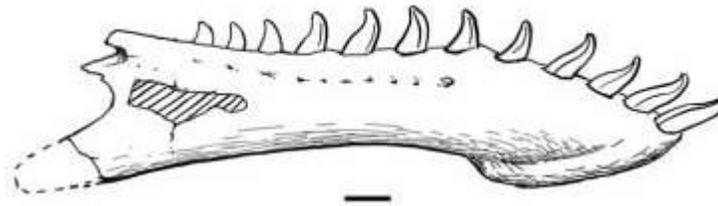


Figure 4.42 Reconstructed dentary of *Masiakasaurus knopfleri*, with full complement of teeth in right lateral view (after Sampson et al. 2001, scale bar 10 mm).

Morphotype 1b, gen. nov., sp. nov.

Diagnosis – Similar to Morphotype 1a, the dentary has strongly heterodont

dentition; central teeth are recurved at the apical side like a utility knife and coarse

serrations on the mesial keel; the caudalmost tooth is large, subtriangular, symmetrical, and keeled; lateral surface of the dentary bears a longitudinal groove.

TTU-P10517

(Figures 4.43, 4.44, 4.45)

Referred specimen **-** Dentary, left side, lateral side exposed

Horizon and locality **-** Boren Quarry (MOTT 3869) Tecovas Formation, Garza County, Texas

Collector **-** Sankar Chatterjee

Description and remarks **-** TTU-P10517 is an incomplete piece of the lateral side of a left dentary, where the rostral and caudal ends are missing. The preserved part is around 1.5 cm in length where the lateral surface is convex and marked by an unusual longitudinal grove. Total dental count in the preserved part is 11, of which six teeth are present; four positions are represented by empty alveoli. The twelfth toot is discernable at the posterior region which is highly obliterated. Central teeth are strongly recurved caudally, compressed sidewise, robust with mesiodistal expansion at the base; keels are serrated with coarse denticles only on the mesial side. Those serrations are inclined about 45° in relation to the long axis of the tooth, but tend to get smaller towards the apex. The eleventh tooth, although it is crushed, is slightly curved, leaf-shaped and shows coarse denticles on both mesial and distal edges. Right below the eleventh tooth, a large, symmetrical upper tooth of the maxilla is plastered on the lateral wall of the dentary; the overlapping nature of the upper tooth indicates that the preserved part of the jaw ramus

belong to the dentary. Heterodonty and is observed at the preserved part of the jaw. There appears to be 13-15 serrations/mm on the mesial keel of the central teeth.

Although TTU-P10517 can be differentiated from TTU-P10514 by the absence of posterior serrations on the distal side and the morphology similar to a utility knife (Figure 4.45), they are considered closer as morphotypes in this work, based on the similar leaf-shaped posterior dentition.
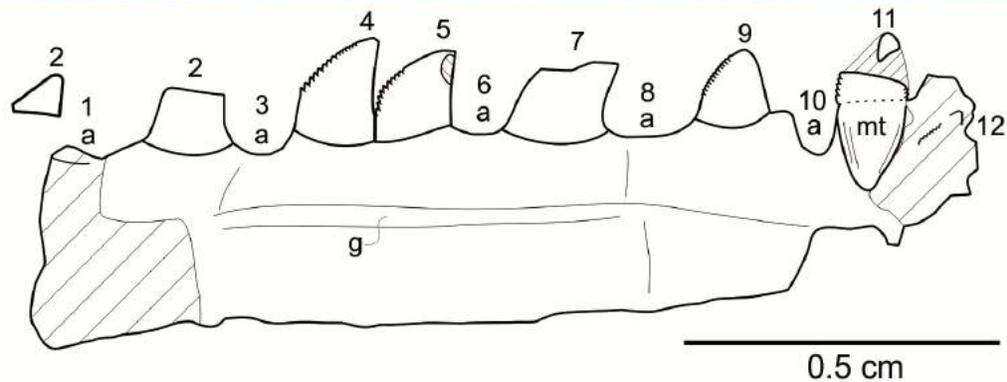


Figure 4.43 Theropoda (TTU-P10517) left side dentary. Abbreviations: **a**, empty alveolus; **g**, longitudinal groove; **mt**, maxillary tooth. Numbers represent total number of teeth, regardless of preservation.

Dental measurements of TTU-P10517

1. mesial-distal basal length (FABL) = ~1 mm

2. tooth crown height = ~2 mm

3. serration density = 13-15 per mm for central teeth

4. serration sizes = coarse

5. apical displacement and crown curvature = ~34.5º for central teeth, ~14º for

    posterior teeth



0.5 cm
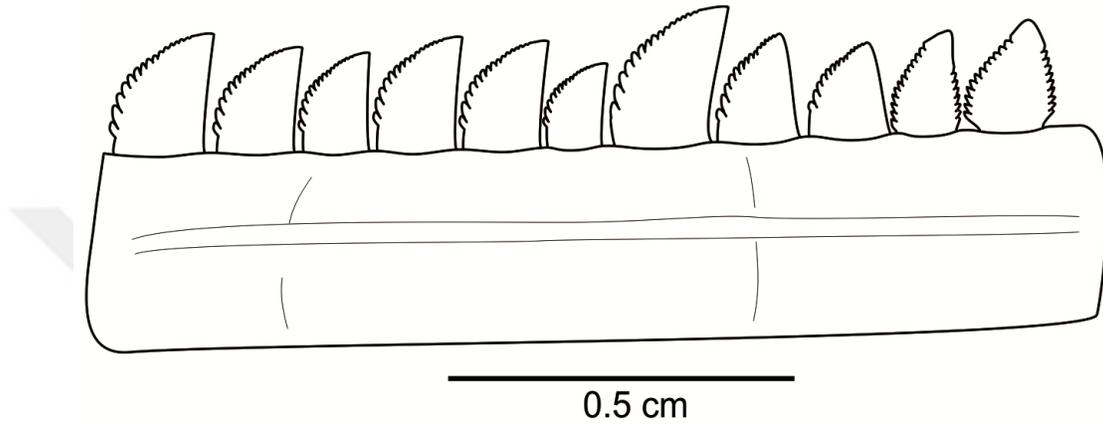
Figure 4.44 Restored right dentary of TTU-P10517.



1 mm
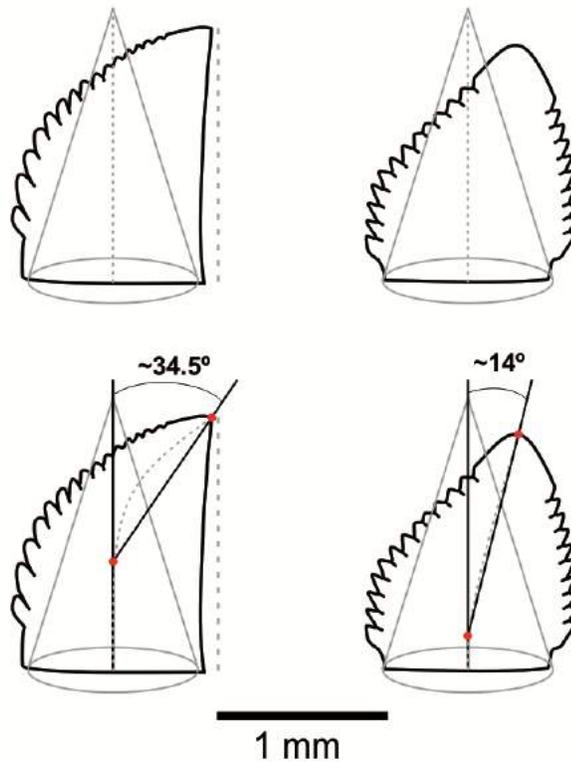
Figure 4.45 Heterodonty of TTU-P10517 with restored teeth: left, strongly serrated central teeth with an apical curvature only at the mesial side; right, eleventh tooth assumes leaf-shaped condition and nearly symmetrical.

Morphotype 2, gen. nov., sp. nov.

Diagnosis - The mesial side of anterior teeth shows sharp angular edge from the tip; whereas the rest of the posterior teeth become increasingly recurved, blade-like and keeled with relatively coarse denticles on both mesial and distal sides. Meckelian fossa curves upward to the level of medial ventral symphysis.

TTU-P10515

(Figures 4.46, 4.47, 4.48)

Referred specimen - Dentary, right side, medial view exposed.

Horizon and locality - Boren Quarry (MOTT 3869) Tecovas Formation, Garza County, Texas

Collector - Sankar Chatterjee

Description and remarks - TTU-P10515 is exquisitely preserved, exposing the medial side of a left dentary. It is slightly longer than 2 cm with parallel alveolar and ventral margins that converge rostrally to the tip. A prominent Meckelian groove runs longitudinally through the central area in between these two margins, but curves upward and extends to the level of the medial symphysis. Alveolar portion is quite distinct with robust and mostly rectangular interdentary plates and associated pits ("special foramina" or "window", Edmund 1957) for replacing tooth. The posterior side of the dentary is crushed.

The total dental count of the preserved part of the jaw is 19, of which 14 teeth are matured, a small replacing tooth in the $16^{th}$ position, and there are 4 empty alveoli. The largest tooth lies in the $17^{th}$ position. The teeth are weakly heterodont, it is not nearly to

the extreme as seen in TTU-P10514. All teeth are laterally compressed and blade-like. The anterior teeth are slim, slightly compressed, and free of serrations; only recurved at the apical region, whereas the rest of the caudal teeth become increasingly recurved, serrated, with mesiodistal expansion at the base. Rostral teeth from 3-8 positions show some unusual morphology where the mesial and distal margins are nearly parallel, except for the upper part of the crown that makes a sharp angular bend from the tip at angle of ~24°. Therefore, the profile becomes similar to that of a utility knife (as observed in the central teeth of TTU-P10517) (Figure 4.48). The mesial serrations are present only at the recurved portion, which are oriented almost parallel to the tooth axis. Strong serrations are present on both distal and mesial sides for the posterior teeth, which are small and pointed in apical direction on both sides. Serrations on the mesial keel tend to get somewhat smaller towards the apex. There are about 12 serrations per millimeter for the posterior teeth on each mesial and distal keel. Serrations tend to get smaller towards the apical portion, at least on the mesial side.

Dental measurements of TTU-P10515

1. mesial-distal basal length (FABL) = ~1 mm
2. tooth crown height = ~2 mm
3. serration density = 8-10 per mm for anterior teeth, ~12 per mm for posterior teeth
4. serration sizes = coarse
5. apical displacement and crown curvature = ~15.5° for anterior teeth, ~24° for central teeth, ~30° for posterior teeth.
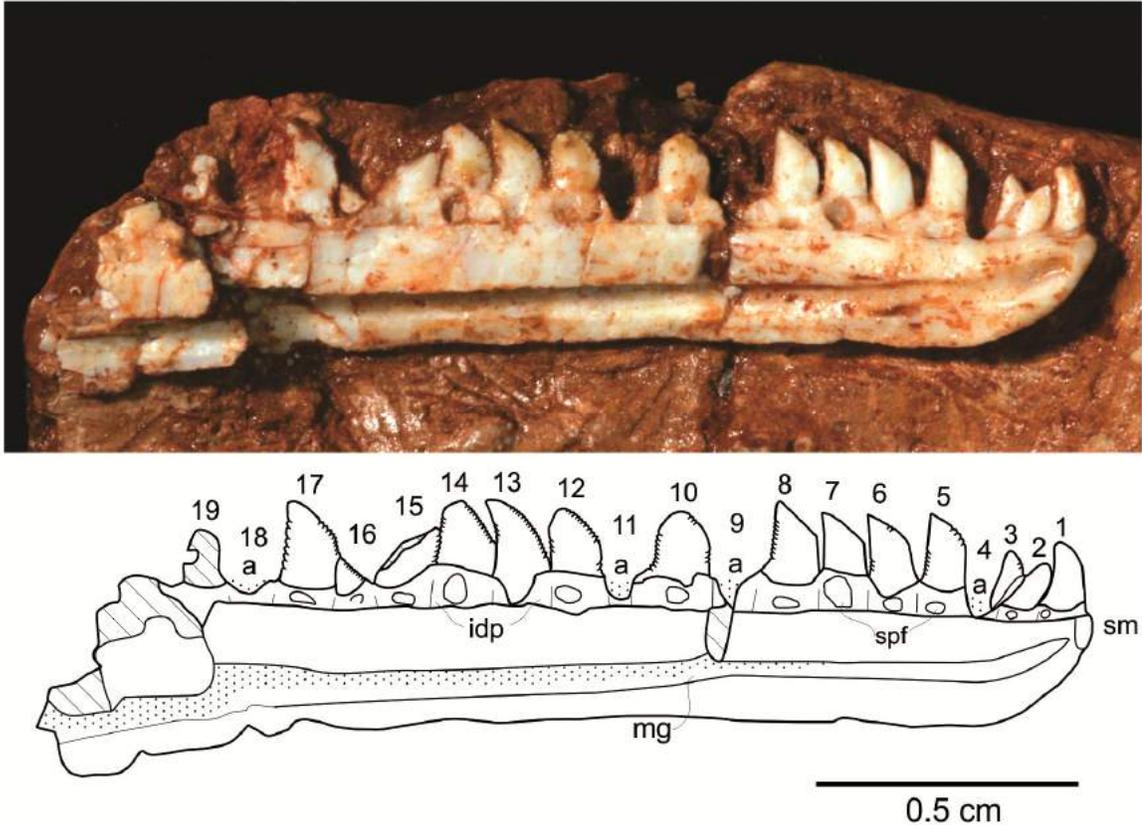
Figure 4.46 Theropoda (TTU-P10515) left side dentary. Abbreviations: **a**, empty alveolus; **idp**, interdentary plates; **mg**, Meckelian groove; **sm**, symphyseal area; **spf**, special foramen. Numbers represent total number of teeth, regardless of preservation.
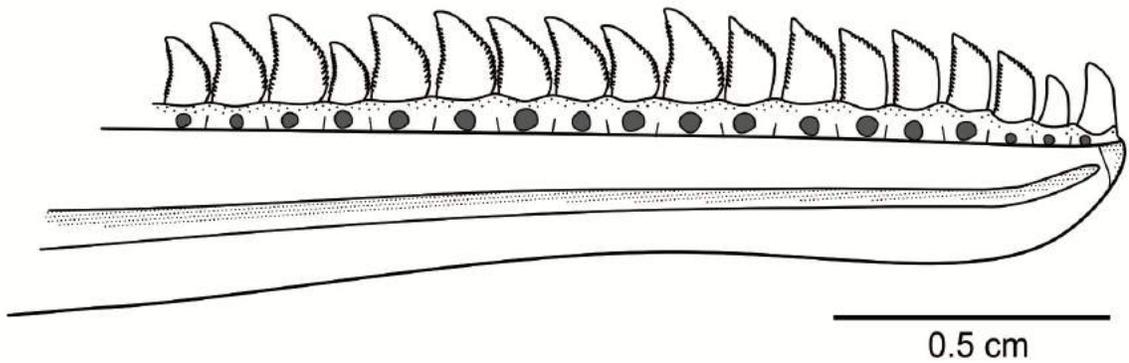


Figure 4.47 Restored left dentary of TTU-P10515.
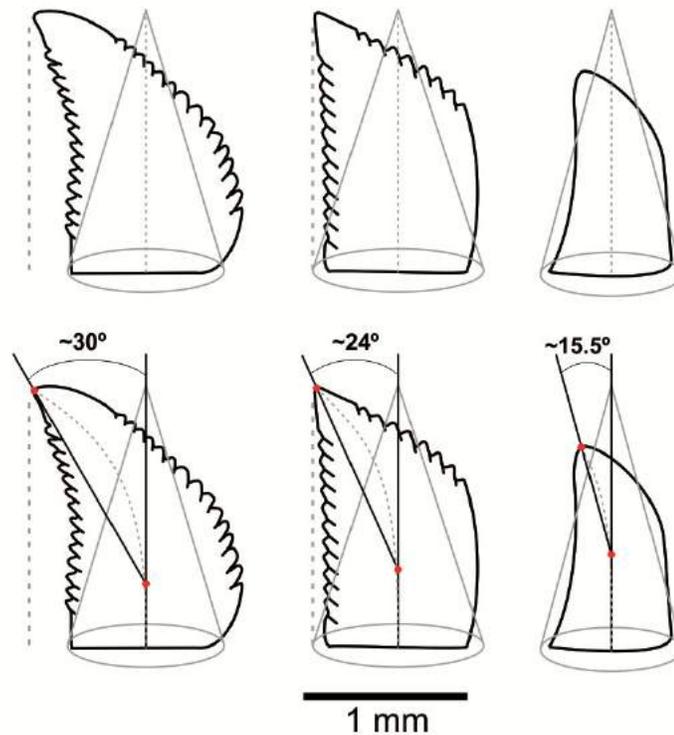
Figure 4.48 Heterodonty of TTU-P10515 with restored teeth: left, highly recurved, laterally compressed and highly serrated posterior teeth; middle, laterally compressed central teeth with serrations along entire distal keel and on the curved apical postion of the mesial keel; right, unserrated, slim and caniniform first and second teeth.


**Morphotypes 3a and 3b**

DINOSAURIA Owen 1842 *sensu* Padian and May 1993

SAURISCHIA Seeley 1887 *sensu* Gauthier 1986

THEROPODA Marsh 1881 *sensu* Gauthier 1986

MANIRAPTORA Gauthier 1986

<u>Brief description</u> **-** Maniraptorans are a diverse group of theropods made up of

alvarezsaurids, therizonosaurus, oviraptorosaurs, deinonychosaurs, and avialans that

evolved true broad contour feathers. They are distinguished from other coelurosaurs by

an encephalized skull; elongated forelimbs; an ulna with curved shaft; a semilunate carpal

with a swivel wrist joint; a bony sternum; an ischium with a broad obturator notch and a

reduced distal symphysis; a backward pointing pubis; and a stiff, dynamic tail which is strengthened by ossified tendons (e.g. Agnolin and Novas 2013). A typical maniraptoran such as *Velociraptor* is shown below (Figure 4.49)



Figure 4.49 Skeletal reconstruction of *Velociraptor mongoliensis* (image credit Scott Hartman 2013)

Description - Soumya Chatterjee, then a high school student, found these unusual and delicate specimens during the summer of 1993 from the bone bed of Post Quarry. The skeletal elements were partly associated and were jacketed for careful preparation in the laboratory (Figure 4.50). Zheng Zhong, who was a graduate student from China and also a skilled preparator, prepared the specimen under a binocular microscope. However, an extensive description of these elements is introduced in this work for the first time. After close examination, it appears that the mudstone block yields two different individuals, a larger and a smaller individual, with intermixed fragments, which can be distinguished from the great size disparity. The larger individual (TTU-P11254a, Morphotype 3a) is about the size of a crow and it is represented by the postorbital-frontal portion of the skull and associated series of cervical vertebrae. The smaller individual (TTU-P11254b, Morphotype 3b) is about the size of a sparrow and it is represented by partial braincase, partial lower jaw, scapular blade, partial pelvis and limb elements.

Intermix of these skeletal fragments resulted in a similar taphonomic condition to those of *Protoavis* (e.g. Chatterjee 1999). However, these two morphotypes cannot be certainly referred to the same taxon as in the case of *Protoavis* specimens, due to the lack of common skeletal elements.

To retrieve and free the bones from the mudstone matrix for future 3-D anatomical study was a challenging job, especially for the smaller individual. For example the limb bones of the smaller individual were extremely delicate and fragile (the shaft diameter is ~2 mm wide). Some of the bones were shattered while exposing for the smaller individual; the fused astragalocalcaneum, a typical diagnostic bone of a theropod was lost forever during the preparation (Sankar Chatterjee, personal communication). These two specimens represent the earliest record of maniraptoran theropods from the Late Triassic deposits and provide critical information of the transition of avialans from theropod ancestors. The small body size and phylogenetic position imply that extreme miniaturization was ancestral for Paraves (Lee et al. 2014).
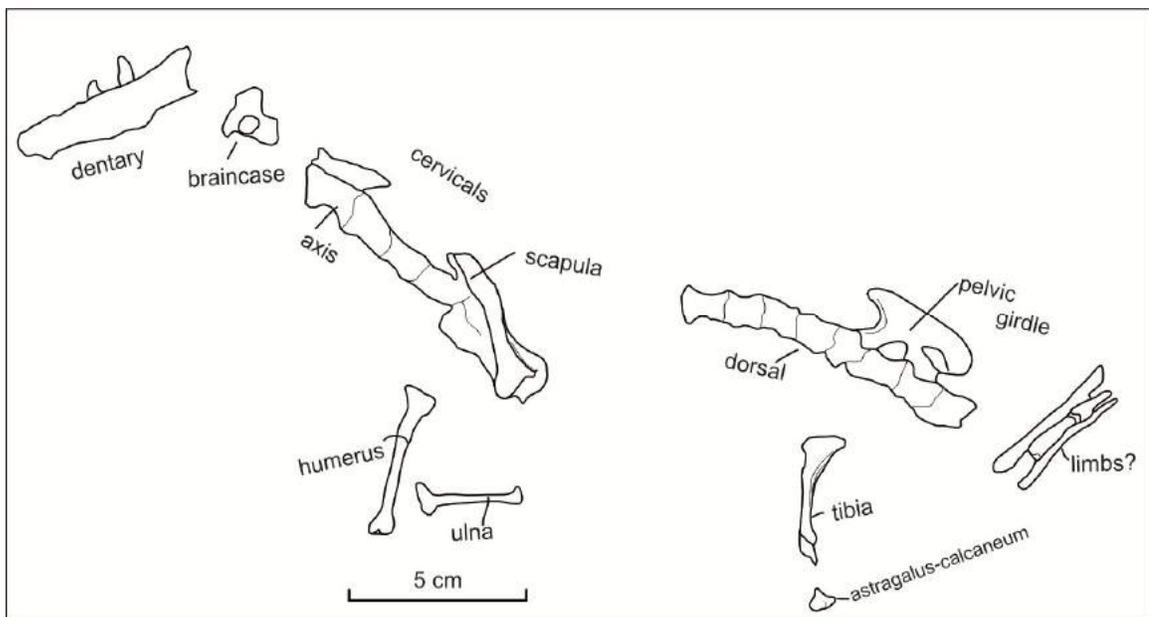


Figure 4.50 Field sketch for TTU-P11254a and TTU-11254b (redrawn after Sankar Chatterjee's field book). Note that the postorbital bone was not depicted in the sketch.

Morphotype 3a, gen. nov., sp. nov.

Diagnosis - Postorbital with anterodorsally curved frontal process; cervicals lacking neural spines with strong hypapophyses and posterior caudals elongated and procoelous.

TTU-P11254a

(Figures 4.51-4.53)

Referred specimen - Right postorbital-frontal, partially articulated vertebral column, isolated caudal vertebrae.

Horizon and locality - Post Quarry (MOTT 3624), Tecovas Formation, Garza County

Collector - Soumya Chatterjee

Description and remarks - The postorbital is a triradiate bone in side view that forms the postero-dorsal margin of the orbit. The dorsal bar extends forward and backward as tapering processes to receive the frontal and squamosal respectively. The frontal process is curved anterodorsally to meet the frontal, as in all maniraptorans (e.g. Turner et al. 2012). The descending process curves around the orbit and is bifurcated ventrally to receive the jugal. Medially the squamosal abuts against the frontal. The frontal is incomplete, but shows a straight median symphysis to articulate with its opposite fellow (Figure 4.51).
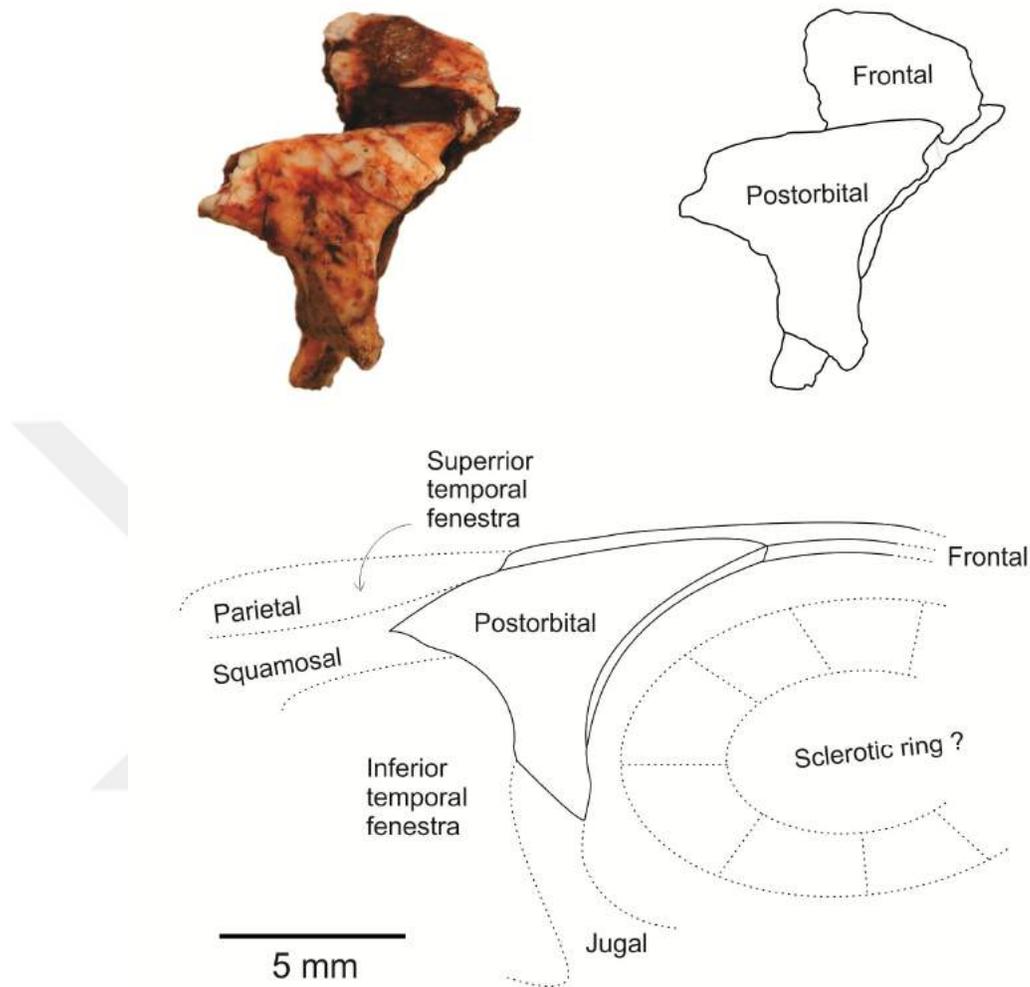
Figure 4.51 Dockum maniraptoran (TTU-P11254a) right postorbital-frontal.

Two articulated segments of vertebral column are preserved: four anterior cervicals and eight posterior cervicals (Figure 4.52). In addition, three isolated caudals are present. The vertebral column appears to be long and lightly built. In the anterior cervical series (C2-C5), the axis is followed by three more cervicals. The centra are elongated and bilaterally compressed with the development of a ventral keel. Anterior to the keel, a prominent hypapophysis is present in all cervicals as in maniraptorans. The centra are platycoelous except for the axis; the latter bears an odontoid process anteriorly

for atlas intercentrum. The three components of the axis–the odontoid, intercentrum, and the axis proper–are fused. The axis is highly elongated in the series, with strongly offset cranial and caudal articular surfaces indicating upward arch of the neck, which was probably long and flexible. The axial neural spine is enlarged, compressed mediolaterally to form a sharp dorsal edge that slopes cranially but extends caudally beyond the postzygapophyses; the postaxial neural spines are dorsoventrally low. In the third cervical, the neural spine is weakly developed and the parapophysis lies low down at the anterior rim of the centrum. In the remaining cervicals the pre- and postzygapophyses are long, horizontally directed, and extend beyond the faces of the centra, indicating great degree of mobility of the neck. In the fifth cervical, the hypapophysis is divided into two ventral flanges in the caudal aspect as seen in some modern birds.
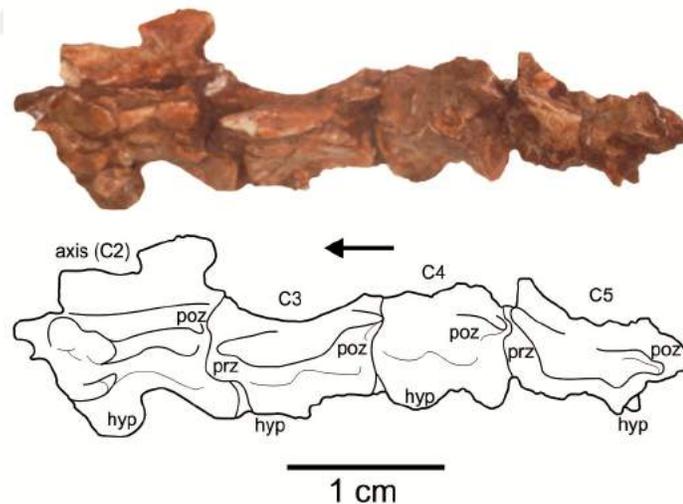


Figure 4.52 Dockum maniraptoran (TTU-P11254a) anterior cervical vertebrae. Abbreviations: **hyp**, hypapophysis; **poz**, postzygapophysis; **prz**, prezygapophysis. Arrow points the anterior direction.

In the posterior cervical series, the zygapophyses become short at the level of the central faces (Figure 4.53). The prezygapophyses are directed more upward; the high degree of tilt of zygapophyseal facets may have restricted lateral bending. The trunk was

rigid. The centra become slightly shorter than those of the cervicals. Unlike the anterior

cervicals, the majority of posterior cervicals bear a double pair of small pleurocoels on

each side of the centra. The centra are amphiplatyan. Ventrally, each centrum bears a pair

of ridges, separated by a median groove. On the right of the posterior cervicals series,

several elongated ribs are present, articulating with the parapophysis and the diapophysis.
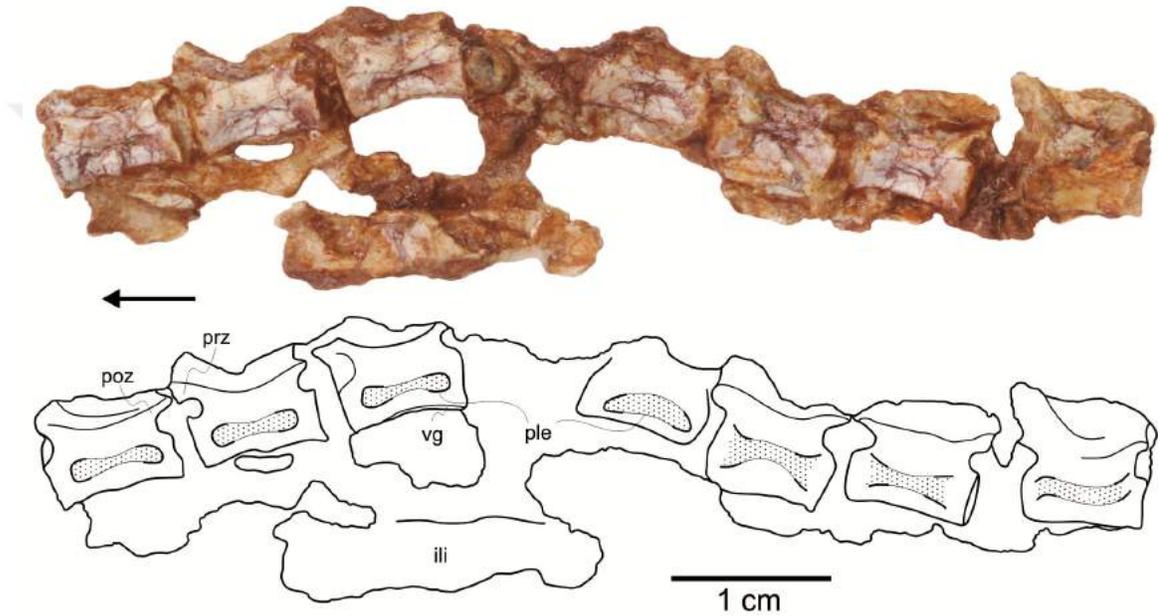


Figure 4.53 Dockum maniraptoran (TTU-P11254a) posterior cervical vertebrae. Abbreviations: **ili**, ilium; **ple**, pleurocoel; **poz**, postzygapophysis; **prz**, prezygapophysis; **vg**, ventral groove. Arrow points the anterior direction.

There are three isolated caudals present in the collection that show transition point

from shorter amphiplatyan centra to longer procoelous centra. The first one represents the

proximal caudal. It is similar in architecture to the dorsal one, but the chevron facets are

present on the caudal aspect of the centrum. The zygapophyses are small, and the neural

spine is fairly tall. The second one is highly unusual, probably representing the posterior

caudal segment. It is low and elongate, narrow in cross-section, and almost twice the

length of the anterior caudal. The centrum is procoelous, where the cranial face is large,

concave, and circular in outline, but the caudal face is convex and elliptical. The prezygapophyses are horizontal; they slightly extend beyond the face of the centrum. The posterior part of a broken vertebra of is attached anteriorly, showing the ball and socket joint. The posterior part of the tail must be extremely flexible for sidewise movement. The third caudal vertebra is similar in design to this one, with procoelous articulation, but much shorter, probably representing more distal segment. Possession of elongated middle caudal vertebrae was previously stated as a potential synapomorphy for *Graciliraptor* and *Microraptor* (Turner et al. 2012, p. 27).

Morphotype 3a (TTU-P11254a) exhibits a suite of maniraptoran attributes (Turner et al. 2012; Agnolin and Novas 2013):

1. Frontal process of the postorbital curved anterodorsally;

2. Axial neural spine compressed mediolaterally;

3. Cervical neural spines short anteroposteriorly (after Makovicky and Sues 1998);

4. Cervical vertebrae with strong hypapophyses (after Gauthier 1986);

5. Elongation of posterior caudal vertebrae (see above).

Morphotype 3b, gen. nov., sp. nov.

Diagnosis - A miniature theropod with extremely slim and delicate limb bones; rostral tip of the dentary edentulous, where symphysis is restricted to ventral part; unserrated teeth; scapula narrow and strap-like; ulna with two distinct humeral facets; retroverted ischium with an incomplete ilio-ischiadic fenestra; tibia-fibula fused; fibula highly reduced.

TTU-P11254b

(Figures 4.54-4.65)

Referred specimen - Associated skeleton of a small theropod including, partial braincase, right dentary, left scapula, left humerus, left ulna, partial pelvic girdle, right tibia-fibula.

Horizon and locality - Post Quarry (MOTT 3624), Tecovas Formation, Garza County

Collector - Soumya Chatterjee

Description and remarks - Only two isolated elements of the skull are preserved: partial braincase and a right dentary. The preserved part of the braincase shows striking resemblance to those of basal avialans such *Protoavis* and *Archaeopteryx* (Chatterjee 1991). The braincase is incomplete, preserving part of the occipital region with a condyle, but the left side of the otic capsule is intact with air-filled sinuses (Figures 4.54 and 4.55). The bones are intimately fused making demarcation of individual bones difficult. The basioccipital is fused with surrounding bones and forms most of the hemispherical condyle, which is constricted to a neck rostrally and then flares again to form a pair of basal tubera. These tubera are separated on the ventral aspect by the basioccipital recess. The left side of the exoccipital bone covers the dorsal aspect of the condyle, thus obliterating the foramen magnum. Each exoccipital bears a foramen for the hypoglossal (XII) nerve on the occiput. Ventral to it, there is a large vagus canal on the occiput, which diverted from the metotic foramen to transmit cranial nerves IX-XI. In this canal, there is a small foramen, possible for the vagus nerve (X) that communicates directly with the endocranial cavity as in maniraptorans and modern birds.

Internally, in the endocranial cavity, the floor of the basioccipital is deeply concave to house the ventral region of the pons Varolii of medullar eminence. In *Protoavis*, there are two separate concavities for the pons. Lateral to the concavity and above the pons, there is a big cavity internally in the otic capsule region, the occipital recess that formed the base of the recessus scalae tympani (Chatterjee 1991). Above this recess, there is a foramen for the vagus nerve (X). Behind it lies the foramen for the hypoglossal (XII).

The left side of the otic capsule is a complex region that is perforated by several foramina, recesses, and pneumatic spaces. The otic capsule is primarily made of exoccipital-ophisthotic complex, but the prootic covers the anterodorsal region. The prootic is probably hourglass-shaped as in birds, but only the ventral expanded region with a narrow shaft is preserved, but the dorsal expanded region is missing; thus the nature of the dorsal tympanic recess remains uncertain. Similarly, the narrow shaft is incomplete. In birds, the upper part of the shaft is pierced by a small foramen for the facialis (VII) nerve, which is missing in the specimen. Rostrally, the concave margin of the prootic forms the caudal margin of the trigeminal foramen (V). Below the expanded base, the prootic is highly excavated and contains the rostral tympanic recess; it extends onto the lateral side of the basal tubera and is highly excavated representing the rostral tympanic recess. The caudal margin of the prootic encloses the otic recess and the rostral margin of the fenestra ovalis. The otic capsule is beautifully preserved and provides critical anatomical information of the middle ear sac region.

## POSTERIOR
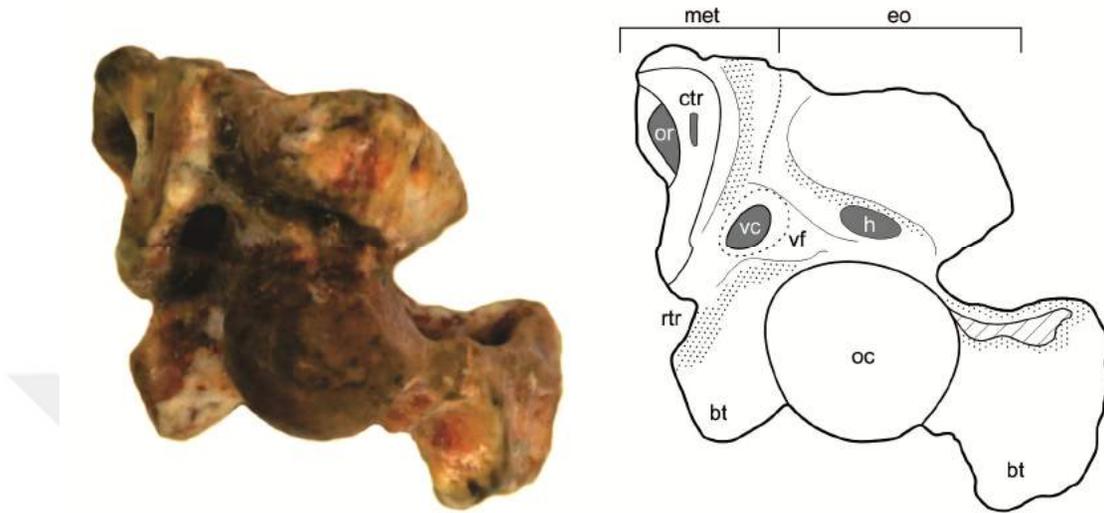


## LATERAL
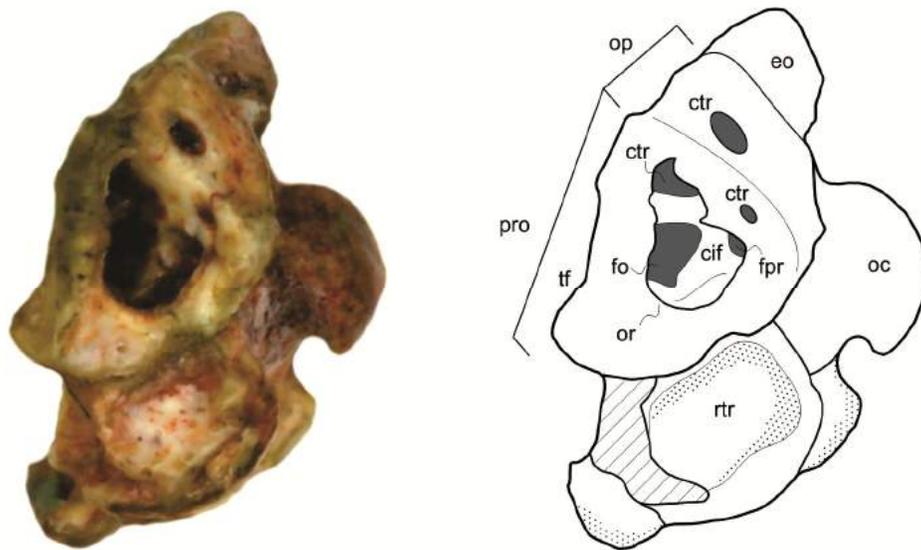


2 mm

Figure 4.54 Dockum maniraptoran (TTU-P11254b) partial braincase. Abbreviations: **bt**, basal tubera; **cif**, crista interfenestralis; **ctr**, caudal tympanic recess; **eo**, exoccipital; **fo**, fenestra ovalis; **frp**, fenestra pseudorotunda; **h**, hypoglossal foramen; **met**, metotic process; **oc**, occipital condyle; **op**, ophistotic; **or**, otic recess; **pro**, prootic; **rtr**, rostral tympanic recess; **tf**, trigeminal foramen (part); **vc**, vagus canal; **vf**, vagus foramen.
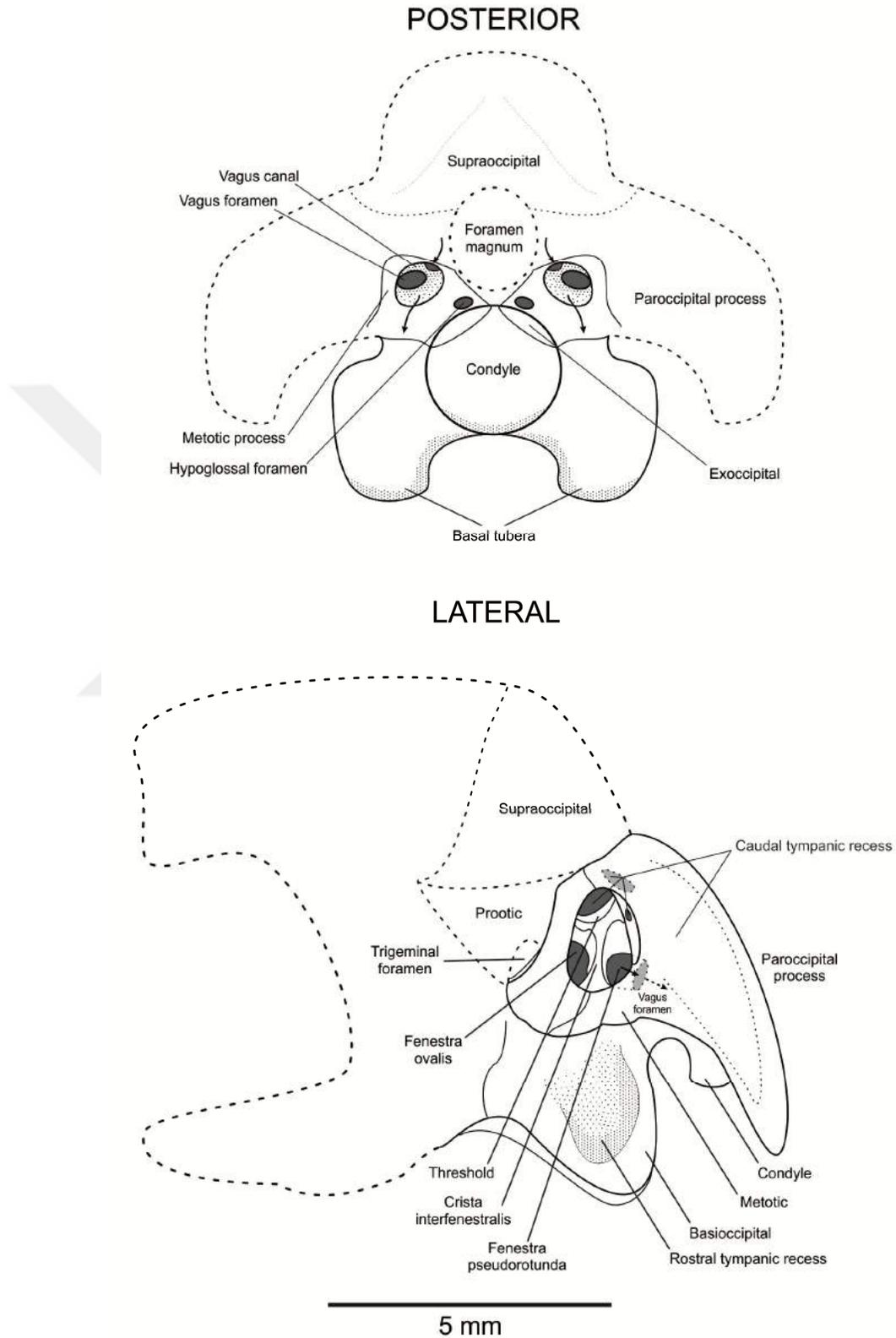
Figure 4.55 Dockum maniraptoran (TTU-P11254b) restored braincase in posterior and lateral views.

The derived state of the otic recess can be seen in this specimen where the rostral one represents fenestra ovalis, the caudal one the fenestra pseudorotundum; these two foramina are separated by the crista interfenestralis of the opisthotic. The crista interfenestralis expands dorsally and slopes from its threshold to the caudal tympanic recess as in *Archaeopteryx* (Walker 1985). A large metotic process covers the rostrodorsal surface of the exoccipital to form the floor and most of the caudal wall of the recessus scalae tympani. As a result, the vagus canal is caudally diverted from the otic capsule to the occiput. In birds, the vagus foramen has severed its lateral connection through the metotic strut and takes a shorter and direct route; it is now directed medially to endocranial cavity. In the Dockum theropod, a transitional stage of the modification of the otic capsule can be seen as in some maniraptorans such as *Troodon* (Currie and Zhao 1993). Here the vagus canal is diverted from the metotic foramen behind the strut and emerges at the occiput as in ceratosaurs. However, there is an additional foramen in the vagal recess for the vagus nerve (X) that made a direct connection to the endocranial cavity as in birds. The main entrance of the caudal tympanic recess is located within the otic recess as in birds, but it extends laterally into the base of the of the paroccipital process as an oval foramen (Figure 4.54). Most of the paroccipital process is missing, except for the base.

Chatterjee (1991, 1997) discussed the modification of the otic recess region in theropods within an evolutionary sequence. Inside the otic recess, there are two foramina on the lateral wall in basal theropods (such as "*Syntarsus*"), separated by a bar of opisthotic, the crista interfenestralis. The rostral one is the fenestra ovalis, which receives the footplate of the stapes. The caudal one is the metotic foramina, which provides an exit

for the IX-XI cranial nerves and possibly the posterior branch of the jugular foramen. In tetanurans, a subscapular cartilage, the metotic strut, is added to the exoccipital, thus enclosing the rostral part of the metotic foramen, with the formation of a secondary tympanic membrane covering the fenestra pseudorotunda. As a result, the vagus foramen in these groups has been diverted backward from the metotic foramen behind the metotic strut and emerges at the occiput (Figure 4.56). With the elongation of the cochlea, the perilymphatic duct is shifted to a new aperture, the fenestra pseudorotunda, at the position of metotic foramen (Figures 4.54 and 4.55). Carrano and Sampson (2008) recognized this caudal diversion of the vagus canal in ceratosaurid *Majungasaurus*, Smith et al. (2011) in therizinosaurian *Falcarius*, while Currie and Zhao (1993) in *Troodon*.
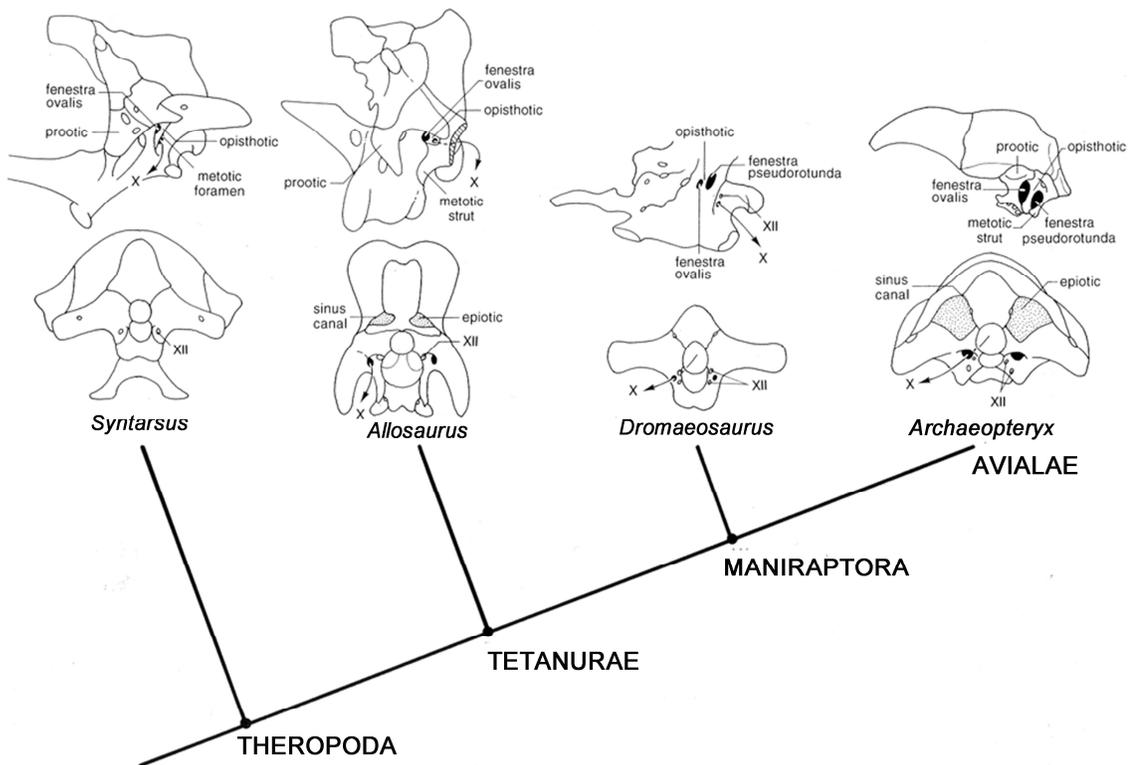


Figure 4.56 The cladogram displaying the braincase evolution in Theropoda (after Chatterjee 1997).
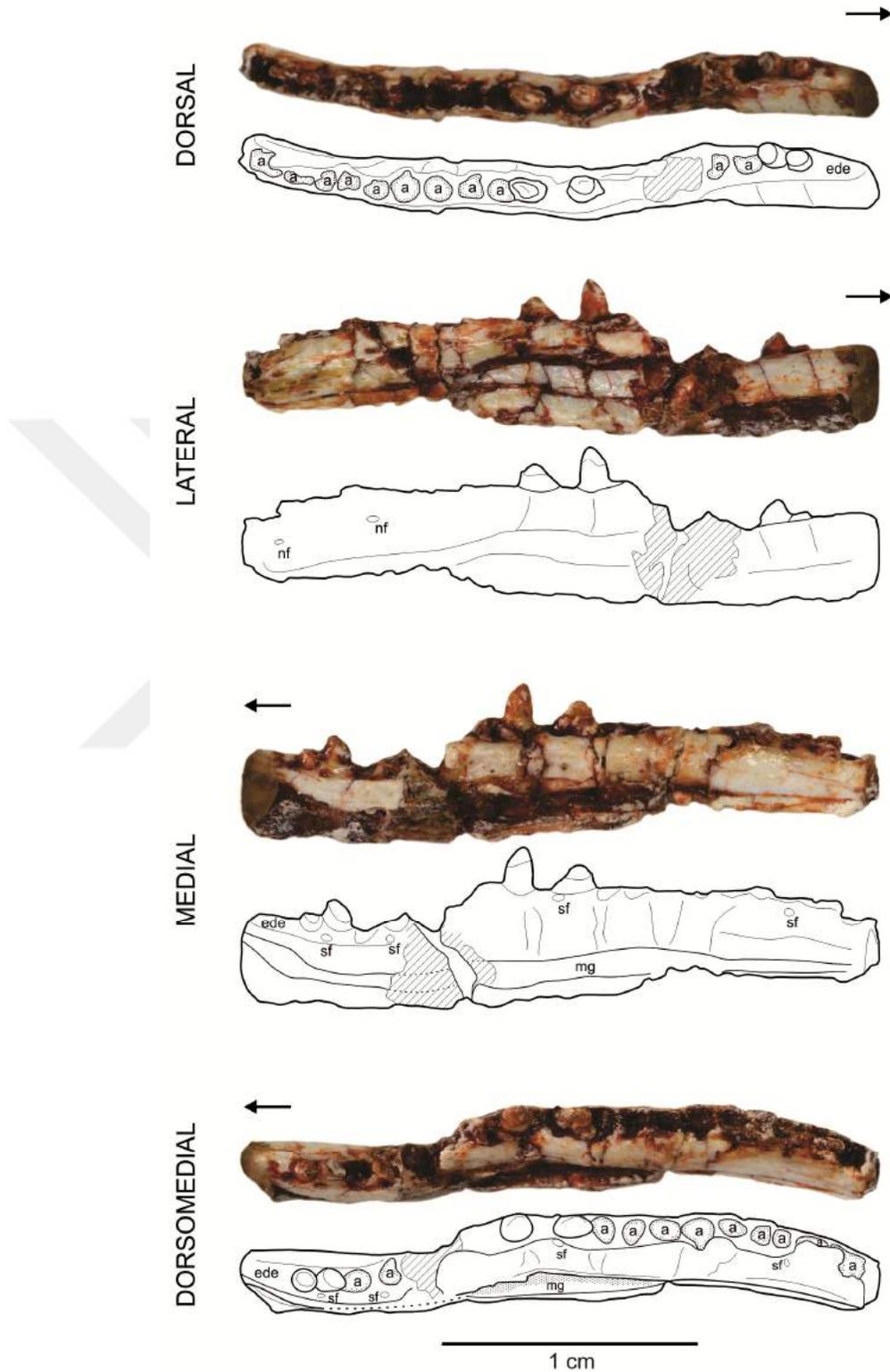
Figure 4.57 Dockum maniraptoran (TTU-P11254b) right side dentary. Abbreviations: **a**, empty alveolus; **ede**, edentulous anterior portion of the dentary; **mg**, Meckelian groove; **nf**, nutrient foramen; **sf**, special foramen.

An additional feature shared by the Dockum theropod and modern birds is system of pneumatic spaces in the bones surrounding the middle ear. Both rostral and caudal tympanic recesses are present in the braincase, but the present of dorsal tympanic recess is uncertain because of the missing region of the prootic. Witmer (1997) discussed the phylogenetic significances of the tympanic recesses in theropods and found a wide range of diversity of these air-filled sinuses in different lineages. However, because of recurrent reversals of these features, their value as identifying a particular clade is diminished. So far, the presence of caudal tympanic recess may be a diagnostic feature in coelurosaurs. The function of this tympanic pneumaticity is still poorly understood.

The right dentary is about 2.5 cm long with an edentulous beak (Figure 4.57). It is a slender element with a narrow elliptical in cross-section. Both the anterior and posterior tips are missing, and jaw ramus is slightly damaged. In non-avian theropods the symphysis is weak making the jaw kinetic at the tips. In contrast, the medial side of the dentary in this specimen shows a rugose symphyseal facet indicating the edentulous portion of the beak has developed bony symphysis as in birds and was probably covered with a sheath or rhamphotheca. Like modern birds, the symphysis was restricted to the ventral side. When the two dentaries were joined, the median conjoined tips would create a longitudinal depression. Behind the symphysis, a narrow Meckelian fossa runs throughout the length of the dentary, but somewhat crushed at places. Most of the teeth are lacking in the specimen. Four predatory teeth are preserved of which three are broken at the tip, and one is intact. Most likely heterodonty developed in the jaw where the rostral teeth are conical, but the caudal teeth are compressed sideways. The complete tooth at the midsection of the jaw shows several dental features. It is compressed labio-

lingually with the development of mesial and distal keels, and is pointed at its tip. But it is not recurved caudally but nearly upright in position. Serrations are weak or absent. There are about 11 empty alveoli, making the preserved dental count 15 or more. Interdental plates are absent, but the lingual side of the alveolar margin shows replacement pits or special windows (Edmund 1957). Empty alveoli and special windows indicate replacement activity. Laterally the dentary shows several foramina for neurovascular canals. Most likely a narrow splenial is inserted at the back of the dentary medially on its ventral surface but the suture is obscured.
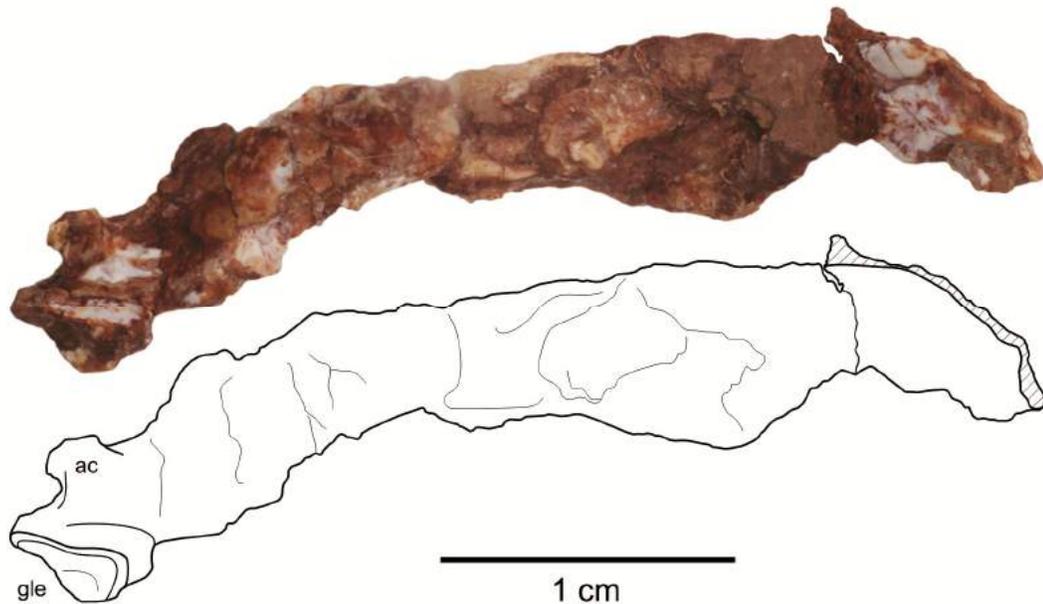


Figure 4.58 Dockum maniraptoran (TTU-P11254b) left scapula (lateral view). Abbreviations: **ac**, acromion process; **gle**, glenoid.

The left scapula is somewhat crushed and found on the top of the axis vertebra (Figures 4.58 and 4.59). The scapular blade is long and narrow, tapers proximally and expands only slightly distally and bears an acromion process, which is laterally everted. The scapular part of the glenoid fossa is slightly concave and faces not only caudally but

also laterally in avian fashion. The coracoid is not found. Unlike nonavian theropods, the coracoid was not fused with the scapula.
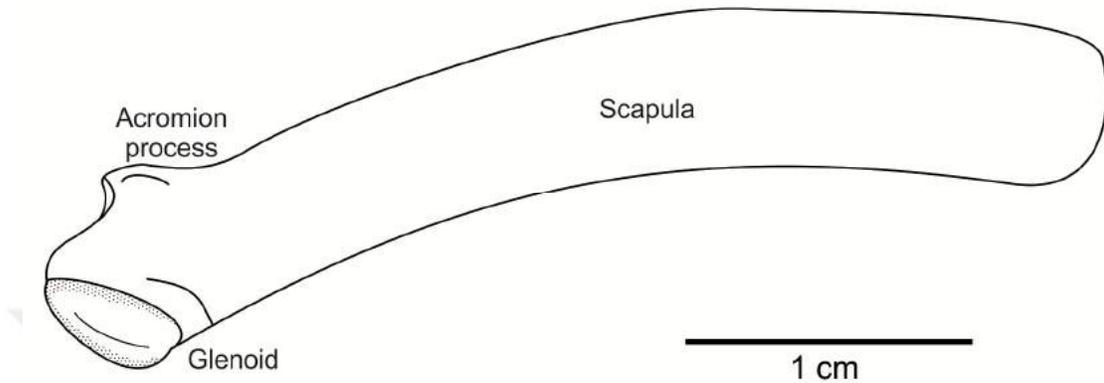


Figure 4.59 Dockum maniraptoran (TTU-P11254b) restored left scapula in lateral view.

The left humerus, the left ulna and two conjoined metacarpal bones are preserved. The bones are extremely slim and delicate. From the preserved part of the limb bones, it appears that the forelimb was quite elongated. The proximal head of the humerus is missing. The shaft of the humerus is long, slender, straight, cylindrical, extremely hollow with thin walls, and circular in cross-section (Figure 4.60). It is expanded distally into two distinct condyli; the lateral radial condyle is larger with a rolling convex surface and is parallel to the axis of the bone. The medial ulnar condyle projects more ventrally than the lateral condyle but is somewhat damaged. These two condyli are separated by a shallow flexor groove.
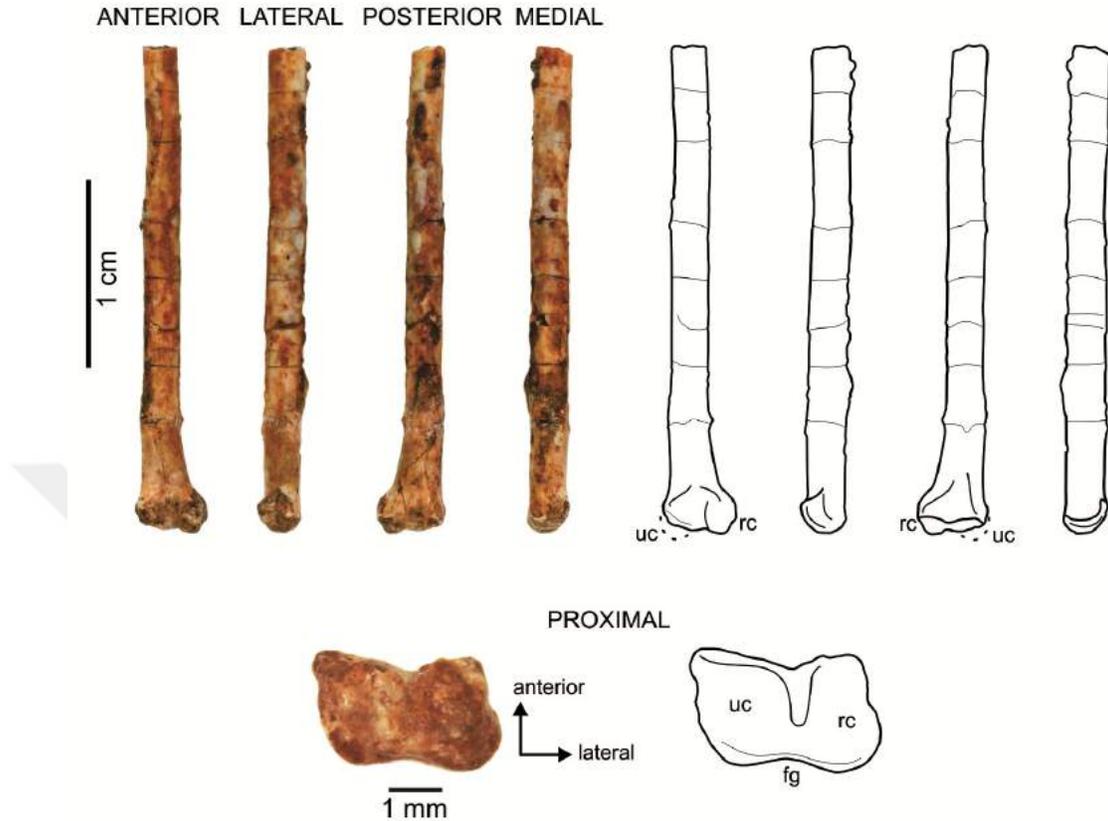
Figure 4.60 Dockum maniraptoran (TTU-P11254b) distal left humerus. Abbreviations: **fg**, flexor groove; **rc**, radial condyle; **ur**, ulnar condyle.

The ulna is a long, slim, and curved bone with expanded proximal and distal ends connected by a narrow cylindrical shaft (Figure 4.61). The proximal articular surface has a modest, pointed olecranon process, and bears two distinct concave articular surfaces separated by a median ridge for the distal condyli of the humerus; the larger one is for the ulnar condyle, the smaller one for the radial condyle. Such distinct articular cotyli are known in birds but not in nonavian theropods. The distal end is slightly damaged on the medial aspect but shows a distinct distal condyle on the posterolateral side which has a convex surface for the articulation of carpal bones (i.e. semilunate carpal joint).
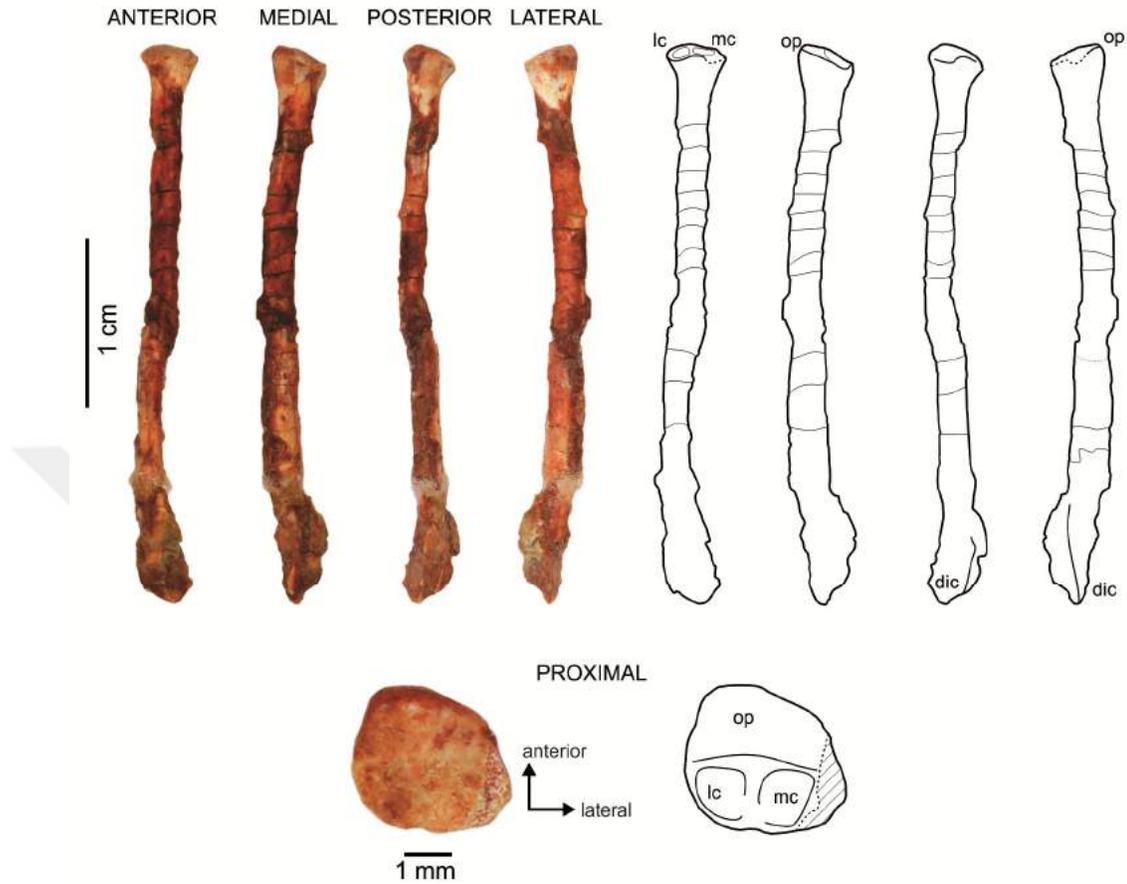
Figure 4.61 Dockum maniraptoran (TTU-P11254b) proximal left ulna. Abbreviations: **dic**, distal condyle; **op**, olecranon process; **lc**, lateral condyle; **mc**, medial condyle.
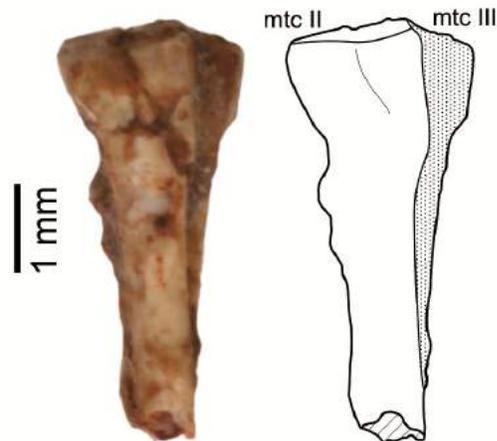


Figure 4.62 Dockum maniraptoran (TTU-P11254b) proximal left metacarpals. Abbreviations: **mtc II**, metacarpal II; **mtc III**, metacarpal III.

Two small, delicate, and long, conjoined bones are identified as the proximal halves of metacarpal bones II and III (Figure 4.62). These two bones are expanded proximally but taper in the shaft. Metacarpal II is more robust than the metacarpal III.

The left pelvic girdle consisting of ilium and pubis is found at the ventral side of the articulated dorsal series (Figures 4.53, 4.63 and 4.64). The ilium is expanded anteroposteriorly to accommodate large number of sacrals, probably more than 5 sacral vertebrae. The long postacetabular process is deep and bears a tall, pointed cranioventral end that is flared at the right angle to the sagittal plane. The ventral side of the postacetabular process is damaged, nonetheless, the shelf-like morphology of the brevis fossa can still be inferred, which have been well developed along the ventral side of the postacetabular process (Novas 1997a; Turner et al. 2012, p. 100). The preacetabular process is shorter than the postacetabular process and tapers to a narrow end caudally. A shallow cuppedicus fossa is present on the ventral side of the preacetabular process. A longitudinal crest that extends along full length of the iliac blade, bounds the cuppedicus fossa, the acetabulum and the brevis fossa on the dorsal side. There is a vertical lamina of thin bone (infracristalis lamina) that covers the upper part of the perforated acetabulum, as seen in modern birds (Baumel and Witmer 1993). Acetabulum is craniocaudally wide with a distinct, avian-style antitrochanter that is restricted to the posterodorsal corner. Pubic peduncle is probably more robust compared to the ischiadic peduncle, where both peduncles are directed ventrally. The medial side of the iliac blade is convex and yields attachment surfaces for the sacral ribs.
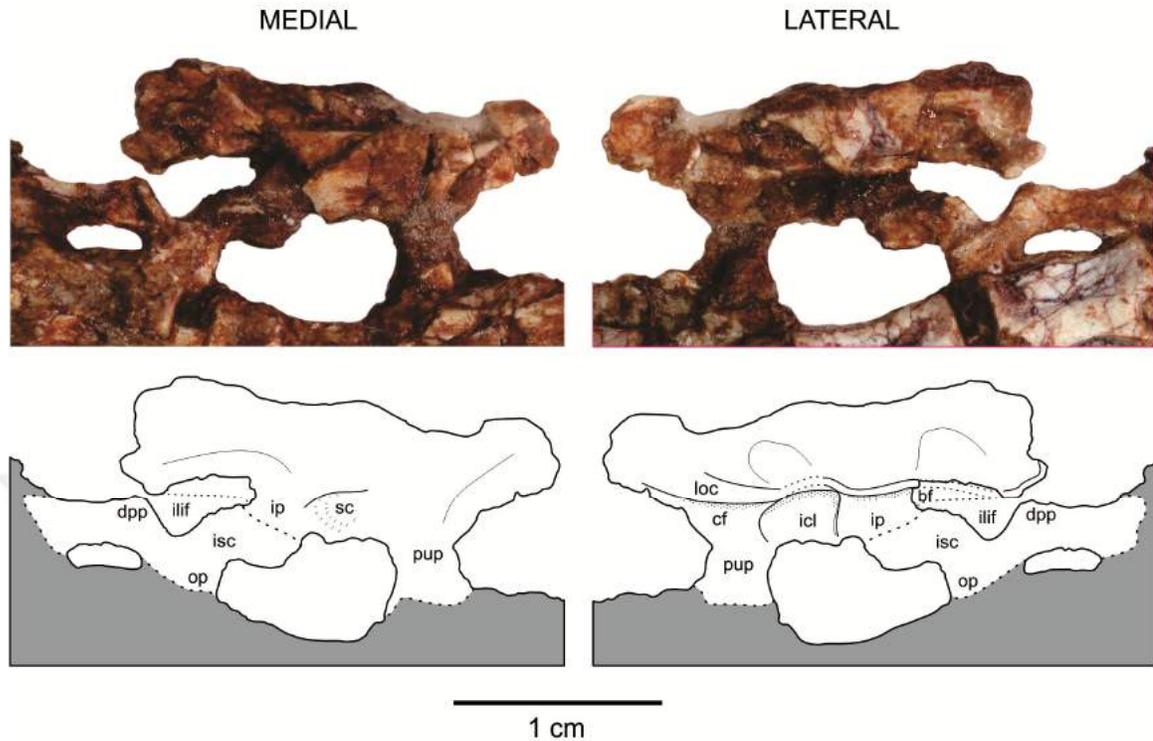
Figure 4.63 Dockum maniraptoran (TTU-P11254b) left ilium. Abbreviations: **bf**, brevis fossa; **cf**, cuppedicus fossa; **dpp**, dorsal posterior process; **icl**, infracristalis lamina; **ilif**, isioischiadic fenestra; **ip**, ischiadic peduncle; **isc,** ischium; **loc**, longitudinal crest; **op**, obturator process; **pup**, pubic peduncle; **sc**, sacral rib attachment.

The ischium is considerably shorter than the ilium. Proximally it is bifurcated into two processes—the caudal one for the ischiadic peduncle of the ilium and the cranial one for the pubis, which is obliterated. Between these two processes, the curved, concave margin forms the caudoventral rim of the acetabulum. The shaft possesses an additional dorsal posterior process as in *Archaeopteryx* (e.g. Ostrom 1976; Agnolin and Novas 2013) and an obturator process around the mid-part as in maniraptorans. The ischiadic shaft is slightly expanded at the distal end. Ischium is positioned closely to the ventral side of the ilium; however a complete enclosing of the ilioischiadic fenestra is absent. A completely closed ilioischiadic fenestra is only recognized in neognaths (e.g. Turner et al. 2012, character 403).
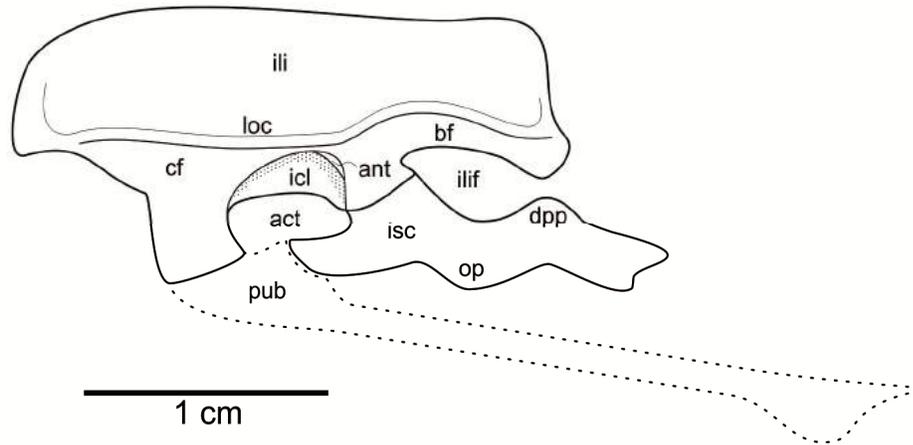
Figure 4.64 Dockum maniraptoran (TTU-P11254b) restored left side of pelvis. Abbreviations: **act**, acetabulum; **ant**, antitrochanter; **bf**, brevis fossa; **cf**, cuppedicus fossa; **dpp**, dorsal posterior process; **icl**, infracristalis lamina; **ili**, ilium; **ilif**, isioischiadic fenestra; **isc,** ischium; **loc**, longitudinal crest; **op**, obturator process; **pub**, pubis.

Among hind limb elements, only left side of the fused tibia-fibula are present in the collection (Figure 4.65). The proximal head of tibia is highly derived with the development cranial and lateral cnemial crests as seen in modern birds. The lateral crest contacts the highly reduced fibula. The proximal articular surface is angled so that the medial margin is elevated with respect to the lateral margin; it contains two articular surfaces for the distal condyles of the femur. The shaft is long, hollow, and oval in cross-section, but the distal end is missing. The fibula is highly reduced, terminates as a narrow tapering rod that extends only to the proximal one-fourth of the length of the tibia as seen in modern birds.
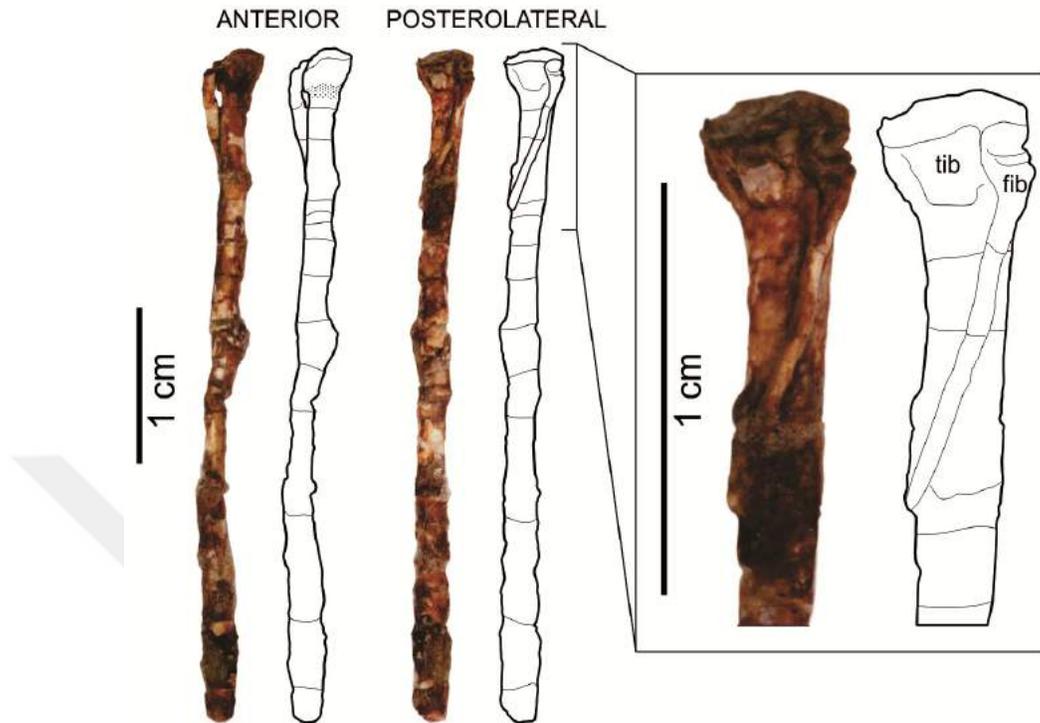
Figure 4.65 Dockum maniraptoran (TTU-P11254b) right tibia and fibula. Abbreviations: **fib**, fibula; **tib**, tibia.

Morphotype 3b (TTU-P11254b) exhibits a suite of derived characters that suggest the maniraptoran affinity (Turner et al. 2012; Agnolin and Novas 2013):

1. Crista interfenestralis depressed within otic recess;

2. Caudal tympanic recess dorsal to crista to crista interfenestralis;

3. Caudal tympanic recess in the otic recess extends to the ophistotic;

4. Occipital condyle subspherical with constricted neck;

5. Acromion margin of scapula laterally everted cranially;

6. Glenoid fossa on scapula faces posterolaterally;

7. Proximal surface of ulna divided into two distinct fossae separated by a median ridge;

8. Ulna with a bowed shaft;

9.  Distal articular surface of ulna convex, semilunate surface;

10. Prominent antitrochanter;

11. Brevis fossa becomes shelf-like, well developed and extends along the full length of the postacetabular process;

12. Presence of an obturator process at the middle part of ischium

There are several derived features present in Morphotype 3b, which show remarkable bird-like characteristics and appear to be present in avialans and modern birds (Chatterjee 1991, 1997), but their distributions at different lineages are not known:

1.  Rostral tympanic recess on ventral surface of prootic;

2.  Threshold on the dorsal surface of crista interfenestralis;

3.  Vagus foramen directed medially to the endocranial cavity;

4.  Dentary symphyseal region restricted ventrally;

5.  Infracristalis lamina ventral to acetabulum;

6.  Additional dorsal posterior process on ischium;

7.  Retroverted ischium;

8.  Partially closed iliosichiadic fossa;

9.  Tibia with cranial and lateral cnemial crests;

10. Highly reduced fibula.

To place these morphotypes in a broad phylogenetic framework of theropods, especially among different taxa of maniraptorans is beyond the scope of the present work. In future, during publication of the work, I intend to undertake detailed phylogenetic analysis using PAUP and other computer algorithms to study sequences of appearance of synapomorphies in the theropod line to birds.

## Dockum Maniraptorans and the Affinity of *Protoavis*

The discovery of new maniraptorans from Dockum sediments reintroduces the long time controversy on the affinity of *Protoavis* and on the early origin of the maniraptorans.

THEROPODA Marsh 1881 *sensu* Gauthier 1986

MANIRAPTORA Gauthier 1986

AVIALAE Gauthier 1986

Brief description **-** Avialans are highly derived maniraptorans represented by basal form such as *Archaeopteryx* (Figure 4.66). They are characterized by three autapomorphies (Agnolin and Novas 2013): (1) caudal margin of the naris nearly reaching or overlapping the rostral border of the antorbital fossa; (2) prominent acromion process; and (3) Postacetabular process shallow and pointed, less than 5-% of the depth of the preacetabular wing at the acetabulum
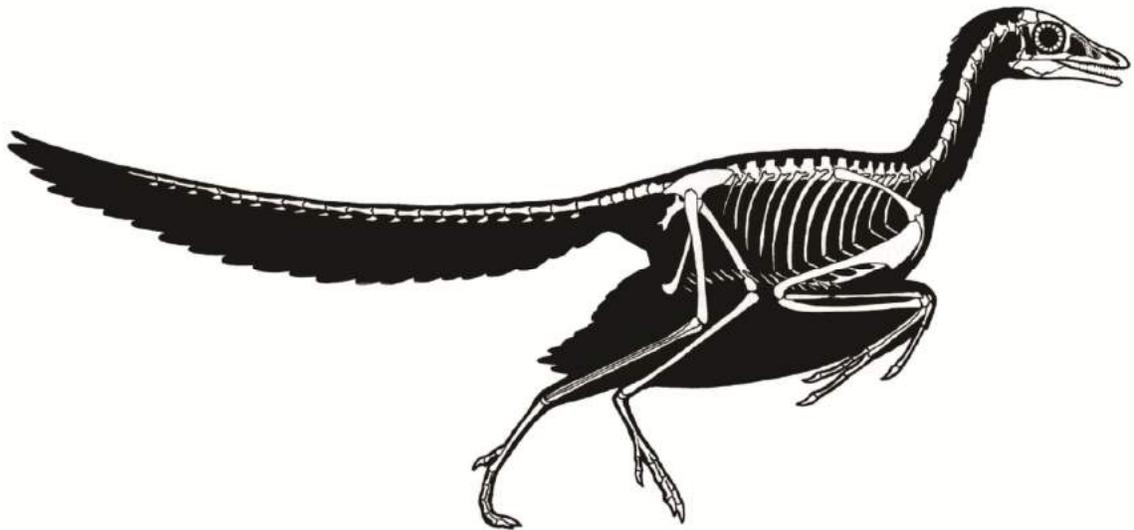


Figure 4.66 Skeletal reconstruction of *Archaeopteryx lithographica* (after Chatterjee 1997)

*Protoavis texensis* Chatterjee 1991

TTU-P9200; TTU-P9200

Holotype **-** Partial skull of a larger individual (TTU-P9200)

Paratype  - Partial skull and postcranial fragments of a smaller individual (TTU-P9201)

Horizon and locality **-** Post Quarry (MOTT 3624), Tecovas Formation, Garza County, Texas

Collector **-** Sankar Chatterjee

Description and remarks **-** The Dockum avialan *Protoavis texensis* has been described previously in detail (e.g. Chatterjee 1991, 1997, 1999) and will not be discussed here.  However, the new maniraptorans differ considerably from *Protoavis* in several aspects. In *Protoavis*, the cervicals are heterocoelous, the preacetabular process of ilium has a prominent descending anteroventral process and the limb bones are much more robust. In contrast, the cervicals are amphiplatyan in the Morphotype 3a (TTU-P11254a), whereas the preacetabular process of ilium lacks an anteroventral process and the limb bones are extremely slim and delicate in the Morphotype 3b (TTU-P11254b). Since many of the avialan characters identified in *Protoavis* are not represented in the Dockum maniraptorans, especially the cranial features, the detailed comparison between the two taxa is not possible.

One of the objections cited against the avian origin of *Protoavis* was based on the "temporal paradox", since the closest relatives of avialans such as maniraptorans generally occurred in the Upper Jurassic-Cretaceous sediments. The current criticism can be dismissed with the maniraptoran discoveries from the same quarry (Post Quarry,

MOTT 3624) of the Dockum Group where *Protoavis* remains have been found. The

Dockum maniraptorans seem to have shared a common ancestor with *Protoavis* as

opposed to a direct ancestry.

# Chapter 5

# Age and Correlation of the Dockum Group

The type sequence of the terrestrial Triassic was first described in southern Germany by Friedrich August von Alberti in 1834 into three distinctive units of terrestrial Buntsandstein (colored sandstone), marine Muschelkalk (clam limestone) and terrestrial Keuper (non-marine reddish beds) in superposition (Ogg 2004, 2012). Recalibrated from the original scheme, this tripartite sequence vaguely corresponds to Lower, Middle and Upper Triassic even today. However, correlation of the Keuper with the standard marine chart is low in resolution, since it is predominantly composed of terrestrial rocks. Thus, the Keuper is correlated with other terrestrial rocks outside of Germany in various localities of continental Europe, and also in Britain. The Chinle-Dockum sequence and the Newark Supergroup are the two main terrestrial sequences in North America during the Late Triassic. Sedimentation in the southwestern basins is predominantly fluvial compared to the lacustrian rift basins of the eastern coast. On the other hand, the deposition is primarily paralic in the Keuper and its European lithostratigraphic equivalents. These terrestrial deposits are rich in archosaur fossils, predominantly in phytosaurs which are excellent zone fossils especially for Europe and North America (e.g. Gregory 1957, 1969, 1972) as well as for Morocco and India (e.g. Dutuit 1977a, 1977b; Chatterjee 1978a).

## Phytosaur-Based Biostratigraphy and Biochronology of the Upper Triassic

The land tetrapod biostratigraphy of the Upper Triassic rocks is established based on phytosaur assemblage zones in correlation with the Keuper type section. Phytosaurs were first discovered in central Europe and best documented in Germanic Keuper from the beginning (e.g. Jaeger 1828; von Meyer and Plieninger 1844; also see Stocker and Butler 2013). *Zanclodon arenaceus* (later referred to *Paleorhinus* by Gregory [1969]) from the Stuttgart Formation (or Schilfsandstein) was traditionally considered as the earliest evidence of phytosaurs within the Keuper. However, most up-to-date works proved that this taxon cannot be affined with Phytosauria anymore (Hungerbühler 2001; Stocker and Butler 2013). Therefore, the stratigraphically lowest phytosaur occurrences are now recorded in the Weser Formation.

Weser Formation is subdivided into three "formations" as Steigerwald Formation, Hassberge Formation (or Kieselsandstein), and Mainhardt Formation (Figure 5.1). It is reported that there are several isolated phytosaur teeth and fragments from the Steigerwald Formation (Lehrbergschichten) without any further possible diagnosis (Seegis 1997; Butler et al. 2013). Nonetheless, the first identified phytosaurs were collected from lower part of the overlying Hassberge Formation (Blassensandstein in Gregory 1969; Butler et al. 2013) (Figure 5.1). These phytosaurs originally named as *Francosuchus* (*F. broilii*, *F. latus* and *F. angustifrons*) and *Ebrachosuchus* (*E. neukami*) (Kuhn 1933, 1936). Although the holotypes of the first two *Francosuchus* species were lost during the Second World War, the two genera are later referred to *Paleorhinus* (Gregory 1962b; Westphal 1976) and this approach is partially applied in following

works (see Chatterjee 1978a; Hunt and Lucas 1991b; Long and Murry 1995). Most

recently, the status of *E. neukami* is reconsidered as a valid taxon where *F. angustifrons*

is recognized as *Paleorhinus angustifrons* (Butler et al. 2013). The recently published

horizon from Poland including *Paleorhinus* provides a direct correlation with the

Hassberge Formation within the continental Europe (Dzik 2001).
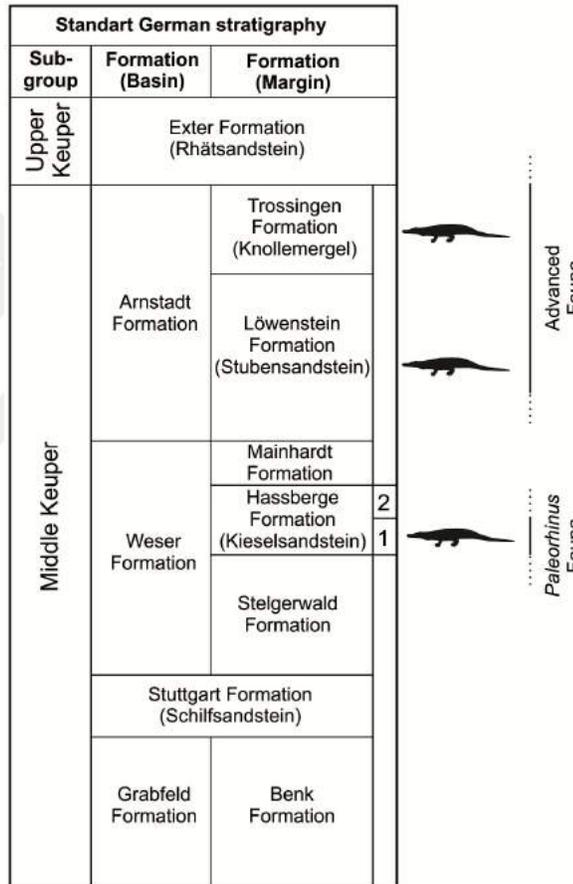


Figure 5.1 Composite lithostratigraphy of the Middle and Upper Keuper including the phytosaur collected levels (after Nitsch 2005; Butler et al. 2013). Horizons 1 and 2 correspond to Blassensandstein and Coburger Sandstein, respectively. Phytosaur bearing levels are marked with black silhouettes, including the faunal zone they belong.

On the other hand, *Nicrosaurus* and *Mystriosuchus* (von Meyer 1860, 1861, 1863;

Gregory 1962a, 1962b; Ballew 1989; Hungerbühler and Hunt 2000) are the Norian

phytosaurs of the Keuper, and both are collected from the middle parts of the

stratigraphically higher Löwensandstein Formation (Stubensandstein Formation) (Figure 5.1). Phytosaur remains from the upper part of the Arnstadt Formation (i.e. Trossingen Formation or Knöllenmergel) were originally referred to *Angistorhinopsis ruetimeyeri* (von Huene 1911, 1922), which is possibly a *Nicrosaurus*-grade phytosaur (Kimmig and Arp 2010) that is currently considered as nomen dubium (see Stocker and Butler 2013) (Figure 5.1).

The occurrence of phytosaur fossils are also long known in Upper Triassic deposits of North America (e.g. Emmons 1856; Mehl 1916). In this context, a direct correlation is provided between Keuper and North American Upper Triassic, mainly based on phytosaur fossils (by Colbert and Gregory, in Reeside et al. 1957; Gregory 1957, 1969).  Historically, the phytosaur diversity and abundance is much greater in the southwestern area (i.e. the Dockum Group and the Chinle Formation, and also the Popo Agie Formation), relative to the eastern Newark Supergroup. Thus, the phytosaur fauna of the southwestern North America, especially of the Dockum Group, has complemented the phytosaur biochronology (Gregory 1972). The *Paleorhinus* Fauna includes basal forms like *Paleorhinus* and *Angistorhinus*; the succeeding "*Rutiodon*" Fauna carries more derived forms (*sensu* Gregory 1962a, 1962b); and the overlying "Advanced" Fauna is characterized by an advanced species of *Rutiodon* with specialized temporal and occipital regions (i.e. *Redondasaurus*, Hunt and Lucas 1993a) which is considered as comparable with the European counterpart *Angistorhinopsis ruetimeyeri*, now nomen dubium (Stocker and Butler 2013, see above). Those phytosaur zones are predominantly based on Dockum and Chinle phytosaurs, due to the rarity of phytosaurs in Newark Supergroup deposits and the missing *Rutiodon* fauna in Keuper.

Gregory's phylogeny is revised extensively some decades later, based on newly arising cladistic method at the time. Cladistic method eliminates the previous classical phylogeny which heavily stresses on the homoplasic characters such as rostral morphology (e.g. Ballew 1989; Hunt 1989a; Stocker 2010). Consequently, the North American genera *Pseudopalatus* (Mehl 1928; Ballew 1989), *Leptosuchus* (Case 1922; Stocker 2010) and *Machaeroprosopus* (Mehl 1916; Parker et al. 2013) which were previously considered within the genus *Rutiodon* (*sensu* Gregory 1962a, 1962b) are restored, in addition to the newly engendered taxon *Smilosuchus* (Long and Murry 1995). This updated phytosaur assemblages of Gregory are later adopted to construct tetrapod faunachrons for the southwestern United States, namely the land vertebrate faunachrons (Lucas 1991, 1993; Lucas and Hunt 1993b). These four land vertebrate faunachrons are later converted into a series of interval zones, of which the boundaries are set predominantly on phytosaur fossil record (Figure 5.2); then it is attempted to cover the Late Triassic land tetrapod faunas in a global scale (Lucas 1998b, 1999, 2010; Lucas et al. 2007).

As well as Gregory's phytosaur framework, Lucas's land vertebrate faunachrons are also predominantly based on the Chinle and Dockum faunas since the indeterminate phytosaurs of the Newark Supergroup only allows ambiguous land vertebrate faunachrons (Huber et al. 1993). Moreover, Newark, Keuper and other land tetrapod bearing Upper Triassic rocks are incorporated into these global faunachrons of Lucas. In 1998, those faunachrons first represent a series of interval zones, marked by the first appearances of the mentioned phytosaurs *Paleorhinus*, *Rutiodon*, *Pseudopalatus* (*sensu* Ballew 1989) and *Redondasaurus* (Lucas 1998b). Subsequent replacements are made in

the following versions, such as the taxon *Parasuchus* is integrated to the scheme for the

new base of Otischalkian as the senior synonym for *Paleorhinus* (Lucas et al. 2007;

Lucas 2010), whereas the Adamanian-Revueltian boundary is also redefined by the first

appearance of an aetosaur, *Typothorax coccinarum*, and therefore the faunachron

boundary is changed in favor of a broader Adamanian by inclusion of the lower part of

the Revueltian (i.e. Lamyan, Hunt et al. 2005; Lucas et al. 2007; Lucas 2010).
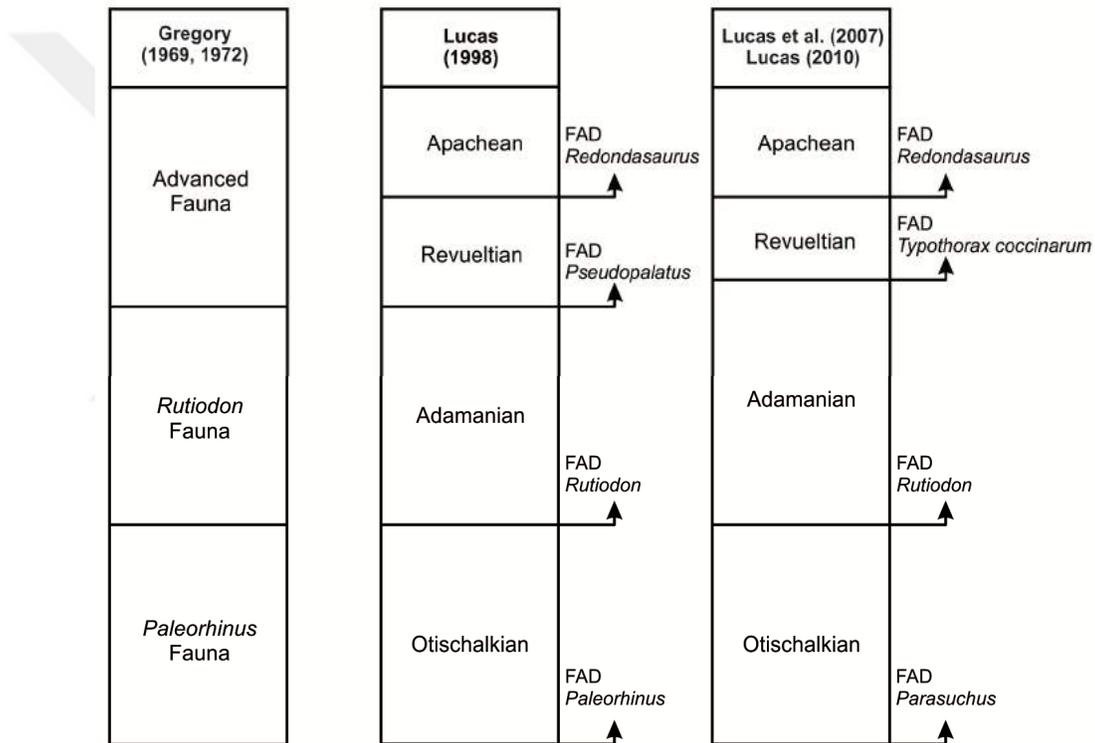


Figure 5.2 Comparison of phytosaur-based biochronology for the continental Late Triassic: Gregory's assemblage zones and Lucas's interval zones. FAD for the first appearance datum.

Modern works have shown that the original framework of Gregory is still valid

based on taxonomy and fossil occurrences, and probably more accurate in determinations

of taxa regarding Lucas's land vertebrate faunachrons (e.g. Rayfield et al. 2005, 2009).

The *Paleorhinus* Fauna mainly includes non-phytosaurid phytosaurians like *Paleorhinus*

(*sensu* Stocker 2010a) including the recently generated taxon *Wannia scurriensis* from

the Santa Rosa Formation (Stocker 2012b). The fossil occurence of *W. scurriensis*, a *Paleorhinus*-grade phytosaur, is stratigraphically lower that of *Paleorhinus* in the Dockum Group. Thus, the Otischalkian faunachron cannot correspond to the *Paleorhinus* Fauna anymore, since the lower boundary of which is defined by the first appearance of *Paleorhinus*. The succeeding *Rutiodon* Fauna includes the genera *Leptosuchus* and *Smilosuchus*, but also the two recent discoveries from the Sonsela Member of the Chinle Formation in Arizona, *Pravusuchus* (Stocker 2010) and *Protome* (Stocker 2012a). The range of the Advanced Fauna is now shifted to cover the taxon range of *Pseudopalatus*, which is recently considered as the junior synonym of *Machaeroprosopus* (Parker et al. 2013). *Redondasaurus,* once seen as the most derived phytosaur, is also accepted as a junior synonym of *Machaeroprosopus* as well (Hungerbühler et al. 2013). In this case, it is unnecessary to use the subdivision of Revueltian and Apachean faunachrons, since the original definition of Gregory's Advanced Fauna has been covering the exact stratigraphic interval. To sum up, Otischalkian and Adamanian basically correspond to the *Paleorhinus* and "*Rutiodon*" faunas of Gregory, whereas Revueltian and Apachean are the equivalents of the Advanced Fauna after the recent taxonomic rearrangement of the taxon *Machaeroprosopus*.

## The Non-Marine versus Marine Correlation of the Upper Triassic

Modern chronostratigraphic type sections of Phanerozoic are always selected in marine sequences which are quite precise due to continuous deposition and wide range distribution; thus the stage boundaries are based on taxon ranges of marine fossils. This principle is followed also in order to subdivide the Upper Triassic sequences by using

ammonoid and conodont taxon ranges. Carnian, Norian and Rhaetian are the three stages of the Upper Triassic, all defined in Northern Calcareous Alps of Austria (Ogg 2004, 2012). Carnian and Norian are historically defined by von Mojsisovics in 1869, as well as their substages in 1895, based on characteristic ammonoids, however the uncertain stratigraphic relationships of two stages were settled in favor of a younger Norian after the more precise establishment of ammonoid taxon ranges (von Mojsisovics 1893). Rhaetian is the first established chronostratigraphic stage of Triassic, based on Kössen limestone strata in Austria (von Gümbel 1861). Especially during the 20th century, the existence of this stage was fiercely debated (cf. Golebiowski 1990; Ogg 2004, 2012). Since 1991, the Rhaetian Stage is officially consented by the International Commission of Stratigraphy and the boundary is recently marked by the first appearance datum of conodont *Misikella posthernsteini* (Krystyn 2010) and dated around 208-209 Ma (Muttoni et al. 2010).

**Traditional Ages of Non-Marine Correlation**

Every terrestrial biozone has to be integrated to the global chronostratigraphic chart to establish a complete history of life. Therefore, one of the main goals for the phytosaur bizones is to establish a marine correlation, as previously attempted. From the very beginning, Keuper and its terrestrial equivalents are tentatively dated as Late Triassic. Concurrently, Gregory (1957, 1969, 1972) did not seek any stage level subdivision for the initial phytosaur biozonation. In order to increase the temporal resolution, it is first assumed a Carnian age for the *Paleorhinus*/*Parasuchus* bearing strata (i.e. the *Parasuchus* Zone) and a Norian age for the *Nicrosaurus-* and *Mystriosuchus-*

grade phytosaur bearing strata of India, Germanic Keuper and North America (Chatterjee 1978a, 1986a); concurred by many others who were distinguishing the phytosaurs of the Dockum and Chinle sequences (e.g. Long and Ballew 1985; Murry 1989a, 1989c; Lucas and Hunt 1989b; Hunt and Lucas 1991b). This outline is also supported by the stratigraphy and overall land tetrapod fauna (e.g. Chatterjee 1986a; Long and Padian 1986; Murry and Long 1989), and also by the early palynologic works on the Euramerican flora (Dunay and Transverse 1971; Dunay and Fisher 1974).

Chronostratigraphic stages are described based on the marine fossil ranges and a direct correlation of marine and terrestrial rocks is hard due to lack common taxa. Therefore, the only other option for a direct correlation between two realms would be the absolute ages. Absolute ages are generally obtained by radiometric dating, but also by astrochronology, i.e. calculating the durations of Milankovitch and Van Houten cyclicity and recalibrating magnetostratigraphic reversals. Although the type section Keuper possesses any marine fossils or magmatic input, it has a well developed cyclic sedimentation pattern (Kozur and Bachmann 2005, 2008). Similarly, the dominant cyclic lacustrine sedimentation of the Newark Supergroup for a period more than 40 million years which responded the periodic climate changes caused by variations in Earth's orbit is feasible for the Late Triassic astrochronologic calculations (e.g. Olsen 1986; Witte et al. 1991; Kent et al. 1995; Kent and Olsen 1999; Olsen and Kent 2000). The other two biostratigraphic tools of palynomorphs (e.g. Cornet 1977; Olsen and Cornet 1985; Kürschner and Herngreen 2010) and conchostracans (clam shrimps, e.g. Kozur and Weems 2005, 2007, 2010) are utilized to sustain the correlation between Keuper and Newark. On the contrary, the main biostratigraphic tool for the Chinle and Dockum rock

sequences are phytosaurs in order to establish a correlation with the Keuper and Newark, nevertheless supplementary data are gathered from palynomorphs (e.g. Litwin et al. 1991; Cornet 1993) and megaflora (e.g. Ash 1967, 1972, 1980, 1987, 1989; Ash et al. 1986). In sum, the correlation between the Keuper, Newark, Chinle and Dockum sequences is entirely based on the terrestrial stratigraphic tools which have resulted by the association of Otischalkian and Adamanian with Carnian, Revueltian with Norian, and Apachean with Rhaetian in broad sense (e.g. Lucas 2010; Lucas et al. 2012) (Figure 5.3).

| Dockum Group | Age | | Chinle Group | Newark Supergroup | Keuper |
|---|---|---|---|---|---|
| Redonda Fm. | Rhaetian | Apachean | Rock Point Formation | Orange Mtn. Basalt | Exter Formation |
| Bull Canyon Formation | Norian | Revueltian | Owl Rock Fm. / Painted Desert Member / Sonsela Member / Blue Mesa Member (Petrified Forest Fm.) | Passaic Formation | Arnstadt Formation |
| Trujillo Fm. | | | | | Mainhardt Fm. |
| Tecovas Fm. | Carnian | Adamanian | Bluewater Creek Formation | Lockatong Formation | Hassberge Fm. / Steigerwald Fm. |
| Santa Rosa Fm. | | Otischalkian | Shinarump Fm. | Stockton Fm. | Stuttgart Fm. |

Figure 5.3 Non-marine correlation of the main terrestrial Upper Triassic deposits. Ages, faunachrons ad the lithostratigraphies of Chinle, Newark and Keuper modified after Lucas et al. (2012) and references therein; lithostratigraphy of the Dockum Group after Lehman and Chattterjee (2005). Note the lithostratigraphic ranking of the Chinle strata is based on Heckert and Lucas's scheme (2002a, 2002b).

**The New Late Triassic Timescale**

Since both Keuper and Newark Supergroup are terrestrial sequences, the correlation of their cyclicity with the marine fossil ranges is essential, in order to test the results and to construct a compact time scale. Tethyan sections provide the global marine strata for Late Triassic, however Turkish and Austrian reference sections display condensed conodont biozones and abrupt lithological variations due to irregular sedimentation rates (e.g. Gallet et al. 1992, 1993, 1994, 1996, 2000). Among the Tethyan

sections, relatively thicker and stratigraphically expanded Pizzo Mondello section in

Sicily (candidate for Norian GSSP) offered the best magnetostratigraphic correlation with

the North American Newark Supergroup (Muttoni et al. 2001). Therefore, an increase in

sedimentation rate in the Norian is assumed and a long Carnian/short Norian (boundary at

~216 Ma) is favored, in accord with the Newark astrochronology (Figure 5.4).
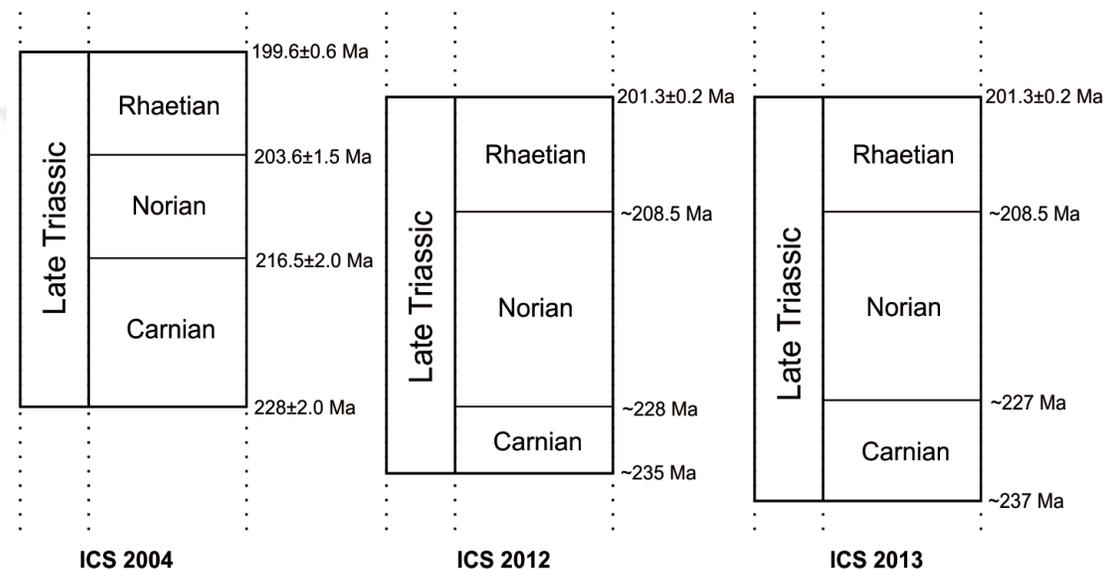


Figure 5.4 Recalibration of the Late Triassic stages, reproduced after the charts of the
International Commission of Stratigraphy (Ogg et al. 2004, 2012; Cohen et al. 2013).

However, the Pizzo Mondello section has a poor conodont fossil record and the

marine megafossils (ammonoids, halobiids) are scarce which complicates the

biostratigraphic correlation with other Tethyan sections, especially in location of the

Carnian-Norian boundary (Muttoni et al. 2001; Krystyn and Gallet 2002). Subsequently

gathered more precise ammonoid, conodont and halobiid biostratigraphy including the

magnetostratigraphic data from the newly discovered Tethyan sections in Austria,

Slovakia and Turkey are used to recalibrate the Carnian-Norian boundary of the Pizzo

Mondello section, indicating lower sedimentation rates for Norian compared to Carnian

and therefore favors a longer Norian (shorter Tuvalian/longer Lacian) which starts around

228-227 Ma (Krystyn et al. 2002; Channell et al. 2003; Gallet et al. 2003; Muttoni et al.

2004). This new boundary initiates by the first appearance of the conodont

*Norigondolella navicula* which is supported by the $\delta^{13}$C proxy which is located within the

Newark magnetozone E7n (Muttoni et al., op. cit.). Magnetistratigraphic age is consistent

with the previously obtained isotopic ages from the lower Norian rhyolites (225±3 Ma,

Gehrels et al. 1987). Moreover, a new composite magnetostratigraphy is constructed

based on the data gathered from these Tethyan sections (Hounslow and Muttoni 2010).

The absolute ages extracted from this new composite chart are preferred and started to

use officially in ICS charts starting from 2012 (e.g. Ogg 2012; Cohen et al. 2013), due to

the facility of a direct correlation with the marine fossil zones (Figure 5.4). Most recent

recalibration of the Newark polarity time scale manifested the true correlation with the

short Carnian-long Norian framework (Olsen et al. 2011).

Besides the data gathered from the sequence stratigraphy (e.g. Lupe and

Silberling 1985; Lucas 1991, 1993; Lucas and Marzolf 1993; Lucas and Huber 1994)

which wouldn't increase the stratigraphic resolution unless any relative or absolute age

data is present, the occurrences of land tetrapod fossils in marine rocks are proposed as

the strongest link for a strong correlation between the phytosaur biozones with the marine

stages. There are only a couple terrestrial tetrapod fossils documented from Tethyan

marine strata which are used in correlation to the marine stages (Lucas 1998b, 2010). The

phytosaur "*Parasuchus*" and the temnospondyl amphibian *Metoposaurus santaecrucis*

which are collected from lower and upper Carnian limestone strata in Austria,

respectively (Hunt and Lucas 1991b; Lucas and Heckert 2000 and references therein) and

both fossils are used to strengthen the correlation between Otischalkian and Carnian. However, the taxonomic status of the Austrian phytosaur is asserted uncertain (Rayfield et al. 2009; Butler 2013), as well as *M. santaecrucis* (Hunt 1993; Schoch and Milner 2000; Milner and Schoch 2004; Sulej 2002, 2007). It is also argued that the beds from which *M. santaecrucis* is collected might represent a correlative for Revueltian (Irmis et al. 2010, p. 42 and references therein). *Eudimorphodon*, *Mystriosuchus* and *Aetosaurus* are reported from the Norian Zorzino limestone (e.g. Wild 1989; Renesto 2006) and also from the Forni Dolomite (e.g. Dalla Vecchia 1995, 2006) which are used to correlate Norian with the Revueltian (Lucas 1998b, 2010). Besides the fact that no pterosaur is hitherto known from Late Triassic of North America except some jaw fragments which were referred to *Eudimorphodon* (see Murry 1986, p. 129), there are some counter arguments based on the geographical restrictions and taxonomic equivalencies of both *Mystriosuchus* and *Aetosaurus* to the associated North American taxa (Irmis et al. 2010, p. 42 and references therein). In any case, common vertebrate fossils in terrestrial and marine deposits are far from providing a complete correlation.

To sum up, no unequivocal land tetrapod fossils are hitherto validated for a direct correlation of terrestrial and marine Upper Triassic rocks. Among other fossil groups which might be used as a biostratigraphic tool, only palynomorphs have the potential for a direct correlation between terrestrial and marine rocks. However, based on rarity of the independently dated successions, taxonomic problems and differential preservation, the biostratigraphic resolution of the palynomorphs is currently quite low which can only be useful at the regional scale (Cirilli 2010). Although the chronostratigraphic stage boundaries are defined based on biostratigraphy, they also possess absolute ages by

geochronology. Possession of numerical ages, gathered either by isotope geochronology or by geomagnetic polarity zones, stand as the only plausible option in most cases for a direct terrestrial-marine correlation due to lack of common fossils between two realms (Figure 5.5).
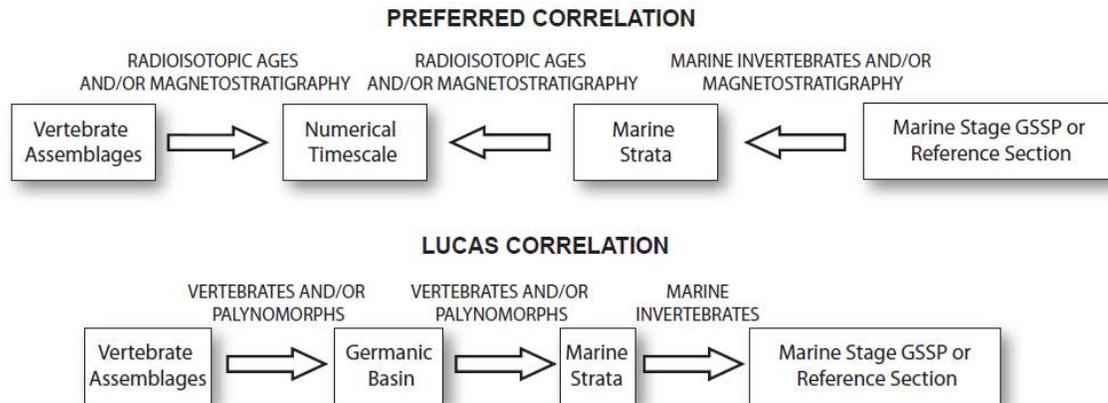


Figure 5.5 Different rationale used in order to correlate terrestrial Late Triassic to the marine reference sections (after Irmis et al. 2010).

## Phytosaur Biostratigraphy and Geochronology of the Chinle-Dockum Sequence

As stated above, biostratigraphy is not a useful tool to correlate terrestrial and marine sequences of the Late Triassic due to the lack of common fossils. Although paleomagnetic works were previously executed for Lower-Middle Triassic (e.g. Steiner and Lucas 1992; Steiner et al. 1993), Upper Triassic (e.g. Molina-Garza et al. 1993, 1995, 1996), uppermost Triassic (e.g. Steiner and Lucas 2000) and Lower Jurassic (e.g. Steiner and Helsley 1974a, 1974b) of the southwestern basins of North America, the scarcity of the cyclical (lacustrine) deposition prevents to obtain a composite set of magnetostratigraphic data. Therefore, the radiometric dating is the only available source to obtain absolute ages for the Dockum Group and the Chinle Formation, as well as for

the Ischigualasto Formation and for many other areas of the world which housed terrestrial Upper Triassic rocks. Since no ash beds are available in Dockum for a direct marine correlation, using land tetrapod biostratigraphy is the only available tool to reflect the absolute ages obtained from the Chinle Formation over the Dockum Group.

Earlier attempts to resolve the geochronology of the Chinle-Dockum sequence were based on U-Pb dating of detrital zircons gathered predominantly from the Chinle Formation (Dickinson and Gehrels 2008, 2009). Accordingly, the analyses give a nominal duration of 217–227 Ma and a maximum duration of 215–229 Ma for the lower sequence, instead of 227-232 Ma and 226-234 Ma for the same parameters, respectively. Similarly for the upper sequence, the nominal and maximum durations yield 207–217 Ma and 205–219 Ma, rather than 210-227 Ma and 208-229 Ma respectively. Therefore, the earlier results for the depositional ages turned out to be at least 5-10 Ma younger than previously expected which were based on biostratigraphic studies (e.g. Lucas 1997). Further studies have provided more precise age data, including recalibrations on the lithostratigraphy of the Chinle Group (e.g. Ramezani et al. 2011, 2014, see below).

**The Land Tetrapod Biostratigraphy and Geochronology of the Chinle Formation**

Similar to the Dockum Group, a rich tetrapod fauna including dicynodont therapsids, temnospondyl amphibians, a large array of archosauromorphs (e.g. Murry 1987a, 1989c; Murry and Long 1989; Long and Murry 1995; Heckert et al. 2005; Parker 2005) and various microvertebrates (e.g. Murry 1989b; Heckert 2004) is documented in the Chinle Formation. The traditional ages gathered from the non-marine correlation of these rocks and the phytosaur biozones within (e.g. Long and Padian 1986; Lucas et al.

2012) are recently recalibrated by the radiometric analyses based on U/Pb zircon dating of the in-situ volcanic ash layers were previously performed for the upper and lower levels of the Chinle Formation (Figure 5.6).

The stratigraphically lowest occurrence of vertebrate fossils in the Petrrified Forest National Park, Arizona is located within the Newspaper Rock Bed of the Blue Mesa Member in the Billings Gap area (Parker and Martz 2011) (Figure 5.6). Alongside of a variety of crurotarsan skeletal elements, a skull of *Leptosuchus* which indicates the *Rutiodon* Fauna and a probable theropod femur are collected from this locality. Dying Grounds is the other locality from the Petrified Forest National Park from which a silesaurid femur is collected close to the top of the Blue Mesa Member ("the Petrified Forest Form", Parker et al. 2006; Langer et al. 2013). *Placerias* and Downs quarries are the two other landmark localities from the lower portion of the Chinle Formation in Romero Springs area, Arizona, which are positioned approximately the same stratigraphic horizon and generally evaluated together (Lucas et al. 1997a). *Placerias* Quarry is widely known for the discovery of dicynodont *Placerias hesternus* (see Taphonomy section), nevertheless, a partial left femur of the lagerpetid *Dromomeron gregorii* (Nesbitt et al. 2009b), some fragments of the herrerasaurid *Chindesaurus bryansmalli* (Long and Murry 1995, p. 174) and the neotheropod *Camposaurus arizonensis* (Lucas et al. 1992, figure 1b-e; Hunt et al. 1998; Nesbitt et al. 2007; Ezcurra and Brusatte 2011) are the three referred taxa from this locality, besides many other undiagnosed dinosauriform specimens (see Nesbitt et al. 2007).

As stated above, the lowermost occurrences of land tetrapods in Chinle are reported from the upper portion of the Blue Mesa Member. Previous dating indicates a very short deposition interval (ca. 1-2 Ma) for the Blue Mesa Member (219.2±0.7 Ma-220.9±0.6 Ma for the base of the member and 218.1±0.7 Ma for the upper portion, see Irmis and Mundil 2008; Heckert et al. 2009; Irmis et al. 2011). Assuming that the Bluewater Creek Member (which is considered synonymous with the Mesa Redondo Member) is laterally continuous with the Blue Mesa Member, at least in most part if not completely (see Heckert and Lucas 2002a, 2002b; Parker 2005; Martz and Parker 2010; Parker and Martz 2011; Irmis et al. 2011), it is concluded that most of the Chinle Formation is younger than 220 Ma (Irmis et al., op. cit.). Especially, the stratigraphic position of the *Placerias* Quarry was in debate, which was initially placed at the base of the Bluewater Creek Member (Lucas et al. 1997a; Heckert and Lucas 2003; Parker 2005) but later considered within the Blue Mesa Member according to the most recent stratigraphic framework (Parker and Martz 2011). This latter view is further supported by the geochronology (Irmis et al. 2011, see above).

However, conflicting results are published in the following works especially for the lower part of the Chinle Formation which provided somewhat older ages (Ramezani et al. 2009, 2011, 2014; also see Atchley et al. 2013). An age of ~225 Ma is obtained from the base of the Blue Mesa Member by in-situ zircon dating manifested that the Chinle Formation is somewhat older, and it is estimated an age of ca. 223 Ma for the lowermost land tetrapod occurrences in Chinle (e.g. the Newspaper Rock Bed), which signifies that the preserved portion of the Adamanian faunachron in Arizona corresponds to early Norian rather than middle to late Norian (Ramezani et al. 2011, 2014, *contra*

Irmis et al. 2011). Moreover, new ages which are gathered from the Bluewater Creek Member type section in New Mexico revealed that the Bluewater Creek Member is in fact, the temporal equivalent of the uppermost Blue Mesa Member to the middle Sonsela Member of the Chinle Formation (Ramezani et al. 2014). In this case, the position of *Placerias* Quarry became the stratigraphically lowest dinosauromorph bearing locality of the Chinle Formation which is constrained at a maximum of 219.39±0.12 Ma (Ramezani et al. 2011, 2014), corresponding to the early-middle Norian (Figure 5.6).

The boundary between the *Paleorhinus* and *Rutiodon* biochrons (Adamanian-Revueltian boundary *sensu* Lucas) in the Petrified Forest National Park is recently demarcated by a "persistent red silcrete bed" within the Sonsela Member (Woody and Parker 2004; Parker and Martz 2009; Parker and Martz 2011). This horizon is stands within the age limits of 218.017±0.088 Ma and 213.124±0.069 Ma based on the U-Pb zircon dating (Ramezani et al. 2011), which is tentatively placed at 216 Ma in this study (Figure 5.6). More derived phytosaurs (*Machaeroprosopus*, as the new senior synonym for *Pseudopalatus*) and aetosaurs (e.g. *Rioarribasuchus*) are introduced with the initiation of the Advanced Fauna, a turnover which is also observed in palynomorph communities (e.g. Litwin et al. 1991; Reichgelt et al. 2013). This turnover once linked with a global climate change and a minor extinction, an event which was hypothesized to had happened at the Carnian-Norian boundary and triggered the rise of dinosaurs over other tetrapods (e.g. Simms et al. 1994; Benton 1994, 2006).
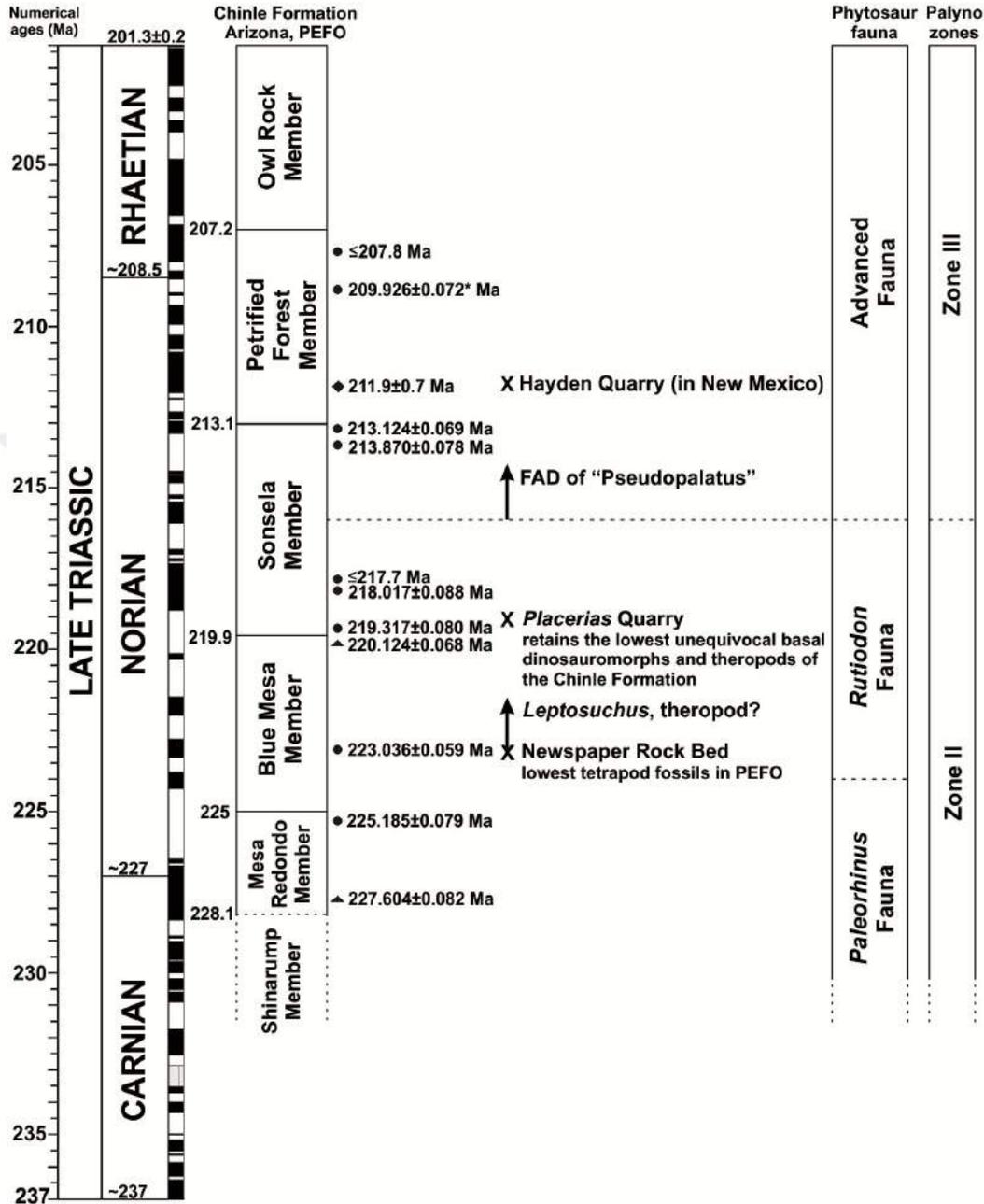
Figure 5.6 Compact stratigraphic chart for the Chinle Formation. FAD for the first appearance datum and PEFO signifies the section within the Petrified Forest National Park. Magnetostratigraphy based on Hounslow and Muttoni (2010), stage boundaries and numerical ages after Cohen et al. (2013), lithostratigraphy after Ramezani et al. (2014; partially following Parker [2005]), dating after Ramezani et al. (2014, black circles) and Atchley et al. (2013, black triangles), phytosaur faunas after Gregory (1969, 1972) and floral zones after Litwin et al. (1991) and Reichgelt et al. (2013). Since no numerical ages gathered, the biostratigraphic boundary passing within the Sonsela Member tentatively placed at 216 Ma, where as the boundary between *Paleorhinus* and *Rutiodon* faunas is tentatively placed at 224 Ma (see text). Asterisk (*) indicates the Black Forest Tuff layer which recalibrated multiple times (see text).

The Petrified Forest Member which immediately overlies the Sonsela Member keeps the record of the earliest unequivocal theropods in the Chinle Formation (Figure 5.6). The Hayden Quarry which is situated at the lower part of the Petrified Forest Member has produced the basal dinosauromorph *Dromomeron romeri* (Irmis et al. 2007a) and various fragments which are referred to the "Hayden Quarry silesaurid", *Chindesaurus bryansmalli* and coelophysids (Irmis et al., op. cit.; also see Kammerer et al. 2012). More recently, the basal theropod *Tawa hallae* was also discovered from the same quarry (Nesbitt et al. 2009c). The fauna of this particular quarry is first to indicate that both dinosaurs and their precursors had lived together within close temporal sequence for more than 15 Ma during the Late Triassic which it is further supported by the U-Pb geochronology (211.9±0.7 Ma, Irmis et al. 2011).

Upper portion of the Petrified Forest Member has also produced many dinosauromorph bearing localities. Both the holotype and some other referred fragments of North American herrerasaurid *Chindesaurus bryansmalli* (Long and Murry 1995, p. 174) whereas various coelophysoid fragments are noted from the Snyder Quarry (Heckert et al. 2003; Nesbitt et al. 2007) and from the Dinosaur Hill locality (Padian 1986, the "Padian theropod" of Nesbitt et al. 2007) in Arizona, Recalibration of the unexpectedly older tuffaceous Black Forest Bed (239±9 Ma, Ash et al. 1992) which is situated within the upper part of the Petrified Forest Member, provided a more precise dates of 213±2 Ma (Riggs et al. 2003) or 211±0.7 Ma (Heckert et al. 2009). In New Mexico, the silesaurid dinosauriform *Eucoelophysis baldwini* was collected from the Sullivan sites at the Orphan Mesa locality (Sullivan and Lucas 1999; Ezcurra 2006).

The uppermost dinosaur bearing quarries are located in the overlying "Upper Siltstone" Member in Ghost Ranch, New Mexico, which corresponds to the Owl Rock Member (Lucas et al. 1997b; Lucas and Heckert 2002a; Parker 2005)(Figure 5.6). The most famous *Coelophysis* Quarry (or the Whitaker Quarry, see Taphonomy section) is placed within this rock unit, where numerous individuals of *Coelophysis bauri* are revealed (e.g. Colbert 1989; Schwartz and Gillette 1994; Nesbitt et al. 2007). An additional basal theropod, *Daemonosaurus chauliodus* is also collected from the same quarry (Sues et al. 2011). Despite the original syntypes of *Coelophysis* is probably collected from some other quarry which stratigraphically below the Whitaker Quarry (Sullivan et al. 1996; Sullivan and Lucas 1999), it is stated that no morphologic contradiction exists between the Cope's original material and the neotype of *C. bauri* (AMNH FR 7224, Nesbitt et al. 2007). Therefore, coined binominal name of *Rioarribasaurus colberti* (Lucas and Hunt 1991a) has been relegated to a junior synonym of *C. bauri*.

**The Land Tetrapod Biostratigraphy and the Geochronology of the Dockum Group**

Most of the Late Triassic land tetrapods of the Dockum Group are documented from various quarries of the Tecovas and Bull Canyon Formations (e.g. Chatterjee 1986; Murry 1986, 1987b, 1989a; Long and Murry 1995; Lehman and Chatterjee 2005) whereas the phytosaurs of the Dockum Group have complemented the global Late Triassic phytosaur biochronology (e.g. Gregory 1972). Unlike the Chinle Formation above, dinosauromorph fossils and their collection sites within the Dockum Group will be evaluated separately in following pages. On the other hand, the geochronology for the

Dockum Group is still rough in outline, which is based on preliminary results of

incomplete sampling as yet (see below).
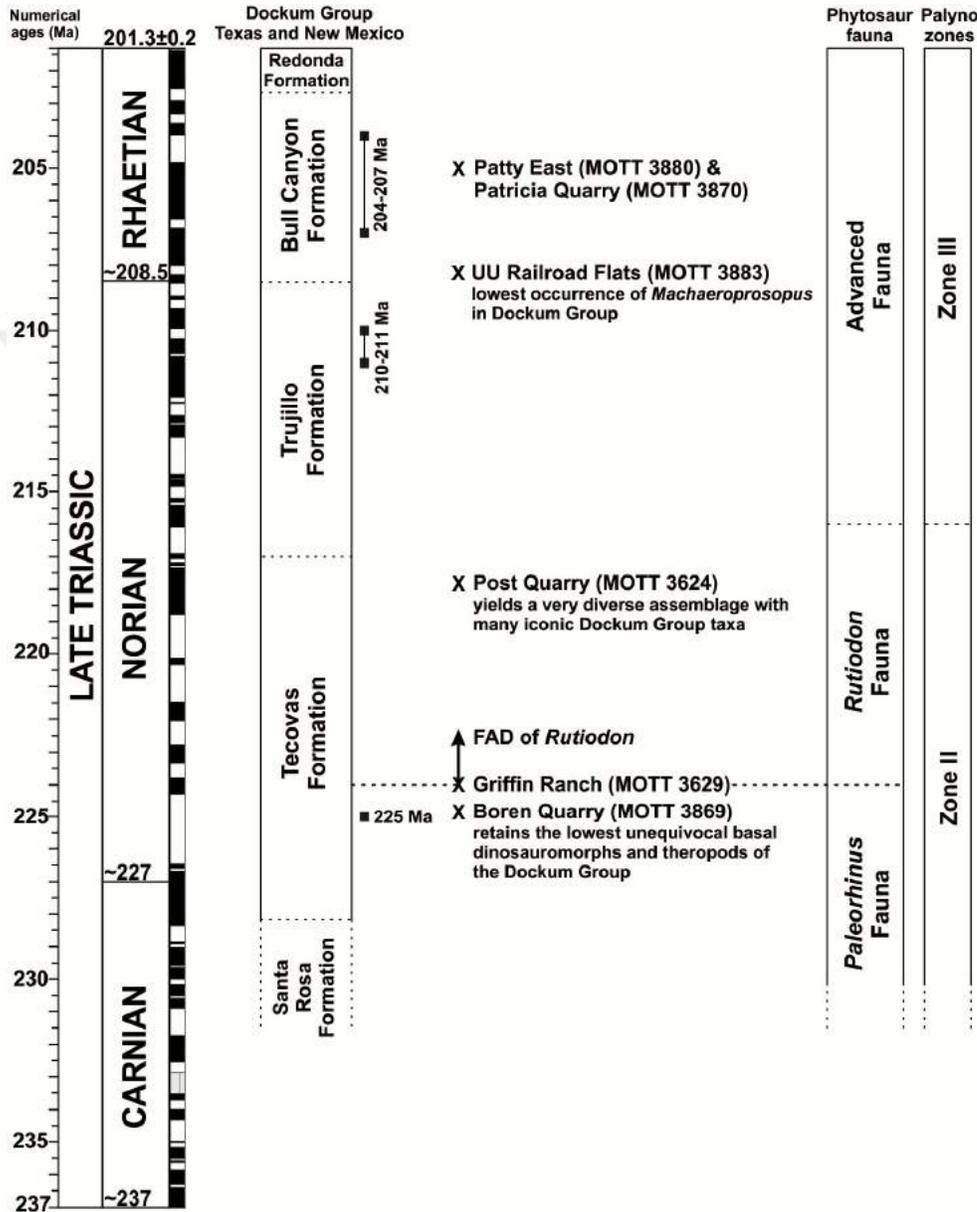


Figure 5.7 Composite stratigraphic chart for the Dockum Group. FAD for the first appearance datum. Magnetostratigraphy based on Hounslow and Muttoni (2010), stage boundaries and numerical ages after Cohen et al. (2013) and lithostratigraphy after Lehman and Chatterjee (2005), phytosaur faunas after Gregory (1969, 1972) and floral zones after Litwin et al. (1991) and Reichgelt et al. (2013). Gathered ages from Rb-Sr dating in black squares are provided by Thomas Lehman, pers. comm. 2014). Note that the boundaries for the phytosaur faunas are lacking numerical ages, but tentatively placed at 224 and 216 Ma, respectively (see text). Undefinite lithostratigraphic boundaries are also shown by dashed lines.

The Santa Rosa Formation and the lower part of the Tecovas Formation bear the *Paleorhinus*-grade phytosaurs, *Wannia scurriensis* and *Paleorhinus* spp. The exact locality for *W. scurriensis* is difficult to mark since the thickness of the Santa Rosa Formation varies largely (Bill Mueller, pers. comm. 2014). *Paleorhinus* specimens are produced from the upper Boren Ranch Sandstone (*sensu* Martz 2008) at Lake Alan Henry, Boren Quarry (MOTT 3869) and various other overlying quarries of the lower Tecovas Formation.  Most of the *Paleorhinus* specimens are collected from the Boren Quarry which covers a large diversity of archosaurs including various aetosaurs, rauisuchians such as *Postosuchus* and *Poposaurus*, alongside of other land tetrapods such as metoposaurs and dicynodonts (see Mueller 2014). Boren Quarry also yields the lowest occurrences of dinosauromorphs and theropods of the Dockum Group (Figure 5.7).

The upper portion of the Tecovas Formation carries *Rutiodon*-grade phytosaurs of *Rutiodon*, *Smilosuchus* and *Leptosuchus*. *Paleorhinus* and *Rutiodon* are both collected from the same locality (Griffin Ranch, MOTT 3629) which is considered as the boundary between two biozones in Dockum and referable as the midpoint for the Tecovas Formation (Bill Mueller, pers. comm. 2014), which is tentatively placed at 224 Ma in this study (Figure 5.7). A direct biostratigraphic correlation between the Dockum Group and the Keuper is only available in part since no equivalent of the *Rutiodon* Fauna in modern sense is present within the Keuper (see Figures 5.1, 5.2 and 5.7). Post Quarry (MOTT 3624) offers the richest and most diversified land tetrapod record available to this interval including phytosaur *Leptosuchus*, various dinosauromorphs and many other archosauromorph and non-archosauromorph taxa (e.g. Martz et al. 2013) (Figure 5.7).

Post Quarry also represents the maximum range of dicynodonts in the Dockum Group (Bill Mueller, pers. comm. 2014).

On the other hand, the Bull Canyon Formation and the overlying Redonda Formation are characterized by the taxon range of *Machaeroprosopus* (*sensu* Parker et al. 2013 and Hungerbühler et al. 2013). The first appearance of *Machaeroprosopus* is recorded in one of the lowermost quarries (UU Railroad Flats [MOTT 3883], Figure 5.7) of the Bull Canyon Formation, however lower occurrences of this taxon (i.e. first appearance of "*Pseudopalatus*") is previously recorded in the Chinle Formation (see previous section and Figure 5.6) It is suggested that the boundary between the *Rutiodon* and the Advanced phytosaur biozones in Dockum Group passes within the Trujillo Formation (e.g. Lehman and Chatterjee 2005), although no phytosaur fossils hitherto described from this formation.

Comprehensive and detailed works on the geochronology of the Dockum Group are still lacking. Detrital biotite Rb-Sr age determinations were briefly mentioned only in a series of abstracts by Long and Lehman (1993, 1994, 2009). The full data and analyses have not been published; however the preliminary results are kindly provided (Thomas Lehman, pers. comm. 2014). The weathered condition of the biotite has likely degraded the quality of the results, and because the six samples were collected over a broad stratigraphic interval, an isochron calculated using all six samples together yield an apparent age that is not useful. The "model" ages determined for each sample individually require assuming an initial Sr value. Nevertheless, the calculated model ages (with assumed initial Sr) do accord with the stratigraphic positions of the samples (Figure 5.7). The lowest (and "freshest") sample is from the upper portion of Boren Ranch

sandstone (*sensu* Martz 2008) at the base of Tecovas Formation and yields a model Rb-Sr age of 225 Ma. The upper Boren Ranch sandstone stands only a couple of meters below the Boren Quarry (MOTT 3869). Two samples from the Trujillo Sandstone yield model Rb-Sr ages of 210 to 211 Ma. The three highest samples, from just below and within the Macy Ranch sandstone of the upper levels of Bull Canyon Formation (including the Patricia Quarry, MOTT 3870) yield model Rb-Sr ages of 204 to 207 Ma (Figure 5.7). This preliminary framework is a promising study to complement the high resolution scheme of Chinle Formation (e.g. Atchley et al. 2013; Ramezani et al. 2014).

## Significance of the Upper Triassic Phytosaur Biostratigraphy and Biochronology

Although the phytosaur fossils occur worldwide in continental Upper Triassic deposits, only a few of those localities besides the Chinle-Dockum sequence offer a complete or near-complete biostratigraphic record including the Keuper and the Upper Triassic deposits of eastern North America, India and Morocco. Unfortunately, none of the latter three provinces provide any geochronologic ages.

### The Land Tetrapod Biostratigraphy of the Keuper

As expanded above, the German Keuper represents the type section for the terrestrial Upper Triassic with a diverse land tetrapod fauna. The Hassberge Formation (Blassensandstein in Gregory 1969; Butler et al. 2013) (Figures 5.1 and 5.8) of Germany includes the *Paleorhinus*-grade phytosaurs of *Ebrachosuchus neukami* and *Paleorhinus angustifrons* (Butler et al. 2013), alongside of various temnospondyls and a discredited

aetosaur *Ebrachosaurus singularis* (synoynmized with *Stagonolepis* in some, e.g. Seegis 2005), of which the holotype is destroyed during the Second World War (Desojo et al. 2013). Compared to the Hassberge Formation, the other two horizons (Stelgerwald and Mainhardt formations) of the Weser Formation are poorly fossiliferous (e.g. Seegis 2005). The genus *Paleorhinus* is also represented in the Krasiejów beds in Poland (Dzik 2001) which becomes the only other reliable correlative for the Hassberge Formation in terms of phytosaur biocorrelation.

Upper Norian-Rhaetian Arnstadt Formation (including Löwenstein and Trossingen formations) and Exter Formations yield a greater variety of land tetrapods, especially marked by the widespread occurrences of terrestrial turtles and temnospondyls (e.g. Seegis 2005; Sues and Fraser 2011). Temnospondyls *Gerrothorax* and *Cyclotosaurus* (e.g. Seegis 2005; Sues and Fraser 2011), phytosaurs *Nicrosaurus* and *Mystriosuchus* (e.g. Hungerbühler and Hunt 2000), aetosaurs *Aetosaurus ferratus* and *Paratypothorax andressorum* (e.g. Desojo et al. 2013), rauisuchian *Teratosaurus suevicus* (von Meyer 1861; Brusatte et al. 2009), sphenosuchian *Saltoposuchus* (e.g. Sereno and Wild 1992) and dinosaurs *Procompsognathus triassicus* (Frass 1913; Ostrom 1981; also see Sereno and Wild 1992 and Knoll 2008); *Efraasia diagnostica* (e.g. Galton 1973) and *Plateosaurus* (*Sellosaurus*) *gracilis* (e.g. Yates 2003) are the most important elements of the land tetrapod fauna, collected from the Löwenstein Formation. A *Nicrosaurus*-grade phytosaur (Kimmig and Arp 2010, but see Stocker and Butler 2013) and dinosaurs *Plateosaurus engelhardti* (von Meyer 1837; Moser 2003), *Ruehleia bedheimensis* (Galton 2001) and *Liliensternus liliensterni* (von Huene 1934; Welles 1984) are the notable elements of the overlying Trossingen Formation. A diverse fossil

array of therapsids and mammalian precursors are collected especially from the layers of the Trossingen and Exter formations (e.g. Seegis 2005).

The German Keuper has also provided basis for the establishment of the phytosaur biozones. Lowest occurrences of phytosaurs within the Keuper are located in Germany, but also in Poland (Dzik 2001), however higher occurrences of phytosaurs which are suitable for biocorrelation only occur in German strata. Therefore, only the *Paleorhinus* and Advanced faunas can be detected within the Keuper, whereas the *Rutiodon*-grade phytosaurs are missing in-between (Figures 5.1 and 5.8).

**The Land Tetrapod Biostratigraphy of Eastern North America**

The eastern rift basins of the North America are filled by an extensive Upper Triassic rock sequence, namely the Newark Supergroup. The vertebrate fauna of the Newark Supergroup is dominated by fish rather than land tetrapods (e.g. Olsen et al. 1982), a situation probably ascribable to the dominant lacustrine facies, analogous to modern-day African Rift Valley. Land tetrapod record is mostly fragmentary and dispersed in various different basins, such as the Newark Basin, the Deep River Basin, the Hartford Basin, the Taylorsville Basin, the Fundy Basin and the Gettysburg Basin (e.g. Huber et al. 1993). The faunal contents of the Newark Supergroup deposits include temnospondyls (e.g. Hunt 1993), cynodonts (e.g. Lucas 1998a; Sues and Hopson 2010), archosauromorphs such as *Doswellia kaltenbachi* (Weems 1980), the only unequivocal phytosaur *Rutiodon carolinensis* (Emmons 1856), various aetosaurs (e.g. Lucas et al. 1998; Desojo et al. 2013), *Postosuchus alisonae* as the only rauisuchian so far (Peyer et

al. 1998) and various ichnotaxa which are mainly represented by footprints (e.g. Cornet and Olsen 1985; Olsen et al. 1992).

The fragmentary nature of the land tetrapod elements and the lack of diagnosable phytosaurs except *R. carolinensis* prevent the construction of any reliable land tetrapod biochronology. Nevertheless, the presence of *R. carolinensis* in the Cumnock Formation of the Deep River Basin (and any other Newark correlatives) is directly referable the *Rutiodon* Fauna (Figure 5.8).

**The Land Tetrapod Biostratigraphy of India**

Upper Triassic deposits of India are exposed mainly in two basins, the Pranhita-Godavari Valley which includes the Lower and Upper Maleri formations and the overlying Lower Dharmaram Formation, and the Son-Mahanadi Basin which yields Tiki Formation, a coeval rock unit with the Maleri Formation (e.g. Kutty and Sengupta 1989; Bandyopadhyay 1999; Sengupta 2003). India possesses wide spectrum of Late Triassic vertebrate fossils (e.g. Chatterjee and Roy Chowdhury 1974; Jain 1990; Jain et al. 1996; Bandyopadhyay 1999; Sengupta 2003; Novas et al. 2011). The Lower Maleri fauna includes many important non-archosaurian tetrapods, such as the metoposaur *Metoposaurus* (Roy Chowdhury 1965), rhynchosaur *Hyperodapedon* (*Paradapedon*) *huxleyi* (Chatterjee 1974; Langer and Schultz 2000), traversodontid *Exaeretodon statisticae* (Chatterjee 1982a) which is recently regarded as an undetermined taxon (Lui 2007), and the protorosaur *Malerisaurus robinsonae* (Chatterjee 1980b). Metoposaurs are also widely documented in the Tiki Formation (e.g. Sengupta 1992, 2003) as well as rhynchosaurs, where a new taxon, *Hyperodapedon tikiensis*, was recently published

(Mukherjee and Ray 2014). *Parasuchus hislopi* (Chatterjee 1978a, 2001) of the Lower

Maleri and Tiki formations is the only phytosaur determined in India so far, whereas

*Tikisuchus romeri* (Chatterjee and Majumdar 1987) of the Tiki Formation is the only

rauisuchid hitherto collected from India. Tiki Formation also housed some possible early

mammalians *Gondwanadon tapani* (Datta and Das 1996) and *Tikitherium copei* (Datta

2005), where only the molars are preserved in both taxa. Following up to the Upper

Maleri Formation, the characteristic metoposaurids, rhynchosaurs and phytosaurs of the

previous Lower Maleri Formation are no longer appearing in the fossil record (e.g.

Bandyopadhyay 1999). Instead, new chigutisaurid temnospondyl (Sengupta 1995) and

possible dicynodonts (e.g. Novas et al. 2011, table 1) appeared in this formation.

Aetosaurs are represented only by their dermal scute fragments in both Maleri and

Dharmaram faunas (e.g. Chatterjee and Roy Chowdhuri 1974; Kutty and Sengupta 1989;

Bandyopadhyay 1999) which are associated with typothoracisine and desmatosuchinae in

recent works (Desojo et al. 2013, p. 209; also see Benton 1983a).

Dinosauromorphs are also represented as a part of this diversity. *Alwalkeria*

*maleriensis* is the earliest dinosaur discovered within the Lower Maleri Formation

(Chatterjee 1987; Chatterjee and Creisler 1994). Although it is previously debated that

the holotype of *A. maleriensis* might include a composite of various different elements

(Rauhut and Remes 2005), at least the illustrated and described femur and astragalus in

the original text display definite theropod characters. Dinosaurs and their kin are better

represented in the upper formations of Upper Maleri and Lower Dharmaram. *Nambalia*

*roychowdhurii* and *Jaklapallisaurus asymmetrica* represent the non-plateosaurid and

plateosaurid sauropodomorphs of the Upper Maleri Formation respectively, alongside of

a guaiabasaurid and two basal dinosauriform specimens, whereas the Lower Dharmaram

Formation has produced some remains of basal sauropodomorphs and neotheropods

(Novas et al. 2011).

Due to the inadequate phytosaur record no land tetrapod biozones established as

yet and thus, a direct biocorrelation is implausible with Euramerican deposits especially

for Upper Maleri and Lower Dharmaram Formations. In this case, only *Parasuchus*

*hislopi* (Chatterjee 1978a, 2001) of the Lower Maleri and Tiki formations which is a

*Paleorhinus*-grade phytosaur indicates the fauna of those two formations belong to the

*Paleorhinus* Fauna of Gregory (Figure 5.8). Additionally, other faunal elements of the

Lower Maleri Formation (e.g. *Metoposaurus*, *Hyperodapedon*, *Exaeretodon* and

*Malerisaurus*) provide an auxiliary biocorrelation with the corresponding faunas of the

Late Triassic. The other phytosaur remains from the overlying Upper Maleri Formation

are tentatively affined to *Rutiodon*-grade phytosaurid phytosaurs (Bandyopadhyay 1999;

Hungerbühler et al. 2002; Stocker and Butler 2013). The phytosaur remains found on the

overlying Lower Dharmaram Formation cannot be referred to any taxon (Hungerbühler et

al., op. cit.).

**The Land Tetrapod Biostratigraphy of Morocco**

The terrestrial Permo-Triassic sequence of Morocco is situated in the modern-day

Argana Valley, at the western part of the High Atlas Mountains. Those sediments are

subdivided into eight distinct layers (T1-T8), where the Triassic sediments include two

formations, Timezgadiouine (T3-T5) and Bigoudine (T6-T8), respectively (e.g. Jalil

1999; Lagnaoui et al. 2013). Of these six layers, only the T4 and T5 contain body fossils

of land tetrapods, whereas T3 and T6 yield tetrapod footprints (Tourani et al. 2010; Lagnaoui et al. 2013). Except a skull fragment in the T4 layer (the Aglegal Member) which belongs to temnospondyl *Cyclotosaurus*, the bulk of the land tetrapod body fossils are concentrated on the T5 layer, or formerly the Irohalene Member (e.g. Jalil 1999). The land tetrapod fauna of Irohalene Member contains metoposaurs *Dutuitsaurus ouazzoui* and *Arganasaurus lyazidi* (e.g. Dutuit 1976; Hunt 1993; Sulej 2002), dicynodonts *Moghreberia* and *Azarifeneria* (e.g. Dutuit 1980, 1988, 1989), phytosaurs *Angistorhinus talainti* (Dututi 1977a) and *Paleorhinus magnoculus* (Dutuit 1977b; *Arganarhinus magnoculus*, Long and Murry 1995), rauisuchian *Arganasuchus dutuiti* (Jalil and Peyer 2007) and silesaurid *Diodorus scytobrachion* (Kammerer et al. 2012). The presence of *Paleorhinus magnoculus* places the Irohalene Member within the *Paleorhinus* Fauna in phytosaur biochronology (Figure 5.8).

Next Page: Figure 5.8 Composite stratigraphic chart for the terrestrial Upper Triassic. FAD signifies the first appearance datum and PEFO signifies the Chinle section within the Petrified Forest National Park. Magnetostratigraphy based on Hounslow and Muttoni (2010), stage boundaries and ages after Cohen et al. (2013). For lithostratigraphic and biostratigraphic sections, including the positions of the quarries, see text and previous figures. Sections from Brazil and Zimbabwe are omitted based on the absence of both numerical ages and phytosaurs (for their correlations, see text).The first appeareance of Ischigualastian dinosaurs is reported from the lowermost part of the Ischigualasto Formation. *Placerias* and Boren quarries reflect the lowest dinosaur occurrences for each sequence, indicating an earlier presence of dinosaurs in North America. The absence of numerical ages from the collection sites of *Wannia scurriensis* (Santa Rosa Formation), *Rutiodon carolinensis* (Cumnock Formation) and *Parasuchus hislopi* and *Alwalkeria maleriensis* (Lower Maleri Formation) prevents their exact stratigraphic placement. A numerical age is also missing for the horizon of *Paleorhinus magnoculus* (Timezgadiouine Formation), although it is noted that this taxon is collected from the base of the Irohalene Member (T5) (e.g. Jalil 1999). Note that the boundaries for the phytosaur faunas are lacking numerical ages, but tentatively placed at 224 and 216 Ma, respectively (see text).
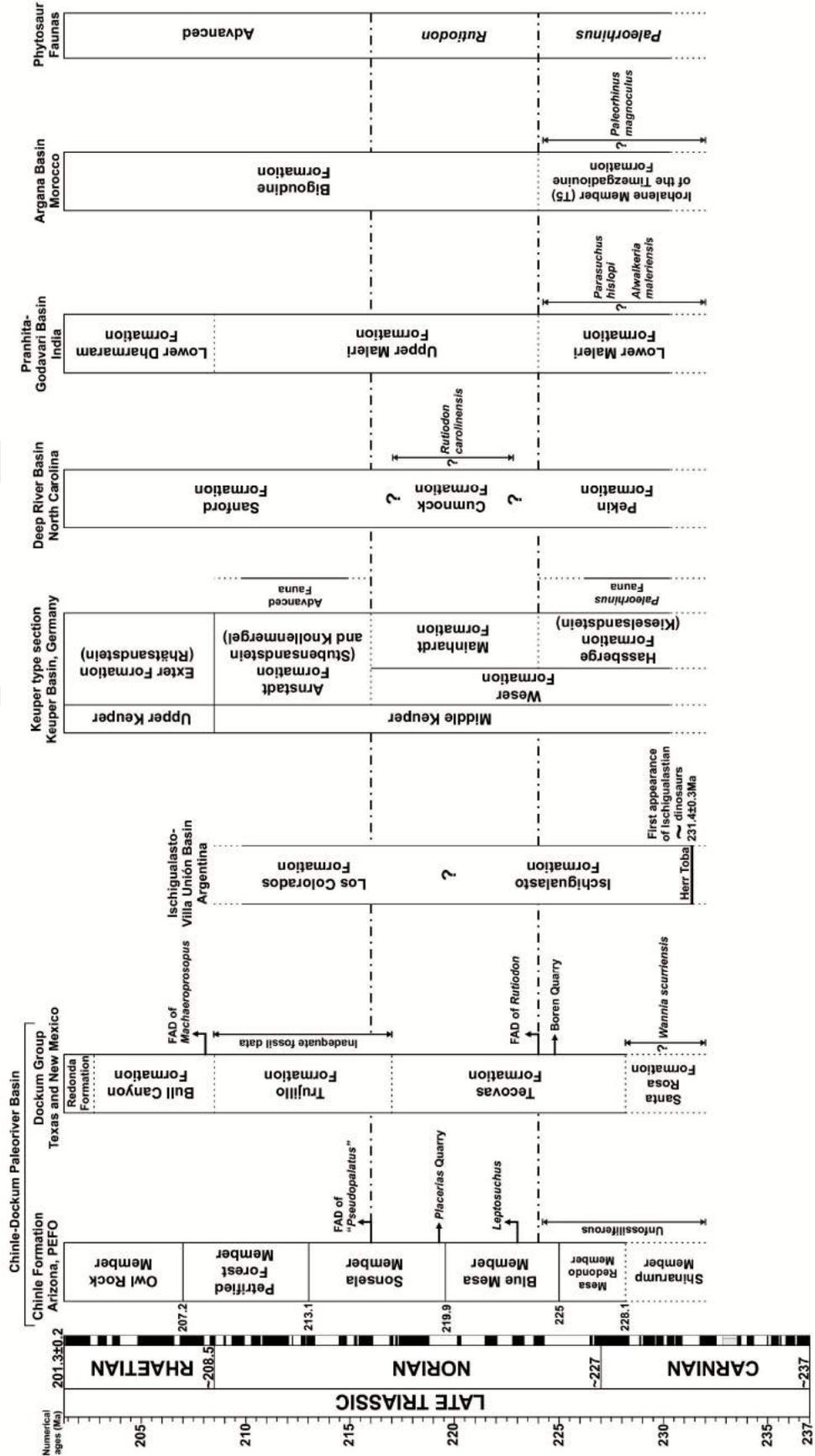
**The Composite Late Triassic Phytosaur Biochronology**

Based on the four main provinces of Europe, North America, Morocco and India which possess different degrees of completeness on the phytosaur fossil record, it appears that the phytosaur biochronology provides a satisfactory biocorrelation at least for the most part (Figure 5.8). Moreover, Ischigualasto and Los Colorados formations can be included within the chart based on the geochronology, despite the absence of phytosaur fossils (Figure 5.8; also see next section). The Dockum Group provides the complete phytosaur biochronology, as previously recognized (Gregory 1972). The Keuper and the Chinle Formation are missing one biochron each. The Newark Supergroup and the Argana sequence have the poorest phytosaur record in abundance, whereas the phytosaur fossils of India are restricted to the *Paleorhinus* biochron.

## Problems with the Global Phytosaur Biochronology and Supplementary Approaches

It is previously explained that the geochronology stands as the only tool to correlate marine and terrestrial sequences, due to the lack of common fossil elements. But is it the same when comparing the terrestrial units with each other? In available cases, as in Late Triassic when all the continents were still coalesced together, the biostratigraphy facilitates a better correlation between the rock units rather than geochronology, based on widely distributed index taxa, in this case, the phytosaurs. However, the absence of a descent phytosaur record in South America compelling the researchers to involve secondary approaches such as geochronology and the use of other land tetrapods.

**The Land Tetrapod Biostratigraphy and the Geochronology of South America**

South America is the only other continent than the Euramerican landmass where Late Triassic vertebrate biozones are established. In contrast with the Eurmarican faunas, the South American land tetrapod zones are established based on therapsids and rhynchosaurs since no phytosaurs are hitherto discovered except a fragmentary lower jaw from the Caturrita Formation (Kischlat and Lucas 2003), however the generic affinity of this animal is still ambiguous (Axel Hungerbühler in Langer et al. 2005a; Stocker and Butler 2013). Based on Bonaparte's (e.g. 1966, 1967, 1982) vertebrate assemblages per formation (the "Reptil Ages" and their local equivalents, Figure 5.9), it is proposed two main rock-independent vertebrate assemblage zones (i.e. Cenozones, Figure 5.9) to establish a formal Middle-Upper Triassic biostratigraphy of Brazil which are the Therapsid Cenozone and the Rhynchosaur Cenozone, followed by a third informal unit, the *Jachaleria* Level, characterized by the presence of these tuskless dicynodonts (e.g. Schultz et al. 1995, 2000; Schultz 2005) (Figure 5.9). In terms of faunal abundance, the lower part of the Rhynchosaur time is dominated by the rhynchosaur "*Scaphonyx*" where the upper part consists almost completely of the traversodontid cynodont *Exaeretodon* (Schultz et al. 2000; Langer 2005a, 2005b; Martinez et al. 2011a, 2013a). All the rhynchosaurs which were previously ascribed to *Scaphonyx* are now classified under the genus *Hyperodapedon*, except *S. sulcagnathus* which is recently referred to a new genus *Teyumbaita* (Langer and Schultz 2000; Montefeltro et al. 2010). Concurrently, this biozone is referred as the *Hyperodapedon* Acme Zone (Langer et al. 2007), as traceable in the lower part of the Ischigualasto Formation and the upper part of the Santa Maria Formation (the Alemoa Member, Figure 5.9) since *T. sulcagnathus* is collected from the

Caturrita Formation. Although *Exaeretodon* is documented in the preceding "*Scaphonyx*"

Zone (namely *Scaphonyx-Exaeretodon-Herrerasaurus* Biozone, Martinez et al. 2013a), it

became the dominant element of the land tetrapod fauna only after the disappearance of

the rhynchosaurs. Such faunal turnover is recently linked with the Carnian-Norian

boundary events (Martinez et al. 2011a). *Exaeretodon* is replaced by the dicynodont

*Jachaleria* in the following biozone, which eclipsed other taxa in abundance as well.

Regardless of the biochronology, dicynodonts were important components of the Late

Triassic tetrapod fauna of South America (e.g. Cox 1965).



Figure 5.9 The composite stratigraphic framework including the vertebrate biochronology of South American Late Triassic (Modified after Schultz et al. 2000). Although all these biozones are originally established as succeeding assemblage zones, recent attempts also provide redefinitions based on intervals between the ranges of index taxa (e.g. Langer 2005b). The subdivision of the Rhynchosauria Cenozone (including both Brazil and Argentina) and the redefinition of the lower boundary of *Jachaleria* Level to include the uppermost part of the Ischigualasto Formation after Langer et al. (2007) and Martinez et al. (2013a).
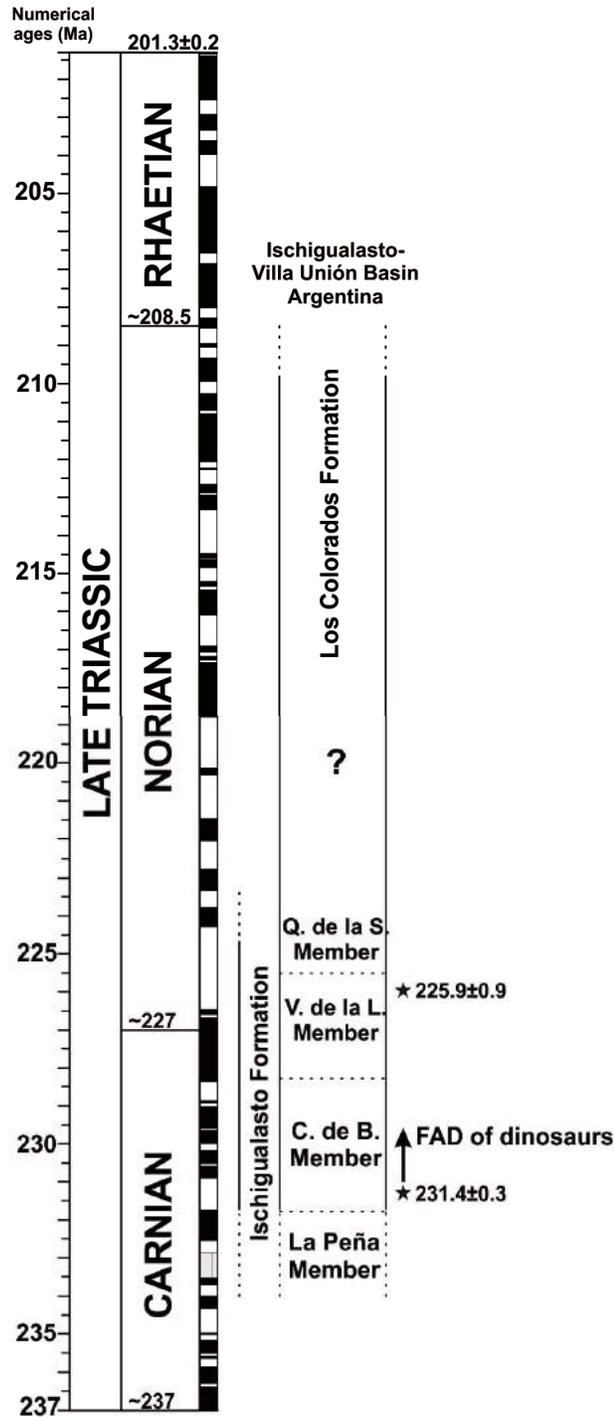
Figure 5.10 Composite stratigraphic chart for the Ischigualasto and Los Colorados formations. FAD for the first appearance datum. The abbreviated members are Cancha de Bochas, Valle de la Luna and Quebrada de la Sal members, respectively. Magnetostratigraphy based on Hounslow and Muttoni (2010), stage boundaries and numerical ages after Cohen et al. (2013) and lithostratigraphy after Currie et al. (2009). Gathered ages labeled in black stars after Rogers et al. (1993) and Martinez et al. (2011a).

Dinosauromorphs are the significant members of the fauna, alongside of various other land tetrapods. The earliest dinosaur precursors *Lagerpeton chanarensis* (Romer 1971; Sereno and Arcucci 1994a), *Lewisuchus admixtus* (Romer 1972a, Bittencourt et al. 2014) and *Marasuchus lilloensis* (Romer 1972b; Sereno and Arcucci 1994b) and *Pseudolagosuchus major* (Arcucci 1987) are discovered from the Ladinian Chañares Formation in Argentina (Figure 5.9). Those early dinosauromorphs constitute about 20% of the total faunal assemblage of terrestrial vertebrates (Martinez et al. 2011a, figure 4). However, the first appearance of dinosaurs in Argentina is documented in the lowermost part of the overlying Ischigualasto Formation (Figures 5.9 and 5.10). All of these earliest dinosaurs are collected from the *Scaphonyx-Exaeretodon-Herrerasaurus* Biozone (which corresponds to the *Hyperodapedon* Acme Zone Figure 5.9); the diversity of Ischigualastian dinosaurs corresponds to the one-third of the recorded land vertebrate genera from this formation, despite their low relative abundance which only corresponds to 10-11% of the total faunal composition of land vertebrates (Martinez et al. 2011a, figure 4). The basal theropod *Eodromaeus murphi* and herrerasaurids *Herrerasaurus ischigualastensis* (Reig 1963; Sereno and Novas 1992) and *Sanjuansaurus gordilloi* (Alcober and Martinez 2010) represent ~70% of all terrestrial carnivores in the Ischigualasto faunal assemblage, whereas the small sized herbivores and omnivores are represented by the basal saurischians *Eoraptor lunensis* (Sereno et al. 1993; Sereno et al. 2013), *Chromogisaurus novasi* (Ezcurra 2008, 2010; Martinez et al. 2013b), *Panphagia protos* (Martinez and Alcober 2009) and the basal ornithischian *Pisanosaurus mertii* (Casamiquela 1967; Bonaparte 1976) (Martinez et al. 2011a). The herbivore/omnivore niche possibly includes the following discoveries of a new silesaurid *Ignotosaurus*

*fragilis* and a new lagerpetid form (PVSJ 883) (Martinez et al. 2013a; the "Ischigualasto forms" of Langer et al. [2013]). In Brazil, on the other hand, the herrerasaurid *Staurikosaurus pricei* (Colbert 1970; Galton 1977; Bittencourt and Kellner 2009), the basal theropod *Pampadromaeus barberenai* (Cabreira et al. 2011) and the basal sauropodomorph *Saturnalia tupiniquim* (Langer et al. 1999) are collected from the upper part of the Santa Maria Formation (*sensu* Andreis et al. 1980; Langer et al. 2007) which correspond to the Alemoa Member/Fauna (Figure 5.9).

Such large diversity of dinosaurs noted to be reappearing in the upper parts of the overlying Los Colorados Formation ("La Esquina Fauna", Figure 5.9) in Argentina, including the theropod *Zupaysaurus rougieri* (Arcucci and Coria 2003; Ezcurra and Novas 2007) and basal sauropodomorphs *Riojasaurus incertus* (Bonaparte 1967, 1971; Bonaparte and Pumares 1995), *Coloradisaurus brevis* (Bonaparte 1978; renamed by Lambert 1983) and *Lessemsaurus sauropoides* (Bonaparte 1999; Pol and Powell 2007b). The faunal gap for dinosauromorphs between the lower part of the Ischigualasto Formation and the upper part of the Los Colorados Formation in Argentina stands as a sampling artifact for the Los Colorados Formation, since the Caturrita Formation in Brazil has produced dinosaurs *Guaibasaurus candelariensis* (Bonaparte et al. 1999, 2007; Langer et al. 2011) and *Unaysaurus tolentinoi* (Leal et al. 2004), and the silesaurid *Sacisaurus agudoensis* (Ferigolo and Langer 2007; Langer and Ferigolo 2013) (the Botucarai Fauna, Langer 2005a; Langer et al. 2007, see Figure 5.9). An additional plateosaurid-like basal sauropodomorph fragment from the Caturrita Formation is recently noted (Bittencourt et al. 2012). This continuous fossil record indicates a stable dinosaur lineage in South American basins during Late Triassic (Figure 5.9). In addition

to the main sequence basins, the sauropodomorph *Mussaurus patagonicus* (Bonaparte and Vince 1979; Pol and Powell 2007a; Otero and Pol 2013) and a heterodontosaurid (Baez and Marsicano 2001) are collected from the Upper Triassic rocks of Patagonia (El Tranquilo Group).

The obtained 227.8±0.3 Ma from $^{40}Ar/^{39}Ar$ dating of Herr Toba bentonite layer which occurs only 20 meters above the base of the formation (Rogers et al. 1993) is later recalibrated to 231.4±0.3 Ma after the statistical optimizations (Renne et al. 2010; Martinez et al. 2011a). In this case, the base of the Ischigualasto Formation is now corresponds to late Carnian (Figure 5.10). This result brings the argument that the origin of dinosaurs is dated to Late Triassic, around 230 million years ago (e.g. Langer et al. 2010; Brusatte et al. 2010b). Another coinciding date is obtained by U-Pb zircon dating of an ash layer within the marine limestone units in Southern Italy which yielded ~231 Ma for upper Carnian (Furin et al. 2006), and might be representing the somewhere near the base of Tuvalian (Heinz W. Kozur in Ogg 2012, p. 704). Absolute ages are also obtained from the upper part of the Ischigualasto Formation by $^{40}Ar/^{39}Ar$ dating of feldspars; however, it is relatively more difficult due to scattered volcanic ash layers and but also due to the contradicting stratigraphic tools (Ramezani et al. 2014). In contrast with an earlier result of ~217 Ma from the upper part Valle de la Luna Member of the Ischigualasto Formation (Shipman 2004; Currie et al. 2009), a more reliable and statistically calibrated date of 225.9±0.9 Ma obtained from the topmost portion of the same member (Martinez et al. 2011a). The lack of radiometric dates in the overlying Los Colorados Formation, on the other hand, mandate a magnetostratigraphic study which provided a conflicting time span from 227 Ma to 216-215 Ma in correlation with the

Newark polarity zones (Santi Malnis et al. 2011). Therefore, an uncertain upper boundary

for the Ischigualasto Formation is indicated at this time (Figure 5.10).

**Absence of the Phytosaur Biocorrelation for South America**

Although extensive continental Upper Triassic sequences occur in both Argentina

and Brazil, it is always challenging to establish a direct biocorrelation between South

America and the rest of the Pangea continents due to the lack of phytosaurs in South

America. Based on the diverse land tetrapod fossil record, India is long regarded as the

reference point for the South American correlation, especially with the North America

(e.g. Chatterjee and Scotese 1999). For example, traversodontids, rauisuchids and

rhynchosaurs from India are very similar to those of Europe, North America, Africa and

South America. On the other hand, phytosaurs and metoposaurs from the Lower Maleri

Formation are comparable to those of North America, Europe and Morocco but they are

conspicuously absent in South America, except one phytosaur fragment from the

Caturrita Formation of Brazil (Kischlat and Lucas 2003).

**Incompleteness of Geochronologic Record**

The Chinle-Dockum Paleoriver Basin and the Ischigualasto-Villa Unión Basin are

only two Late Triassic provinces where it can be obtained radiometric dates. As expanded

above, a complete geochronology for the Chinle Formation has been recently published

(Ramezani et al. 2011, 2014; Atchley et al. 2013). In contrast, the dating of the Dockum

and the Ischigualasto/Los Colorados sediments are still in preliminary phases (Figure

5.10). Therefore, geochronology by itself cannot be adequate at the moment to correlate terrestrial Upper Triassic deposits.

## The Biostratigraphic Significance of Dinosauromorphs

The terrestrial Upper Triassic units of South America require another tool for a global biochronology because of the absence of phytosaurs and the incompleteness of the geochronology. Recent discovery of the Lower Maleri dinosaur fauna provides a strong biotic link between India and South America (Novas et al. 2011). In the present work, it is provided the biostratigraphic utility of the dinosauromorphs for the first time for a direct correlation predominantly between North America and South America. This framework is corroborated by the recent work of radioscopic data, gathered from the Chinle Formation of Arizona and the Ischigualasto Formation of Argentina (see above).

### Biostratigraphy of Dockum Dinosauromorphs

Dockum dinosauromorphs have a notably large diversity and wide stratigraphic range predominantly in Texas (also see Descriptions chapter). Boren Quarry (MOTT 3869) which is situated at the lowermost portion of the Tecovas Formation is probably the most significant fossil locality of this work, since it provides the earliest records of theropods in the North America (TTU-P10514; TTU-P10515; TTU-P10517). One fragmentary and one complete tibia (TTU-P10546; TTU-P19803) are also collected from the Boren Quarry which might represent a new dinosauromorph taxon. Otis Chalk Quarry 3 (TMM 31100-1306 or MOTT 2000) which is stands slightly higher in the stratigraphic column has produced the holotype of the lagerpetid *Dromomeron gregorii* and associated

paratypes (Nesbitt et al. 2009b) and the proximal portion of a left femur which is referred to *Chindesaurus bryansmalli* (TTM 31100-523, Long and Murry 1995; Nesbitt et al. 2007). The proximal portion of a left tibia (TTU-P09408) which is diagnosed as an indeterminate dinosauriform is the only dinosauromorph remain from the overlying Kirkpatrick Quarry (MOTT 3628).

Among all the dinosauromorph bearing quarries, Post Quarry (MOTT 3624) from the uppermost Tecovas Formation is one of the most significant of all, not just by its peculiar taphonomy which is previously expanded (see Taphonomy chapter) but also by including the largest diversity of dinosauromorphs from the Dockum Group (Figure 5.11). The Post Quarry dinosauromorph assemblage includes lagerpetid *Dromomeron gregorii* (TTU-P11282, see in Martz et al. 2013; TTU-P18331; TTU-P20046), silesaurid *Technosaurus smalli* (TTU-P9021), an indeterminate dinosauriform tibia (TTU-P11127), a herrerasaurid which possibly related to *Chindesaurus bryansmalli* (TTU-P10082) and various coelophysoids/basal neotheropods (TTU-P10071; TTU-P11044) and even more derived theropods (TTU-P11254a and TTU-P11254b).

Both species of *Dromomeron* are represented in the Tecovas Formation. Alongside with many other unidentifiable bone fragments, the three hind limb fragments which are referred to *Dromomeron* spp. (i.e. WTAMU specimens) despite the unknown stratigraphic position of their collection site. An isolated ilium of *Chindesaurus bryansmalli* (UMMP 8870) is also collected from the Tecovas Formation in Crosby County (Long and Murry 1995; Nesbitt et al. 2007), of which the exact locality is unknown (Figure 5.11).

**Phytosaur Zonation**

Advanced Fauna
*Machaeroprosopus* spp.

*Rutiodon* Fauna
*Rutiodon* sp.
*Smilosuchus* spp.
*Leptosuchus* spp.

*Paleorhinus* Fauna
*Paleorhinus* spp.
*Wannia scurriensis*

**Dockum Dinosauromorphs**

Neotheropoda
X TTU-P16789 — X TTU-P10534
TTU-P12587
TTU-P12790
X TTU-P10072
X TTU-P11175 — X TTU-P14786
TTU-P12531
TTU-P10071
X TTU-P10082 — X TTU-P11044
TTU-P11254a
TTU-P11254b
X TMM 31100-523

Herrerasauridae

Theropoda indet.
TTU-P10514
TTU-P10515
TTU-P10517
X

Dinosauriform indet.
X TTU-P09021 — X TTU-P11127
X TTU-P09480

Technosaurus smalli

Dinosauromorph indet.
TTU-P11282
X TTU-P18331
TTU-P20046
X TMM 31100-1306

Dromomeron gregorii
X TTU-P10546
TTU-P19803

Dromomeron romeri
TTU-P12537
X TTU-P12539

**Aforecited Quarries**

Patty East (MOTT 3880) &
Patricia Quarry (MOTT 3870)
Macy Ranch (MOTT 3927)
Lott Kirkpatrick (MOTT 3634)
Headquarters S (MOTT 3898) &
Headquarters NW (MOTT 3899)
UU Railroad Flats (MOTT 3883)
Post Quarry (MOTT 3624)
Griffin Ranch (MOTT 3629)
Kirkpatrick Quarry (MOTT 3628)
Otis Chalk Quarry (MOTT 2000)
Boren Quarry (MOTT 3869)

**Lithostratigraphy of the Dockum Group in Texas**

Bull Canyon Formation
204-207 Ma

Trujillo Formation
210-211 Ma

Tecovas Formation

Santa Rosa Formation
~225 Ma

RHAETIAN
~208.5 Ma
NORIAN
CARNIAN
~227 Ma

Previous Page: Figure 5.11 Biostratigraphy and taxon ranges of the Dockum Group dinosauromorphs in Texas, including the related phytosaur fauna. Chronostratigraphy and ages after Cohen et al. (2013), the Dockum ages represented by black squares are provided by Thomas Lehman (pers. comm. 2014). The WTAMU specimens and the *Chindesaurus* ilium from Crosby County (UMMP 8870) cannot be placed due to their uncertain stratigraphic positions. Specimen NMMNH P-4569, *Gojirasaurus quayi* (Carpenter 1997) and rest of the referred material for *Chindesaurus bryansmalli* (Long and Murry 1995) are collected from the New Mexico outcrops of Dockum; therefore they are not included to the chart.

Theropods are better represented compared to other dinosauromorphs in the fossil record of Bull Canyon Formation; however this situation might represent a collection artifact (Figure 5.11). Alongside of two *Dromomeron romeri* hind limb elements (TTU-P12537; TTU-P12539), a complete tibia and an isolated head of a femur which belong to herrerasaurids (TTU-P11175; TTU-P12531) and a distal tibia of a coelophysoid theropod (TTU-P14786) are gathered from the Headquarters South (MOTT 3898) and Headquarters Northwest (MOTT 3899) localities. Herrerasaurids appear also in abundance in stratigraphically higher localities. It is unearthed a partial skeleton of a herrerasaurid (TTU-P10072) from the Lott Kirkpatrick (MOTT 3634), a proximal right femur (TTU-P12587) and a postcervical vertebra (TTU-P12790) from the Macy Ranch (MOTT 3927), and a dorsal vertebra (TTU-P16789) from the Patricia Quarry (MOTT 3870) localities, respectively. A remarkable tibia (TTU-P12587, see Nesbitt et al. 2007) from the Macy Ranch locality (MOTT 3870) resembles to a dilophosaurid-grade theropod in morphology, although the size is only the half of a typical dilophosaurid (e.g. Welles 1984).

Additionally, several other theropods are also noted from various localities of the Bull Canyon Formation in New Mexico. A partial skeleton (NMMNH P-4569) which is

later diagnosed as an indeterminate saurischian is noted from the Guadalupe County (e.g. Hunt 1994, 1996, 2001; Nesbitt et al. 2007, p. 229). A partial femur and various vertebral centra (NMMNH P-4415; NMMNH P-16656; NMMNH P-17325) which are referred *Chindesaurus bryansmalli* (Long and Murry 1995) are collected various localities of eastern New Mexico, whereas the coelophysoid *Gojirasaurus quayi* is defined from the Quay County (Carpenter 1997).

## Biocorrelation between North America and South America Based on Dinosauromorphs

The relative abundance and distribution of dinosaurs makes a good biostratigraphic tool for the Upper Triassic continental sediments of Argentina and Brazil. Presences of herrerasaurid dinosaurs have linked the lower part of the Ischigualasto Formation and the Alemoa Member of the Santa Maria Formation (the same interval also corresponds to the acme zone for the rhynchosaur *Hyperodapedon* (e.g. Langer et al. 2007), whereas the upper parts of the Caturrita and Los Colorados formations can be correlated by using prosauropod dinosaurs (Langer 2005a, figure 8) (Figures 5.9 and 5.12). More recently, newly discovered dinosaur fauna from the Upper Triassic sequence of the Pranhita-Godavari Basin in India implied an opportunity for a direct intercontinental correlation for South America, based on saurischians (Novas et al. 2011, figure 6). Similarly in this work, the diverse and well distributed dinosauromorph fauna of the Dockum Group may provide a stronger biostratigraphic link between the two continents. The Dockum Group might be a better candidate in correlation with the South American sequences, since the dinosauromorph diversity of the Dockum Group is larger

compared to the Chinle Formation, and the lowermost occurrences of dinosauromorphs (i.e. lower part of the Tecovas Formation) are only present in the Dockum Group whereas the corresponding interval of the Chinle Formation is unfossiliferous (Figures 5.6, 5.7, 5.8, 5.11 and 5.12).
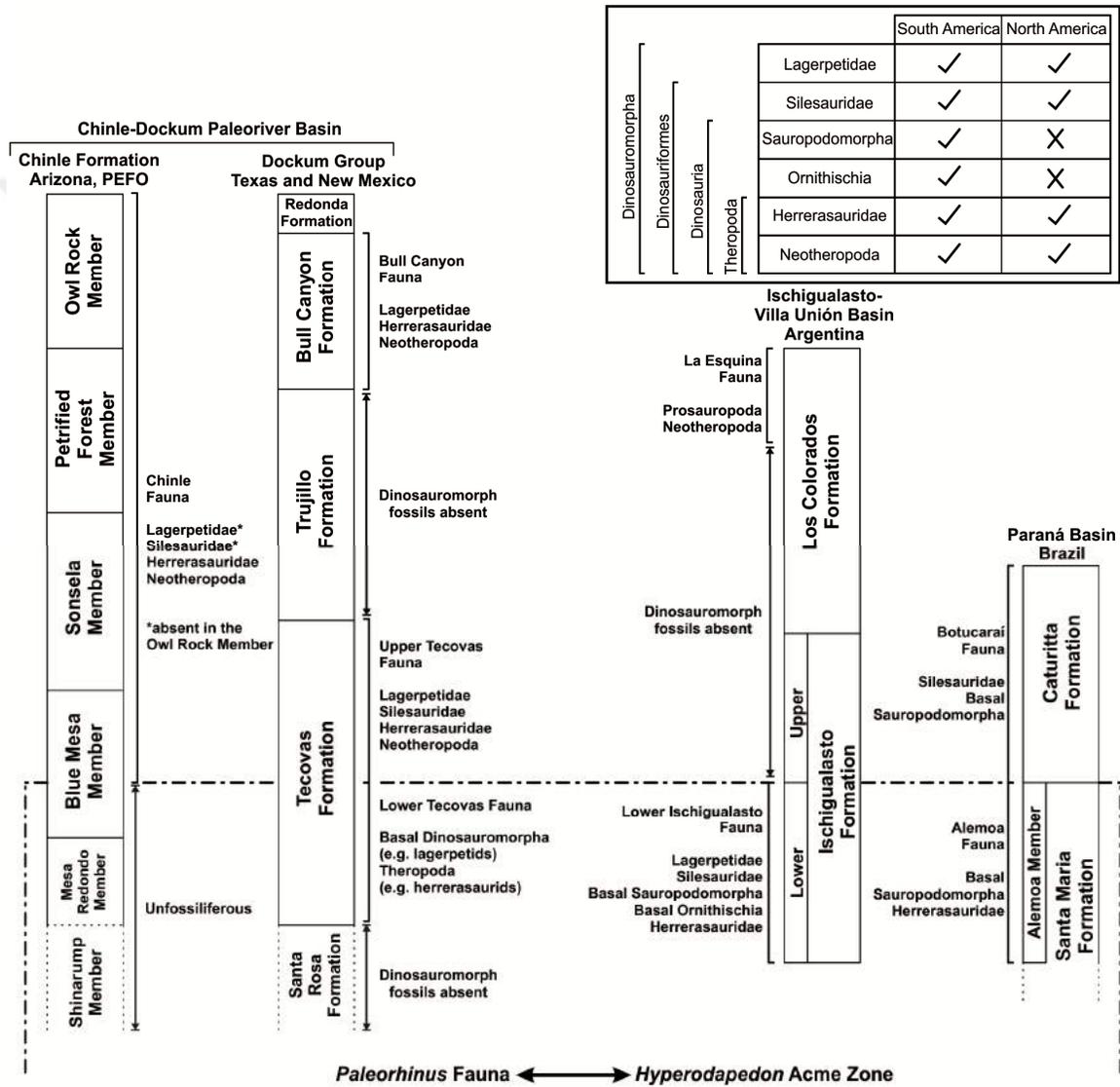


Figure 5.12 Main stratigraphic sequences of North and South America, and referred dinosauromorph faunas (for details see text and previous figures). As visible on the top right corner, sauropodomorphs and ornithischians are the two main elements missing in the North American faunas.

South America, especially the Ischigualasto Formation is widely known not only for having the earliest records of dinosaurs but also for keeping the record of dinosaur precursors with recently reported lagerpetid and silesaurid individuals (Martinez et al. 2013a). As detailed above, Late Triassic dinosauromorph fauna of North America displays a large diversity comparable to the South American counterpart, despite the absence of basal sauropodomorphs and basal ornithischians. Despite the low taxonomic resolution, dinosauromorphs might establish a direct biocorrelation between North and South America in the future works (Figure 5.12). Nevertheless, the common occurences of earliest dinosaurs stand as another unequivocal biostratigraphic tool after the significant discoveries from the lower Tecovas Formation which complements the previously known dinosaurs from the Gondwana continents. The time interval when the dinosaurs first appeared coincides with the *Paleorhinus* Fauna, as documented in the lower Tecovas Formation, and the equivalent biochron of the *Hyperodapedon* Acme Zone (*sensu* Langer et al. 2007, also see Martinez et al. 2013a), not only the two biozones seem roughly equivalent based on the geochronology, but also on the vertebrate biostratigraphy since both fauna have co-existed in the Lower Maleri Formation of India and in the Lossiemouth Sandstone of Scotland despite the absence of *Paleorhinus*-grade phytosaurs in this part of Laurasia (Figures 5.8, 5.11 and 5.12).

# Chapter 6

# Paleobiogeography of Late Carnian-Early Norian Land Tetrapods

The late Carnian-early Norian world has witnessed a global radiation of the archosaurs and other land tetrapods all over the Pangea, as manifested by the fossil record. This significant interval can be portrayed by the peak abundance of rhynchosaurs, the radiation of phytosaurs, aetosaurs and possibly crocodylomorphs, as well as by the first appearance of dinosaurs. There are multiple geologic provinces with coeval terrestrial deposits as shown below, including the Germanic Keuper and its European correlatives (e.g. Poland, Britain), the rift basins of eastern North America and northwestern Africa (i.e. Morocco), the Chinle-Dockum Paleroriver Basin from the southwestern North America, the Upper Triassic sequences of the Ischigualasto-Villa Unión and Paraná basins of Argentina and Brazil, the Pebbly Arkose Formation of Zimbabwe and the Lower Maleri and Tiki formations of the Indian subcontinent (Figure 6.1).
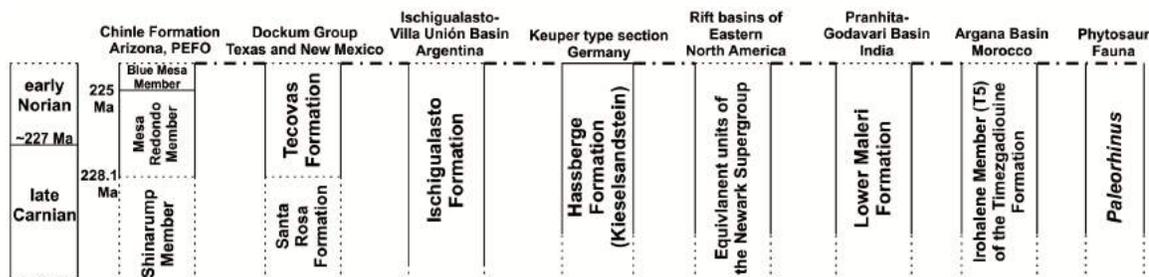


Figure 6.1 The late Carnian-early Norian terrestrial stratigraphy (simplified from Figure 5.8). Sections from Brazil and Zimbabwe are omitted based on the absence of both geochronology and phytosaurs (for their correlations, see text). The upper boundary for the *Paleorhinus* Fauna is tentatively placed at 224 Ma (see text and previous figures).

## The Late Carnian-Early Norian Land Tetrapod Faunas

### The Land Tetrapod Fauna of Keuper

The Hassberge Formation of German Keuper and its laterally equivalent beds in Krasiejów, Poland display a large diversity of terrestrial tetrapods, including index fossils such as phytosaurs and metoposaurs (Figure 6.2). *Metoposaurus diagnosticus krasiejowensis* (Milner and Schoch 2004) is the index temnospondyl of that horizon. *Ebrachosuchus neukami* and *Paleorhinus angustifrons* from Hasseberge Formation, alongside with another species of *Palorhinus* from Poland (Dzik 2001, which still awaits species level designation) refers to the *Paleorhinus* Fauna (Butler et al. 2013) of late Carnian-early Norian age. The only European rauisuchian hitherto discovered from this interval, *Teratosaurus* (*Polonosuchus*) *silesiacus*, is reported from the Krasiejów beds of Poland (Sulej 2005; Brusatte et al. 2009). The aetosaur *Stagonolepis olenkae* (Dzik et al. 2000; Sulej 2010) and the pioneering dinosauromorph discovery of *Silesaurus opolensis* (Dzik 2003) are also known from the Krasiejów beds. However, no dinosaurs (*sensu* Padian and May 1993) hitherto discovered from this interval of Keuper. Not only dinosaurs, but also herbivorous therapsids are also absent in the Keuper fauna (e.g. Maisch et al. 2009).

The aetosaur *Stagonolepis robertsoni* (Agassiz 1884; Walker 1961), dinosauriform *Saltopus elginensis* (von Huene 1910; Benton and Walker 2011; Langer et al. 2013) and the rhynchosaur *Hyperodapedon gordoni* (Huxley 1859; Benton 1983b) are collected from the Lossiemouth Sandstone of Scotland. The genus *Hyperodapedon* provides a direct correlation between the Lossiemouth Sandstone and the South American (i.e. Ischigualasto and Santa Maria formations) and Indian (i.e. Lower Maleri

Formation) counterparts (see below), therefore indicating a late Carnian-early Norian age (Figures 6.1 and 6.2).

**The Land Tetrapod Fauna of Morocco**

Across the proto-Atlantic Ocean, the Timezgadiouine Formation of the Argana Group/Formation in Morocco has yield a variety of tetrapods, except dinosaurs (e.g. Jalil 1999) (Figure 6.2). The Irohalene Mudstone Member (or the T5 layer), which occurs at the upper portion of the Timezgadiouine Formation, is especially rich in land tetrapod assemblage. The Irohalene Fauna includes various land tetrapod taxa, such as metoposaurs *Dutuitsaurus ouazzoui* and *Arganasaurus lyazidi* (e.g. Dutuit 1976; Hunt 1993; Sulej 2002), phytosaur *Angistorhinus talainti* (Dututi 1977a) and *Paleorhinus magnoculus* (Dutuit 1977b; *Arganarhinus magnoculus*, Long and Murry 1995), rauisuchian *Arganasuchus dutuiti* (Jalil and Peyer 2007) and silesaurid *Diodorus scytobrachion* (Kammerer et al. 2012). Dicynodont taxa *Moghreberia* and *Azarifeneria* are erected based on the fragmentary material (e.g. Dutuit 1980, 1988, 1989; also see Jalil and Peyer 2007), which are later considered synonymous with North American genus *Placerias* (e.g. Cox 1991; Lucas 1998a). Archosaurs of these rift basins are not abundant, where only the Argana Basin displays a large diversity. However, various vertebrate ichnotaxa reported from each side of Atlantic (e.g. Cornet and Olsen 1985; Lagnaoui et al. 2012) indicate a larger diversity for the Late Triassic tetrapod assemblage for this region. The *Paleorhinus* Fauna of the Irohalene Mudstone Member is correlated with the Hasseberge Formation of the Keuper (Figure 6.1).

**The Land Tetrapod Fauna of North America**

In North America, the Newark Supergroup is a very extensive rock unit which accumulated into various basins in eastern North America (both United States and Canada), but the correlation of these deposits can be very challenging due to the scarcity of fossils (Figures 6.1 and 6.2). Stockton Formation of the Newark Basin is the poorest known of all the Newark Supergroup formations (Olsen 1980a) and has produced only one diagnostic terrestrial tetrapod fossil so far, which is the problematic capitosaurian *Calamops paludosus* from the lower horizons (Olsen 1980b; Sulej 2002). Upper part of the Stockton Formation, as well as overlying Lockatong Formation, probably belongs to *Rutiodon* Fauna (~middle Norian) since most of the phytosaur remains are referred to this taxon (Olsen 1980b). Some phytosaur and rauisuchian fragments from the Falling Creek Member/Formation of the Taylorsville Basin (Weems 1980) might represent another late Carnian-early Norian assemblage for the Newark Supergroup, since it enables a direct correlation with the lower part of the Tecovas Formation with the common presence of *Doswellia kaltenbachi*, a taxon which is only known from this two localities. Similarly in the Wolfville Formation (Fundy Basin, Nova Scotia), the presence of *Metoposaurus bakeri*, which is specific to the lower part of the Tecovas Formation, might establish a direct correlation (Baird 1986; Hunt 1993) (see below). Aetosaur and "rauisuchian" remains are highly fragmented and no dinosaurs or phytosaurs are recovered from this formation (Sues and Fraser 2010, p. 129 and references therein). Reported rhynchosaur (e.g. Baird 1964; Chatterjee 1980a; Lucas and Heckert 2002b and references therein) and traversodontid (Sues et al. 1992) fossils are highly fragmentary. Although it is suspected for a temporal equivalency, the land tetrapod faunas of Deep River Basin (e.g. Lucas et

al. 1998; Peyer et al. 2008; Heckert et al. 2012) and Richmond Basin (e.g. Sues and Olsen 1990; Sues 1992; Sues et al. 1994; Lucas 1998a; Sues and Hopson 2010) may not be used for a direct stratigraphic correlation at the time.

The late Carnian-early Norian Dockum land tetrapod fauna is definitely one of the richest deposits in North America (Figures 6.1 and 6.2). Metoposaurs are widely represented in the Dockum Group. "*Metoposaurus bakeri*" (Long and Murry 1995; same as *Buettneria bakeri*, Sulej 2007) is restricted to the lower part of the Tecovas Formation, whereas *Apachesaurus* and *Koskinonodon* (replacement name for *Buettneria*, Mueller 2007) have longer stratigraphic ranges. Both taxa are collected from the Tecovas Formation and continued to the Bull Canyon Formation. The non-metoposaurid temnospondyl *Latiscopus disjunctus* (Wilson 1948) is also noted from the Otis Chalk locality. Remains of the *Paleorhinus*-grade phytosaurs (plus *Angistorhinus*, e.g. Lucas et al. 2002b) and various aetosaur taxa like *Calyptosuchus*, *Desmatosuchus* and *Tecovasuchus* (e.g. Desojo 2013, table 1) are abundantly found in the lower part of the Tecovas Formation, where rauisuchians like *Poposaurus* and *Postosuchus* appear even in some of the lowermost sections like Boren and Kirkpatrick quarries. And as expanded above, the lowermost occurrences of Dockum dinosauromorphs are marked in the same quarries which include basal dinosauromorphs and theropods, complimenting the previously published sites in South America and India. Dicynodont fossils are collected from the lower sections of the Tecovas Formation but their record is very fragmentary (Mueller and Chatterjee 2007). Similarly, rhynchosaurs are only represented by some unpublished jaw fragments, predominantly from the lower sections of the Tecovas Formation (e.g. McCarthy Ranch, MOTT 0690). The preexisting putative rhynchosaur

*Otischalkia elderae* is now regarded as an invalid taxon (e.g. Mukherjee and Ray 2014; Bill Mueller pers. comm. 2014, see Chapter 2).

The equivalent portion of the Chinle Formation is very poorly fossiliferous and thus, it is not included in this section.

Popo Agie Formation of Wyoming has yielded a variety of tetrapods (e.g. Branson and Mehl 1928; Colbert 1957; Parrish and Carpenter 1986) and might be another correlative of the Tecovas Formation. It includes various metoposaur taxa (e.g. Sulej 2002), phytosaurs *Paleorhinus* and *Angistorhinus* (Mehl 1913, 1928; Stocker and Butler 2013), aetosaur *Desmatosuchus* (Lucas 1994), various rauisuchians like *Poposaurus gracilis* (Mehl 1915; Weinbaum and Hungerbühler 2007; also see Nesbitt et al. 2013), dicynodonts as *Eubranchiosaurus* (Williston 1904; Kammerer et al. 2013) and rhynchosaurs (e.g. Lucas et al. 2002a; Lucas and Heckert 2002b).

**The Land Tetrapod Fauna of India**

Tetrapod fauna of the Lower Maleri Formation is notably diverse. Metoposaur and phytosaur fossils are ubiquitous, a condition which is highly comparable to the Hasseberge Formation (Hunt 1993; Sankar Chatterjee, per. comm. 2014) (Figures 6.1 and 6.2). *Metoposaurus maleriensis* (Roy Chowdhury 1965) and *Parasuchus hislopi* (Chatterjee 1978a, 2001) are the two significant taxa which characterizes the *Paleorhinus* Fauna of the Lower Maleri Formation. The Tiki Formation in India, though less diverse, has yielded similar *Paleorhinus* Fauna of the Lower Maleri Formation. Aetosaurs in Lower Maleri Formation are known from isolated scutes (e.g. Chatterjee and Roy Chowdhuri 1974; Kutty and Sengupta 1989; Bandyopadhyay 1999). The only single

rauisuchian taxon hitherto described is *Tikisuchus romeri* from the Tiki Formation (Chatterjee and Majumdar 1987). No dinosauromorphs are described from the Lower Maleri Formation, except the theropod *Alwalkeria maleriensis* (Chatterjee 1987; Chatterjee and Creisler 1994). Herbivorous therapsids are represented by traversodontids like *Exaeretodon statisticae* (e.g. Chatterjee and Scotese 1999). In the Lower Maleri Formation, rhynchosaurs are probably the most prolific tetrapods, represented by several well preserved skeletons of the genus *Hyperodapedon* (Chatterjee 1974; Langer and Schultz 2000; Mukherjee and Ray 2014).

| | Dicynodontia/Traversodontidae | Rhynchosauria | Temnospondyli | Phytosauria | Aetosauria | Rauisuchia | Non-Dinosaurian Dinosauromorpha | Dinosauria |
|---|---|---|---|---|---|---|---|---|
| Hassberge Formation (Keuper) and European equivalents | X | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | X |
| Timezgadiouine Formation | ✓ | X | ✓ | ✓ | ✓ | ✓ | ✓ | X |
| relevant formations of the Newark Supergroup | ? | ? | ✓ | ? | X | ? | X | X |
| Tecovas Formation (lower part) (and Popo Agie Formation?) | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Lower Maleri Formation | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | X | ✓ |
| Ischigualasto Formation (lower part) | ✓ | ✓ | X | X | ✓ | ✓ | ✓ | ✓ |
| Santa Maria Formation (upper part) | ✓ | ✓ | X | X | ✓ | ✓ | X | ✓ |
| Pebbly Arkose Formation | X | ✓ | X | X | X | X | X | ✓ |

Figure 6.2 Late Carnian-early Norian distribution of major terrestrial tetrapods in different parts of the globe. Note the grey areas which represent the absence of temnospondyls (metoposaurs) and phytosaurs in South America and southern Africa, while basal dinosaurs are absent in most of Laurasia. Question mark (?) indicates unconfirmed stratigraphic positions of the fossiliferous horizons.

**The Land Tetrapod Fauna of South America**

South American Late Triassic basins are notable in two aspects; the faunal dominance of non-archosaur herbivores and the appearance of earliest dinosaurs (e.g. Benton 1983a) and their relatives (Figures 6.1 and 6.2). Lower section of the Ischigualasto Formation and the upper section of the Santa Maria Formation are

characterized by the *Hyperodapedon* Acme Zone (Langer et al. 2007). Alongside of rhynchosaurs, therapsids were also quite abundant including larger sized herbivores of traversodontids like *Exaeretodon* and smaller carnivorous therapsids such as *Diegocanis* (e.g. Martinez et al. 2011b, 2013a), as well as dicynodonts like *Ischigualastia* (Cox 1962, 1965).

Although basal dinosauromorphs at this stage are known from the Ischigualasto Formation (Martinez et al. 2013a), basal theropods like *Pampadromaeus barberenai* (Cabreira et al. 2011), *Eodromaeus murphi* (Martinez et al. 2011a) and various herrerasaurids (e.g. Reig 1963; Colbert 1970; Galton 1977; Sereno and Novas 1992; Bittencourt and Kellner 2009; Alcober and Martinez 2010), basal saurischians *Eoraptor lunensis* (Sereno et al. 1993; Sereno et al. 2013), *Saturnalia tupiniquim* (Langer et al. 1999), *Chromogisaurus novasi* (Ezcurra 2008, 2010; Martinez et al. 2013b) and *Panphagia protos* (Martinez and Alcober 2009), and the basal ornithischian *Pisanosaurus mertii* (Casamiquela 1967; Bonaparte 1976) represent a large basal dinosaur diversity in South American basins even at the initial stage. Terrestrial suchians of aetosaurs and rauisuchians are also well represented in this interval (Desojo et al. 2013; Nesbitt et al. 2013). *Aetosauroides scagliai* (Casamiquela 1960) and *Aetobarbakinoides brasiliensis* (Desojo et al. 2012) are the two aetosaur taxon erected up to now. The shuvosaurid *Sillosuchus longicervix* (Alcober and Parrish 1997) and rauisuchian *Saurosuchus galilei* (Reig 1959) are the Argentinian members of the clade Rauisuchia, whereas only one rauisuchid, *Rauisuchus tiradentes* (von Huene 1938) is collected from the upper Santa Maria Formation, which corresponds to the

*Hyperodapedon* Acme Zone (Langer et al. 2007). No temnospondyls or phytosaurs are documented from any of the aforecited formations.

**The Land Tetrapod Fauna of Africa**

The Pebbly Arkose Formation from Zimbabwe stands as another representative of a late Carnian-early Norian rock unit, by the presence of an isolated dinosaur femur which in referable to *Saturnalia* (Raath 1996; Langer et al. 2010). Additionally, there are some specimens of *Hyperodapedon* reported from this formation (Raath et al. 1992; Lucas and Heckert 2002b) (Figure 6.2). A late Carnian age was previously suggested for the "Isalo II" beds of Morondava Basin, Madagascar (Lucas 1998b, 2010), where a diverse land tetrapod fauna is reported including sphenodontids, procolophonids, dicynodonts, traversodontids, rhynchosaurs and even basal sauropodomorphs (e.g. Flynn et al. 1998, 1999, 2000, 2010). The assumed dinosaur fragments are now regarded as a basal archosauromorph (*Azendohsaurus*, Flynn et al. 2010), which was the main biostratigraphic tool for this horizon, therefore, this assemblage now seems to be older than the late Carnian mainly based on the absence of aetosaurs and dinosaurs and the controversial phylogeny of the Madagascar rhynchosaur *Isalorhynchus* (Langer 2005b, pp. 222-223 and references therein). No significant land tetrapod faunas are reported from Australia and Antarctica (Schultz 2005).

## Late Carnian-Early Norian Continental Paleobiogeography and Paleoclimatology

In the Pangean world, the distribution of land tetrapods was widespread during late Carnian-early Norian time. An extensive radiation is noticed in herbivorous aetosaurs, therapsids and rhynchosaurs, carnivorous rauisuchians and omnivorous/carnivorous dinosauromorphs. This worldwide radiation of land tetrapods can be evaluated in terms of climate, orogeny and ecology (i.e. freshwater systems).

### Climate

Different climatic regimes over the Pangea during Late Triassic have been recognized (e.g. Scotese 2001, Figure 6.3). The Chinle-Dockum Basin was clearly in the equatorial tropical climatic regime of Laurasia that might have favored widespread radiation of tetrapods. The Keuper Basin in Europe and the rift basins of the future Atlantic Ocean (i.e. eastern North America and the Argana Basin of Morocco) lay at the paratropical climatic regime of Laurasia; the widespread *Paleorhinus* Fauna across the proto-Atlantic is apparent. On southern continents, the Ischigualasto-Villa Unión Basin of Argentina, the Paraná Basin of Brazil, the Western Cabora Bassa Basin of Zimbabwe (e.g. Raath et al. 1992) and the Pranhita-Godavari Basin of India occupied around the same latitude of the warm temperate climatic regime of southern hemisphere. This situation might bring us to an earlier assumption of a monsoonal Pangea (e.g. Robinson 1973), at least for the late Carnian-early Norian interval, since it is assumed a trend of aridity at least for some part of the Pangea from late Norian until the end of the period (Tucker and Benton 1982). Despite the presence of multiple climatic provinces, this

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pattern of early dispersal of land tetrapods indicate that those climatic regimes had little influence on the radiation of land tetrapods



Figure 6.3 The late Carnian-early Norian paleobiogeographic map, displaying the provinces and radiation of fully terrestrial early dinosaurs and subaqueous phytosaurs and temnospondyls (e.g. metoposaurs) (e.g. Map projection modified after Scotese 2013). The paleoclimatic boundaries are taken after Scotese (2001).

**Orogeny**

There were two main mountainous regions in the Late Triassic Pangea, namely the Late Paleozoic Central Pangean Mountains (Appalachian-Mauretanide-Hercynian orogenies, e.g. Otto-Bliesner 1998) and remnants of the Proterozoic East African Orogeny on the southern Africa, Antarctica and India (the Mozambique Belt, e.g. Stern 1994; Kröner and Stern 2004). Nevertheless, such geographic barriers across the Pangea were not posing serious hindrance for land tetrapods with different stance and locomotor abilities, as exemplified not only by the worldwide radiation of archosaurs with an erect posture but also by the global distribution of sprawler rhynchosaurs (Figure 6.2, including *Hyperodapedon gordoni* of Scotland). Although it is not coined in the present work, the

wide fossil occurrence of sphenodontian lepidosaurs within the terrestrial Upper Triassic deposits might represent similar type of example (e.g. Fraser 1986, 1993; Sues and Reisz 1995; Lehman and Chatterjee 2005; Bonaparte and Sues 2006).

**Freshwater Ecology**

On the other hand, late Carnian-early Norian distribution of land tetrapods of the freshwater habitats such as metoposaurs and phytosaurs is restricted to Western Europe, North America and India, which is conspicuously absent in South America (Figures 6.2 and 6.3). The uneven distribution of this subaqueous fauna is puzzling because coeval basins of both South American (and southern African) and Indian occurred at the same latitude. The rift basins of the Eastern North America and Morocco might have established a convenient route for metoposaurs and phytosaurs to track freshwater resources between the Keuper Basin and the Chinle-Dockum Paleoriver Basin. Similarly in India, the Godavari Rift provided a suitable habitat for these subaquatic tetrapods. In this context, this subaquatic assemblage had to have a freshwater route to India (Figure 6.3). The presence of coeval deposits is still needed to be discovered in southwestern Europe or northeastern Africa, since only some fragmentary phytosaur fossils are reported only from Italy and Turkey so far. However, these phytosaurs either signifies younger deposits (Renesto 2006, 2008) or it requires better taxonomic resolution (Buffetaut et al. 1982; Stocker and Butler 2013), respectively. On the other hand, terrestrial tetrapods such as rhynchosaurs, traversodontids and dinosaurs are common between India and South America. India maintained subaquatic links with Europe, North

America and Morocco, and the terrestrial link with South America during the late Carnian-early Norian time.

The Ischigualasto Formation represents a fluvial sequence with well preserved flora and fauna (e.g. Colombi and Parrish 2008). In this case, what prevented the migration of metoposaur-phytosaur assemblage from India to South America or from North America to South America during late Carnian and early Norian? Previous works suggested that no phytosaurs have exceeded 45° latitudes north and south during the Late Triassic (Olsen and Galton 1984; Cornet and Olsen 1985), which is apparently reflecting a sampling bias (e.g. Brusatte et al. 2012). Nevertheless, the southern basins of South America, Africa and India were located in relatively lower latitudes; climatic provinciality seems to have little influence on these freshwater tetrapods during late Carnian-early Norian (Figure 6.3). In case no collecting bias exists, the main cause for the absence of phytosaurs and metoposaurs in South America (and probably in southern Africa) might be the punctuation of the freshwater routes between the continents by geographic barriers, mountain ranges in our case (see above). Even in this theory, the ongoing parameters might have altered towards the end of the Triassic since phytosaurs had appeared in the South American fossil record, as evidenced in the Caturrita Formation of Brazil (Kischlat and Lucas 2003). On the other hand, the physical barriers which prevent phytosaur-metoposaur extension did not affect the distribution of fully terrestrial tetrapods, as detailed above. In this case, absences of the dinosaur fossils in Newark, Argana and Keuper regions imply sampling biases.

**The Origin and Early Radiation of Dinosaurs**

The origin and early evolution of dinosaurs have been debated for more than a century. The order Dinosauria of Owen (1842), which was originally established as a natural group, was later regarded as a polyphyletic (unnatural) group in the literature for a long time and it was disassociated into two camps, Saurischia and Ornithischia, based on the different pelvic patterns (Seeley 1887). Besides the propubic pelvis pattern, saurischians were also diagnosed for their bipedal tendencies and their origins had linked to the bipedal thecodonts of the Triassic even from the very beginning (e.g. Watson 1917, text-figure 2). Especially, *Euparkeria* and *Ornithosuchus* were the primary candidates from which the saurischians would have evolved (e.g. Walker 1965; Cruickshank 1979). Nevertheless, the consensus was set that saurischians, ornithischians and all later archosaurs arose from the ancestral order Thecodontia of Owen (1859) (e.g. Romer 1968, 1972c). Even the pioneering discoveries of the *Lagerpeton* and *Lagosuchus* (now *Marasuchus*) from the Chañares Formation of Argentina (Romer 1972c) were not credited as the ancestors of the dinosaurs at that time, since the ankle joint trends in archosaur phylogeny was not resolved at the time (e.g. Chatterjee 1978a, 1982b). The origin of ornithischians had remained obscured until the discovery of the *Pisanosaurus mertii* (Casamiquela 1967; Bonaparte 1976).

Bonaparte (1976) was first to realize that saurischians and ornithischians share a common descent within the same thecodont group (the "Pseudosuchia", *sensu* von Zittel 1887), since no other groups of thecodonts are derived enough to provide a separate ancestry for dinosaurs. Apparently, there was a sampling bias to think that the dinosaurs were polyphyletic. Bonaparte's foresight is verified when the cladistic analysis is

introduced to the archosaur phylogeny which resulted in omission of Owen's paraphyletic group of Thecodontia and in recognition of dinosaurs as a distinctive monophyletic clade (Gauthier 1984, 1986). Cladistic works also revealed that *Lagerpeton* and *Marasuchus* are indeed closely related to dinosaurs, whereas *Euparkeria* and *Ornithosuchus* are replaced as a stem taxon and a derived crurotarsan, respectively, unrelated to the dinosaur ancestry (Gauthier 1986; Benton and Clark 1988; Sereno 1991b).

With the wide acceptance of the phylogenetic analysis, Argentina has been considered as the center for the dinosaur origin during the past few decades because of close temporal and cladistic relationships of immediate dinosaur ancestors such as *Lagerpeton*, *Marasuchus* in the Middle Triassic Chañares Formation and the early dinosaurs such as *Eoraptor* and *Herrerasaurus* in the overlying Late Triassic Ischigualasto Formation (Sereno and Novas 1992; Sereno et al. 1993; Sereno and Arcucci 1993, 1994). Coeval records of early dinosaurs are also documented from the neighboring Santa Maria Formation of Brazil (e.g. Langer et al. 2010). The Lower Maleri Formation of India and the Pebbly Arkose Formation of Zimbabwe are the other two coeval dinosaur localities hitherto known from the southern landmasses, in which *Alwalkeria maleriensis* (Chatterjee 1987; Chatterjee and Creisler 1994; Rauhut and Remes 2005) and an undetermined prosauropod femur (Raath 1996; cf. *Saturnalia* in Langer et al. 2010) are described respectively. However, both formations lack immediate predecessors of the dinosaurs.

A new picture of dinosaur phylogeny is beginning to emerge in the last decade, when a new group of quadruped herbivorous dinosauromorphs, including *Silesaurus* from Poland (Dzik 2003), *Sacisaurus* from Brazil (Ferigolo and Langer 2007) and also

*Technosaurus* from Texas (Chatterjee 1984) are gaining importance as the sister group of dinosaurs. After this new phylogenetic framework, the role of *Marasuchus* and other allied forms from South America has been considerably diminished regarding the origin and early evolution of dinosaurs. In return, North America might have preserved some critical evidence for the origin and early radiation of dinosaurs. An expanded distribution for the basal dinosauromorph group, the Lagerpetidae, is reported from both Chinle and Dockum sequences with the recent discoveries of *Dromomeron* spp. (Irmis et al. 2007a; Nesbitt 2009b). Until then, the lagerpetids were only represented by *Lagerpeton chanarensis* from the Middle Triassic of Argentina (Romer 1971; Sereno and Arcucci 1994a). In this context, the Dockum-Chinle Basin appears as a potential rival to South American basins by having not only the basal dinosaur but their immediate ancestors. Dinosaurs are only represented by theropods in the Chinle-Dockum Basin so far.

Based on the conclusive evidences, the earliest dinosaurs are reported from the Ischigualasto Formation (Argentina), Santa Maria Formation (Brazil), Pebbly Arkose Formation (Zimbabwe), Lower Maleri Fomation (India) as well as from the Tecovas Formation (United States) of which the earliest fossils are introduced in this study. This picture indicates not only a quick radiation within the warm-temperate zone of the southern continents, but also a spread towards further north (*contra* Nesbitt et al. 2007; Brusatte et al. 2010b; Langer et al. 2010; Irmis et al. 2011) (Figure 6.3). Dinosaurs co-existed with various land tetrapod groups during the Late Triassic, some of which were much larger in size. The small size of the early dinosaurs (only a couple of meters long) was possibly the reflection of this competitive pressure (Novas 1997). The dinosaur disparity had only shifted towards larger body sizes for herbivorous prosauropods in late

Norian with the availability of abundant coniferans after a turnover for the terrestrial communities (e.g. Benton 1983a; Benton et al. 2014). On the other hand, theropods existed at the shadow of rauisuchians until the end of Triassic Period whereas ornithischians remained low in diversity until Jurassic Period. Size increase and relative abundance of both groups only appeared after the Triassic-Jurassic extinctions where all the crurotarsans except crocodylomorphs had gone extinct.

## Implication of the Early Dinosauromorph Record in North America

Recent works suggests that both non-dinosaurian dinosauromorphs and early dinosaurs existed together in the Chinle-Dockum Basin. Well represented non-dinosaurian dinosauromorphs include *Dromomeron* spp. (Irmis et al. 2007a; Nesbitt et al. 2009b), *Technosaurus smalli* (Chatterjee 1984) and *Eucoelophysis baldwini* (Sullivan and Lucas 1999; Ezcurra 2006) are the three erected dinosauromorph taxa, besides various bone fragments from various quarries but unassigned to a specific taxon (e.g. Parker et al. 2006, Langer et al. 2013, see above).

On the other hand, the history of dinosaurs in North America extends back to the days of first paleontological expeditions in this continent. As one of the earliest dinosaur discoveries, *Coelophysis bauri* (Cope 1889) is the second Late Triassic dinosaur recognized after *Plateosaurus engelhardti* (von Huene 1837) and it was the only complete dinosaur from North American Late Triassic until the 21st century. From both Dockum and Chinle sequences, various theropod specimens were attributed to *Coelophysis* sp. (e.g. Padian 1986; Lehman and Chatterjee 2005; Irmis et al. 2007a; Nesbitt et al. 2007). *Segisaurus halli* is the first theropod diagnosed in North America

other than *Coelophysis*, based on a partial postcranial skeleton (Camp 1936; Carrano et al. 2005). Nonetheless, the scarcity of Late Triassic dinosaurs in North America was a longtime recognized fact (e.g. Romer 1975).

A series of new theropods are discovered by the end of the century, including *Chindesaurus bryansmalli* (Long and Murry 1995), *Gojirasaurus quayi* (Carpenter 1997, which might represent another species of *Coelophysis* [Nesbitt et al. 2007]), *Camposaurus arizonensis* (Hunt et al. 1998; Nesbitt et al. 2007; Ezcurra and Brusatte 2011), *Tawa hallae* (Nesbitt et al. 2009c) and *Daemonosaurus chauliodus* (Sues et al. 2011). Although none of them were complete skeletons except *C. bauri* and *T. hallae*, those discoveries are quite significant by means of displaying the large dinosaur diversity, at least in the southern part of North America.

Discoveries from the Eagle Basin in the northern Colorado and Utah also have contributed the dinosauromorph diversity in North America. Various specimens belong to *Dromomeron romeri*, silesaurids including the "Eagle Basin form" and coelophysoids (Small 2009; Langer et al. 2013). The Eagle Basin cannot be directly correlated with the main Chinle-Dockum Paleoriver sequence, nonetheless, a middle to late Norian (~Revueltian) age has been suggested based on the faunal similarity of land tetrapod elements (Bryan Small pers. comm. 2014).

Such large diversity of dinosauromorphs in the southwestern North America may shed new light on the early origin and diversity of dinosaurs, preferable to the earlier attempts which were based on the classical non-marine stratigraphy (e.g. Hunt 1990; Hunt et al. 1998). Following the stratigraphic replacement of the *Placerias* Quarry into the Blue Mesa Member and concurring geochronology for the base of this member (~218

Ma, see the discussion above), it was previously suggested the *Placerias* Quarry is the lowermost quarry in the Chinle Formation which has produced the earliest dinosauromorphs and basal theropods of North America and thus, the radiation of dinosaurs seems diachronous which initiated in South America, then spread to North America with a delay of more than 10 million years (Irmis et al. 2011). Although the absolute dating and the earliest dinosauromorph occurrences are verified for the *Placerias* Quarry, it is recently revealed that the *Placerias* Quarry is actually situated higher in stratigraphy, probably at the lowermost portion of the Sonsela Member (Ramezani et al. 2014). The same study also suggested that the lower portion of the Chinle Formation is much older, by stating an age of ~225 Ma for the base of Blue Mesa Member and ~228 Ma for the base of Mesa Redondo Member (Ramezani et al., op. cit.; Figures 5.6 and 5.8). However, except a possible dinosaur fragment collected from the Newspaper Bed of the Blue Mesa Member which is the lowermost fossiliferous horizon of Chinle Formation (Parker and Martz 2011), lack of land tetrapod fossils for the lowermost portion of the Chinle Formation prevents further implications on the early origin and radiation of dinosaurs.

On the other hand, Tecovas Formation of the Dockum Group may unfold the beginning of the age of dinosaurs. Tecovas Formation is considered as the stratigraphic equivalent of the Blue Mesa Member and probably of the Mesa Redondo Member from the Chinle Formation. Moreover, it also becomes comparable with the Ischigualasto Formation of Argentina, upper part of the Santa Maria Formation of Brazil, the Lower Maleri Formation of India and possibly with the Pebbly Arkose Formation of Zimbabwe, based on the early dinosaur occurrences (Figures 6.2 and 6.3). Three of the lowermost

Tecovas Formation quarries, Boren Quarry (MOTT 3869), Otis Chalk quarries (MOTT 1998-2000) and Kirkpatrick Quarry (MOTT 3628) have produced various dinosauromorph fossils, including the hitherto earliest dinosaurs of the North America unearthed from the Boren Quarry as well as a fragment of the proximal femur which is ascribed to *Chindesaurus* (Long and Murry 1995; Nesbitt et al. 2007) from the overlying Otis Chalk Quarry. These quarries include the lowermost quarries with dinosaur fossils of North America, since the equivalent horizons of the Chinle Formation are unfossiliferous and no dinosaur fossils are hitherto discovered in the Newark Supergroup. Despite the raw geochronology of the Tecovas Formation, the co-existence of earliest dinosaurs within the same biostratigraphic interval (the *Paleorhinus* Fauna and the *Hyperodapedon* Acme Zone) suggests the temporal equivalency for the aforecited rock units. This new input is compatible with the main biostratigraphic implication in the study of Ramezani et al. (2011, 2014) which implies a global synchronous rise of dinosaurs rather than a diachronous start which initiated in South America (*contra* Nesbitt et al. 2007; Brusatte et al. 2010b; Langer et al. 2010; Irmis et al. 2011). In this case, the Chinle-Dockum Paleoriver Basin emerges as an important area for the dawn of dinosaurs, and moreover, it may be equally important to the South American counterparts which the prevailing theory points out as the centre of origin for dinosaurs. Thus, it appears that the early dinosaurs may not be restricted to a single geographic province but their distribution might be global in the Pangaean world, even from the very beginning.

# Chapter 7

# Conclusions

The Upper Triassic Dockum Group is a fluvial rock sequence with limited lacustrine deposition. The sedimentation of the Dockum Group is triggered by the reactivation of the preexisting Precambrian rift basin by the initial Central Atlantic rifting, in which the clastics of the uplifted basement rocks had started to accumulate. Besides displaying different taphonomic patterns, the Dockum Group sediments are remarkably rich in vertebrate fossils, especially in archosaurs. In the Dockum Group quarries of Texas, it is represented a successive series of dinosauromorph taxa, ranging from lagerpetids to theropods. Most of these specimens are kept in the repository of the Museum of Texas Tech University, which are all elaborately described here in a phylogenetic context for the first time, in addition to some loaned specimens from the West Texas A&M University (i.e. WTAMU specimens). The documented dinosauromorph specimens include a new basal dinosauromorph taxon (TTU-P10546; TTU-P19803) and new theropod morphotypes diagnosed on isolated jaw fragments (TTU-P10514, TTU-P10515 and TTU-P10517) from the Boren Quarry (MOTT 3869), and intermixed skeletal fragments (TTU-P11254a and TTU-P11254b) from the Post Quarry (MOTT 3624), together with many other hitherto unpublished specimens. Such extensive documentation of dinosauromorphs revealed a much larger diversity and higher relative abundance for this clade in the Dockum Group, complementing the most recent dinosauromorph discoveries from the Chinle Formation and the Dockum Group (e.g. Irmis et al. 2007a; Nesbitt et al. 2009b, 2010).

In contrast to the classical non-marine stratigraphic framework, recalibrated marine stages and high resolution geochronology now enables to reconcile Upper Triassic terrestrial and marine sequences. Therefore, the phytosaur biochronology of North America, Europe, India and Morocco where the phytosaur fossil are ubiquitous is also recalibrated. The lack of common elements, with the exception of India, prevents a direct biostratigraphic correlation between northern and southern continents, as exemplified between North America and South America. Since a complete geochronology of the terrestrial Upper Triassic has not been achieved yet, dinosaurs might be a more direct biostratigraphic tool for the Late Triassic biochronology especially between North and South America, despite the low taxonomic resolution. The common occurrences of the earliest dinosaurs in North America and South America provides better stratigraphic resolution by establishing a direct faunal correlation for the late Carnian-early Norian interval, since the same interval coincides with the *Paleorhinus* Fauna in northern continents and India, and with the abundance zone of the rhynchosaur *Hyperodapedon* in South America (e.g. Langer et al. 2007; Martinez et al. 2013a).

The earliest record of dinosauromorphs from one of the lowermost quarries of the Tecovas Formation, i.e. the Boren Quarry (MOTT 3869), is particularly important of being the stratigraphically lowest dinosaur bearing rock unit in North America. Preexisting theories indicate that the dinosaurs originated in South America and the radiation of dinosaurs is a two-step process which initiates with an early radiation in South America and possibly in other Gondwana continents, and then it spreads to Laurasia where we especially document the dominance of sauropodomorph dinosaurs in late Norian herbivorous niche (e.g. Irmis et al. 2011). However, the dinosauromorph

fossils are well documented in each level of the Dockum sequence, especially the ones in the lowermost portion of Tecovas Formation would allow a better correlation with the Ischigualasto Formation and the coeval strata for the first time. Although the geochronology of the Ischigualasto Formation points out the earliest dinosaur assemblage, the dinosaurs collected from the coeval deposits of South America, North America, Africa and India brings the possibility that the dinosaurs might have achieved wider dispersal even from the very beginning.

The center of origin for dinosaurs is difficult to pinpoint. Both Ischigualasto and the Tecovas formations are the two prime candidates for being the center of origin for dinosaurs by yielding each step of dinosauromorph evolution. In case for the Dockum Basin, the Santa Rosa Formation which underlies the Tecovas Formation and the Middle Triassic Anton Chico Formation stand as promising research areas to document the deep roots of dinosaurs and other non-dinosaurian dinosauromorphs.

Therefore it can be concluded that:

- The richer and taxonomically more diverse dinosauromorph fauna represented in the Dockum Group is now available for phylogenetic and biostratigraphic studies.

- Dinosaurs originated in the late Carnian-early Norian interval which corresponds to the *Paleorhinus* Fauna in the northern continents (and India) and to the *Hyperodapedon* Acme Zone in the southern continents.

- The earliest dinosaurs occurred synchronously even from the very beginning, as documented in Dockum Basin of North America, Ischigualasto-Villa Unión and Paraná basins of South America, Western Cabora Bassa Basin in southern Africa

and In Pranhita-Godavari Basin in India. However, the current fossil record suggests that the Tecovas Formation of the Dockum Basin and the Ischigualasto Formation of the Ischigualasto-Villa Unión Basin are the two principal candidates for being the center of origin for dinosaurs.

- The Ischigualasto Formation of Argentina preserved the most complete record of early dinosaurs, including sauropodomorphs and ornithischians, before their rise to dominance in the Early Jurassic. On the other hand, the Tecovas Formation of North America preserves the most complete record of theropod dinosaurs, as primarily documented from Boren and Post quarries.

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