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ADVANCES IN LATE TRIASSIC VERTEBRATE PALEONTOLOGY BASED ON NEW MATERIAL FROM PETRIFIED FOREST NATIONAL PARK, ARIZONA

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Abstract—Recent collecting of vertebrate fossils in Petrified Forest National Park as the result of an ongoing inventory of fossil localities has produced numerous important new specimens. These include phytosaur skulls and partial skeletons, aetosaur partial skeletons and isolated, but complete, osteoderms, as well as new dinosaur material that contributes new information to a currently poor dinosaur record from the Late Triassic of Arizona. Stratigraphic placement of phytosaur and aetosaur fossils from the park shows that several index taxa used for Late Triassic land vertebrate faunachrons overlap and that revision of these faunachrons is needed.

Keywords: Petrified Forest National Park, Arizona, Late Triassic, Chinle Formation, vertebrate paleontology, dinosaurs

INTRODUCTION

Petrified Forest National Park (PEFO) was established as a national monument in 1906 by President Roosevelt to protect the "mineralized remains of the Mesozoic forest" that are found within the Upper Triassic Chinle Formation. The park and surrounding area has been renowned for its paleontological resources and research potential for over 150 years since the Whipple expedition discovered the Black Forest in 1853 (Whipple et al., 1855). Ash (1972) and Long and Murry (1995) provided detailed histories regarding the past paleontological research in the park. Since these publications, Ash and colleagues have continued describing the fossil flora (e.g., Ash, 1973, 1977, 1985, 1991, 1999, 2000, 2001; Creber and Ash, 1991, 2004; Litwin et al., 1991; Ash and Creber, 2000), while Spencer Lucas and Andrew Heckert of the New Mexico Museum of Natural History have published several detailed papers on the local stratigraphy (e.g., Lucas, 1995; Heckert and Lucas, 1998, 2002). Heckert (2004) also provided a detailed analysis of the microvertebrates from the lower part of the Chinle Formation in the park. Good (1998) described the freshwater bivalves and gastropods, while Hasiotis and Dubiel (1995) presented evidence for insect nests. Adrian Hunt, then at the Mesalands Dinosaur Museum, noted several new dinosaur localities in the park as part of his ongoing "Dawn of the Dinosaurs" project (Hunt et al., 1996, 1999). Other important work includes Demko (1995) and Demko et al. (1998) on plant taphonomy. Robert Long made additional extensive collections of vertebrates and invertebrates in 1997, however none of this has been described (Long, 1997 unpublished field notes).

In 2001, the park launched an exhaustive inventory of its paleontological resources (Parker, 2002; Parker and Clements, 2004). As a result of this work numerous new specimens have been collected. This paper provides a preliminary discussion of these discoveries and their implications for the paleontology and biostratigraphy of the Chinle Formation.

Stratigraphy and Age

Petrified Forest National Park (Fig. 1) contains some of the best exposures of the Upper Triassic Chinle Formation in the southwestern United States. In PEFO, the Chinle Formation is approximately 300 m thick (Billingsley, 1985a,b; Heckert and Lucas, 2002; Creber and Ash, 2004) and can be divided into five units from oldest to youngest: the Mesa Redondo, Blue Mesa, Sonsela, Petrified Forest and Owl Rock members (Fig. 2; Woody, 2003). Heckert and Lucas (2002) essentially agree with this division, however they use the terminology of Lucas (1993) in which the Chinle is elevated to group status. Following this terminology the park contains three formations, Bluewater Creek (=Mesa Redondo), Petrified Forest, and Owl Rock. The Petrified Forest Formation is further divided into three members, Blue Mesa, Sonsela, and Painted Desert (=Petrified Forest Member of Woody [2003]). The terminology of Woody (2003), which presents a minor variation of the older Chinle nomenclature, is preferred for this work.

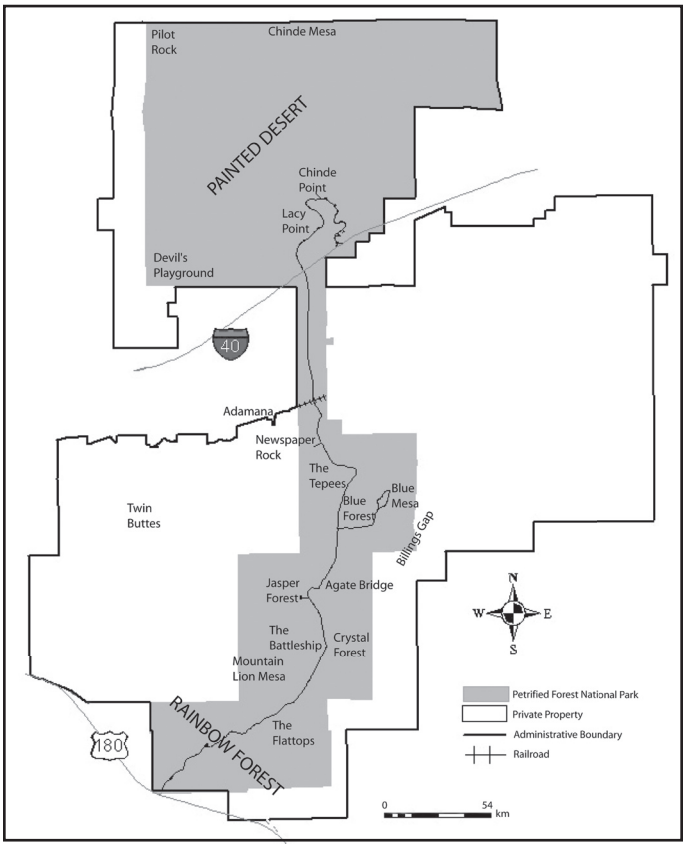

FIGURE 1. Locality map of Petrified Forest National Park showing the relevant geographical areas mentioned in the text.

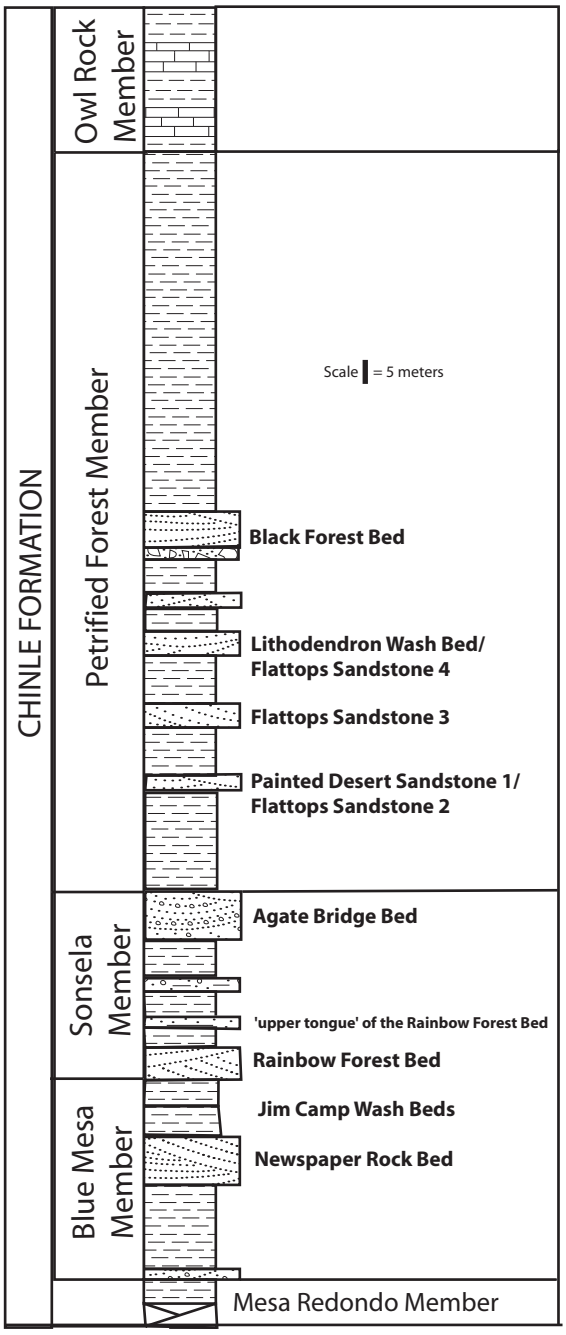

FIGURE 2. Generalized stratigraphic column for the Chinle Formation in Petrified Forest National Park (modified from Heckert and Lucas, 2002).

Contrary to Dubiel et al. (1999), Therrien et al. (1999), and Hasiotis et al. (2001), there is no conclusive evidence for the presence of the Moenkopi Formation or the Shinarump Member of the Chinle Formation in the park. Supposed Shinarump Member outcrops in the Tepees area overlie a reddish-purple mudrocks that do superficially resemble the "mottled strata" or upper Moenkopi; however, exposures to the west of the park demonstrate that these rocks represent the upper portion of the Mesa Redondo (=Bluewater Creek) Member. Thus, Heckert and Lucas (1998, 2002) were correct in assigning the exposures in the park to their Bluewater Creek Formation.

Chinle Formation exposures in the park span the late Carnian through early-middle Norian stages based on palynomorphs (Litwin et al., 1991) and vertebrates (Lucas and Heckert, 1996), with the Carnian-Norian boundary most likely occurring in the lower portion of the Sonsela Member (Albright et al., in prep). Riggs et al. (2003) have proposed an isotopic date of 209 Ma for the Black Forest Bed (Petrified Forest Member) based on detrital zircons; although these authors suggest that the true date of the bed may be closer to 214 Ma.

Paleontological Locality Designations for PEFO

Parker (2002) discussed the ambiguities regarding the designation of paleontological localities in PEFO. Diverse numbering schemes have been used by several institutions, with different locality names and numbers often being assigned to the same sites. Long and Murry (1995) presented an appendix listing all known PEFO vertebrate localities as of 1990. The scheme used by these authors provided each locality with a sequential number and the prefix PF. Unfortunately the same scheme has been used by Ash (unpubl. data) for plant localities. Since Long and Murry's scheme has already entered the literature, it would be confusing to present a new scheme, therefore the numbers provided by Long and Murry have been retained except that the prefix has been modified to PFV for the vertebrate localities. It is strongly recommended that this scheme be used in all future references to PEFO localities and has already been followed by Heckert and Lucas (2002) and Hunt et al. (2002).

INSTITUTIONAL ABREVIATIONS

GR = Ruth Hall Museum, Ghost Ranch, New Mexico; **MNA** = Museum of Northern Arizona, Flagstaff; **NMMNH** = New Mexico Museum of Natural History and Science, Albuquerque; **PEFO** = Petrified Forest National Park, Arizona; **UCMP** = University of California Museum of Paleontology, Berkeley; **UMMP** = University of Michigan Museum of Paleontology, Ann Arbor.

SYSTEMATIC PALEONTOLOGY

AMPHIBIA Linnaeus, 1758

TEMNOSPONDYLI Zittel, 1888

STEREOSPONDYLI Fraas, 1889

METOPOSAURIDAE Watson, 1919

Metoposauridae indet.

Metoposaurs are one of the most commonly recovered fossils in PEFO, especially from the Blue Mesa Member. Several elements, mostly pectoral, have been collected as a result of the current inventory. The most important discoveries consist of two partial skulls of small individuals. The first (PEFO 31184) is from the Bowman locality (PFV 89) within the Sonsela Member and the second (PEFO 33977) is from the Giving Site (PFV 231), which is in the Petrified Forest Member. Neither has been completely prepared and at this time it is premature to assign them to genus.

Buettneria Case, 1922

Buettneria perfecta Case, 1922

Sulej (2002) and Milner and Schoch (2004) argue that the criteria regarding the lacrimal used by Hunt (1993) to distinguish *Buettneria perfecta* from *Metoposaurus diagnosticus* are not valid and that further study is needed to determine whether *Buettneria* is a synonym of *Metoposaurus*. Nonetheless, until further review is conducted, PEFO material will continue to be assigned to the genus *Buettneria* as it traditionally has.

A very small interclavicle (PEFO 34036; Fig. 3A), recovered from the Dying Grounds area (PFV 122), is of interest because juvenile metoposaur material is rare (e.g., Zanno et al., 2002). A second specimen of interest is a partial right clavicle (PEFO 23383) from the Phytosaur Basin area (PFV205). Although represented by

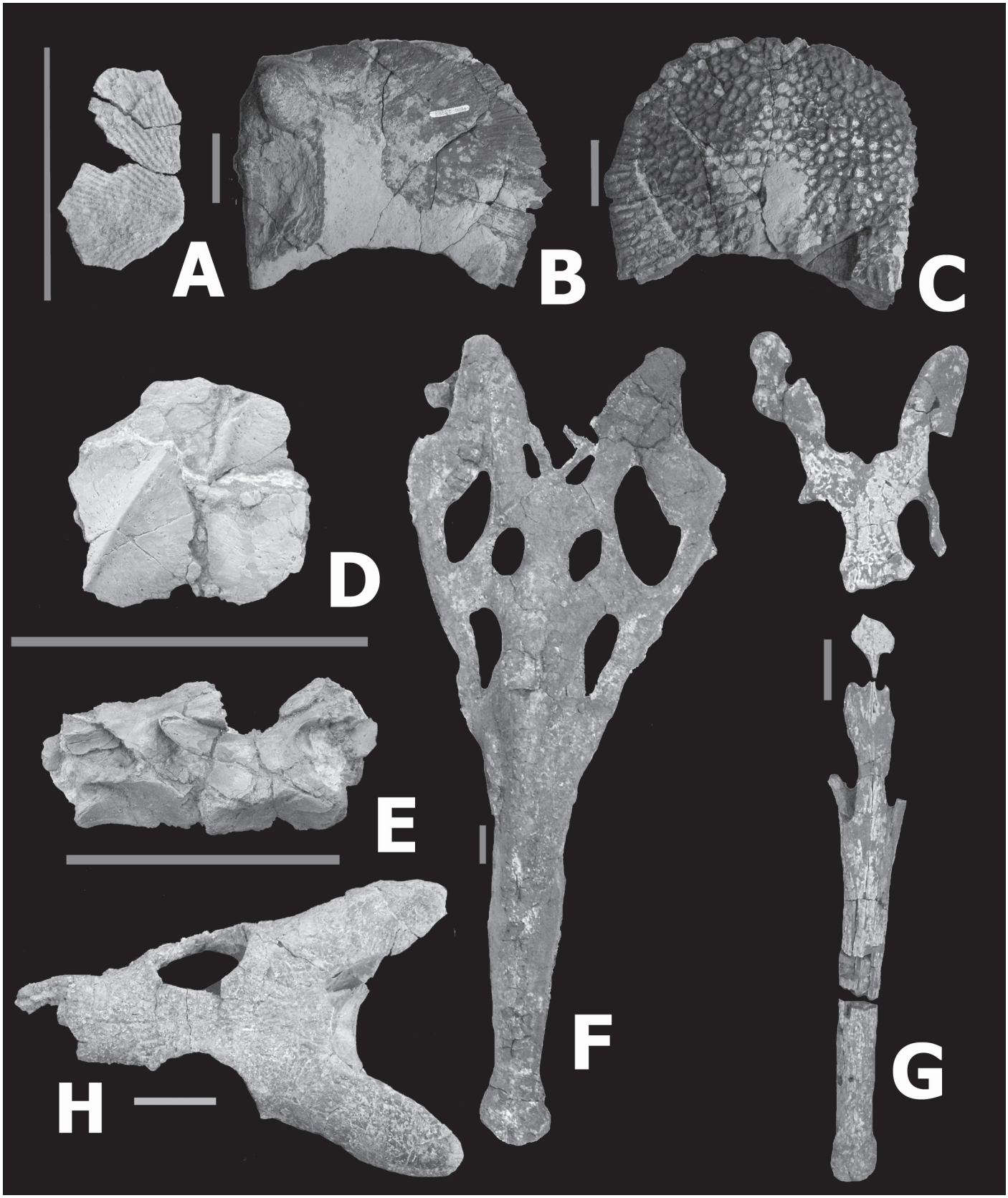

FIGURE 3. New metoposaur (A-C), archosauromorph (D-E), and phytosaur (F-G) material from the park. **A**, *Buettneria perfecta* juvenile interclavicle fragment (PEFO 34036) in dorsal view; **B-C**, *Buettneria perfecta* proximal right clavicle (PEFO 23383) in **B**, dorsal, and **C**, ventral views; **D**, *Vancleavea* sp. osteoderms (PEFO 33978) in dorsal view; **E**, *Vancleavea* sp., articulated caudal vertebrae (PEFO 33978) in lateral view; **F**, *Leptosuchus* sp. skull (PEFO 31218) in dorsal view; **G**, *Leptosuchus adamanensis* skull (PEFO 34034) in dorsal view; **H**, *Pseudopalatus* sp. skull (PEFO 31207) in dorsal view. Scale bars = 5 cm.

only the proximal portion (Figs. 3B-C) it is possible to estimate an original length for this element using averages of data given by Colbert and Imbrie (1956). Colbert and Imbrie (1956: tables 1-3) provide clavicular widths and lengths for metoposaurids from the southwestern United States. This data was compiled into a spreadsheet to obtain an average clavicular length/width ratio. Clavicular length (CL) can be determined by multiplying this ratio by the clavicular width. PEFO 23383 has a clavicular width of 231 mm. Using the above formula suggests that this element had a length of approximately 470 mm, making it one of the largest metoposaur clavicles collected from the southwestern United States. No element listed by Colbert and Imbrie (1956) has a CL of more than 443 mm (a single specimen from the Lamy quarry of New Mexico), and the average CL of all of the elements provided by these authors is only 337 mm.

EUREPTILIA Olsen, 1947

DIAPSIDA Osborn, 1903

ARCHOSAUROMORPHA Benton, 1985

TRILOPHOSAURIA Romer, 1956

***Trilophosaurus* sp.**

Long and Murry (1995) documented *Trilophosaurus* from PEFO on the basis of caudal vertebrae from two localities, Agate Bridge N (PFV 161) and Saurian Valley (PFV 97), and an uncatalogued ilium from PFV 97, collected by UCMP crews in the 1980s. However, these vertebrae represent caudals from an indeterminate archosaur and cannot be assigned with certainty to *Trilophosaurus* (RBI pers. obs.), and the ilium could not be relocated. Murry (1989) assigned three fragmentary teeth (PEFO 3893-3895) from the Dying Grounds locality (PFV 122) to *T. buettneri*. Murry (1989; Fig. 7h) figured one of these teeth (PEFO 3893), yet it is unclear why this occurrence is not listed by Long and Murry (1995). Heckert (2004) agreed with Murry's identification and also assigned these teeth to *T. buettneri* based on Murry's illustration.

In 2003, jaw fragments of a large trilophosaurid were discovered at the Flag Canyon locality (PFV 191) within the Sonsela Member. These teeth possess distinct cingula and represent a new taxon (Mueller and Parker, in review).

ARCHOSAUROMORPHA *incertae sedis*

***Vancleavea* Long and Murry (1995)**

***Vancleavea* sp.**

Small and Downs (2002) provided a preliminary description of a new armored reptile (GR 138) from the Whitaker quarry at Ghost Ranch, New Mexico. According to these authors, characters of the skull, osteoderms, and femur, suggest placement of this taxon within the Archosauriformes. However, these characters may have a broader distribution and other characters only suggest inclusion within Archosauromorpha. Although these specimens have yet to be formally described, Hunt et al. (2002) assigned them to the enigmatic taxon *Vancleavea*. *Vancleavea campi* was described by Long and Murry (1995) from fragmentary material collected from PEFO in the 1960s. The holotype is probably from the Blue Mesa Member in the area of the Blue Forest, though the exact locality and association of these elements is unknown and the type specimen (PEFO 2427) was originally mixed with phytosaur teeth and bone fragments from larger tetrapods, probably metoposaurs.

Hunt and Wright (1999) documented occurrences of *Vancleavea* from the Petrified Forest Member of PEFO from the Zuni Well Mound (PFV 215), Dinosaur Hill (PFV 40), and RAP Hill (PFV 216) localities. In 2003, a partial skeleton (PEFO 34035; Figs. 3D-E) of *Vancleavea* was collected from Zuni Well Mound, although this specimen has not yet been prepared. In 2004, a second fragmentary skeleton (PEFO 33978) was collected from The Giving Site (PFV 231). Both of these new specimens possess the diamond-shaped osteoderms (Fig. 3D) that are characteristic of GR 138 and the holotype of *Vancleavea campi* (PEFO 2427).

ARCHOSAURIA Cope, 1869

PSEUDOSUCHIA Gauthier, 1986

PHYTOSAURIA Jaeger, 1828

PHYTOSAURIDAE Jaeger, 1828

***Leptosuchus* Case, 1922**

***Leptosuchus* sp.**

Phytosaurs represent the most common fossil vertebrate recovered from the park, although skulls are generally rare. Camp (1930) described several phytosaur skull specimens from the Petrified Forest area, including the holotype skull and skeleton of the phytosaur "*Machaeroprosopus*" (=*Leptosuchus*) *adamanensis* from the Annie's Canyon locality (PFV 123), located high in the Blue Mesa Member. Two newly recovered skulls from the park can be referred to *Leptosuchus* based on their possession of elongate, deep squamosals that are not knoblike and supratemporal fenestrae that are open in dorsal view (Long and Murry, 1995). PEFO 31218 (Fig. 3F) is from the Saurian Valley N locality (PFV 99) in the Sonsela Member and consists of a complete skull that has been dorsoventrally flattened at the posterior end. This skull occurs approximately 8 m stratigraphically above the type locality of "*Machaeroprosopus lithodendrorum*" (Camp 1930), which Long and Murry (1995) assigned to *Leptosuchus crosbiensis*. PEFO 31218 is 107 cm in length and possesses an extremely robust rostrum that has a slight swelling of the posterior premaxilla as in *Leptosuchus* (=*Smilosuchus*) *gregorii* and other brachyrostral phytosaurs. The rostrum is also slightly crested. This specimen is heavily encrusted with hematite coatings, as are most fossils from the Devil's Playground area of the park, and has not yet been fully prepared. Although the squamosals strongly resemble those of *L. adamanensis* in being elongate and deep, the stratigraphic position of the quarry and the robust nature of the skull suggest that it may possibly represent a small specimen of *L. gregorii*. Current understanding of the variation of squamosal morphology in *Leptosuchus* makes it difficult to determine whether Long and Murry's (1995) characters are valid for species determination.

A relatively complete skeleton lacking the skull (PEFO 26695) was collected from the Gobstopper Hill locality (PFV 263) within the general area of "Phytosaur Basin." This skeleton consists of an almost complete pelvis, limb bones, scapulocoracoid, and numerous vertebrae, ribs, and gastralia. The preservation of elements is exquisite and this specimen represents one of the best phytosaur postcranial skeletons collected from Arizona to date. PEFO 26695 occurs in the Blue Mesa Member just below the base of the Sonsela Member.

***Leptosuchus adamanensis* (Camp, 1930)**

A fragmentary skull (PEFO 34034) collected from the Battleship N locality (PFV 169) in 2004 consists of the skull roof, including both squamosals, and much of the rostrum, as well as the right mandibular ramus (Fig. 3G). PEFO 34034 measures approximately 81 cm in length, while the holotype of *L. adamanensis* (UCMP 26699) measures 109.5 cm. The squamosals are elongate and deep, while the supratemporal fenestrae are open and exposed dorsally, allowing referral to *Leptosuchus*. Following Long and Murry (1995) we refer this specimen to *L. adamanensis* on the basis of the partially crested rostrum, and squamosals that are rounded, as opposed to those of *Leptosuchus crosbiensis*, which are squared off. This specimen was recovered from the Rainbow Forest Bed, which in PEFO represents the base of the Sonsela Member (Heckert and Lucas, 2002; Woody, 2003) and co-occurs with the aetosaurs *Stagonolepis*

and *Paratypothorax* as well as the metoposaur *Buettneria perfecta*. This specimen represents the highest stratigraphic occurrence of *Leptosuchus adamanensis* in the park.

PSEUDOPALATINAE Long and Murry, 1995
***Pseudopalatus* Mehl, 1928**
***Pseudopalatus* sp.**

In 2002 a partial skull (PEFO 31207) consisting of the skull roof and portions of the braincase were collected from just above the Rainbow Forest Bed and below the Agate Bridge Bed near Mountain Lion Mesa (PFV 295). A wide postorbito-squamosal bar and supratemporal fenestra that are slit-like in dorsal view (Fig. 3H) allow assignment of this specimen to *Pseudopalatus* (Long and Murry, 1995). However, the squamosals are anteroposteriorly shortened, the squamosal tips are not knob-like, and the squamosal fossa extends to the tip of the squamosal, unlike any known pseudopalatine. Parker and Irmis (2004) tentatively referred this skull to *P. mccauleyi* based on the morphology of the squamosals and the exoccipitals, however until more complete material is found, this skull is best referred to *Pseudopalatus* sp. This specimen co-occurs with the aetosaur *Typothorax* at PFV 295 and is the lowest occurrence of a pseudopalatine phytosaur in the park, ~3 m above the Rainbow Forest Sandstone.

ARCHOSAURIA Cope, 1869
PSEUDOSUCHIA Gauthier, 1986
STAGONOLEPIDIDAE Lydekker, 1887

Next to phytosaur remains, aetosaurs are the most frequently recovered vertebrate fossils in the park. Long and Ballew (1985) prominently featured the aetosaurs of PEFO in their discussion of the taxonomic utility of aetosaur plate ornamentation. This included listings of material by locality. It should be noted, however that much of this material is extremely fragmentary and in many cases not identifiable below the level of Stagonolepididae indet. Contrary to Long and Ballew (1985), almost none of the material referred by these authors to *Desmatosuchus* belongs to that taxon. For example, UCMP 126901 and UCMP 126837 are unidentifiable fragments while UCMP 126838 is a paramedian plate of *Paratypothorax* sp. with the lateral and medial margins broken off.

***Desmatosuchus* Case, 1920**
***Desmatosuchus haplocerus* (Cope, 1892)**

Although almost none of the specimens from the PFNP referred to *Desmatosuchus haplocerus* by Long and Ballew (1985) and Long and Murry (1995) pertain to that taxon, *D. haplocerus* does occur at PEFO. Currently, known material is restricted to several fragmentary paramedian plates (PFV 202/PEFO 23338; PFV 212/PEFO 26668) (Figs. 4B-D) and a fragmentary lateral plate (PFV 198/PEFO 31177) (Fig. 4E), all from the Blue Mesa Member in the Blue Forest area. The paramedian plates are dorsoventrally thickened with the complex tongue-and-groove articulation characteristic of *Desmatosuchus* (Long and Ballew, 1985), while the lateral plate is similar to the more anterior cervical lateral plates of UMMP 7476 (holotype of *D. spurensis*; Case, 1922). A plate from locality PFV 294 (MNA V697) was illustrated by Long and Ballew (1985: figs. 7a-b) as a cervical lateral plate but actually represents an incomplete dorsal lateral plate (Parker, 2003). This specimen is from the Petrified Forest Member and co-occurs with the aetosaur *Typothorax coccinarum* and is referable a new species of *Desmatosuchus* (Parker, 2003; in press).

***"Desmatosuchus" chamaensis* Zeigler, Heckert and Lucas, 2002**

PEFO 31162 (Fig. 4F) is an anterior caudal paramedian plate of "*Desmatosuchus*" *chamaensis* from the Karen's Point locality (PFV 75). Parker (2003) demonstrated that "*D.*" *chamaensis* shares almost no characters with *Desmatosuchus*, instead is more closely related

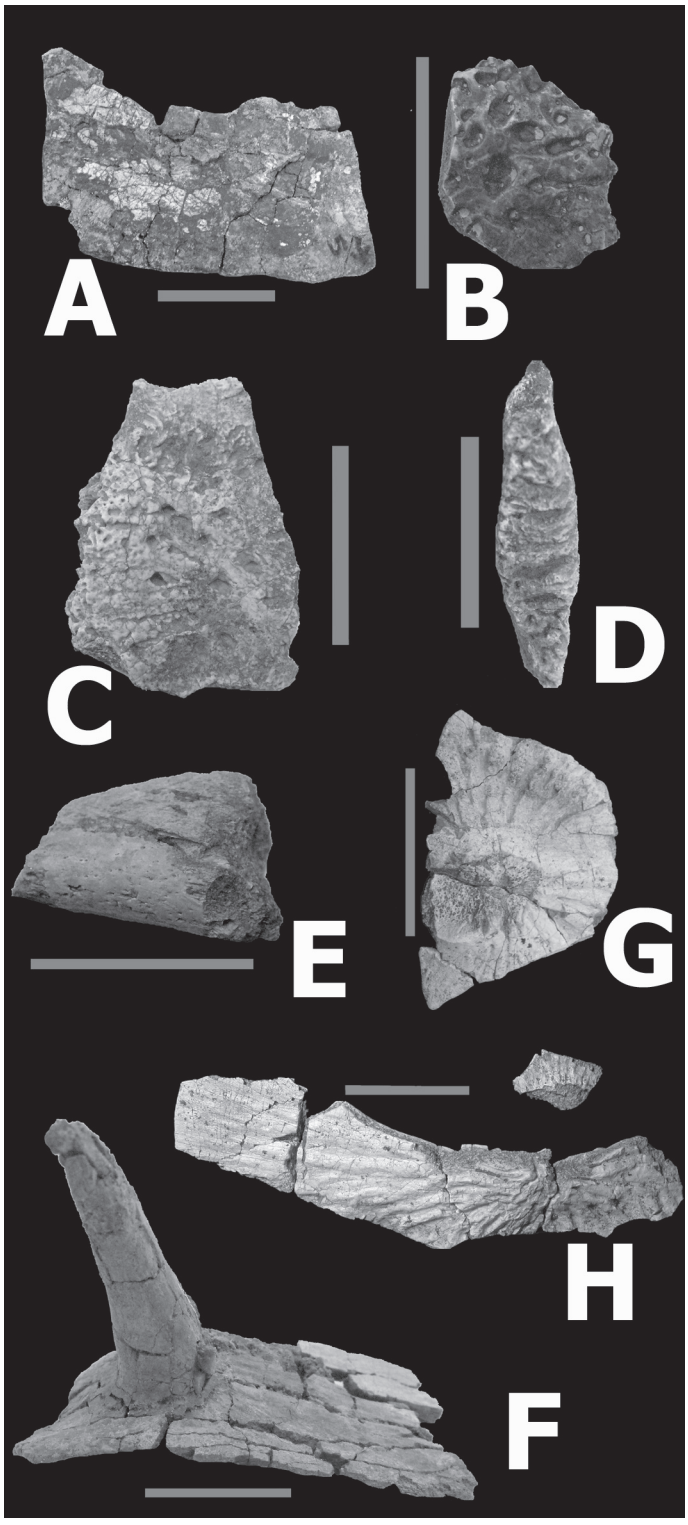

FIGURE 4. New aetosaur material from the park. **A**, *Stagonolepis wellesi* right cervical paramedian plate (PEFO 31217) in dorsal view; **B**, *Desmatosuchus haplocerus* paramedian plate fragment (PEFO 23338) in dorsal view; **C-D**, *Desmatosuchus haplocerus* paramedian plate fragment (PEFO 26668) in **C**, dorsal and **D**, medial views; **E**, *Desmatosuchus haplocerus* cervical lateral plate fragment (PEFO 31177) in lateral view; **F**, "*Desmatosuchus*" *chamaensis* anterior caudal paramedian plate (PEFO 31162) in anterior view; **G**, "*Desmatosuchus*" *chamaensis* lateral plate fragment (PEFO 34040) in lateral view; **H**, "*Desmatosuchus*" *chamaensis* partial paramedian plate (UCMP 129829) in dorsal view. Scale bars = 5 cm.

to *Paratypothorax*, and represents a distinct genus. PEFO 31162 co-occurs with the aetosaur *Typothorax coccinarum* above the Flattops Two Bed of the Petrified Forest Member and represents the first occurrence of this taxon outside of New Mexico. One fragmentary lateral plate (PEFO 34040) (Fig. 4G) and UCMP 129829 (Fig. 4H), a partial paramedian plate, are also referable to this taxon and were also collected from PFV 75.

Stagonolepis Agassiz, 1844

Stagonolepis wellesi (Long and Ballew, 1985)

Stagonolepis wellesi was described by Long and Ballew (1985) from the articulated posterior half of a partial skeleton (UMMP 13950) collected by E. C. Case from the Tecovas Formation of Texas (Case, 1932). Charles Camp collected *Stagonolepis* armor from the *Placerias* quarry in the early 1930s and a partial carapace (UCMP 27225) from the Blue Hills near St. Johns, Arizona in 1926. Unfortunately none of this material was described until the work of Long and Murry (1995), and except for a dentary fragment and several cervical vertebrae from UCMP 27225, the specimens do not appear to represent portions of the carapace not preserved in the holotype. In 1982 Michael Parrish discovered a partial carapace (UCMP 126844) from the Agate Bridge NW locality (PFV 162), which was illustrated by Long and Ballew (1985: pl. 5), however this specimen consists only of fragmentary paramedian and lateral plates from the dorsal region.

In 2002, another partial carapace referable to *Stagonolepis wellesi* (PEFO 31217) was collected from a sandy mudstone facies of the Rainbow Forest Bed at the Battleship NW locality (PFV 169). Preparation of this specimen is currently underway and preliminary work shows that this specimen also consists mainly of the posterior portion of a carapace, including the pelvis, anterior caudal vertebrae and associated armor. However, one plate collected during the excavation appears to be from the anterior dorsal or posterior cervical portion of the carapace, suggesting that elements anterior of the pelvis may be present in the unprepared material. The rectangular shape (wider than long), small size, low dorsal eminence, and faint ornamentation of this plate (Fig. 4A) are common for aetosaur cervical plates including those of *Stagonolepis robertsoni* and *Aetosaurus ferratus* (Walker, 1961). The dorsal eminence is strongly offset medially as in *Paratypothorax* (Long and Ballew, 1985). The plate is flat and not arched as in the dorsal paramedians of *Stagonolepis robertsoni* (Walker, 1961) and has an overall crescentic shape in dorsal view further supporting placement in the cervical series. Another interesting character of PEFO 31217 is that the neural spines of the anterior caudals are extremely high, being at least twice the height of the centrum. Although this portion of the column is present in the holotype of *Stagonolepis wellesi*, the neural spines of the caudal vertebrae are crushed, so they cannot be easily compared with the present specimen. Case (1932: plate III) reconstructed them as being 1.5 times the height of the centra. Although not well represented by the known material, the anterior caudal vertebrae of *Stagonolepis robertsoni* also appear to have tall neural spines (Walker, 1961: Fig. 10b). High neural spines in the anterior caudals are a feature also seen in phytosaurs (e.g., Case, 1927: plate I).

Stagonolepis sp.

In 2004, another aetosaur carapace was collected from near old Highway 180 (PFV 304) in the southern portion of the park that is also referable to *Stagonolepis*. This specimen consists principally of armor plates, vertebrae and ribs and is currently undergoing preparation. This specimen is significant since it was collected several meters above the Rainbow Forest Bed of the Sonsela Member and represents the highest known stratigraphic occurrence of *Stagonolepis*. Most of this specimen is currently unprepared, although characteristics of several prepared paramedian plates suggest that it may be distinct from *Stagonolepis wellesi*.

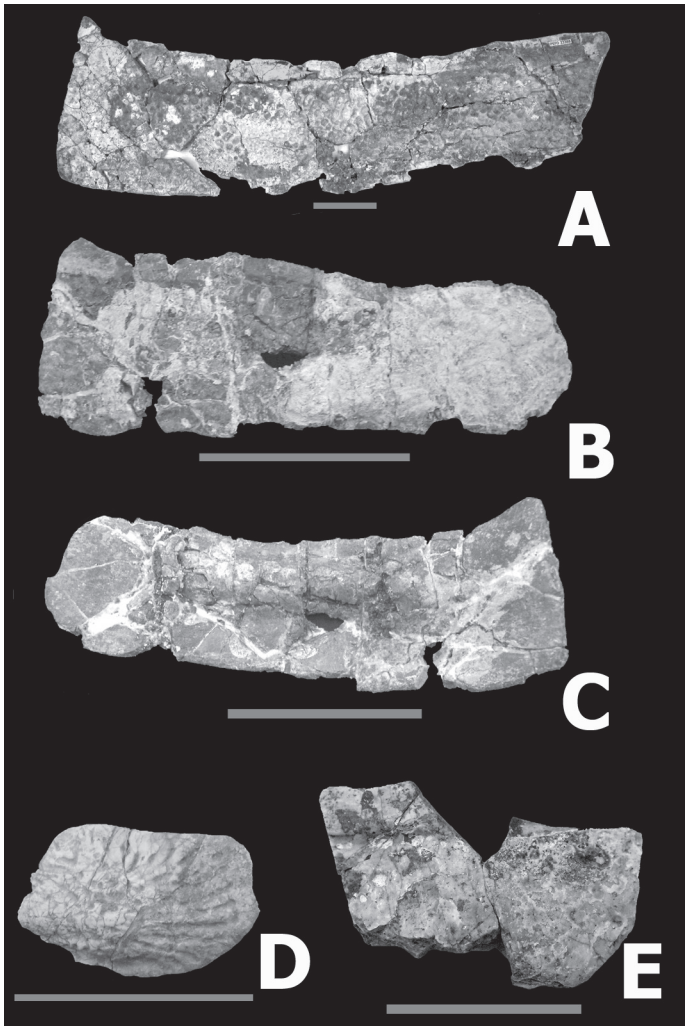

FIGURE 5. New *Typothorax* material from the park. **A**, *Typothorax coccinarum* paramedian plate (PEFO 23388) in dorsal view; **B-C**, *Typothorax coccinarum* paramedian plate (PEFO 33979) from a juvenile individual in **B**, dorsal and **C**, ventral views; **D**, *Typothorax* sp. lateral plate (PEFO 33980) from a juvenile individual in dorsal view; **E**, *Typothorax coccinarum* paramedian plate fragment (PEFO 26694) in dorsal view. Scale bars = 5 cm.

Typothorax Cope, 1875

Typothorax coccinarum Cope, 1875

Typothorax coccinarum is the most commonly recovered aetosaur from Norian aged strata in the southwestern United States. Significant finds made in recent years include a paramedian plate from PFV 70 (PEFO 23388; Fig. 5A) with a width of 432 mm, which represents the largest *Typothorax* plate found to date. The Giving Site (PFV 231) yields a wealth of *Typothorax coccinarum* material including a partial sacrum with associated armor, and two juvenile specimens. The juvenile specimens (Figs. 5B-D) demonstrate that the ornamentation of *Typothorax* plates did not change through ontogeny.

Another important specimen is a partial paramedian plate of *Typothorax coccinarum* (PEFO 26694) from the "Camp Butte Sandstone" (=Rainbow Forest Bed) in the Phytosaur Basin locality (PFV 121) below Blue Mesa. While represented by only a fragment (Fig. 5E), this plate can be referred to *Typothorax* based on the presence of a raised anterior bar, combined with prominent ventral strut

and a dorsal ornamentation consisting of small rounded pits in a non-radial ornamentation. Furthermore, the plate represents *T. coccinarum* and not *T. antiquum* based on dense pitting and the dorso-ventral flexion of the plate. This flexion is present in *T. coccinarum* (Martz, 2002) and never in *T. antiquum* (Lucas et al., 2002: p. 222). This plate represents the lowest known occurrence of *T. coccinarum* and is approximately 5 m stratigraphically below the *Stagonolepis* specimen from PFV 304.

Paratypothorax Long and Ballew, 1985

Paratypothorax sp.

According to Long and Ballew (1985) and Long and Murry (1995) *Paratypothorax* is a rare constituent of the PEFO fauna, however, specimens referable to this taxon have been routinely recovered in recent years. The best specimen to date is a partial carapace (PEFO 3004) from the Sonsela Member of the Crystal Forest that was described by Hunt and Lucas (1992). Since this time *Paratypothorax* plates have been recovered from several localities in the park including PFV 169, PFV 177, PFV 178, PFV 259, and PFV 272. All of these occurrences are from the Sonsela Member. In addition, some plates assigned to *Stagonolepis* and *Desmatosuchus* by Long and Ballew (1985) and Long and Murry (1995) actually represent *Paratypothorax* plates. Examples include UCMP 126963 and UCMP 126838, both of which were originally assigned to *Desmatosuchus*. Both of these specimens were also recovered from the Sonsela Member.

cf. *Paratypothorax* sp.

Numerous plates have been collected from the park that are similar to *Paratypothorax* yet not directly referable to that taxon. This material consists of paramedian and lateral plates from at least four localities in the Sonsela Member that are similar to a new *Paratypothorax*-like genus from Texas being described by Jeff Martz and Bryan Small. The PEFO material will be described by the authors in a separate paper.

ARCHOSAURIA Cope, 1869

PSEUDOSUCHIA Gauthier, 1986

RAUISUCHIDAE Huene, 1942

Postosuchus Chatterjee, 1985

Postosuchus kirkpatricki Chatterjee, 1985

Postosuchus elements are rare at PEFO, consisting mainly of isolated elements found in the Blue Mesa, Sonsela, and Petrified Forest members. Long and Murry (1995) assigned mostly fragmentary pelvic and limb elements to this taxon. The most diagnostic specimen is a left ilium (PEFO 4851) from the Dry Tank SE locality (PFV 55), which is probably located within the Sonsela Member. Newly recovered material includes isolated left and right postorbitals (PEFO 34044) of the same individual from the Agate Bridge N locality (PFV 161), which is at the top of the Blue Mesa Member. A partial skeleton referable to *Postosuchus* (PEFO 33954) was collected from the Giving Site (PFV 231) in 2004. Located stratigraphically low in the Petrified Forest Member, this material consists of left and right astragali and calcanea (Fig. 6A), numerous vertebrae, and limb and pelvic fragments. A distal fibula of *Postosuchus* (PEFO 33958; Fig. 6B) was also collected from this locality. In addition, a badly weathered femur (PEFO 31183) from the Bowman locality (PFV 89) is possibly also referable to *Postosuchus*. This site is in the Jim Camp Wash Beds (medial portion of the Sonsela Member *sensu* Heckert and Lucas, 2002).

ARCHOSAURIA Cope, 1869

PSEUDOSUCHIA Gauthier, 1986

POPOSAURIDAE Nopsca 1928

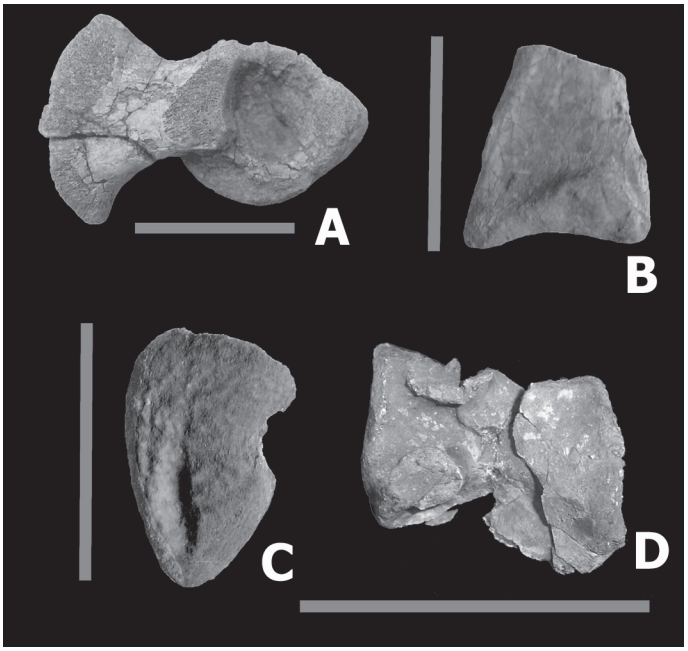

FIGURE 6. "Rauisuchian" (A-B), chatterjeeid (C), and "sphenosuchian" (D) material from the park; **A**, *Postosuchus kirkpatricki* right calcaneum (PEFO 33954) in medial view; **B**, *Postosuchus kirkpatricki* distal fibula (PEFO 33958) in anterior view; **C**, *Chatterjeea* sp., proximal femur (PEFO 34038) in proximal view; **D**, "*Parrishia mccreai*" anterior cervical vertebra (PEFO 26681) in left lateral view. Scale bars = 5 cm.

Chatterjeea Long and Murry, 1995

Chatterjeea sp.

New chatterjeeid material has been collected from three sites in the Painted Desert portion of the park, including limb bone fragments and vertebrae from PFV 297, several limb bones from PFV 231 (Fig. 6C), and a proximal femur from PFV 300. This material more than doubles the known chatterjeeid material for the park. It should be noted that the chatterjeeid pelvic and limb material listed by Long and Murry (1995) from the Dinosaur Hollow locality (PFV 20) is missing and has not been formally catalogued. Also, a distal femur (UCMP 126751) from the Flattops West locality (PFV 71) assigned to *Chatterjeea* by Long and Murry (1995) is actually referable to Dinosauria indet.

ARCHOSAURIA Cope, 1869

PSEUDOSUCHIA Gauthier, 1986

CROCODYLOMORPHA Walker, 1968

"SPHENOSUCHIA" Hoffstetter, 1955

"*Parrishia*" Long and Murry, 1995

"*Parrishia mccreai*" Long and Murry, 1995

"*Parrishia mccreai*" was named by Long and Murry (1995) for a robust form of sphenosuchian from the *Placerias* quarry. These authors differentiated "*Parrishia*" from *Hesperosuchus* on the basis of the vertebral centra being more robust and the lack of dorsoventrally offset articular faces of the cervical centra. Clark et al. (2001) considered "*Parrishia*" a *nomen dubium* and pointed out that a cervical centrum figured by Long and Murry (1995: figs. 174a, b) does possess dorsoventrally offset articular faces. A partial postcranial skeleton (PEFO 26681) collected from the Blue Mesa Member (PFV 261) at PEFO contains numerous vertebrae from throughout the vertebral column. The centra are extremely robust and most closely resemble those assigned to *Parrishia* by Long and Murry (1995). However, several of the cervical centra

possess articular faces that are strongly offset dorsoventrally (Fig. 6D). The *Hesperosuchus agilis* skeleton (UCMP 129740) from the Dinosaur Hill locality (PFV 40) described by Parrish (1991) shows that the anteriormost centra of the cervical series have strongly offset articular faces, while this offset diminishes in the more posterior centra. PEFO 26681 shows this same progression; therefore the neck orientation of *Parrishia* does not differ from that of *Hesperosuchus* (*contra* Long and Murry, 1995). As a result, the only difference between the vertebrae of *Parrishia* and *Hesperosuchus* is the robustness of the elements in the former.

ARCHOSAURIA Cope, 1869

PSEUDOSUCHIA *incertae sedis* Gauthier, 1986

***Revueltosaurus* Hunt, 1989**

***Revueltosaurus callenderi* Hunt, 1989**

Revueltosaurus callenderi was described by Hunt (1989) based on isolated teeth as a probable ornithischian dinosaur from the Upper Triassic Bull Canyon Formation of New Mexico. Later papers (e. g., Padian, 1990; Hunt and Lucas, 1994; Hunt and Wright, 1999; Heckert, 2002) affirmed the ornithischian identity of these teeth, although other authors (e. g., Sereno, 1991a; Norman et al., 2004) have doubted the validity of this genus. Padian (1990) was the first to document the occurrence of *R. callenderi* in PEFO in the form of isolated teeth from the Dinosaur Hill locality (PFV 40). *Revueltosaurus* teeth are a commonly recovered element in a narrow stratigraphic interval in the Petrified Forest Member of PEFO (Hunt and Wright, 1999) including the RAP Hill (PFV 216) and Zuni Well Mound (PFV 215) localities. In 2004, a quarry consisting almost exclusively of skeletal material referable to *R. callenderi* was discovered in the Painted Desert at PEFO (PFV 297), adjacent to the Giving Site (PFV 231). This material, preliminarily described by Parker et al. (2005), demonstrates that *Revueltosaurus* in not an ornithischian dinosaur. Skeletal material of *R. callenderi* has also been recovered from the Giving Site (PFV 231) and skeletal material collected by the UCMP from Dinosaur Hill also is assignable to *R. callenderi*. Both PFV 297 and PFV 231 are in the same stratigraphic interval (below the Black Forest Bed of the Petrified Forest Member) as are all of the other occurrences of *R. callenderi* at PEFO.

DINOSAURIFORMES *incertae sedis* Sereno, 1991b

***Chindesaurus* Long and Murry, 1995**

***Chindesaurus bryansmalli* Long and Murry, 1995**

Chindesaurus bryansmalli was described as an herrerasaurid by Long and Murry (1995) from a fragmentary skeleton from the Dinosaur Hollow locality (PFV 20) in the Petrified Forest Member. Long and Murry (1995) assigned other material from the park and Texas to this taxon, however, Hunt et al. (1998) have demonstrated that these fossils cannot be conclusively assigned to *Chindesaurus*. Given that the current state of basal dinosaur relationships is ambiguous at best, it is unclear whether *Chindesaurus* represents an herrerasaurid, as many characters used to assign it to this clade are actually dinosauriform plesiomorphies. Furthermore, even if *Chindesaurus* is an herrerasaurid, the position of the Herrerasauridae is controversial, and the clade may lie outside of the Theropoda (Langer, 2004) or the Dinosauria (Fraser et al., 2002).

A second *Chindesaurus* specimen (PEFO 33982) was collected in 2004 from the Giving Site (PFV 231). Unfortunately this material consists only of ilium fragments, a proximal femur, and several vertebral centra. Nevertheless, the proximal femur (Fig. 7A) is identical to the holotype femur in having a characteristic squared off and elongate head. This represents only the second documented confirmed occurrence of *Chindesaurus* from North America.

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1887

THEROPODA Marsh, 1881

COELOPHYSOIDEA Holtz, 1994

***Coelophysis* Cope, 1889**

***Coelophysis* sp.**

Unquestionably theropod material from PEFO is extremely rare, with only a single partial theropod skeleton (UCMP 129618) described by Padian (1986) and assigned to the genus *Coelophysis*. UCMP 129618 was collected from the Dinosaur Hill locality (PFV 40). This specimen is important because it represents the first relatively complete *Coelophysis* material collected outside of the Whitaker Quarry at Ghost Ranch, New Mexico, and opened discussion of the taxonomic validity of the genus *Coelophysis* (Padian, 1986). Besides UCMP 129618, Long and Murry (1995) do not list any other theropod material occurring from the park and all of the uncatalogued specimens from the park in the UCMP collections that are assigned to the Saurischia either are not dinosaurian or are too fragmentary to confirm (WGP and RBI pers. obs.). However, a distal femur (UCMP 126751) from the Flattops area of the park and assigned to *Chatterjeea elegans* by Long and Murry (1995) is referable to Dinosauria indet. While it is extremely difficult to differentiate between the distal femora of dinosaurs and chatterjeeids, in this specimen the fibular groove opens with an obtuse angle and the margin of the fibular condyle in this groove is strongly rounded (Fig. 7B). This is the condition found in dinosaurs (Fig. 7D) whereas in chatterjeeids the fibular groove opens at nearly a 90° angle and the margin of the fibular condyle is subangular (Fig. 7C).

Long and Murry (1995) assigned a proximal femur from the Battleship NW locality (PFV 169) to the ?Prosauropoda; the element is extremely weathered and according to Hunt et al. (1998) does not represent a dinosaur. Colbert (1989) referred caudal centra from the Agate Bridge N locality (PFV 161) to *Coelophysis*, however these elements are also not dinosaurian (Hunt et al., 1996).

Hunt et al. (1996) and Hunt and Wright (1999) documented numerous new dinosaur fossils from the park, however none of these have ever been formally described or illustrated. Furthermore, with the exception of a partial dentary (Hunt et al., 1996) the majority of these specimens consist of isolated vertebral centra. Unfortunately, isolated theropod vertebrae cannot be distinguished from those of chatterjeeids, so these records cannot be confirmed (S. Nesbitt, pers. comm., 2004). The most important specimen is a partial coelophysoid skeleton from the Jeremiah's Perch locality (PFV 278). This specimen was never completely excavated and has not been formally described (Hunt and Wright, 1999).

Collected material from the Giving Site (PFV 231) in 2004 includes the partial skeletons of three coelophysoids. These specimens have not yet been completely prepared, though preliminary research has shown them to be identical to UCMP 129618 (Figs. 7E-F). In addition, a small proximal femur (PEFO 33984: Figs. 7G-H) from the same locality and a proximal femur (PEFO 31187; Figs. 7I-J) from the Bowman Locality (PFV 89) possess a sloping posterior margin adjacent to the greater trochanter and therefore are probably referable to the Theropoda.

CONCLUSION

Since the revitalization of the paleontology program at PEFO in 2001, numerous new specimens and localities have been discovered. Probably the two most important new sites are the *Revueltosaurus* Quarry (PFV 297) and the Giving Site (PFV 231). To date, the Giving Site has produced the remains of bivalves, lungfish, indeterminate phytosaurs, small metoposaurs, the archosauromorph *Vancleavea*, the pseudosuchians *Typothorax* (includ-

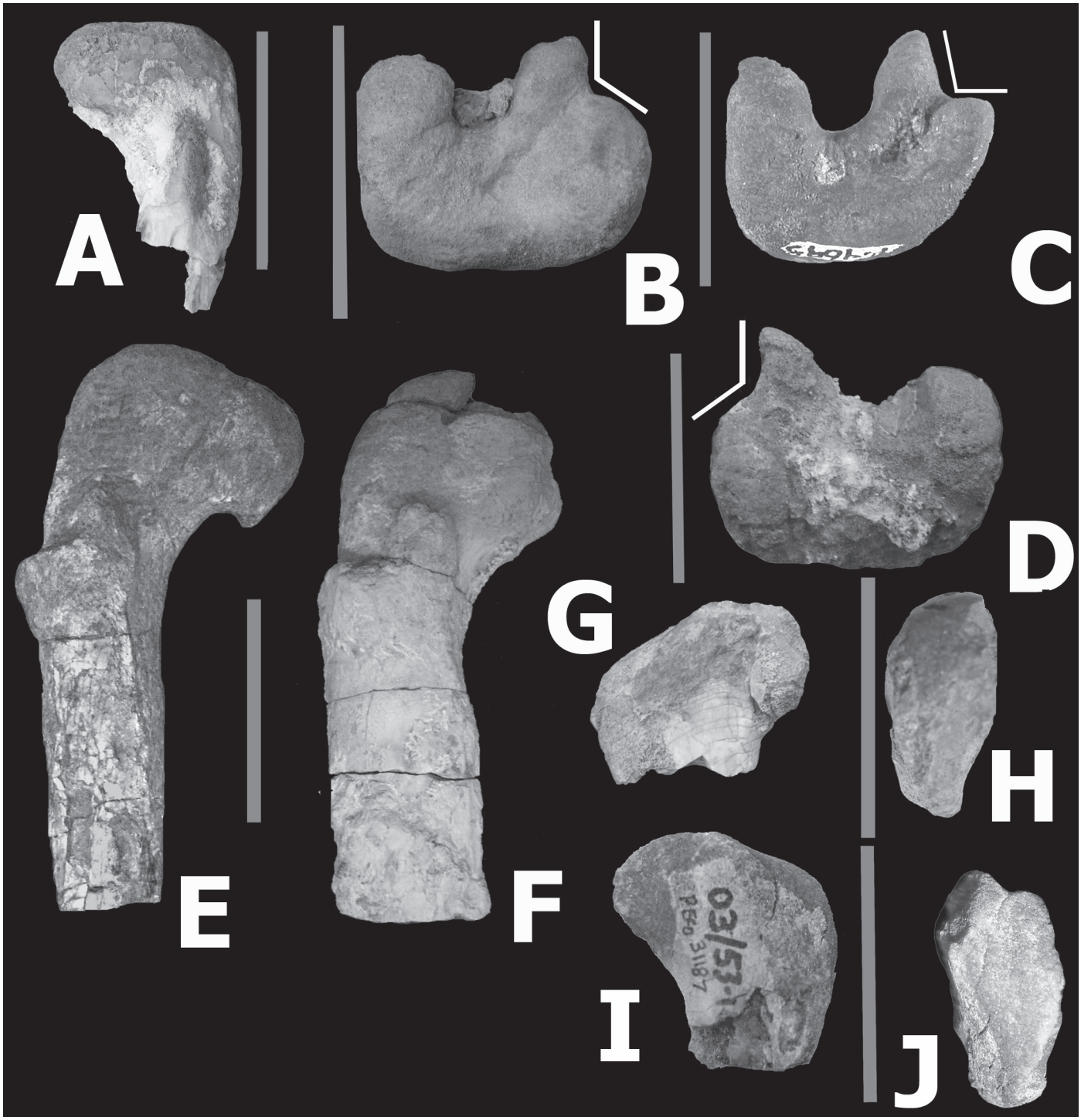

FIGURE 7. Dinosauriform (A) and dinosaur material (B, D-H) from the park. A, *Chindesaurus bryansmalli* proximal left femur (PEFO 33982) in anterior view; B, indeterminate dinosaur distal femur (UCMP 126751) in distal view; C, *Chatterjeea* sp. distal femur (NMMNH P-4695) from the Bull Canyon Formation in distal view; D, *Coelophysis* sp. distal femur from PFV 231 in distal view; E, *Coelophysis* sp. proximal femur (UCMP 129618) in anterior view; F, *Coelophysis* sp. proximal femur from PFV 231 in anterior view; G-H, theropod proximal femur (PEFO 33987) in G, anterior view and H, proximal view; I-J, theropod proximal femur (PEFO 31187) in I, posterior view and J, proximal view. Scale bars for (A-F) and (I-J) = 5 cm. Scale bar for (G-H) = 3 cm.

ing the first reasonably complete juvenile material), *Chatterjeea*, *Postosuchus*, and *Revueltosaurus*. In addition, the site has yielded no fewer than three coelophysoid partial skeletons and only the second documented occurrence of *Chindesaurus bryansmalli*. Furthermore, numerous vertebrae and limbs from indeterminate reptiles and archosaurs have been recovered. Finally, the site has provided the first instance in the park of plant compression fossils (leaves) being found in direct association with a vertebrate (*Typothorax* sacrum).

Other key specimens recovered in recent years from the park include two carapaces of *Stagonolepis*; numerous plates of a new aetosaur taxon; the first occurrence of "*Desmatosuchus*" *chamaensis* outside of New Mexico; two skulls of *Leptosuchus adamanensis*; one skull of *Pseudopalatus*, and a new species of *Trilophosaurus*.

Most importantly, the stratigraphic position of these specimens has been carefully documented allowing for the insertion of these localities into the newly proposed stratigraphic scheme for the park for the purposes of a detailed biostratigraphic analysis.

Biochronological Implications

Lucas and Hunt (1993) formally named four land-vertebrate faunachrons based on non-marine vertebrates for the Late Triassic of the western United States. These faunachrons predominately use phytosaurs and aetosaurs as index taxa. New discoveries of aetosaurs and phytosaurs in conjunction with detailed stratigraphic work are providing a robust vertebrate biochronology (Woody and Parker, 2004) for Chinle Formation strata in the vicinity of PEFO. This work, as well as research in western Texas (Lehman and Chatterjee, in press), suggests that taxa traditionally used to divide the Late Triassic of the southwest United States into faunachrons (e. g., *Stagonolepis* and *Typothorax*) overlap (Fig. 8).

Aetosaurs

The partial skeleton of *Stagonolepis* sp. mentioned previously from PFV 304 represents the highest occurrence of this taxon from the park, situated in the lower portion of the Jim Camp Wash beds. This locality is 10 m below the prominent silcrete marker bed that Woody (2003) noted occurs in numerous localities within the Jim Camp Wash beds, generally between 7-15 m above the Rainbow Forest bed (Fig. 9a). Thus, while the Rainbow Forest bed is not locally exposed at PFV 304, we would place it no more than 5 m below the quarry based upon this observation. In addition, PFV 304 is 15.8 m beneath a prominent sandstone horizon that represents an upper tongue of the Rainbow Forest bed. Another important locality in the Rainbow Forest area (PFV 89) occurs within and just above this bed and contains *Paratypothorax* and *Typothorax* (Fig. 9b).

Another high occurrence of *Stagonolepis* is from the Battleship NW locality (PFV 169) where a carapace of *S. wellesi* (PEFO 31217) was collected in 2002. This locality is within a sandy mudstone facies laterally equivalent to a prominent sandstone body that represents the Rainbow Forest Bed (Heckert and Lucas, 2002). This site occurs approximately 10 m beneath the silcrete marker bed, which caps a nearby butte (Fig. 9e).

The lowest occurrence of *Typothorax coccinarum* (PEFO 26694) is from the Rainbow Forest Bed at Blue Mesa (PFV 121, Fig. 9F). The second lowest occurrence is from site PFV 295, where *Typothorax coccinarum* co-occurs with the phytosaur *Pseudopalatus*. PFV 295 is located in the basal Jim Camp Wash beds within a few meters of the Rainbow Forest Bed, where it is exposed in Starving Man Wash (Figs. 9C-D),

The lowest occurrence of *Paratypothorax* is from the Rainbow Forest beds at PFV 169 (uncatalogued specimen) and PFV 178 (Long Logs: PEFO 31190). The highest occurrence is from Hell Wash (PFV 39), which is low in the Petrified Forest Member, below Painted Desert Sandstone #1 (Billingsley, 1985; Long and Murry, 1995). Long and Murry (1995) list an occurrence of *Paratypothorax* from the Black Forest (PFV 3), however this plate is badly weathered and indeterminate.

Phytosaurs

The highest occurrence of *Leptosuchus adamanensis* (PEFO 34034) is from the Rainbow Forest bed at PFV 169, where it co-occurs with the aetosaurs *Stagonolepis wellesi* and *Paratypothorax* sp. *Leptosuchus adamanensis* also occurs in a prominent sandstone in the Devil's Playground area of the park (PFV 99). This skull (PEFO 31218) occurs 8 m above the type locality of "*Machaeroprosopus lithodendrorum*" (=*Leptosuchus crosbiensis*). Although direct correlations have not been made between beds in the Devil's Playground and the southern half of PEFO, it has long been recognized that these beds are older than those directly to the north and east in the Painted Desert (Long and Murry, 1995). Heckert and Lucas

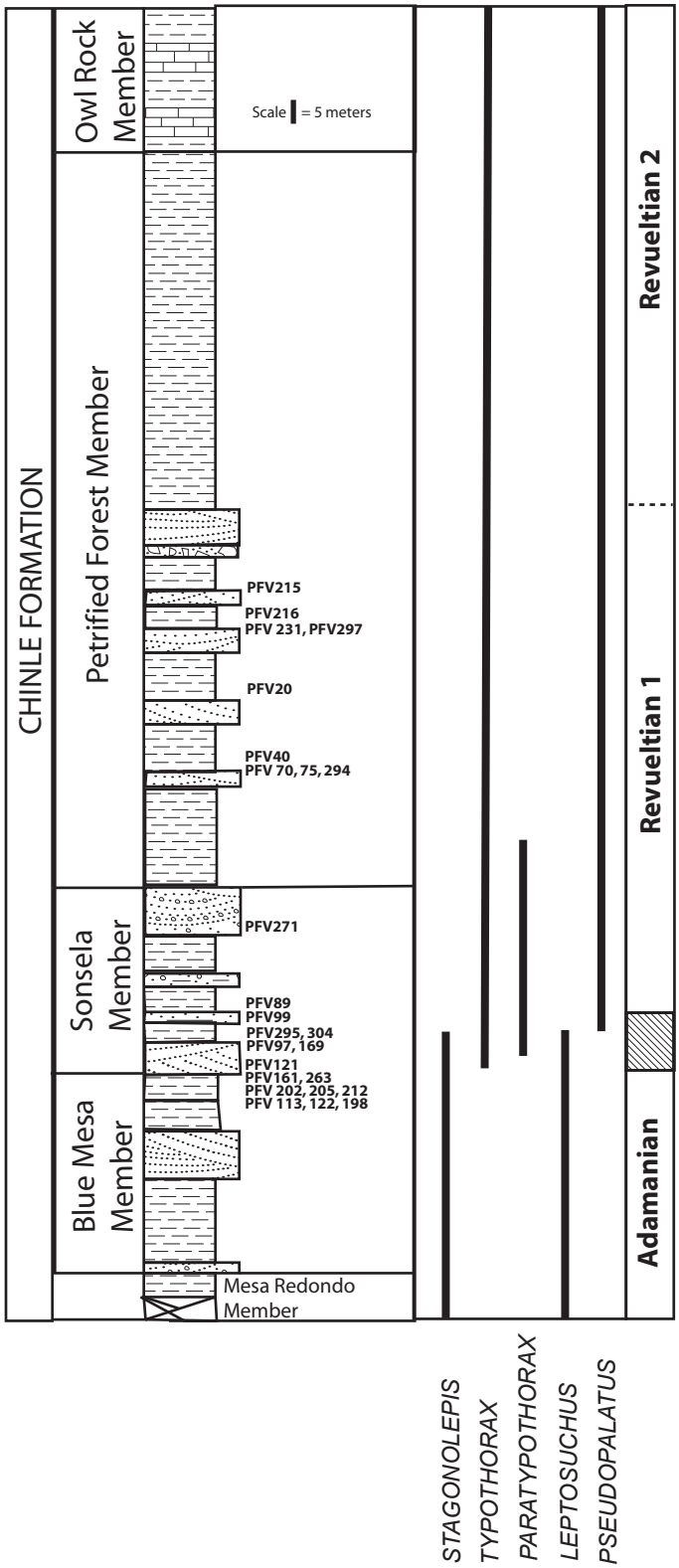

FIGURE 8. General stratigraphic column of PEFO showing position of localities discussed in to text as well as stratigraphic ranges for phytosaur and aetosaur index taxa. Cross-hatching depicts overlap between proposed faunachrons.

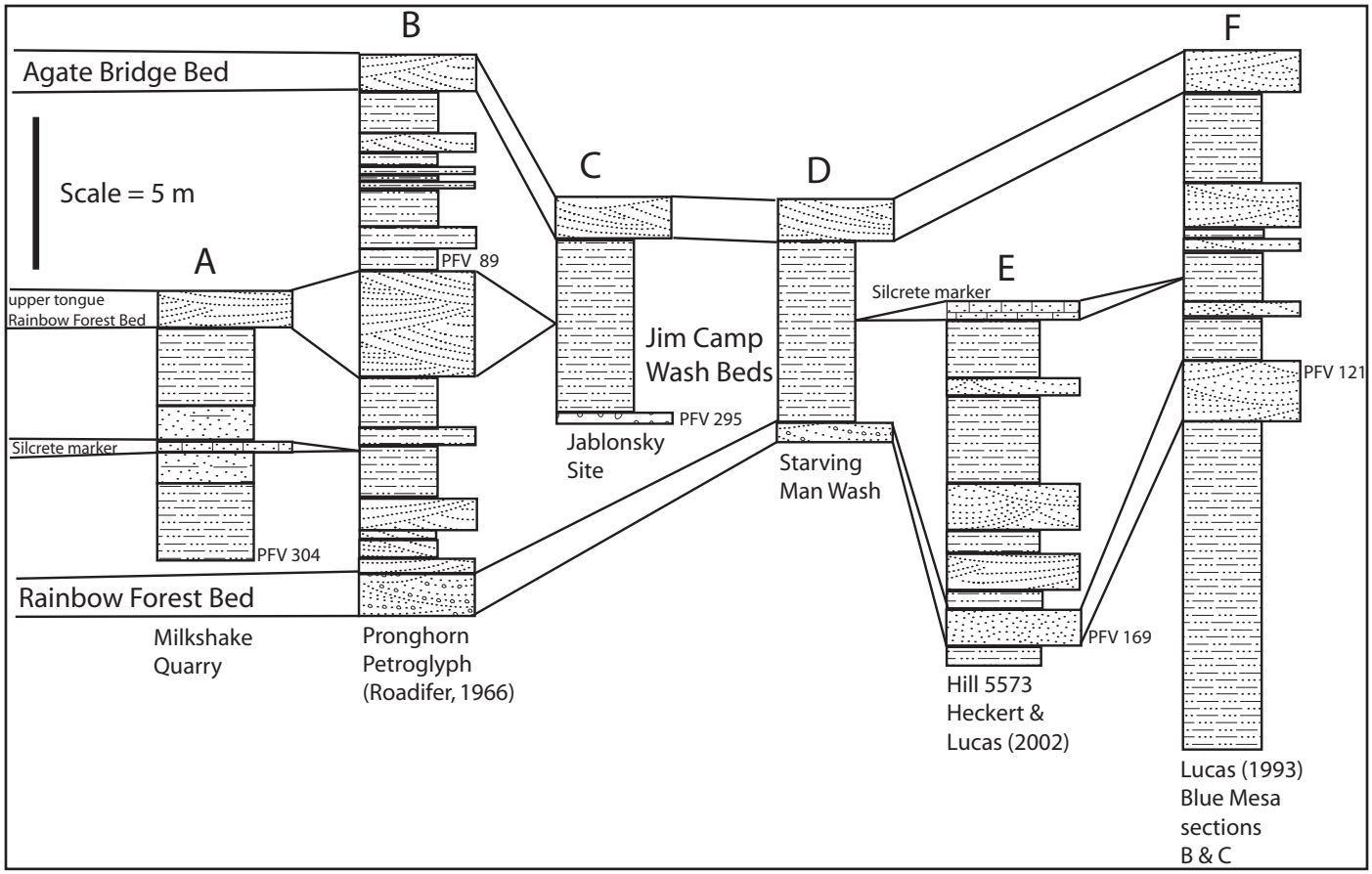

FIGURE 9. Correlation of stratigraphic columns from PEFO showing the positions of localities with fossils important to a local biochronology.

(2002) and Woody (2003) assigned these exposures to the Sonsela Member and the sandstone that contains PFV 99 is most likely equivalent to the Rainbow Forest bed.

The lowest occurrence of *Pseudopalatus* is PEFO 31207 from PFV 295, which is situated only a few meters above the Rainbow Forest bed. Therefore, although stratigraphic occurrences of the phytosaurs *Leptosuchus* and *Pseudopalatus* come within a few meters of each other they do not currently overlap (Fig. 8). This is also the case in Texas (Lehman and Chatterjee, in press).

The overlap of *Typothorax coccinarum* and *Stagonolepis* in the Sonsela Member warrants caution in using these taxa as index fossils for the Late Triassic. However, this overlap is slight (less than five m) and could be expected for a transitional fauna such as that represented within the Sonsela Member. Therefore, these taxa can still be used as a proxy for relative stratigraphic position, however final determination of age would require other lines of evidence (e. g., lithology, pollen, paleomagnetism).

Leptosuchus and *Pseudopalatus* still appear to be viable index taxa, however the use of phytosaurs as a whole has been drawn into question by Lehman and Chatterjee (in press) based on recent discoveries from Texas, which place *Parasuchus* (=*Paleorhinus*), *Pseudopalatus*, and *Redondasaurus* together in the same quarry at the base of the Bull Canyon Formation (Revueltian). Thus, a revision of the land-vertebrate faunachrons as initially conceived by Lucas and Hunt (1993) is necessitated.

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