AN INVENTORY OF MESOZOIC MAMMALS AND NON-MAMMALIAN THERAPSIDS IN NATIONAL PARK SERVICE AREAS

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Abstract—Body and trace fossils of Mesozoic mammals and non-mammalian therapsids have been documented in nine National Park Service areas, along with one probable occurrence and one case where fossils have been found immediately outside of a monument’s boundaries. To date, body fossils of Mesozoic mammals are documented from geologic formations in three NPS areas: the Aguja Formation (Upper Cretaceous) of Big Bend National Park; the John Henry Member of the Straight Cliffs Formation and the Wahweap Formation (Upper Cretaceous) of Bryce Canyon National Park; and the Morrison Formation (Upper Jurassic) of Dinosaur National Monument. A probable Mesozoic mammal bone has also been recovered from the Morrison Formation of Curecanti National Recreation Area. Bones of non-mammalian Mesozoic therapsids have only been reported from the Chinle Formation (Upper Triassic) of Petrified Forest National Park, although fossil remains have also been found just outside of the boundary of Navajo National Monument in the Navajo Sandstone (Lower Jurassic). Tracks generally attributed to tritylodonts or similar derived non-mammalian therapsids are known from Lower Jurassic formations of Capitol Reef National Park, Colorado National Monument, Dinosaur National Monument, Glen Canyon National Recreation Area, and Zion National Park. Burrows that may have been dug by non-mammalian or mammalian therapsids have been reported from Canyonlands National Park, Curecanti National Recreation Area, and Dinosaur National Monument.

INTRODUCTION

The Cenozoic history of mammals has long overshadowed the Mesozoic history of mammals and their relatives. There are several factors implicated in this: 1) most Mesozoic mammals were small and left behind small, fragile fossils that are easily overlooked and require a dedicated effort to collect, almost always via microvertebrate screen-washing techniques; 2) most Mesozoic mammals can broadly be described as rodent-like in their overall appearance, and perhaps because of this commonplace appearance have not captured the imagination of the public; and 3) other Mesozoic vertebrates, particularly dinosaurs, are more popular and require different collecting logistics. However, disregarding Mesozoic mammals leaves out more than half of mammalian history. Depending on whether one favors a crown group Mammalia or broader Mammalia incorporating all forms with the mammalian dentary-temporal jaw joint, anywhere from 100 to 160 million years of the mammal record occurred during the Mesozoic, compared to 66 million years and counting for the Cenozoic. Either definition, of course, also omits the various non-mammalian therapsids that coexisted with the mammal line into the Jurassic. From the North American perspective, perhaps the most notable of these non-mammalian Mesozoic therapsids are the dicynodonts, large herbivores represented in Triassic rocks of the southwestern United States, and tritylodonts, late-surviving non-mammalian cynodonts represented by skeletons and probably tracks and burrows from Lower Jurassic rocks of the same region. By the end of the Jurassic, the clearly non-mammalian therapsids were extinct in North America, but anatomical mammals had diversified into several groups of generally rodent-sized herbivores, insectivores, and omnivores. Most of these groups disappeared before the end of the Cretaceous, leaving Late Cretaceous mammalian faunas dominated by multituberculates and various metatherian (marsupial) and eutherian (placental) mammals. In North America, significant mammalian faunas have been known from Upper Jurassic and Upper Cretaceous rocks since the 19th century. Mammals from between about 145 and 85 Ma (a gap comparable in length to the entire Cenozoic) have only been described since 1980.

The record of Mesozoic mammals and their relatives found on National Park Service (NPS) lands mirrors that of North America at large: limited, but with areas of high diversity and significant fossils. Body fossils of mammals have been recovered from three or four NPS units, all documented since 1984: Big Bend National Park (BBIE), Bryce Canyon National Park (BRC), Dinosaur National Monument (DINO), and probably Curecanti National Recreation Area (CURE) (Fig. 1). DINO and probably CURE have Morrison Formation fossils from the Late Jurassic, BRC has fossils from the Straight Cliffs and Wahweap formations of the middle and Late Cretaceous, and BBIE has fossils from the Aguja Formation of the Late Cretaceous. In addition to the various Late Jurassic and Cretaceous sites with true mammals, there are a number of NPS units with trace or body fossils that pertain to non-mammalian therapsids or could belong to mammals or non-mammalian therapsids. Because these fossils are also an important part of the story of mammal evolution, they are included here. Most examples are trace fossils from the Early Jurassic, such as Brasilichnium probably produced by tritylodonts, but there is one example of more distantly related Late Triassic forms. Units with fossils that fall under these categories include Canyonlands National Park (CANY), Capitol Reef National Park (CARE), Colorado National Monument (COLM), Curecanti National Recreation Area (GLCA), Petrified Forest National Park (PEFO), and Zion National Park (ZION), with an additional record just outside the boundary of Navajo National Monument.
BODY FOSSILS OF MESOZOIC MAMMALS
Big Bend National Park (BIBE)

Vertebrate fossils from Upper Cretaceous rocks of the Big Bend region have been of interest as a point of comparison to the famous fossils of Alberta and the northern United States. Aside from the difference in latitude, the Cretaceous Big Bend had a slower rate of sedimentation because it was farther from uplifts that supplied sediment (Lehman, 1991). The Big Bend area has produced mammal fossils from the Upper Cretaceous (upper Campanian to possibly lower Maastrichtian) Agua Formation. The best-known locality is Oklahoma Sam Noble Museum of Natural History (OMNH) VP58/Texas Memorial Museum (TMM) 43057, which is the source of the Terlingua local fauna. This locality is 8 km north-northeast of Study Butte, just west of BIBE boundaries. The mammals from this productive microsite have been described in detail by Rowe et al. (1992), Weil (1992), and Cifelli (1994). Within BIBE, mammals have been found in the Talley Mountain area, in the south-central part of the park (Sankey, 1998, 2008; Sankey and Gose, 2001). Five microsites have been found here in 20 m of the Agua Formation section. Like the Terlingua local fauna, these sites are in the lower part of the upper shale member, with a Late Campanian age (Sankey, 2008). The two sites differ in setting: the Terlingua site is estuarine, while the Talley Mountain sites are from fluvial channels in a marshy floodplain (Sankey and Gose, 2001). The Talley Mountain sites have produced wood and thousands of fossils of chondrichthyans, osteichthyans, amphibians, turtles, lizards, crocodilians, dinosaurs, birds, and mammals. Mammals are represented by 44 specimens. Sankey (2008) noted several mammal taxa, including the multituberculates *Cimolomys* sp., *Mesodma* sp., cf. *Cimexomys*, and cf. *Paracimexomys*, the marsupial *Alphodon* cf. *A. halleyi*, indeterminate multituberculates and marsupials, and other unidentified mammals (Fig. 2).

References to mammals in the Javelina Formation or Member within BIBE are sometimes encountered in the literature (Standhardt, 1986, 1995; Schiebout et al., 1987). The sites involved are Paleocene in age (Standhardt, 1986, 1995; Schiebout et al., 1987; Kielan-Jaworowska et al., 2004; Lofgren et al., 2004), and the terminology derives from an alternative conception of Big Bend stratigraphy (compare Schiebout et al. [1987] to Turner et al. [2011]). Under the framework of the most recent mapping (Turner et al., 2011), they would be included in the Paleocene portion of the Black Peaks Formation instead. Localities in question include the Dogie, Tom’s Top, and Glenn Eleven sites (Standhardt, 1986; Lofgren et al., 2004). Because they are Paleocene, they will not be considered further here.

**Bryce Canyon National Park (BRCA)**

Microvertebrate sites in BRCA were first identified in 1989, in the Wahweap Formation of the Hat Shop area (Eaton [2013], which attributed the sites to the John Henry Member of the Straight Cliffs Formation; revised stratigraphy after J.G. Eaton, personal commun. 2014). The true abundance of microvertebrate fossils in BRCA was not realized until 2003, when collectors led by Jeffrey Eaton (Weber State University) began blind-washing material from promising mudstone horizons and discovered multiple microvertebrate localities (Eaton, 2005). This encouraged further work, and from 2006 to 2010 more than 100 fossil localities were found in BRCA (Eaton, 2013). Two Upper Cretaceous stratigraphic units in the park are known to have yielded mammal fossils: the John Henry Member of the Straight Cliffs Formation (upper Coniacian through Santonian) and the Wahweap Formation (middle Campanian to upper Campanian) (Eaton et al., 2013). The stratigraphy of BRCA has been subject to revision, and the early localities originally assigned to the John Henry Member, including Museum of Northern Arizona (MNA) 1186, 1187, and 1188, are now placed in the Wahweap Formation (J.G. Eaton, personal commun. 2014). The first report of Mesozoic mammals in BRCA appears to have been a marsupial tooth recovered with other microvertebrate fossils during test screening of material (Eaton, 1994), from a site in the Wahweap Formation of the Hat Shop now known as MNA 1187 (J.G. Eaton, personal commun. 2014).

The mammalian fauna of the John Henry Member is of particular interest because of its age: late Coniacian and Santonian terrestrial vertebrates are poorly represented in North America. Particularly important among these localities is Natural History Museum of Utah (UMNH; formerly Utah Museum of Natural History) VP locality 424, the richest Santonian microsite known from North America. Sites in the John Henry Member in BRCA have yielded dental fossils from an assemblage including triconodonts (indeterminate and cf. *Aliciconodon* sp.), multituberculates (*Cedarmomy* sp. cf. *C. hutchisonii*, *Cimolodon similis*, *Cimolodon sp.* cf. *C. similis*, *Cimolodon sp.* cf. *C. foxi*, cf.*Cimolodon sp.*, *Cimolomys* sp. A and B, cf. *Cimolomys* sp. A and B, *Dakotamys* sp., *Dakotamys shalespeari*, *Mesodma* sp. cf. *M. minor*, *Mesodma* sp., and cf. *Mesodma* sp.), spalacotheres (*Spalacotherium* sp. and *Symmetrodontoides* sp.), and marsupials (indeterminate “didelphomorph”, *didelphid*, and *pediomysid* sp. cf. *Iugomortiferum*, and cf. *Vulparaphodon* sp.) (Fig. 3). UMNH VP locality 1156, near Shakespear Point, has produced the holotype molar of multitubulate *Dakotamys shalespeari* (BRCA 3020/UMNH VP 19160; Eaton, 2013) (Fig. 3B).

The first microvertebrate locality from BRCA to be described in print was UMNH VP loc. 77, a Wahweap Formation locality within Campbell Canyon (Munk, 1998). It has produced fossils of multituberculates (*Cedarmomy* sp. cf. *C. hutchisonii*, *Cimolodon* sp., *Mesodma* cf. *M. formosa*, and cf. *Mesodma* sp.) and marsupials (an indeterminate pediomysid, cf. *Alphodon* sp., and cf. *Vulparaphodon* sp. cf. *V. creber* (Eaton et al., 1998; Eaton, 2013), as well as chondrichthyans (*Kirklandia* sp. cf. 1993; osteichthyans (Eaton et al., 1998), anurans (Roček et al., 2010), salamanders, chelonians, lizards, crocodilians, and dinosaurs (Eaton et al., 1998). This site was also briefly discussed in Eaton (1999). Other BRCA sites in the Wahweap Formation have yielded additional multituberculates (*Cimolodon* sp. cf. *C. foxi*, *Cimolomys* sp., cf. *Cimolomys* sp., *Meniscoceous* sp., *Mesodma* sp. cf. *M. archibaldi* minor, and cf. *Paracimexomys* sp.) and marsupials (indeterminate “didelphomorphs”, cf. *Aptostodon* sp., *Lepidosternum* sp., and cf. *Vulparaphodon* sp.) (Eaton, 2013).

**Curecanti National Recreation Area (CURE)**

The Brushy Basin Member of the Morrison Formation at CURE has yielded a probable mammal bone and large burrows that may be mammalian in origin. The bone, probably a limb bone, was found during field work by Anthony Fiorillo and Fred Olson in 1995 at Dino Cove (Koch et al., 2006). Large vertebrate burrows have been found just west of Dinosaur Beach (Koch et al., 2006), which Odier (2006)
from cranial Spalacotheridium and isolated teeth of the multituberculate holotype (Fig. 4). Engelmann (2004) described a palate (DINO 14989) in the literature. Engelmann and Callison (1998) described the triconodont cf. A. exiguus, LM2, D, UMNH VP 17294 (lingual view), symmetrodont ?Spalacotheridium sp., LM4; and E, UMNH VP 17294 (occlusal stereopair), symmetrodont ?Spalacotheridium sp., LM4?. Photos provided by J. Eaton (Weber State University) and arranged by JST. Each scale bar is 1 mm.

attribution to mammals.

Dinosaur National Monument (DINO)

Body fossils of Mesozoic mammals are known from the Morrison Formation at Rainbow Park. Microvertebrates have been recovered from two horizons, separated by about 5 m (Chure and Engelmann, 1989). The two horizons are designated DNM 94 and 96 (Turner and Peterson, 1999; Foster, 2003), with DNM 96 being the higher of the two (Turner and Peterson, 1999). They both are within the upper Brushy Basin Member (Engelmann and Callison, 1998). These sites have yielded an assemblage of freshwater snails, possible hybodont shark spines, teeth and scales of actinopterygians (Chure and Engelmann, 1989), salamanders, frogs, chelonians, sphenodontians, lizards, snakes, crocodylomorphs, several dinosaur genera, and several mammal genera (Foster, 2003). Mammals reported from DINO include multituberculates Ctenacodon laticeps, C. serratus, C. n. sp., Glirodon grandis, and Psalodon n. sp. (Gregson et al., 2010), triconodonts Priacodon (Foster, 2003), Triconolestes curvicuspis, and an unidentified form (Gregson et al., 2010), an unidentified spalacotheriid symmetrodont (Gregson et al., 2010), the dryolestoids Amblytherium gracilis, A. debilis, Araeodon intermissus, Dryolestes priscus, Euthalasus cordiformis, and Herpetarius arcautos (Gregson et al., 2010), and indeterminate mammals (Foster, 2003). Foster (2003) also included the docodont Docodon, but this has not been confirmed and now appears unlikely (Foster et al., 2006).

Several specimens have been discussed at greater length in the literature. Engelmann and Callison (1998) described the triconodont Triconolestes curvicuspis from DNM 96, based on DINO 10780, a molar fragment. Engelmann and Callison (1999) described the “plagiaulacoid” multituberculate Glirodon grandis from cranial material discovered at Rainbow Park and the Fruita Paleontological Area just outside of COLM, with partial skull DINO 10822 as the holotype (Fig. 4). Engelmann (2004) described a palate (DINO 14989) and isolated teeth of the multituberculate Ctenacodon.

**FIGURE 4. Ventral view of a cast of the type skull (DINO 10822) of Glirodon grandis, from Rainbow Park in DINO. Photo provided by D. Chure (NPS–DINO).**

The dicynodont therapsid Placerias has long been reported from the Chinle Formation of PEFO and the Petrified Forest in general. Fossils of Placerias were among the specimens discovered by Annie Alexander and Louis Kellogg of the University of California Museum of Paleontology (UCMP) in 1921, drawing the interest of Charles Camp (Welles, 1972). A few Placerias specimens from PEFO are in the collections of the UCMP (Fig. 5). This genus is reported from the Blue Mesa Member in the park (Long and Murry, 1995; Lucas and Heckert, 2002; Heckert et al., 2005; Irmis, 2005a; Lucas et al., 2007).

**TRACE FOSSILS OF NON-MAMMALIAN THERAPSIDS**

The Glen Canyon Group and correlatives span the uppermost Triassic and Lower Jurassic in the Colorado Plateau region. These formations are not historically noted for preserving abundant vertebrate body fossils, but they do preserve abundant vertebrate tracks. A handful of ichnogenera are represented in each formation. One of these, Brasiliichnium, is regarded as the tracks of a small therapsid (Lockley et al., 2004; Irmis, 2005b; Hunt and Lucas, 2007). This ichnogenus has been reported from at least four of the six formations that either make up the Glen Canyon Group or are equivalents: the Wingate Sandstone of the uppermost Triassic and lowest Jurassic on the east side of the plateau (Lucas et al., 2005, 2006a); the Navajo Sandstone at the top of the Glen Canyon Group (Irmis, 2005b); the roughly coeval Aztec Sandstone west of the plateau (Hunt and Lucas, 2007); and the Nugget Sandstone (or Glen Canyon Sandstone) on the north side of the plateau (Engelmann et al., 2010), roughly equivalent to the entire Glen Canyon Group (Sprinkel et al., 2011). However, use

**FIGURE 5. A portion of a Placerias dentary (UCMP 27095) from the “Dying Grounds” locality (UCMP 7038; PEFO 122) in PEFO. Scale bar is 5 cm. Photo taken by D. Strauss (UCMP).**

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of the ichnogenus may be improper for the Wingate Sandstone; true *Brasilichnium* is distinguished by the small relative size of the manus prints, which are not relatively as small in Wingate “*Brasilichnium*” (Lockley, 2011). *Brasilichnium*-like tracks are present in the other two formations: the marginal lacustrine facies of the lower Whitmore Point Member of the Moenave Formation (roughly coeval with the Wingate Sandstone on the west side of the plateau) (Milner and Spears, 2007), and the Kayenta Formation between the Moenave/Wingate interval and the Navajo Sandstone (Smith and Santucci, 2001). The diversity and systematics of tracks described as *Brasilichnium* have yet to be fully described (Lockley et al., 2004), so unexpected surprises may be lurking. Burrows in the Moenave Formation (Tanner and Lucas, 2009), Navajo Sandstone (Lucas et al., 2006b; Riese et al., 2011) and Nugget Sandstone (Engelmann and Chure, 2008; Engelmann et al., 2014) have also been attributed to therapsids. Body fossils of Glen Canyon Group therapsids are represented by a fairly diverse fauna from the Kayenta Formation (Lucas et al., 2005 for a review) and an indeterminate tritylodont from the Navajo Sandstone (Irmis, 2005b). Several NPS units have examples of therapsid trace fossils from these rock units.

**Canyonlands National Park (CANY)**

The therapsid ichnofossils of CANY consist of vertebrate burrow complexes from wet interdune eolian deposits in the lower Navajo Sandstone, found in and around the park (Hasiotis et al., 2007). The burrows are described as branched and interconnected elliptical tunnels and chambers covering areas of 5 x 7 m to 10 x 15 m. Most of the burrows are close to horizontal and have smooth walls. The networks are often found in groups. Hasiotis et al. (2007) interpreted the networks as having been excavated by therapsids, possibly with social habits.

**Capitol Reef National Park (CARE)**

Santucci et al. (1998) noted in passing that tritylodont tracks had been reported from the Kayenta Formation of CARE.

**Colorado National Monument (COLM)**

Lucas et al. (2006a) reported therapsid tracks from the Wingate Sandstone of COLM. These tracks were found on fallen blocks of the sandstone in Ute Canyon, and probably came from the basal quarter of the formation. One example is shown in Figure 4C of Lucas et al. (2006a).

**Dinosaur National Monument (DINO)**

DINO has both tracks and potential therapsid burrows in the Nugget Sandstone. *Brasilichnium* tracks (Fig. 6) are abundant on five horizons near the top of the formation at one site. More than 300 tracks were found on one surface (Engelmann et al., 2010). Good (2013) noted the association of *Brasilichnium* tracks with arachnid tracks at this site. Poorly preserved possible therapsid burrows were reported by Engelmann et al. (2014) from a site near Cub Creek in the monument (DMN 488). Engelmann et al. (2014) interpreted the burrows as having been excavated by therapsids or scorpions. Good (2013) also found a similar burrow at Orchid Draw.

**Glen Canyon National Recreation Area (GLCA)**

*Brasilichnium* has been reported from the Navajo Sandstone of Slick Rock Canyon (Lockley et al., 1998; Santucci et al., 1998), Iceberg Canyon, and the vicinity of the confluence of the Colorado and San Juan rivers (Lockley et al., 2014), and from the lower Navajo Sandstone near the mouth of Escalante Canyon, where unusually deep examples have been found (Lockley et al., 2014; Kayenta–Navajo transition zone of their usage). *Brasilichnium* appears to be very abundant locally in the recreation area (A. R. C. Milner, personal commun. 2014). Additional unpublished tracks have been observed at several locations, including one site with hundreds of tracks (Fig. 7.; VLS, personal obs.). Tracks have also been found associated with examples of the theropod dinosaur track *Grallator* and a beetle trackway (A. R. C. Milner, personal commun. 2014).

**Zion National Park (ZION)**

Smith and Santucci (2001) reported a locality in the Kayenta Formation with a footprint similar to *Brasilichnium*.

**OTHER REPORTS**

**Navajo National Monument (NAVA)**

The indeterminate Navajo Sandstone tritylodont skeleton was discovered just outside of one of NAVA’s units. The specimen, SMU 70527, was recovered by Southern Methodist University workers from the vicinity of Eggshell Arch, about 2.4 km east of NAVA’s Inscription House Ruin unit (Winkler et al., 1991). Winkler et al. (1991) postulated that the specimen was related to the Kayenta Formation tritylodont *Kayentatherium*, but Sues et al. (1994) and Irmis (2005b) regarded it as indeterminate.

**CONCLUSIONS**

The record of Mesozoic mammals and their close relatives in NPS administered areas is limited at this time, but includes productive microsites and notable ichnofossils. Among them are specimens of mammals from BRCA that lived between the well-known Late Jurassic and Late Cretaceous faunas, tracks of possibly gregarious near-mammals at DINO, and several sites with burrows. It is likely that additional exploration will yield more of both body fossils and ichnofossils, and increased interest in both microvertebrate fossils and traces can only help. Many NPS units include exposures of the same formations discussed here, and the Mesozoic rocks of the NPS areas...
that are already known to yield vertebrate or trace fossils of mammals and their relatives have hardly been exhausted. Further finds will add to our knowledge of what is still a poorly known portion of mammal evolution and history.

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