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DIMINUTIVE METOPOSAURID SKULLS FROM THE UPPER TRIASSIC BLUE HILLS (ADAMANIAN:LATEST CARNIAN) OF ARIZONA

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Abstract—We describe two tiny metoposaurid specimens from the lower part of the Chinle Group in the Blue Hills of east-central Arizona. The more complete of these specimens is an incomplete skull anterior to the orbits (45 mm preorbital length) and numerous skull roof and palate fragments. The less complete specimen is a 25-mm-long skull roof fragment surrounding the left orbit. Based on the sutural relationships of the skull bones anterior to the orbit, we identify the more complete specimen as a juvenile of *Buettneria perfecta* Case, 1922 and tentatively identify the less complete specimen as *Apachesaurus gregorii* Hunt, 1993. These fossils are particularly important because they indicate that cranial sutures do not change significantly during metoposaurid ontogeny.

Keywords: juvenile, metoposaur, ontogeny, Petrified Forest, Adamanian

INTRODUCTION

The Blue Hills in east-central Arizona have long been known as a classic Upper Triassic tetrapod collecting area (Fig. 1). C.L. Camp of the University of California Museum of Paleontology (UCMP) first collected there in the 1920s. Subsequently, other UCMP parties, the Smithsonian Institution, and the Museum of Northern Arizona (MNA) worked in the Blue Hills. Recently, we have begun to collect from this area for the New Mexico Museum of Natural History (NMMNH) (Heckert et al., 1999). Here, we briefly summarize the stratigraphy of the Blue Hills before describing two tiny metoposaurid specimens from this area. The more complete of these (MNA V8415) was found at MNA locality 1393 by one of us (SEK) and was very briefly described by Morales (1993). The second specimen was "discovered" by one of us (ABH) in the UCMP collections of uncataloged material collected by Camp in 1926.

Abbreviations: MNA = Museum of Northern Arizona, Flagstaff; NMMNH = New Mexico Museum of Natural History and Science, Albuquerque; UCMP = University of California Museum of Paleontology, Berkeley.

STRATIGRAPHY AND AGE

The Upper Triassic stratigraphy of the Blue Hills is remarkably straightforward. Two formations of the Chinle Group are present, the Bluewater Creek Formation overlain by the Petrified Forest Formation (Fig. 1). The Petrified Forest Formation is subdivided into a lower Blue Mesa Member, medial Sonsela Member, and upper Painted Desert Member. The vast majority of vertebrate fossils collected in the Blue Hills were found in low badlands developed primarily in bentonitic mudstones of the uppermost Bluewater Creek Formation and the Blue Mesa Member (Lucas et al., 1997; Fig. 1). Both fossils we describe here were collected in this stratigraphic interval.

The more complete specimen, MNA V8415, was collected from MNA locality 1393 low in the Blue Mesa Member of the Petrified Forest Formation. This locality occurs on a south-facing slope above a west-facing wash. The fossiliferous horizon is within a purple mudstone covered with a dense surface concentration of calcrete (siderite) nodules. Larger bones on the surface include indeterminate reptilian vertebrae, fragments of aetosaur scutes, and skull fragments of large metoposaurs. In 1998 we returned to the site and recollected it as NMMNH locality 4127, gathering a small fauna of indeterminate osteichthyans, metoposaurs, phytosaurs, and other archosauromorphs.

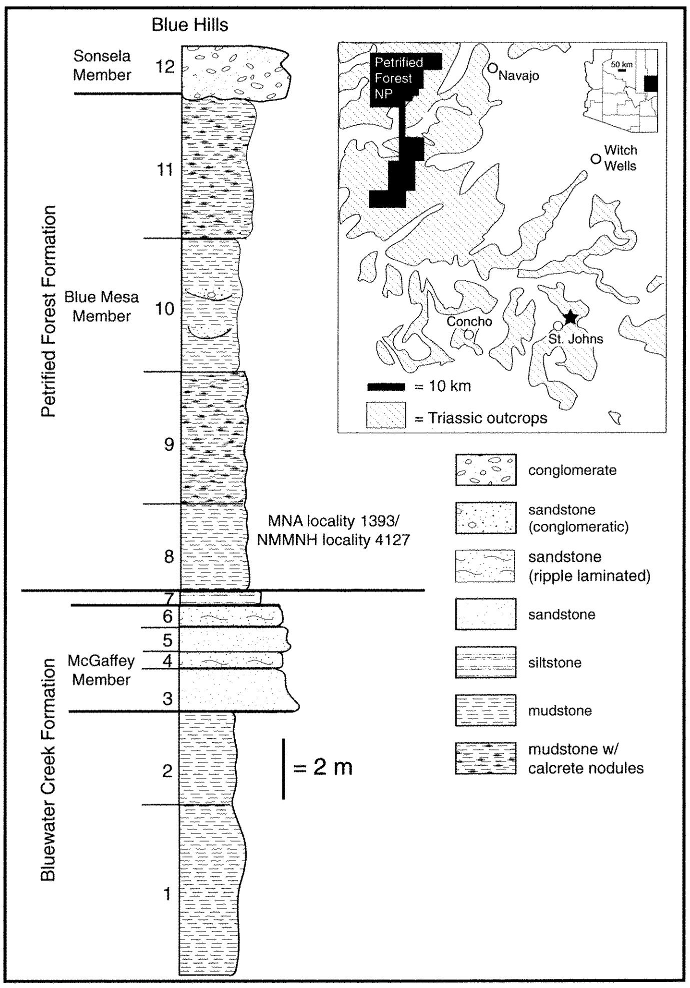

FIGURE 1. Stratigraphic section, generalized geologic map, and index map showing the geographic and stratigraphic location of the Blue Hills localities discussed here (star on the geologic map).

The provenance of the less complete specimen, UCMP V7308/175145, is more problematic. The UCMP has only a few localities to designate all of Camp's collecting areas in the Blue Hills. Camp (1930) and Camp and Welles (1956) noted that numerous Blue Hills microvertebrate fossils occurred in peculiar deposits that they termed "meal pots." Rob Long of the UCMP showed one of us (SGL) several of these localities in 1989. Based on subsequent fieldwork in the area, we have determined that most of these localities are stratigraphically low in the Blue Mesa Member (Fig. 1). It appears likely that UCMP V7308/175145 thus is from a similar horizon to locality MNA 1393/NMMNH 4127. We doubt that the specimens are from the exact same locality because their preservation is strikingly different.

There is little doubt about the age of the upper Bluewater Creek Formation and the Blue Mesa Member of the Petrified Forest Formation in the Blue Hills. Vertebrate fossils from the Blue Hills, including the holotype of *Rutiodon* (=*Machaeroprosopus*) *zunii* (Camp, 1930) and the aetosaur *Stagonolepis wellesi* (Long and Ballew, 1985), indicate an Adamanian (latest Carnian) age (Lucas et al., 1997). Indeed, the fauna of the Blue Hills closely resembles the type Adamanian fauna, found in the Blue Mesa Member of the Petrified Forest National Park, 75 km to the west-northwest (Heckert and Lucas, 1997; Lucas et al., 1997). Lucas (1998) considered *Rutiodon* and *Stagonolepis* index taxa of the Adamanian land-vertebrate faunachron, of latest Carnian (Tuvalian) age. It is worth noting that the large metoposaurid amphibian *Buettneria perfecta* Case, 1922 is common in strata of Adamanian age, whereas the smaller metoposaurid *Apachesaurus* is exceedingly rare in these strata (Hunt, 1993; Hunt and Lucas, 1993).

DESCRIPTION

MNA V8415 is an incomplete, small (45 mm preorbital length) metoposaurid skull. Three fragments combine to create an almost complete and relatively well preserved representation of the skull anterior to the orbits (Fig. 2). What is absent or damaged on one side can be mirrored, producing an accurate picture of this portion of the skull (Fig. 3).

The largest of the three anterior skull fragments is complete from the medial suture laterally to the right lateral margin of the skull roof (Figs. 2B-C, 3B). It contains a complete right premaxilla and right nasal. The right maxilla is elongate, forming the lateral margin, but has been fractured transversely, so the postorbital portion is missing. The fracture continues from the right maxilla into the central portion of the right nasal. The right naris, formed by the premaxilla, nasal, and maxilla, is undamaged. Its dorsal aperture is larger than the ventral. The anterior portions of the right frontal, prefrontal, and lachrymal are intact anterior to the orbit, and the orbital margin is evident on the posterolateral portion of the prefrontal and the medioposterior portion of the lachrymal. Preservation of the most anterior margin of the right orbit is fortuitous as it allows generic-level identification. Based on the preserved anterior margin, the orbit is at least 10 mm wide (Fig. 2B). The lateral line crosses the lachrymal. Left of the medial suture, the medial portion of the left premaxilla and nasal are intact.

The left half of the anterior portion of the skull of MNA V8415 suffered more damage (Fig. 2A,D). It is broken into two pieces, and a small area posterior to the left naris is missing. The larger of the two elements constitutes the left margin of the dorsal surface, and a more extensive palatal area. It is composed of the posterolateral portion of the left premaxilla, which is damaged medially, and the anterior portion of the left lachrymal. This element has been reconstructed on the anterior maxilla and suffered some minor fracturing posteriorly. The lateroposterior margin of the left premaxilla is present, preserving the lateral margin of the left naris.

The smaller fragment from the left half of the anterior portion of the skull is isolated from the other two pieces. It is bordered by the medial suture, left lachrymal and maxilla. This piece contains the posterior portion of the left nasal, a small posteromedial piece of the left maxilla, and the anterior sections of the left frontal and prefrontal. The left frontal, prefrontal, lachrymal, and maxilla are damaged by a transverse fracture immediately anterior to the left orbit, so that the orbital margin is not preserved on this side.

Some palatal structure is preserved on the ventral surface of all three elements (Fig. 2C-D). The largest element contains 11 peg-like marginal teeth on the right premaxilla. They are antero-posteriorly compacted and buccal-lingually elongate. Thirty small, conical marginal teeth follow along the right maxilla. The right vomer is undamaged, the anterior portion of the parasphenoid is present, and most of the right palataline is intact, lacking only the portion sutured to the pterygoid. These bones preserve the anterior quarter of the right palatal vacuity. Seven peg-like teeth traverse the right vomer. The row ends laterally with one large fang, and a depression of similar size located anterior to the fang. A line of 13 small, circular vomerine teeth extends posteriorly behind the fang. Posterior to the vomer-palatal suture of the palatine lies an antero-posterior row of four small oval teeth crowded into a transverse row along the anterior margin of the right palatal vacuity. These are followed by a row of several small conical teeth oriented medially along the lateral margin of the right palatal vacuity in the palatine, which ends posteriorly with one larger tooth. The right element is damaged in a transverse plane through the anterior quarter of the palatal vacuity across the parasphenoid and palatine, and the posterior portion is absent.

The left ventral surface is less fragmentary than its dorsal counterpart. The incomplete left premaxilla contains five of the compressed marginal teeth. Twenty-two small conical marginal teeth of the maxilla follow these. The medial portion of the left vomer is sutured to the right vomer and contains five transverse, peg-like teeth complementary to the seven found on the right vomer. These also end laterally, after bridging a missing section of the row, on the left fragment of the skull, with a large fang and a similarly-sized portion of unprepared matrix. The medial and lateral portions of the left vomer are intact, as is the anterior section of the left palatal. Nine small circular teeth are found in a row oriented medially on the left vomer, complementary to the 13 present on the right vomer. Only the anteriormost margin of the left palatal vacuity is intact, and all bones extending or existing posterior to this plane are missing as a result of this fracture.

There exist four other fragmentary skull roof margins with intact edges of unknown anatomical position. Ten bone fragments of the palate have been recognized but currently remain unidentified as to particular elements represented. There are also two lower jaw fragments, one of which preserves two tooth sockets. Nineteen other unidentified sculptured elements are present with the specimen, some of which are most likely skull or interclavicle fragments. Several of these are illustrated in Figure 2.

All sculptured elements exhibit detailed preservation of the ornamentation. The pitting is mostly small circular indentations, showing little elongation. Some minor lengthening of the sculpture can be seen on the anterior portion of both the left and right maxilla, which may correlate with the elongated nature of this bone relative to others preserved in the skull. Elongation of the sculpturing is also exhibited in the posterior portion of the nasals. Overall, most of the pitting is subcircular and is not as elongate as that typically seen in larger metoposaur skulls (e.g., Hunt, 1993, figs. 6,11).

Overall the skull anterior to the orbital margin is nearly complete. The small portions of damaged bone can be mirrored from their undamaged counterparts. The preservation is satisfactory enough to have preserved sutures, lateral line canals, and sculpturing patterns that can be used in species identification and ontogenetic studies.

A second diminutive metoposaur specimen, UCMP

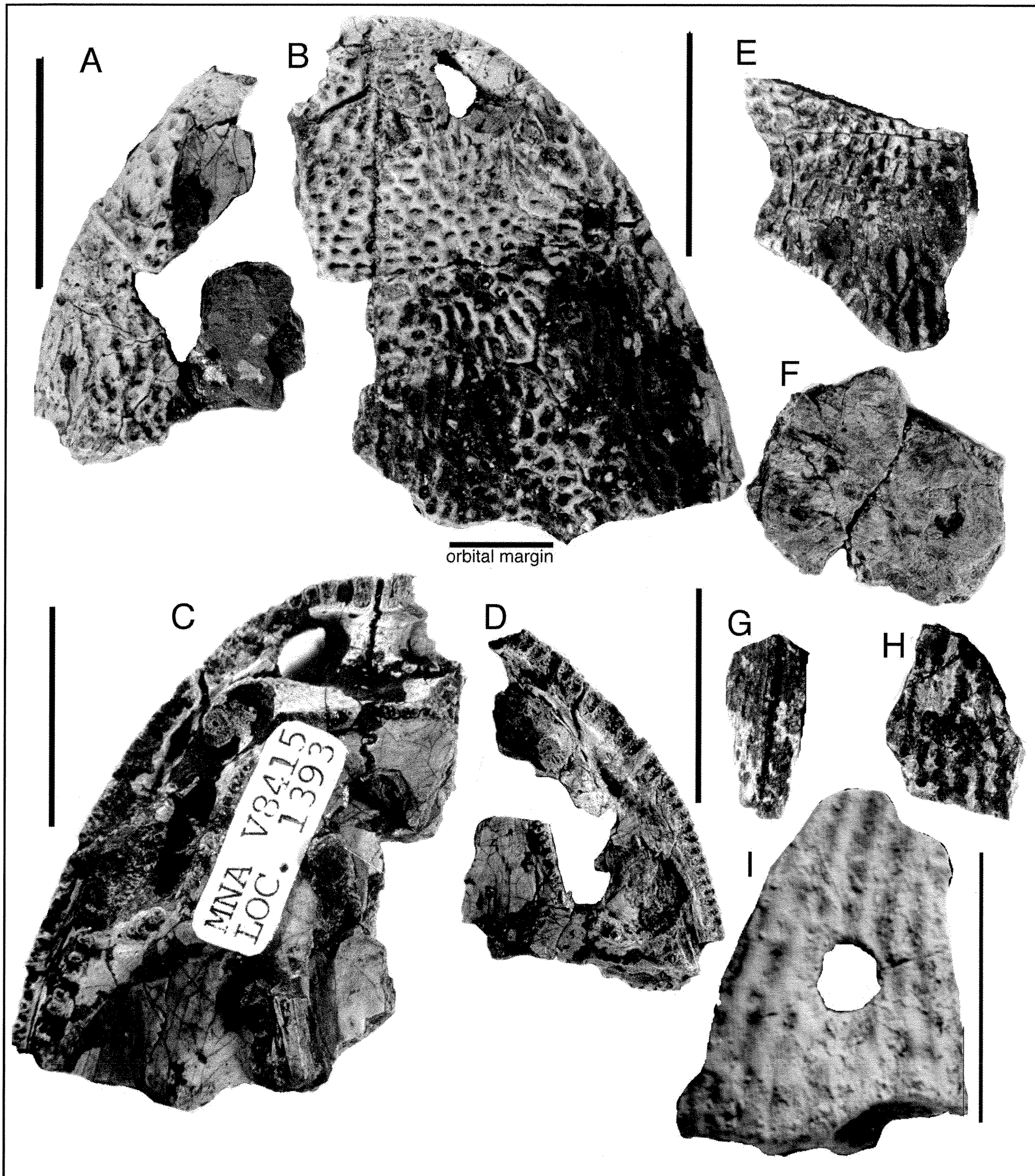

FIGURE 2. Photographs of MNA V8415 (A-H), juvenile of *Buettneria*, and UCMP 175145 (I), adult of *Apachesaurus*. **A**, **D**, Left anterior skull margin in **A**, dorsal and **D**, ventral views; **B**, **C**, Right anterior skull fragment in **B**, dorsal and **C**, ventral views. **E-H**, Miscellaneous skull roof (E,G,H) and palatal (F) skull fragments, in dorsal (E,G,H) and ventral (F) views; **I,** UCMP 175145, left skull roof fragment including left orbit in dorsal view. All scale bars = 2 cm.

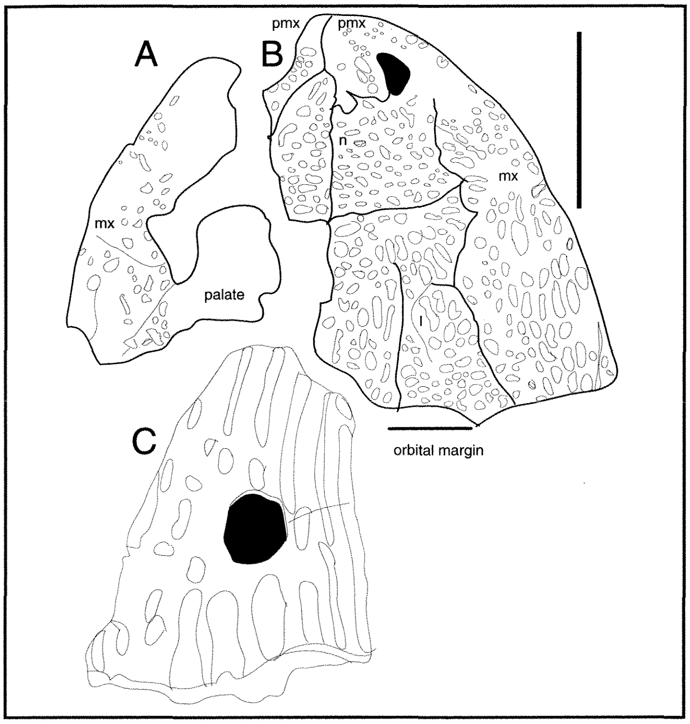

FIGURE 3. Drawings of MNA V8415 (A-B) and UCMP 175145 (C). **A**, Left anterior skull margin in dorsal view; **B**, right anterior skull fragment in dorsal view; **C**, left orbit? in dorsal view. l = lachrymal, mx = maxilla, n = nasal, pmx = premaxilla.

V175145, was discovered by one of us (ABH) in the UCMP collections as part of the abundant material collected by Camp from UCMP locality 7308 in the Blue Hills in the 1920s. This specimen consists of a single fragment approximately 25 mm long and 20 mm wide surrounding the left orbit (Fig. 2I). The orbit is situated near the center of the fragment and is 5 mm long and 4 mm wide. There are no obvious sutures visible in dorsal view, and the ventral surface is largely unprepared, although it clearly does not contain teeth. The ornamentation of the dorsal skull surface consists of long ridges and grooves that are subparallel to the long axis of the skull. The preservation of this specimen is considerably different than that of MNA V8415, so it was probably derived from a different locality.

DISCUSSION

We cannot justify placing these fossils in a new taxon due to their small size or skull proportions. Incorporation of the character states observed here into previous phylogenetic analyses (Davidow-Henry, 1989; Hunt, 1989, 1993) suggests that the more complete of these specimens represents a juvenile of *Buettneria*, and the less complete skull represents a specimen of *Apachesaurus*. The identification of MNA V8415 is based on the observation that the lachrymal enters the orbit and is excluded from the nares. *Buettneria* is the only metoposaurid with a lachrymal composing part of the orbital margin (Hunt, 1993). The small size of UCMP 175145, combined with the lack of any evidence that the lachrymal enters the orbit, supports assignment of this specimen to *Apachesaurus*. The remaining character states are indeterminate due to the lack of pectoral, vertebral, or posterior skull remains.

There has been considerable argument over the nature of small metoposaurid remains. Studies of temnospondyl ontogeny (Davidow-Henry, 1989; Schoch, 1995), variation (e.g., Colbert and Imbrie, 1956; Getmanov, 1987), and phylogeny (e.g., Kathe, 1999; Schoch, 1999; Yates and Warren, 2000) indicate that: (1) metoposaurids possess relatively small, anteriorly placed orbits as adults; (2) labyrinthodont orbits, like those of many vertebrates, are relatively large early in ontogeny; and (3) there is great plasticity in the development of the temnospondyl skull. MNA V8415 has a relatively large orbit and subcircular pitting of the skull roof, characteristics of juvenile metoposaurs. UCMP V175145, while smaller in absolute terms, has a much smaller orbit (relatively), based on the preserved anterior margin of MNA V8415 (Fig. 2A), and possesses considerably more elongated sculpturing on the skull roof, presumably as a function of growth.

The position of the orbits, pineal foramen, and skull bone proportions are all subject to change as a result of growth (Davidow-Henry, 1989; Schoch, 1995; Kathe, 1999). Although it does not pertain to these specimens, tabular horn development and otic notch depth may also be affected by ontogeny. Studies of capitosaurid growth indicate that the orbits and the pineal foramen migrate posteriorly with growth, whereas the depth of the otic notch remains constant relative to size (Davidow-Henry, 1989). Davidow-Henry (1989) also noted that elongation of dorsal pitting may indicate where the most rapid growth occurred.

The characteristics of orbit and pineal foramen position are of no use for classifying these anterior skull fragments. MNA V8415, however, lacks the sculptural elongation usually found on metoposaurids. This could be taken to indicate a lack of rapid growth in this specimen, further supporting our hypothesis that this is a juvenile individual. Conversely, the elongate ridges and grooves of UCMP 175145 could be taken to represent more typical adult metoposaur morphology, thus indicating that *Apachesaurus* is indeed a valid genus and not based on ontogenetic variation of one of the larger metoposaurs.

CONCLUSIONS

There is little that can be said about the juvenile characteristics of metoposaurids, largely because of a fragmentary fossil record. Until we know more about the stages of metoposaurid development it is most parsimonious to classify small specimens based on adult morphology. This makes the logical assumption that their size is ontogenetically representative unless some definitive characteristics that hint at an independent origin are found.

The ontogeny of metoposaurids demands further examination. Compiling the specimens believed to represent juveniles in an effort to characterize growth stages in metoposaurs is a desperately needed endeavor. Thus, while we are confident that MNA V8415 represents a juvenile of *Buettneria* and that UCMP 175145 represents a sub-adult or older *Apachesaurus*, we recognize that further study and attempts to collect the exceedingly rare small metoposaurs could overturn these identifications. Our identification is based on the assumption that key sutural relationships of the metoposaurid skull do not change over ontogeny. We suggest that, while much overall plasticity exists in the metoposaurid skull with growth, this is not reflected in the sutural relationships used to define the metoposaurid taxa *Buettneria* and *Apachesaurus*.

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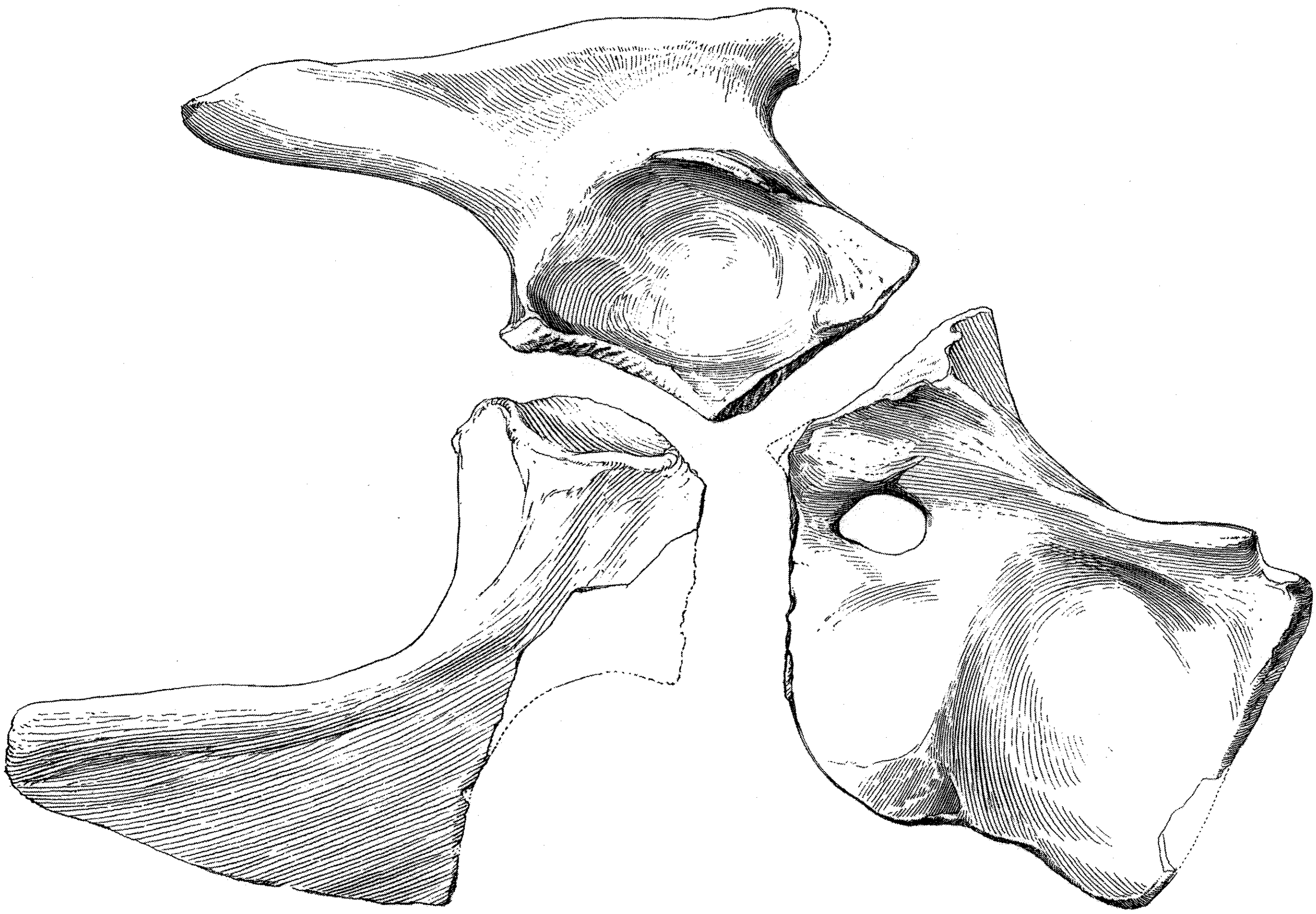
APPENDIX—DESCRIPTION OF MEASURED SECTION

Blue Hills

Measured section begins at UTM 12654220E, 3821725N and ends at 12654148E, 3822025N in the SW1/4 SE1/4 sec. 24, T13N, R28E. Strata considered to be flat-lying. Section measured 7 October 1994 by S. G. Lucas and A. B. Heckert.

unit	lithology	thickness (m)
Chinle Group:		
Petrified Forest Formation:		
SonselaMember:		
12	Sandstone; bluish white (5B9/1) to white (N9) fresh, weathers moderate orange (10R7/4); fine- to medium-grained, moderately well-sorted, slightly micaceous sublitharenite; ripple laminated; some clay pellet conglomerates; well-indurated; slightly calcareous; forms a bench.	1.3+
unconformity (Tr-4 unconformity)		
Blue Mesa Member:		
11	Mudstone; same colors and lithologies as unit 9.	4.8
10	Mudstone and sandstone; mudstone is grayish purple (5P4/2); not calcareous; some yellowish gray (5Y8/1), very poorly sorted conglomeratic sandstones; sandstones are fine-grained to conglomeratic, with numerous rip-ups of blue and purple mudstone lithologies; litharenite composed primarily of mudstone chips; not calcareous; mudstone and sandstone alternate in bands approximately 0.5-m-thick. Approximate horizon of NMMNH L-4127/MNA 1393.	4.6
9	Mudstone; grayish blue (5PB4/2), bentonitic; some yellowish gray (5Y8/1) to olive gray (5Y4/1) calcrete and siderite nodules up to 5 cm long; mudstone is not calcareous; nodules are very calcareous.	4.5
8	Mudstone; yellowish gray (5Y7/2) to medium bluish gray (5B5/1); bentonitic; slightly silty; calcareous; NMMNH L-3379 (SGL 94-105) at base; some lenticular ripple laminated sandstones in basal 0.5 m.	3.3
	Thickness of Blue Mesa Member:	17.2 m
Bluewater Creek Formation:		
upper member:		
7	Mudstone and siltstone; pale red (10R6/2) with yellowish gray (5Y7/2) mottles; mottles are calcareous.	0.7
McGaffey Member:		
6	Sandstone; same colors and lithology as unit 4.	0.3
5	Sandstone; same colors and lithology as unit 3.	1.0
4	Sandstone; grayish red (10R4/2) to medium gray (N5); very fine- to fine-grained, well-sorted, micaceous litharenite; well-indurated; ripple laminated; weakly calcareous; forms a bench; *Neocalamites* horizon.	0.7
3	Sandstone; pale red (10R6/2) to yellowish gray (5Y7/2); fine- to medium-grained, subrounded, well-sorted litharenite; very micaceous; calcareous.	2.4
	Thickness of McGaffey Member:	4.4 m
lower member:		
2	Mudstone; pale reddish brown (10R5/4); bentonitic; not calcareous.	2.3
1	Mudstone; pale blue (5PB7/2) to grayish blue (5PB5/2); bentonitic.	6.0+
	Thickness of incomplete Bluewater Creek Formation:	13.4 m



Pelvis of *M. adamanensis* (type), x1/2. Right side, lateral view (from Camp, 1930, fig. 16, p. 79, reproduced at 70% original size).