

MANDIBLES OF JUVENILE PHYTOSAURS (ARCHOSAURIA: CRURROTARSI) FROM THE UPPER TRIASSIC CHINLE GROUP OF TEXAS AND NEW MEXICO, USA

ANDREW B. HECKERT¹, HILLARY S. JENKINS², SPENCER G. LUCAS³ AND ADRIAN P. HUNT³

¹ Department of Geology, Appalachian State University, ASU Box 32067, Boone, NC 28608-2067 USA, email: heckertab@appstate.edu;

² Department of Earth & Planetary Sciences, Harvard University, 20 Oxford Street, Cambridge, MA, 02138 USA;

³ New Mexico Museum of Natural History & Science, 1801 Mountain Road NW, Albuquerque, NM 87104, USA

Abstract—Here we describe five specimens of juvenile phytosaurs from several localities in the Upper Triassic Chinle Group of Texas and New Mexico. These include three specimens from localities in the Tecovas Formation (Texas) of Adamanian age and one each from the Revueltian-age Bull Canyon Formation and Apachean-age Travesser Formation of New Mexico. Although all of the specimens are incompletely preserved mandibles, they are unquestionably phytosaurian based on their elongate mandibles with an extensive symphyseal region that is of essentially constant height and has at least some contribution from the splenial. We use the length (in mm) per preserved tooth socket as a proxy for ontogenetic stage, ranking the specimens from very young (~4-6 mm/socket) to juvenile (~9 mm/socket). There are distinct differences in tooth spacing, contribution of the splenial to the symphysis, angle of tooth eruption, and other features that vary in these specimens independent of age. This suggests that taxonomic information is available from the mandible pending further description and characterization of adult specimens of known taxa.

INTRODUCTION

Phytosaurs are an extinct clade of Upper Triassic archosaurs known from most modern continents (Westphal, 1976). They are among the most commonly found and collected fossils in Upper Triassic strata in the American Southwest (e.g., Long and Murry, 1995). As is typical in vertebrates, the skull is the most taxonomically and phylogenetically diagnostic element, to the extent that existing taxonomic schemes and phylogenetic hypotheses make no reference to the lower jaw, let alone additional postcrania (e.g., Ballew, 1989; Hungerbühler and Hunt, 2000; Hungerbühler, 2002; Stocker, 2010, 2012). There are now modern hypotheses explaining some of the variation in phytosaur skulls in terms of sexual dimorphism (Zeigler et al., 2003a,b), as has been proposed in the past (Camp, 1930, among others). However, there has been little discussion of ontogenetic variation, largely due to a relative dearth of specimens, but even obviously subadult to juvenile skulls have been assigned to distinctive genera (e.g., “*Arganarhinus*” Long and Murry, 1995—rebutted by Fara and Hungerbühler, 2000). Demonstrably juvenile phytosaur specimens in the literature are extremely rare, with cranial material other than “*Arganarhinus*” reported by Dzik and Sulej (2007) from the Krasiejów locality in Poland, Zeigler et al. (2003b) from the Snyder quarry and by Rinehart et al. (2009) from the Ghost Ranch *Coelophys* (Whitaker) quarry, the latter two both in north-central New Mexico. Heckert et al. (2001) and Spielmann and Lucas (2012, figs. 32-33) reported the very tip of a juvenile snout in addition to a subadult (and very large adult) skull of *Redondasaurus* from the Redonda Formation in Apache Canyon in eastern New Mexico. Postcranial remains of juvenile phytosaurs were described by Zeigler et al. (2003c), again from the Snyder quarry, and by Renesto (2008) from the Argillite di Riva di Solto Shale in Italy. Irmis (2007) examined the pattern of vertebral fusion of phytosaurs using numerous specimens from Upper Triassic strata in the American West, although he was only able to document a few specimens with definitively juvenile characteristics, associated with skulls.

Abbreviations: NMMNH, New Mexico Museum of Natural History and Science, Albuquerque; UMMP, University of Michigan Museum of Paleontology, Ann Arbor.

PROVENANCE

The specimens described herein come from localities in Crosby and Potter counties, Texas, and Quay and Union counties, New Mexico

(Fig. 1). Crews working with E.C. Case of the UMMP collected the Crosby County specimens (UMMP V9607 and 11753) from the Tecovas Formation in the 1920s (Murry, 1989; Long and Murry, 1995). Case’s crews moved north and worked the area around Sierrita de la Cruz creek later in the 1920s and into the 1930s, when they collected UMMP 13534, also from the Tecovas Formation near the Oldham-Potter county line. The NMMNH specimen is from Quay County and was collected as part of Hunt’s (1994) dissertation work and was previously mentioned by Hunt (2001). The Union County NMMNH specimen was collected as part of other projects in that region (e.g., Lucas et al., 1987) and is described in detail for the first time here.

Of the two Crosby County specimens, UMMP V9607 has no other information recorded with it, but UMMP 11753 comes from west of Walker’s Tank, a known Case locality (Murry, 1989; Long and Murry, 1995). Nearly all of Case’s Crosby County localities are in the Tecovas Formation (Murry, 1989; Long and Murry, 1995), although larger vertebrate fossils occur locally in the underlying conglomerates of the Camp Springs Formation (pers. obs.). The Tecovas Formation in Crosby County yields a diverse fauna that includes Adamanian index fossils such as the aetosaurs *Stagonolepis* (= *Calyptosuchus*) *wellesi*, *Desmatosuchus haplocerus*, and *Tecovasuchus chatterjeei* (Murry, 1989; Long and Murry, 1995; Martz and Small, 2006), so the UMMP specimens we describe here are clearly of Adamanian age (Lucas et al., 2007; Lucas, 2010). The localities in the vicinity of Rotten Hill, including Case’s “Sweetly Cruize” sites such as the one yielding UMMP 13534 are also developed in the Tecovas Formation (Murry, 1989; Lucas et al., 2001), and yield a typical Adamanian fauna, including the holotype of *Stagonolepis* (= *Calyptosuchus*) *wellesi* and *Desmatosuchus haplocerus* (Murry, 1989; Long and Murry, 1995; Lucas et al., 2001).

The Quay County specimen, NMMNH P-4192, is from NMMNH locality 76 in the badlands of the Bull Canyon Formation developed around Barranca Creek (Fig. 1). These strata are homotaxial with the strata that yielded the type assemblage of the Revueltian land-vertebrate faunachron in the adjoining Revuelto Creek badlands (Lucas and Hunt, 1993; Lucas, 1998; Lucas et al., 2007). Although P-4192 is the only specimen from locality 76, other Bull Canyon Formation localities in the area yield numerous fossils of Revueltian index fossils such as the phytosaur *Pseudopalatus* and the aetosaurs *Typhothorax coccinarum* and *Aetosaurus arcuatus*, all index taxa of the Revueltian (Lucas and Hunt, 1993; Heckert and Lucas, 1998; Hunt, 2001; Lucas et al., 2007; Heckert

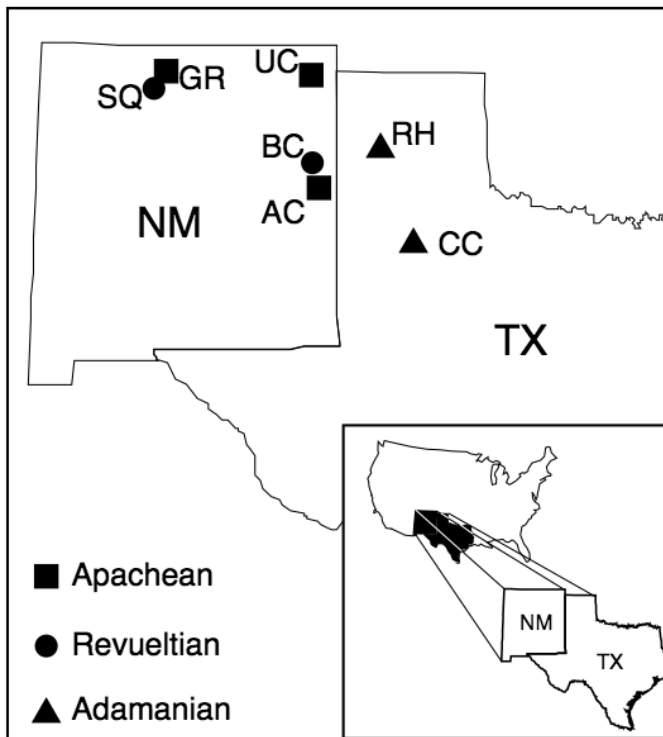


FIGURE 1. Geographic distribution of localities described in the text, with biochronology according to Lucas et al. (2007). AC, Apache Canyon, Quay County (Redonda Fm); CC, Crosby County (Tecovas Fm); GR, Ghost Ranch (Rock Point Fm); NM, New Mexico; RC, Revuelto Creek, Quay County (Bull Canyon Fm); RH, Rotten Hill (Tecovas Fm); TX, Texas; UC, Union County (Travesser Fm).

et al., 2010; Lucas, 2010). This specimen was listed, but not described, in Hunt (2001).

The Union County specimen, NMMNH P-7139, is from NMMNH locality 557 in the Travesser Formation of northeastern New Mexico (Fig. 1). Associated fossils include two phytosaur teeth (NMMNH P-17724) and two fragments of phytosaur osteoderms (P-17721), none of which are diagnostic to lower taxonomic levels. The Travesser Formation in Union County yields a sparse tetrapod fauna, the most important fossil being a phytosaur skull reported by Stovall and Savage (1939) and assigned to *Redondasaurus* by Hunt and Lucas (1993), an assignment disputed by some (e.g., Long and Murry, 1995) but upheld by Spielmann and Lucas (2012) in their recent revision of the genus. Lucas et al. (1987) demonstrated that the *Redondasaurus* skull described by Stovall and Savage (1939) was actually collected in the Travesser Formation, not, as Stovall and Savage (1939) originally proposed, the Sloan Canyon Formation. Based on this *Redondasaurus* occurrence, the Travesser Formation is considered Apachean in age, so this is the geologically youngest specimen we describe here.

DESCRIPTION

Here, we provide detailed descriptions of the juvenile phytosaur fossils from Texas and New Mexico. These include all three specimens from the Adamanian-age Tecovas Formation of Texas: UMMP V9607 (Fig. 2), UMMP 13534 (Fig. 3A-C), and UMMP 11753 (Fig. 3D-F) as well as the Revueltian-age Quay County specimen (NMMNH P-4182—Fig. 4A-D) from the Bull Canyon Formation and the Apachean-age Travesser Formation specimen from Union County, NMMNH P-7139 (Fig. 4E-H). Some measurements and other observations (detailed in the “Discussion” section) are provided in Table 1.

Adamanian Specimens from the Tecovas Formation of West Texas

UMMP V9607: The first specimen we describe, UMMP V9607 (Fig. 2), consists of four fragments. The largest fragment comprises the anterior portion of the lower jaw but lacks the rostral tip (Fig. 2A-C). The fragment is 122.3 mm long, ovoid in cross-section, and narrows slightly toward the anterior end of the jaw. The ventral surface is flat in lateral view (Fig. 2C), which is the primary reason we consider this is a dentary fragment and not part of the premaxillae. The left side of the jaw preserves 12 tooth sockets. These sockets are remarkably similar in size and relatively evenly spaced, although on the left side there is some indication that the sockets are paired, with each socket of the pair slightly closer to the other than either is to sockets anterior and posterior to the pair. Sockets 4 and 6 contain incomplete teeth (counting from the first preserved socket). The right side of the jaw preserves 14 tooth sockets with incomplete teeth in sockets 10, 12, and 14. Sockets 5 and 6 are conjoined (Fig. 2A-B). There is a single row of nutrient foramina parallel to the tooth margin on each side. Sutures of the specimen were clearly unfused; there is a gap between the two elements ventrally, although this may be an artifact of preservation.

The second fragment of UMMP V9607 consists of the right splenial along the medial symphysis (Fig. 2F-I). This fragment is 80.7 mm long and 22.2 mm tall. The specimen is curved, with the anterior portion of the fragment forming part of the medial symphysis (Fig. 2H) and the posterior portion deflected laterally (Fig. 2G). The ventral side of the specimen is highly textured with small ridges radiating outward from the center (Fig. 2I). The lateral edge (as preserved) is deeply grooved, creating a trough-like region along the edge of the specimen. Faint tooth socket grooves are visible along the lateral edge as well (Fig. 2G). There are remnants of 10 of these sockets. Clearly, much of the bone was unossified (cartilaginous), but we interpret the lateral texture as the incipient sutural surface for the dentary. Interestingly, the tooth sockets on this fragment are much more closely spaced than in the conjoined dentary fragment.

Two anterior lower jaw fragments (the third and fourth fragments of UMMP V9607) are also present. These are parts of the left (Fig. 2E) and right (Fig. 2D) dentaries of the anteriormost region of the lower jaw. The left dentary tip contains two tooth sockets and widens slightly anteriorly. It is 7.3 mm long and 11.8 mm tall. A groove along the anterior face of the specimen suggests the presence of an additional tooth socket. The lateral surface of the specimen possesses small, scattered foramina as well. The right dentary fragment is 15.7 mm long and 15.0 mm tall. As in the left dentary, the specimen widens toward the anterior portion of the jaw. It preserves two tooth sockets. The larger, anterior socket possesses an incomplete tooth, exposed along the anterior (mesial) side. This tooth is 18.5 mm tall as preserved. Tooth enamel is visible on the tooth and appears to end 10.0 mm up from its base. The tooth curves slightly along the length of the socket.

UMMP 13534: A second specimen from the Tecovas Formation, UMMP 13534, consists of the anterior portion of the lower jaw of a juvenile phytosaur (Fig. 3A-C), and is the single most complete specimen described here. Portions of both the right and left side of the jaw are present. The jaw fragment is somewhat deformed but possesses clear suture lines running down the midline. The left side of the jaw is offset from the right and therefore lies higher along the suture line. The total length of the specimen is 297 mm. The left side of the jaw preserves 35 evenly spaced tooth sockets. Sockets 21, 23, and 30 reveal small, unerupted teeth. The right side of the jaw preserves 33 tooth sockets, also evenly spaced along the fragment. Tooth socket 29 possesses an unerupted tooth as well. The tooth sockets range in size from 2.9 to 6.2 mm in diameter. The largest tooth sockets are near the posterior end of the jaw, however three pairs of large sockets are located on the anteriormost portion of the jaw. This anterior portion of the jaw is bulbous and slightly enlarged to accommodate these larger teeth. There is a slight

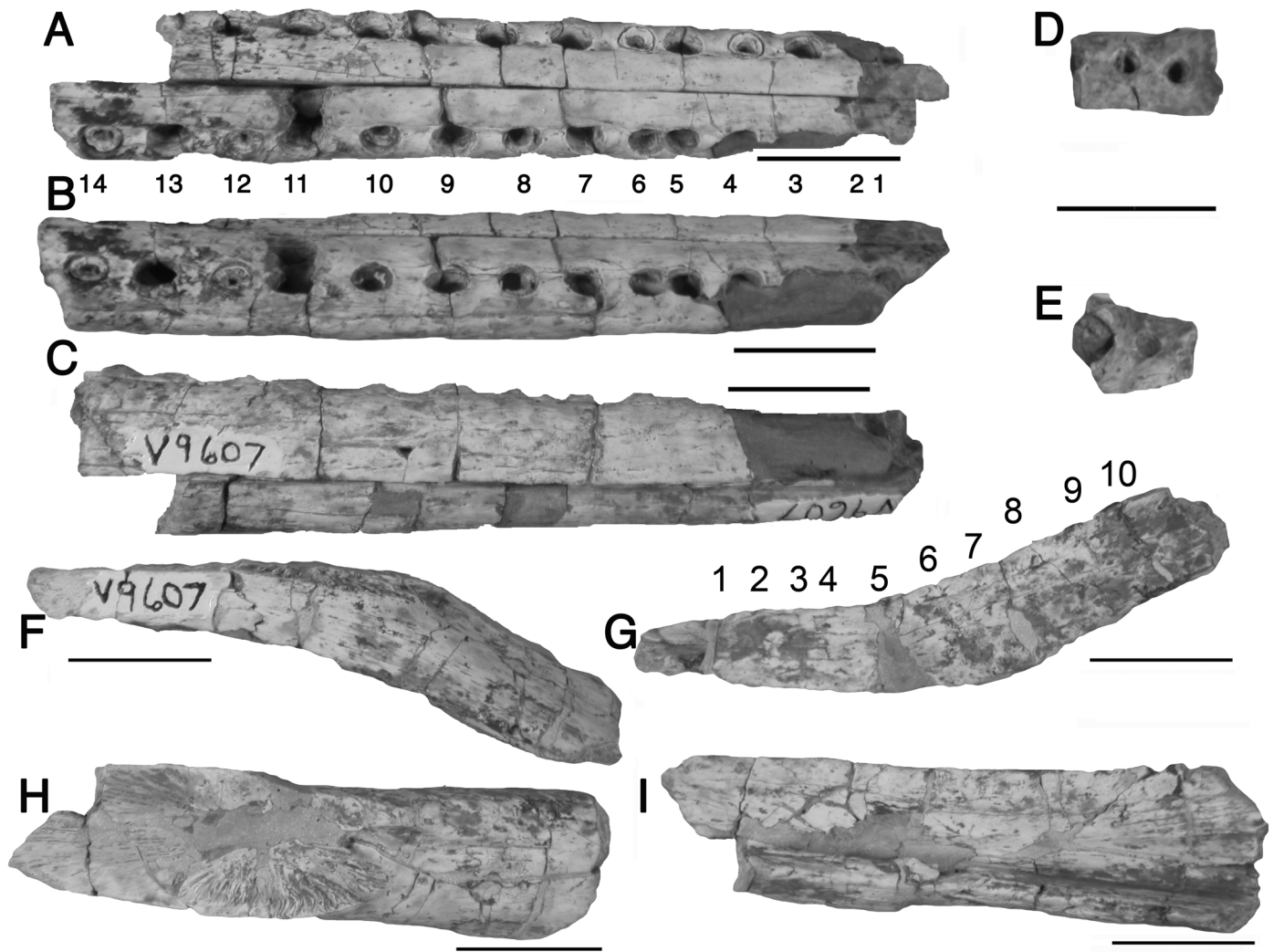


FIGURE 2. Juvenile phytosaur lower jaw fragments (UMMP V9607) from the Tecovas Formation, Crosby County, Texas. **A-C**, Lower jaw fragment in **A**, dorsal, **B**, right lateral, and **C**, ventral views. **D-E**, Lower jaw “bulb” fragments in dorsal view. **F-I**, Right splenial extending from medial symphysis posteriorly in **F**, ventral, **G**, dorsal, **H**, medial, and **I**, oblique lateral views. Numbers refer to tooth socket positions. All scale bars = 2 cm.

upward curvature along the jaw tip as well. The specimen is composed almost entirely of the left and right dentaries, however, part of the left splenial is barely visible on the medial side of the specimen (Fig. 3B-C). The posterior limit of the medial symphysis is visible along the posterior end of the specimen. The bifurcation is more apparent on the underside of the fragment, but is also visible along the top of the specimen.

UMMP 11753: The third Tecovas Formation specimen, UMMP 11753, is the left side of an incomplete phytosaur lower jaw (Fig. 3D-F). The fragment is composed entirely of the left dentary anterior to the posterior edge of the medial symphysis and is 173 mm long. There is little size variation along the width and height of the specimen. The jaw fragment possesses a flat medial surface that we interpret as the midline, although it is less textured than is typical of midline sutures, perhaps reflecting the presence of abundant cartilage (Fig. 3E). The fragment preserves 19 tooth sockets that are relatively evenly distributed along the length of the jaw with the exception of a poorly preserved area between sockets 8 and 9 that probably held 1-2 additional teeth (Fig. 3F). Sockets 2, 14, and 18 include remnants of teeth. The size of the tooth sockets varies slightly, with somewhat smaller sockets in the anterior portion of the jaw. Sockets 3 and 4 appear conjoined, as do sockets 6 and 7 and, as in V9607, there is some indication of “pairing” of tooth sockets. The lateral edge of the specimen is extremely regular, exhibiting little texture or variation along the lateral surface. There is a prominent

row of nutrient foramina adjacent to the tooth row, and two narrow grooves extend along the dorsal edge of the fragment paralleling each other for the length of the jaw. The anterior portion of the jaw widens and appears to tilt upward in a manner typical of the edge of the jaw.

Revueltian Specimen from the Bull Canyon Formation of Eastern New Mexico

The Bull Canyon Formation specimen, NMMNH P-4182, comprises two fragments of a juvenile phytosaur lower jaw, with just enough bone missing to prevent reconstruction with complete confidence (Fig. 4A-D). Both fragments consist of left and right dentary fragments sutured together. The first fragment preserves the anteriormost portion of the jaw and is 48.7 mm long and 9.0 mm tall. This fragment preserves 11 tooth sockets in the left dentary. Incomplete teeth are visible in sockets 1-3, 6-7, and 9-11 (counting from the first preserved socket). The right dentary contains 9 tooth sockets with incomplete teeth visible in sockets 2-9. The distance between each tooth socket increases posteriorly on both sides. The width of the anteriormost portion of the jaw is 10.9 mm and it is slightly wider than the rest of the jaw, which is narrowest immediately posterior to this bulge. The anteriormost tooth sockets along both dentaries in this region are much larger than those that follow, as is typical of phytosaurs. The midline suture is visible between the two dentaries as well and is preserved as a groove or sulcus (Fig. 4A-B,



FIGURE 3. Juvenile phytosaur lower jaw fragments from Tecovas Formation of Potter County (A-C) and Crosby County (D-F), Texas. A-C, Lower jaw fragment (UMMP 13534) in A, ventral, B, dorsal, and C, lateral views. D-F, Left dentary fragment (UMMP 11753) in D, lateral, E, medial, and F, dorsal views. Numbers refer to tooth socket positions. All scale bars = 2 cm.

D). The groove between the two dentaries widens toward the posterior end of the fragment. Both dentaries possess a row of nutrient foramina along their lateral faces, just ventral to the tooth sockets. The tooth sockets along both dentaries are set at an angle from the vertical, causing the teeth to project more laterally than dorsally. The ventral side of the fragment contains multiple elongate grooves parallel to the tooth rows. The bone along both dentaries rises slightly around each tooth socket, resulting in a grooved and bumpy surface.

The second, larger fragment of this specimen is located slightly more posteriorly along the lower jaw. This fragment is 57.3 mm long and 11.1 mm tall. The maximum width of the specimen is 14.1 mm. The fragment contains 8 tooth sockets on the left side and 9 on the right, probably representing sockets 12-20 of the jaw as a whole. The first six of these sockets on the left side of this fragment possess teeth, and the right side possesses nine tooth sockets with incomplete teeth in sockets

1, 3, 5, 7, and 9 (counting from the anterior margin of the fragment, these are obviously teeth in the range of 10-20 or so for the dentary overall). The sockets along both dentaries appear evenly spaced. A replacement tooth in the 9th tooth socket in this right dentary fragment is visible in cross-section due to the break of the fragment. The tooth is angled 45° from the vertical, projecting into the lateral face of the dentary. The depth of the tooth socket is 7.1 mm. The dentary bone, as on the first fragment, appears molded around the tooth sockets resulting in an irregular bumpy surface. Both the left and right dentaries display this pattern although the effect is less dramatic in the left dentary. The suture line between the two dentaries is visible on both the dorsal and ventral sides of the fragment. This suture is not as well preserved as in the more anterior fragment, but is, again, a low, U-shaped groove or sulcus that is slightly wider than in the anterior fragment. The two fragments very nearly fit, so only one, or at most two, tooth positions may be missing.

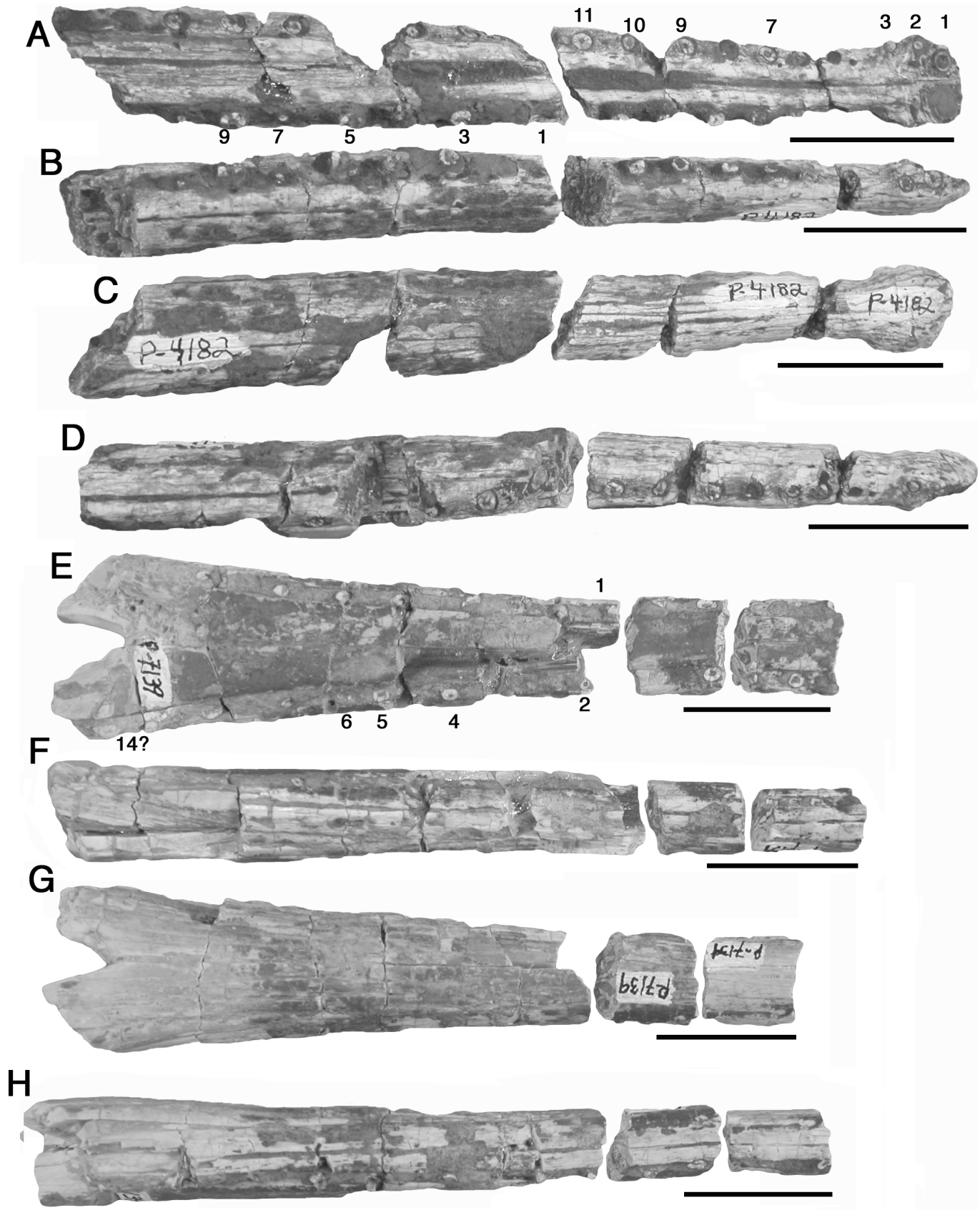


FIGURE 4. Phytosaur lower jaw fossils from Bull Canyon (NMMNH P-4182) and Sloan Canyon (NMMNH P-7139) formations, eastern New Mexico. **A-D**, NMMNH P-4182, lower juvenile jaw fragments in **A**, dorsal, **B**, right dorso-lateral, **C**, ventral, and **D**, ventro-lateral views. **E-H**, Lower juvenile jaw fragments (NMMNH P-7139) in **E**, dorsal, **F**, dorso-lateral, **G**, ventral, and **H**, ventro-lateral views. Numbers refer to tooth socket positions—in **A** these are for the anterior fragment (above) and the posterior fragment (below). All scale bars = 2 cm.

TABLE 1. Measurements of juvenile phytosaurs described here. Different fragments indicated by “a,” “b,” etc. All measurements in mm.

Specimen	Length (mm)	# tooth positions	mm/tooth position	Splénial visible in symphysis	“age rank” youngest (1) to oldest (5)
UMMP V9607a	122	14	8.7	N	3 (tie)
UMMP V9607b	81	10	8.1	Y	
UMMP 13534	297	35	8.5	Y	3 (tie)
UMMP 11753	173	19	9.1	?	5
NMMNH P-4182a	49	11	4.5	Y*	1
NMMNH P-4182b	57	9	6.4	Y*	
NMMNH P-7139	79	13-14	5.6-6.1**	Y	2

*splénial present but only visible in cross-section.

**depending on tooth count of 13 (6.1) or 14 (5.6).

Thus, these fragments well preserve the first 20 or so tooth sockets, roughly equivalent to the anterior half of the tooth row of a typical phytosaur. Lines of nutrient foramina are visible along the lateral faces of the dentaries, however, the lines are located more ventro-laterally due to the angle of the tooth sockets. Deep grooves are visible along the ventral face of the fragment as well.

Apachean Specimen from the Travesser Formation of Northeastern New Mexico

The juvenile phytosaur from the Travesser Formation, NMMNH P-7139, consists of three fragments of the lower jaw of a juvenile phytosaur (Fig. 4F-H), again with just enough material missing or lost to prevent reconstructing the three as one piece. The largest fragment comprises the left and right dentaries extending from the medial symphysis anteriorly and preserves approximately 13-14 tooth positions, mostly on the right side. The fragment is 78.9 mm long and 13.0 mm tall. The width of the fragment at the medial symphysis is 25.9 mm. The left side preserves 8 tooth sockets, all possessing incomplete teeth and probably contained additional sockets between these teeth, although these are poorly preserved and obscured by a concretionary matrix. The sockets are approximately evenly spaced. The first tooth socket is exposed in cross-section, and the depth of the socket is quite shallow at 2.6 mm. The angle of the tooth inside this first socket is about 35° from vertical. The right side contains 13 tooth sockets. Sockets 1, 4, 5, 6, and 8 through 13 all contain incomplete teeth (counting from the first preserved socket). The first tooth socket is exposed in cross-section, and the depth of the socket is 4.6 mm. Again, the tooth sockets are fairly evenly spaced, but the distance between sockets in both dentaries does vary some, ranging from 2.4 to 7.8 mm. Both dentaries contain a row of nutrient foramina just under the tooth sockets along their lateral faces. The suture line between the two dentaries is visible along both the dorsal and ventral faces as well (Fig. 4E,G). The ventral face of the fragment contains multiple grooves that run parallel to the nutrient foramina. The fragment widens considerably approaching the medial symphysis, the bone appearing to bend laterally toward the posterior end.

The second fragment of NMMNH P-7139 is 13.6 mm long, 14.0 mm wide and 10.3 mm tall. The fragment contains portions of both the left and right dentaries immediately anterior to the larger fragment, however, the orientation of the fragment anteriorly and posteriorly is unclear, so our reconstruction (Fig. 4E-H) is tentative. Two tooth sockets are visible on each side. Three of the four preserved sockets contain incomplete teeth. One tooth socket is exposed in cross-section, and the depth of the socket is 5.9 mm. The socket is oriented 45° from vertical. The suture line between the two dentaries is visible along the ventral surface as well as the anterior and posterior surfaces. Two other suture lines that

may represent the anterior extent of the splénial are visible along these surfaces on either side of the dentary suture. The distance between the two suture lines widens as they approach both the dorsal and ventral surfaces but narrows in between. The distance between the two suture lines appears the smallest in the center of the fragment at the base of the tooth sockets. Seven nutrient foramina are visible along the anterior and posterior surfaces as well. One foramen appears at the ventral base of the dentary suture line. The other six appear symmetrically on either side of the suture line. The first symmetrical pair lies ventral to the left and right dentary tooth sockets and connects to the row of foramina visible along the lateral surface. The second pair of foramina lies just dorsal to the tooth sockets. The third symmetrical pair lies just at the base of the tooth sockets on either side of the dentary suture line. The two other suture lines run through this pair of foramina.

The third fragment is quite similar to the second, 13.1 mm long, 13.7 mm wide, and 9.0 mm tall. Both left and right dentary fragments are present but, as in the previous fragment, it is unclear to which side each belongs. Both sides contain three tooth sockets. Five of the six total tooth sockets contain incomplete teeth. Three tooth sockets are exposed and are 4.6 mm, 6.0 mm, and 7.1 mm deep. The teeth again appear to grow at a 45° angle from vertical. The dentary suture line is visible on both the anterior and posterior ends of the specimen. There are also two symmetrical suture lines running on either side of the dentary suture line. The distance between the two suture lines widens slightly as they approach the ventral and dorsal faces of the specimen. Seven foramina are visible on the posterior and anterior ends of this specimen as well. The first foramen lies at the ventral base of the dentary suture line. The other six foramina lie symmetrically in pairs along the anterior and posterior faces. The first pair lies just ventral to the tooth sockets and feeds into nutrient foramina rows visible along the lateral faces of the specimen. The second pair lies just dorsal to the tooth sockets, and the third pair lies at the base of the tooth sockets and is intercepted by the two suture lines that run on either side of the dentary suture line.

DISCUSSION

Given the preponderance of larger phytosaur fossils in the Chinle Group, we are confident that the fossils described here do in fact represent juveniles, and not individuals of diminutive or dwarfed species. Although there may have been small phytosaur taxa, the presence of numerous larger (m-scale skulls) phytosaurs demonstrates that numerous juvenile and subadult phytosaurs must have occupied the ecosystem, whereas evidence for small phytosaur taxa is lacking. The very few small, diagnostic postcranial remains of phytosaurs recovered from Upper Triassic strata both in the Chinle Group (Irmis, 2007) and Upper Triassic of Italy (Renesto, 2008) possess unfused vertebrate sutures and other features diagnostic of juveniles, so we are confident that these skull and jaw fragments represent juvenile animals and not diminutive phytosaur taxa.

We assign all of these specimens to Phytosauria based on the presence of one or more of the following features, originally enumerated by Hungerbühler (2000): (1) elongate mandible; (2) extensive symphyseal region; (3) splénial contributes to symphysis; (4) mandible more or less constant in height over the length of the symphysis. These are all features that Hungerbühler (2001) used to determine that “*Zanclodon*” *arenaceus* was distinct from known phytosaurs. Although none of the specimens are complete, it is evident that all had a lengthy mandible. More compelling is the extensive conjoined symphyseal region on most specimens, with the symphysis clearly extending posteriorly well beyond the 10th tooth position, a characteristic unique to phytosaurs among contemporaneous archosauromorphs (Hungerbühler, 2000). As documented in the description, the splénial clearly contributes to the symphysis in most of these specimens, the only possible exception being the incomplete left dentary UMMP 11753. Finally, all of the preserved specimens maintain a near constant height posteriorly, unlike other archosauromorphs, where the tooth-bearing portion of the dentary

often becomes progressively deeper posteriorly. Hungerbühler (2000) also listed an elongate, slit-like external mandibular fenestra as characteristic of phytosaurs, but this is not preserved in any of the specimens we describe here.

In an attempt to ascertain the relative ontogenetic stage of each individual, we calculated the ratio of preserved tooth sockets per mm of preserved bone (Table 1). Although this measurement could be influenced by a taxonomic feature such as the total number of positions in the jaw, we feel it is a useful way to approximate relative ontogenetic ages. As Table 1 shows, NMMNH P-4182 is the ontogenetically youngest individual, with an overall average of only 5.3 mm per tooth position. Nearly as small is NMMNH P-7139, with only 5.6-6.1 mm per tooth position (depending on whether to interpret the specimen as having 13 or 14 positions). UMMP V9607 is one of the ontogenetically oldest (average length > 9 mm/tooth socket). As adult phytosaurs often have teeth, especially posterior teeth, that exceed 10 mm in mesio-distal length (e.g., Hungerbühler, 2000), this ratio firmly establishes all of these specimens as juveniles to, at most, subadults.

Due to the incomplete nature of these fossils, none can be assigned to a genus with certainty. Based on the available stratigraphic and biostratigraphic evidence, the Tecovas Formation specimens can be assigned to a taxonomic morass variously ascribed to *Rutiodon*, *Leptosuchus*, *Machaeroprotoposus*, and *Smilosuchus* (Case, 1922; Camp, 1930; Gregory, 1962; Long and Murry, 1995; Hungerbühler, 2002). The Bull Canyon Formation specimen likely pertains to *Pseudopalatus*, the principal phytosaur found there (e.g., Hunt, 2001), and the Travesser Formation specimen likely pertains to *Redondasaurus*, the only phytosaur reported from that unit (Spielmann and Lucas, 2012).

The main reason we cannot assign these specimens to a genus is that phytosaur taxonomy generally, and cladistic hypotheses in particular, have all but ignored the lower jaw. Indeed, mandibles are only illustrated in Long and Murry (1995) when in articulation with skulls, and thus only in lateral view. Similarly, the most recent phylogenies of phytosaurs (Hungerbühler, 2002; Stocker, 2010) make no mention of any characters except those of the skull. This is partly because many skulls are found without lower jaws, but is unfortunate because it ignores potentially informative morphological data, and is puzzling given that Hungerbühler (2001) proposed six synapomorphies of Phytosauria in the mandible. There are several features in one or more of these specimens that may be diagnostic, or at least ontogenetically informative, including tooth spacing and number, degree of heterodonty, angle of tooth eruption relative to the jaw, and details of sutural arrangements with other bones, especially the splenial (see following text).

All known phytosaurs have some form of rostral expansion or “bulb,” where both the premaxillae and the anterior dentaries are markedly wider at the tip of the snout than they are immediately posteriorly. Generally this “bulb” has at least three, and sometimes four, tooth positions on each side of the midline in both the dentary and the mandible. In Hungerbühler’s (2000) description of heterodonty in *Nicrosaurus* these are the “tip of snout” and “tip of mandible” sets of teeth. Hungerbühler (2000) reported three tip of mandible teeth on each side in *Nicrosaurus*, a condition widespread among phytosaurs (e.g., Camp, 1930; Ballew, 1989; Long and Murry, 1995). Thus, the presence of three teeth in each side of NMMNH P-4172 (Fig. 4A-C) probably does not hold much phylogenetic information, although it does indicate that taxa from this timeframe possess three larger sockets per side even relatively early in ontogeny.

Although post-rostral “bulb” teeth tend to be spaced relatively evenly, there are exceptions, for example, the somewhat paired tooth spacing evident in the anterior fragment of UMMP V9607 (Fig. 2A) and UMMP 11753 (Fig. 3D-E). In these specimens, the tooth sockets appear to be arranged in pairwise fashion, with each member of the pair slightly closer to the other member than either is with the next most anterior or posterior tooth. The possible functional significance of this is

unclear, although it is tempting to consider that it has something to do with alternate tooth replacement and perhaps maintaining each pair as a single functional position at all times, following Edmund (1960). The distribution of this trait among mature phytosaur specimens needs to be evaluated for its possible taxonomic significance.

Hungerbühler’s (2000) extensive documentation of tooth morphology in *Nicrosaurus* explained the nature and significance of heterodonty within that taxon and laid a basis for future work. Interestingly he only illustrates upper teeth, and his classification of bipartite and tripartite heterodont phytosaurs rests entirely on characteristics of the upper dentition. He did note the transition from slightly ridged, round symphyseal teeth in the dentary to “unstriated, bicarinate, and lingually flattened teeth which generally resemble posterior maxillary teeth” (Hungerbühler, 2000, p. 39), suggesting that documentation of this trend in phytosaur lower jaws could be significant.

Phytosaur skulls and jaws often suffer serious postmortem distortion, complicating reconstruction of features such as the angle of tooth eruption. Thus it is difficult to know what significance to attach to non-vertically oriented teeth in NMMNH P-4172 and P-7139. Functionally, we interpret this as an indication of piscivory in these narrow-snouted taxa, with the teeth splayed out to provide both catching and holding functions, as hypothesized by Hunt (1989; see also Hungerbühler, 2000).

A potentially diagnostic characteristic that does vary among the specimens described here is the sutural arrangement of the midline symphysis. In some specimens (e.g., UMMP 13534, Fig. 3A-C; NMMNH P-7139, Fig. 4E-H) the splenial projects well into the symphysis, extending anteriorly for much of the preserved specimen. Other specimens (e.g., UMMP V9607, Fig. 2A-C) show almost no contribution of the splenial to the preserved anterior symphyseal region, even if it is a substantial portion of the posterior symphysis (Fig. 2H). UMMP V9607 and UMMP 13534 therefore probably represent different taxa, as the splenial’s contribution to the symphysis appears more minimalistic and the tooth spacing is different. UMMP V11534 could represent the same taxon as UMMP 11753, which appears similarly homodont, with the tooth sockets exhibiting paired spacing. In our studies of other phytosaur specimens we have also noted that there are times when the splenial actually forms the medial margin for parts of the tooth row, and we interpret the splenial of UMMP V9607 as one such example here, albeit in the juvenile state of development. Hungerbühler (2001; see also Kischlat and Lucas, 2003) identified the presence of a symphyseal platform, or antero-posteriorly long and flat region formed by the conjoined mandibles, as a phytosaurid (= phytosaurs more derived than *Parasuchus*) characteristic, something shared by all of the specimens described here. Nesbitt (2011) considered the presence of a dentary-splenial mandibular symphysis extending more than one-third of the length of mandible a phytosaurian characteristic, the only synapomorphy of the group that can be identified in the specimens described here and essentially a single character lumping together four criteria of Hungerbühler (2001) that we used to identify these specimens as phytosaurian. More extensive documentation of these features in adult phytosaur specimens may reveal whether these features have taxonomic significance.

CONCLUSIONS

Juvenile phytosaur specimens are difficult to interpret, as they retain a relatively simplistic dentition and few taxonomically significant characteristics. More extensive documentation of subadult to adult specimens associated with skulls is necessary to maximize the taxonomic value of phytosaur mandibles generally and these juvenile specimens in particular. Features that do vary among these specimens include tooth spacing, degree of heterodonty, angle of tooth eruption, and the sutural arrangement of the symphysis, all of which could reveal more taxonomic information. We advocate using a proxy such as mm/tooth position to evaluate the ontogenetic stage of immature phytosaur specimens.

ACKNOWLEDGMENTS

We appreciate the loan of the UMMP specimens, originally authorized by G. Gunnell of that institution. H.S. Jenkins' work on this project was supported by the Sara F. Langer Award for Research in

Geology while an undergraduate at Wellesley College. Various volunteers associated with the NMMNH helped collect and prepare the NMMNH specimens described here. Reviews of an earlier version of the manuscript by J. Kimmig, S. Renesto and R.M. Sullivan improved the content presented here.

REFERENCES

- Ballew, K.L., 1989, A phylogenetic analysis of Phytosauria from the Late Triassic of the western United States; *in* Lucas, S.G. and Hunt, A.P., eds., Dawn of the Age of Dinosaurs in the American Southwest: Albuquerque, New Mexico Museum of Natural History, p. 309-339.
- Camp, C.L., 1930, A study of the phytosaurs with description of new material from western North America: *Memoirs of the University of California*, v. 19, p. 174.
- Case, E.C., 1922, New reptiles and stegocephalians from the Upper Triassic of western Texas: *Carnegie Institution Publication*, v. 321, 84 pp.
- Dzik, J. and Sulej, T., 2007, A review of the early Late Triassic Krasiejów biota from Silesia, Poland: *Palaeontologica Polonica*, v. 64, p. 3-27.
- Edmund, A.G., 1960, Tooth replacement phenomena in the lower vertebrates: *Life Sciences Museum Royal Ontario Museum Contributions*, v. 52, p. 1-190.
- Fara, E. and Hungerbühler, A., 2000, *Paleorhinus magnoculus* from the Upper Triassic of Morocco: A juvenile primitive phytosaur (Archosauria): *Comptes Rendus Academie des Sciences, Paris, Sciences de la Terre et des Planetes*, v. 331, p. 831-836.
- Gregory, J.T., 1962, The relationships of the American phytosaur *Rutiodon*: *American Museum Novitates*, v. 2095, p. 1-22.
- Heckert, A.B. and Lucas, S.G., 1998, First occurrence of *Aetosaurus* (Reptilia:Archosauria) in the Upper Triassic Chinle Group (USA) and its biochronological significance: *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, v. 1998, p. 604-612.
- Heckert, A.B., Lucas, S.G., Hunt, A.P. and Harris, J.D., 2001, A giant phytosaur (Reptilia: Archosauria) skull from the Redonda Formation (Upper Triassic: Apachean) of east-central New Mexico: *New Mexico Geological Society, Guidebook 52*, p. 171-178.
- Heckert, A.B., Lucas, S.G., Rinehart, L.F., Celeskey, M.D., Spielmann, J.A. and Hunt, A.P., 2010, Articulated skeletons of the aetosaur *Typothorax coccinarum* Cope (Archosauria: Stagonolepididae) from the Upper Triassic Bull Canyon Formation (Revueletian: early-mid Norian), eastern New Mexico, USA: *Journal of Vertebrate Paleontology*, v. 30, p. 619-642.
- Hungerbühler, A., 2000, Heterodonty in the European phytosaur *Nicrosaurus kapffi* and its implications for the taxonomic utility and functional morphology of phytosaur dentitions: *Journal of Vertebrate Paleontology*, v. 20, p. 31-48.
- Hungerbühler, A., 2001, The status and phylogenetic relationships of "*Zanclodon*" *arenaceus*: the earliest known phytosaur?: *Paläontologische Zeitschrift*, v. 75, p. 97-112.
- Hungerbühler, A., 2002, The Late Triassic phytosaur *Mystriosuchus westphali*, with a revision of the genus: *Palaeontology*, v. 45, p. 377-418.
- Hungerbühler, A. and Hunt, A. P., 2000, Two new phytosaur species (Archosauria, Crurotarsi) from the Upper Triassic of southwest Germany: *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, v. 2000, p. 467-484.
- Hunt, A.P., 1989, Cranial morphology and ecology among phytosaurs; *in* Lucas, S.G., and Hunt, A.P., eds., Dawn of the Age of Dinosaurs in the American Southwest: Albuquerque, New Mexico Museum of Natural History, p. 349-354.
- Hunt, A.P. and Lucas, S.G., 1993, A new phytosaur (Reptilia: Archosauria) genus from the Uppermost Triassic of the western United States and its biochronological significance: *New Mexico Museum of Natural History and Science, Bulletin 3*, p. 193-196.
- Hunt, A.P., 1994, Vertebrate paleontology and biostratigraphy of the Bull Canyon Formation (Chinle Group, Upper Triassic), east-central New Mexico with revisions of the families Metoposauridae (Amphibia: Temnospondyli) and Parasuchidae (Reptilia: Archosauria) [Ph.D. dissertation]: Albuquerque, University of New Mexico, 404 p.
- Hunt, A.P., 2001, The vertebrate fauna, biostratigraphy and biochronology of the type Revuelitian faunachron, Bull Canyon Formation (Upper Triassic), east-central New Mexico: *New Mexico Geological Society, Guidebook 52*, p. 123-152.
- Irmis, R.B., 2007, Axial skeleton ontogeny in the Parasuchia (Archosauria:Pseudosuchia) and its implications for ontogenetic determination in archosaurs: *Journal of Vertebrate Paleontology*, v. 27, p. 350-361.
- Kischlat, E.-E. and Lucas, S.G., 2003, A phytosaur from the Upper Triassic of Brazil: *Journal of Vertebrate Paleontology*, v. 23, p. 464-467.
- Long, R.A. and Murry, P.A., 1995, Late Triassic (Carnian and Norian) tetrapods from the southwestern United States: *New Mexico Museum of Natural History and Science, Bulletin 4*, 254 p.
- Lucas, S.G., 1998, Global Triassic tetrapod biostratigraphy and biochronology: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 143, p. 347-384.
- Lucas, S.G., 2010, The Triassic chronostratigraphic scale: history and status: *Geological Society, London, Special Publications*, v. 334, p. 17-39.
- Lucas, S.G. and Hunt, A.P., 1993, Tetrapod biochronology of the Chinle Group (Upper Triassic), western United States: *New Mexico Museum of Natural History and Science, Bulletin 3*, p. 327-329.
- Lucas, S.G., Hunt, A.P. and Hayden, S.N., 1987, The Triassic System in the Dry Cimarron Valley, New Mexico, Colorado, and Oklahoma: *New Mexico Geological Society, Guidebook 38*, p. 97-117.
- Lucas, S.G., Heckert, A.B. and Hunt, A.P., 2001, Triassic stratigraphy, biostratigraphy and correlation in east-central New Mexico: *New Mexico Geological Society, Guidebook 52*, p. 85-102.
- Lucas, S.G., Hunt, A.P., Heckert, A.B. and Spielmann, J.A., 2007, Global Triassic tetrapod biostratigraphy and biochronology: 2007 status: *New Mexico Museum of Natural History and Science, Bulletin 41*, p. 229-240.
- Martz, J.W. and Small, B.J., 2006, *Tecovasuchus chatterjeei*, a new aetosaur (Archosauria: Stagonolepididae) from the Tecovas Formation (Carnian, Upper Triassic) of Texas: *Journal of Vertebrate Paleontology*, v. 26, p. 308-320.
- Murry, P.A., 1989, Geology and paleontology of the Dockum Formation (Upper Triassic), West Texas and eastern New Mexico; *in* Lucas, S.G. and Hunt, A.P., eds., Dawn of the Age of Dinosaurs in the American Southwest: Albuquerque, New Mexico Museum of Natural History, p. 102-148.
- Nesbitt, S.J., 2011, The early evolution of archosaurs: Relationships and the origin of major clades: *Bulletin of the American Museum of Natural History*, v. 392, 292 p.
- Renesto, S., 2008, Remains of a juvenile phytosaur from the Late Triassic of northern Italy: *Revista Italiana di Paleontologia e Stratigrafia*, v. 114, p. 155-160.
- Rinehart, L.F., Lucas, S.G., Heckert, A.B., Spielmann, J.A. and Celeskey, M.D., 2009, The paleobiology of *Coelophysis bauri* (Cope) from the Upper Triassic (Apachean) Whitaker quarry, New Mexico, with detailed analysis of a single quarry block: *New Mexico Museum of Natural History and Science, Bulletin 45*, 260 p.
- Spielmann, J.A. and Lucas, S.G., 2012, Tetrapod fauna of the Upper Triassic Redonda Formation, east-central New Mexico: The characteristic assemblage of the Apachean land-vertebrate faunachron: *New Mexico Museum of Natural History and Science, Bulletin 55*, 119 p.

- Stocker, M.R., 2010, A new taxon of phytosaur (Archosauria: Pseudosuchia) from the Late Triassic (Norian) Sonsela Member (Chinle Formation) in Arizona, and a critical reevaluation of *Leptosuchus* Case, 1922: *Palaeontology*, v. 53, p. 997-1022.
- Stocker, M.R., 2012, A new phytosaur (Archosauriformes, Phytosauria) from the Lot's Wife Beds (Sonsela Member) within the Chinle Formation (Upper Triassic) of Petrified Forest National Park, Arizona: *Journal of Vertebrate Paleontology*, v. 32, p. 573-586.
- Stovall, J.W. and Savage, D.E., 1939, A phytosaur in Union County, New Mexico, with notes on the stratigraphy: *Journal of Geology*, v. 47, p. 759-766.
- Westphal, F., 1976, Phytosauria; in Kuhn, O., ed., *Handbuch der Paläoherpetologie: Thecodontia: Handbuch der Paläoherpetologie/Encyclopedia of Paleoherpology*: Stuttgart, Gustav Fischer Verlag, p. 99-120.
- Zeigler, K.E., Lucas, S.G. and Heckert, A.B., 2003a, Variation in the Late Triassic Canjilon quarry (Upper Chinle Group, New Mexico) phytosaur skulls: Evidence of sexual dimorphism: *Paläontologische Zeitschrift*, v. 77, p. 341-351.
- Zeigler, K.E., Heckert, A.B. and Lucas, S.G., 2003b, Phytosaur (Archosauria: Parasuchidae) cranial and mandibular material from the Upper Triassic Snyder quarry (Petrified Forest Formation, Chinle Group): *New Mexico Museum of Natural History and Science, Bulletin 24*, p. 81-88.
- Zeigler, K.E., Heckert, A.B. and Lucas, S.G., 2003c, An illustrated atlas of the phytosaur (Archosauria: Parasuchidae) postcrania from the Upper Triassic Snyder quarry (Petrified Forest Formation, Chinle Group): *New Mexico Museum of Natural History and Science, Bulletin 24*, p. 89-103.