PHYTOSAUR (ARCHOSAURIA: PARASUCHIDAE) CRANIAL AND MANDIBULAR MATERIAL FROM THE UPPER TRIASSIC SNYDER QUARRY (PETRIFIED FOREST FORMATION, CHINLE GROUP)

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Abstract—The Upper Triassic Snyder quarry has produced the remains of several pseudopalatine phytosaurs that we refer to *Pseudopalatus buceros*. This material includes at least four complete skulls (two are fully prepared), two partial skulls, as well as numerous isolated cranial elements that pertain to additional individuals (MNI = 11). Here, we describe these elements in detail and review sexual dimorphism in phytosaurs. We also note that taphonomic distortion of phytosaur skulls can lead to misidentification due to changes in shape and position of features, such as the supratemporal fenestrae, that have long been considered key to diagnosing different phytosaur genera.

Keywords: phytosaur, *Pseudopalatus*, crania, mandibles, Upper Triassic, skull

INTRODUCTION

The Snyder quarry, New Mexico Museum of Natural History (NMMNH) locality 3845, is an extremely rich Late Triassic bonebed near Ghost Ranch in north-central New Mexico (Fig. 1). The bonebed is in a wide, shallow fluvial channel composed of an intraformational conglomerate containing mud pebbles and quartz granules. Over the course of three field seasons, various vertebrate taxa have been recovered from the quarry, most notably the primitive theropod *Eucoelophysis* sp., the aetosaurs *Typothorax coccinarum* and *Desmatosuchus chamaensis*, and the phytosaur *Pseudopalatus buceros* (Sullivan and Lucas, 1999; Heckert et al., 2000; Zeigler et al., 2001, 2002a,b). Phytosaurs dominate the Snyder quarry assemblage, with 11 skulls or partial skulls discovered so far. These skulls range in size from a hatchling (estimated skull length of 0.3 m) to a fully mature adult (estimated skull length of >1 meter). The majority of the skulls appear to be from individuals of subadult age (skull lengths of ~0.7 - 1.0 m). Of the skulls recovered, four have been fully prepared, and we describe that material here, as well as isolated cranial elements and several mandibles.

Phytosaurs are an extinct clade of superficially crocodile-like archosaurs that had an essentially Pangean distribution during the Late Triassic (Gregory, 1962a,b; Westphal, 1976; Hunt and Lucas, 1991; Hungerbühler, 2002). During the Late Triassic, phytosaur genera appear to turn over at least two or three times, depending upon the taxonomic scheme used (e.g., Ballew, 1989; Hunt, 1994; Long and Murry, 1995; Hungerbuhler, 2002). Due to their widespread geographic distribution and relatively brief stratigraphic ranges, phytosaurs have often been used as index fossils in biostratigraphic correlations, and to subdivide Triassic time biochronologically (Colbert and Gregory, 1957; Gregory, 1962a,b; 1969; Hunt and Lucas, 1991; Lucas, 1998). Unfortunately, an essentially complete phytosaur skull is necessary to identify a phytosaur to genus level in any recent taxonomic scheme (e.g., Ballew, 1989; Hunt, 1994; Long and Murry, 1995; Hungerbühler, 2002). Although there are several quarries that yield multiple phytosaur skulls (Camp, 1930; Lawler, 1974; Chatterjee, 1978; Long et al., 1989; Zeigler et al., 2002b), little has been done to study phytosaur death assemblages that appear to represent discrete populations of a single species (Zeigler et al., 2002b). Accordingly, after briefly considering the stratigraphy and age of the Snyder quarry and the taxonomy of the phytosaurs from the quarry, we provide detailed descriptions of much of the phytosaur material that has been prepared thus far. We then discuss the variation seen in this population sample and address the sources of that variation, including both sexual dimorphism (following Zeigler et al.,
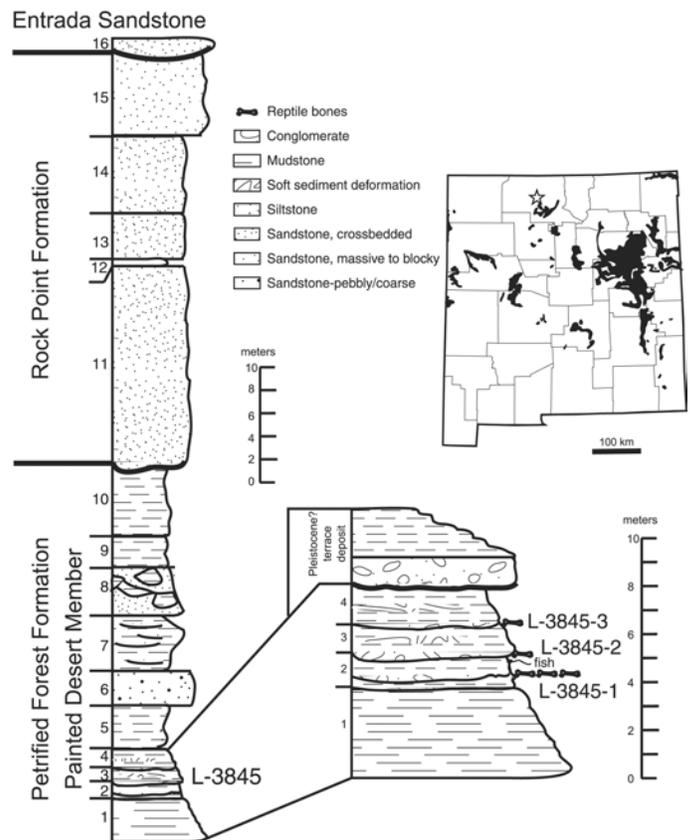
FIGURE 1. Index map showing location of the Snyder quarry site in north-central New Mexico, distribution of Triassic outcrops (from Heckert et al., 2000), and stratigrahic section at the quarry.

2002b) and taphonomic variation, a topic not adequately addressed in previous studies

STRATIGRAPHY AND AGE

The Snyder quarry is stratigraphically high in the Upper Triassic Petrified Forest Formation of the Chinle Group. It is approximately 60 m below the base of the Middle Jurassic Entrada Sandstone and approximately 28 m below the base of the Upper Triassic Rock Point Formation of the Chinle (Fig. 1). The presence of the Revueltian index

taxon *Typothorax coccinarum* in association with *Pseudopalatus*-grade phytosaurs in this quarry indicates that it is within the Revueltian (early-mid Norian) land-vertebrate faunachron (LVF) of Lucas and Hunt (1993; Lucas, 1998; Heckert et al., 2000). The nearby Canjilon quarry lies at a similar, if not identical, stratigraphic level (Hunt and Lucas, 1993; Heckert et al., 2000; Zeigler et al., 2002b).

TAXONOMY

Every phytosaur taxonomic scheme published since the early twentieth century has required an essentially complete skull to provide a genus-level identification (McGregor, 1906; Huene, 1915; Camp, 1930; Gregory, 1962a,b; Westphal, 1976; Ballew, 1989; Hunt, 1994; Long and Murry, 1995; Hungerbühler, 2002). Presently, several schemes are in use by various workers (e.g., Ballew, 1989; Hunt, 1994; Long and Murry, 1995; Hungerbühler, 2002), although we tend to follow Ballew (1989), with some modification [e.g., we recognize *Redondasaurus* as a valid taxon (Hunt and Lucas, 1993b; Hungerbühler, 2002)].

Also relevant to this study is Lucas et al.'s (2002) discussion of the holotype of "*Belodon*" *buceros* Cope (1881), which, like the Snyder quarry phytosaurs, was found in the Painted Desert Member of the Petrified Forest Formation in the Chama basin. Lucas et al. (2002) determined that the oldest available generic name for "*B.*" *buceros* is *Pseudopalatus* Mehl, 1928. *Belodon* is, by all accounts, a *nomen dubium* based on teeth (e.g., Hunt and Lucas, 1989; Hunt, 1994). The next available name, *Machaeroprosopus validus* Mehl 1922 is based on a specimen that is now lost and that, as illustrated by Mehl (1922), differs from any other known taxon. Accordingly, we utilize Mehl's later (1928) name *Pseudopalatus* for the holotype of "*Belodon*" *buceros* as *Pseudopalatus buceros* (Cope) (Lucas et al., 2002; Zeigler et al., 2002a).

Within *Pseudopalatus*, several species have been identified. Most recent authors (e.g., Ballew, 1989; Hunt, 1994; Long and Murry, 1995; Hungerbühler, 2002) recognize a relatively gracile morph with a long, slender snout and an abrupt, steep-sided crest connecting the snout to the nares. Typically this morph is assigned to *Pseudopalatus pristinus* (Mehl, 1928; Ballew, 1989; Hunt, 1994; Long and Murry, 1995). A second, more robust "species" with a less slender snout and more fully developed narial crest extending well anterior of the narial openings is typically identified as *Pseudopalatus andersoni* (Camp, 1930; Ballew, 1989; Hunt, 1994).

Presently, we only recognize a single species of *Pseudopalatus*, *P. buceros*. What all of the previously cited taxonomic schemes failed to address properly was the population sample of phytosaurs from the Canjilon quarry, which is stratigraphically equivalent to the Snyder quarry (Zeigler et al., 2002b). Zeigler et al. (2002b), however, documented that the only anatomical differences between "*P. pristinus*" and "*P. andersoni*" skulls from the Canjilon quarry lie in the size and shape of the premaxillae, which form the anterior portion of the narial crest. Thus, although the Canjilon quarry sample had been previously studied (e.g., Lawler, 1974; Ballew, 1989; Hunt, 1994; Long and Murry, 1995), Zeigler et al. (2002b) were the first to document this sexual dimorphism.

Phytosaur skulls from the Snyder quarry possess the key characteristics of *Pseudopalatus* as identified by previous workers and interpreted by Lucas et al. (2002) and Zeigler et al. (2002a). Specifically, all sufficiently well-preserved phytosaur skulls from the Snyder quarry have supratemporal fenestrae that are laterally compressed and short in dorsal view. This, when combined with squamosal bars that project well posterior to the occiput, and an occipital complex that is u-shaped in dorsal view, confirm their identification as *Pseudopalatus*, specifically *P. buceros sensu* Lucas et al. (2002; Zeigler et al., 2002a). Following Zeigler et al. (2002b), we identify specimens with a short, abrupt volcano-like narial crest as females of the species and specimens with the more elongate, robust and gradually sloping crest as males.
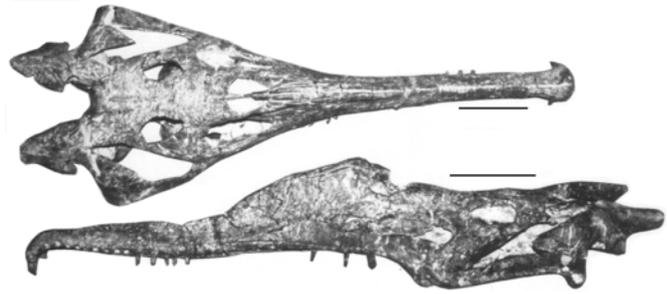
FIGURE 2. NMMNH P-31292, juvenile skull of *Pseudopalatus buceros* from the Snyder quarry in **A**, dorsal, **B**, left lateral and **C**, ventral views. Scale bars = 10 cm.

DESCRIPTION OF CRANIAL MATERIAL

Complete or Associated Crania

NMMNH P-31292 is a complete skull of a subadult *Pseudopalatus*-grade phytosaur (Fig. 2). The dorsal portion of the skull deck is slightly crushed dorso-ventrally, and the left side is partially crushed ventrally and medially. Overall, however, the symmetry of the skull is mostly maintained, suggesting that postmortem breakage and distortion is minimal. The skull is 790 mm long and 270 mm wide at its widest portion (across the quadratojugals). The snout is 420 mm long from its anterior tip to the anterior border of the nares. The post-snout portion of the skull is 370 mm from the anterior border of the nares to the posterior edge of the squamosals. Additional measurements are provided in Table 1. The skull is narrow, with the squamosal bars extending almost straight back from the quadratojugal and parietal with only a slight angle towards the lateral margins of the skull. The maxillae are narrow and almost below the nasal and the rostral crest, which results in a very steep crest and a narrow outline to the skull. This specimen is nearly identical in proportions to the type specimen of

TABLE 1. Selected measurements of phytosaur skull NMMNH P-31292.

Dorsal surface

Length of skull (tip of snout to posterior edge of squamosals)	790 mm
Length of skull (tip of snout to posterior edge of occipital condyle)	675 mm
Maximum width of skull (across quadratojugals)	270 mm
Length of snout (tip of snout to ant. border of nares)	420 mm
Post-snout length (ant. border of nares to post. edge squamosals)	370 mm
Maximum width of snout	95 mm
Maximum height of crest	110 mm
Maximum length of nares	60 mm
Maximum width of nares	22 mm
Maximum length of orbit (average)	63 mm
Maximum width of orbit (average)	40 mm
Minimum interorbital width	46 mm
Length of cranial table (through supratemporal fenestrae)	182 mm
Width of cranial table (across supratemporal fenestrae)	115 mm
Length of supratemporal fenestrae (right fenestra only)	30 mm
Width of supratemporal fenestrae (right fenestra only)	10 mm
Supratemporal interfenestral width	45 mm
Maximum length of lateral temporal fenestra (average)	149 mm
Maximum width of lateral temporal fenestra (average)	51 mm
Lateral temporal interfenestral width	125 mm
Maximum length of antorbital fenestra (average)	105 mm
Maximum width of antorbital fenestra (average)	33 mm
Antorbital interfenestral width	75 mm
Maximum width of squamosals (average)	73 mm
Maximum length of squamosal bar (average)	102 mm
Intersquamosal width (mid-squamosal to mid-squamosal)	130 mm

Ventral surface (measurements are right side only)

Maximum length of palatine	100 mm
Maximum width of palatine	30 mm
Maximum width of pterygoid	64 mm
Maximum width across ectopterygoid flanges	85 mm
Maximum width across medial edges of quadrates	117 mm

FIGURE 3. NMMNH P-39700, adult skull of *Pseudopalatus buceros* from the Snyder quarry in right lateral view. Scale bar = 10 cm.

Belodon buceros Cope (Huene, 1915, fig. 4; Lucas et al, 2002, fig. 3). The widening of the skull at the quadratojugals is greater than in comparable size skulls of *Pseudopalatus pristinus*, but contrasts with phytosaurs such as *Redondasaurus gregorii* and *Rutiodon* (=*Smilosuchus*) *gregorii,* which have very wide skulls (Hunt, 1994; Long and Murry, 1995; Heckert at al., 2001). Zeigler et al. (2002a) is a much more detailed description of this skull, including a brief comparison of the phytosaur genera *Pseudopalatus*, *Nicrosaurus* and *Mystriosuchus*. Following Zeigler et al. (2002b), we identify this skull as a male *Pseudopalatus buceros* based on the presence of a robust narial crest.

A nearly complete skull of a male *P. buceros*, NMMNH P-39700, is nearly identical to P-31292, but is slightly longer (Fig. 3). This skull has been crushed on the left side and is twisted to the left as well. Interestingly enough, none of the ventral aspect has been preserved. This specimen was found upside-down in the field and we suspect that the more delicate palatal elements were crushed or otherwise destroyed either shortly after death or during post-mortem fossilization processes.

NMMNH P-36000 is a partial skull of *Pseudopalatus* that includes the skull roof (frontals to parietals), both squamosals and most of the occipital complex as one piece, and separately, the right and left jugals (incomplete), the right quadrate and a portion of the right quadratojugal, the anterior rim of the right orbit, pieces of the right and left maxillae and a fragment of the right premaxilla (Fig. 4). All of these skull fragments were removed from a single jacket and were once articulated. The skull roof is 123 mm anteroposteriorly and is broken anteriorly at or near the frontal-nasal suture (Fig. 4A). Bones that are present include both frontals, both postfrontals (left is incomplete), both parietals, both squamosals (left is incomplete), as well as most of the occipital complex. Neither orbit nor prefrontal is present. The supratemporal fenestrae are present; however, extreme distortion of the skull has caused both fenestrae to splay open so that they appear much longer and wider than is normal in pseudopalatines. The frontals are 29 mm wide and 69 mm long, though they are probably not complete. The postfrontals are 25 mm wide and 30 mm long and are approximately square in outline. The right squamosal is 154 mm long and 40 mm wide. The right supratemporal fenestra is 23 mm wide and 62 mm long, whereas the left one is only 13 mm wide and 60 mm long.

The left jugal is an arcuate bone fragment with two branches at an acute angle that form the ventral and anterior rims of the lateral temporal fenestra (Fig. 4B). The ventral branch is a flattened rod that is smooth and is 18 mm dorsoventrally, 115 mm anteroposteriorly and 5 mm mediolaterally. The anterior branch is fractured, but would be a wide, flat triangle of bones that articulates with the maxilla and the lacrimal. It has a moderately sculptured surface, and is 110 mm anteroventrally to posterodorsally and 5 mm mediolaterally. Medially, the anterior branch has a projecting ridge, 10 to 18 mm mediolaterally, that is part of a sutural zone between the jugal and the palatal bones. This suture runs along the anteroventral rim of the lateral temporal fenestra, creating a horizontal shelf. Anterior and somewhat ventral to this shelf is a shallow concavity. The right jugal is similar in morphology to the left, but it is less complete (Fig. 4C). The right jugal is an L-shaped fragment with little of the anterior fenestral rim left intact. The medial shelf of the suture zone is much more distinct in the right jugal, so that muscle scars are plainly evident on the sculptured surface just
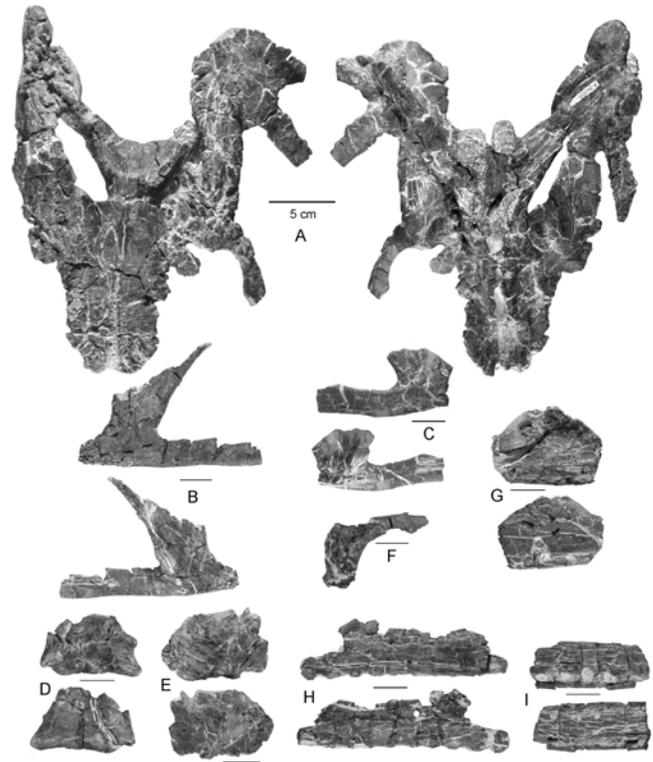
FIGURE 4. NMMNH P-36000, a partial juvenile skull of *Pseudopalatus buceros*. **A**, Dorsal (left) and ventral (right) views of the skull deck. **B**, Left jugal in lateral (top) and medial (bottom) views. **C**. Right jugal in lateral (top) and medial (bottom) views. **D**, Right quadrate in anterior (top) and posterior (bottom) views. **E**, Right quadratojugal fragment in medial (top) and lateral (bottom) views. **F**, Anterior rim of right orbit. **G**, Right maxilla fragment in medial (top) and lateral (bottom) views. **H**, Left maxilla fragment in lateral (top) and medial (bottom) views. **I**, Right premaxilla fragment in lateral (top) and medial (bottom) views. Scale bars are 2 cm unless otherwise labeled.

ventral to the shelf. The fragment is 86 mm anteroposteriorly, 37 mm dorsoventrally, 6 mm mediolaterally and 17 mm mediolaterally at the medial shelf.

The right quadrate is in good condition and is broken only at its dorsal surface (Fig. 4D). It is trapezoidal in outline, being 50 mm mediolaterally across the base and 23 mm mediolaterally across the dorsal break. It is 35 mm dorsoventrally and 17 mm anteroposteriorly. There is a small process halfway up the medial surface that is broken. The ventral surface is a smooth rod that articulates with the mandible. The anterior and posterior faces of the quadrate are smooth and flat. On the lateral edge, the suture with the quadratojugal has split open and is partially infilled with matrix. The fragment of the quadratojugal that is preserved is an ovoid plate that is separate from the quadrate (Fig. 4E). This plate of bone is 55 mm anteroposteriorly, 34 mm dorsoventrally and 6 mm mediolaterally at its thickest point. It is moderately concave on the medial side and is badly fractured.

The right anterior rim of the orbit is a separate fragment that is a gentle arc in outline (Fig. 4F). It is heavily sculptured on the dorsal surface and rises up posteriorly into a thin ridge that borders the orbit itself. This fragment is 59 mm anteroposteriorly on its longest dimension, 41 mm mediolaterally at its widest and 18 mm dorsoventrally at its thickest. A portion of the prefrontal suture is visible on the medial part of the dorsal surface.

One fragment of each of the maxillae is preserved. The right fragment may be from the anterior margin of the narial crest, whereas the left fragment appears to be from a more posterior position in the

left maxilla. The right maxillary fragment is a trapezoidal plate of bone that changes from a vertical plate to a horizontal ledge by a right angle turn at the tooth row (Fig. 4G). It is 50 mm dorsoventrally, 65 mm anteroposteriorly, 11 mm mediolaterally near the top of the bone and 23 mm mediolaterally at the tooth row. There are 3½ alveoli present with no teeth. There is a hint of sculpturing on the more dorsal half of the lateral side. The horizontal shelf on the ventral aspect has sutural "ribbing" on the ventral and medial sides and is, in general, much thicker and more robust than the vertical plate. The bone fragment becomes thicker anteriorly with a flat plate rising anteriorly from the vertical lateral plate. This indicates that this fragment is probably fairly close to the premaxilla-maxilla suture just anterior to the narial crest. The left maxillary fragment is a long bar of bone that is concave medially (Fig. 4H). It is 122 mm anteroposteriorly, 33 mm dorsoventrally at its highest point and 15 mm mediolaterally at the tooth row. There are 10 alveoli present, but no teeth. This fragment thickens ventrally into the tooth row, but without the dramatic shelf seen in the right maxillary fragment. There is a thin sulcus on the lateral face just above the tooth row. This specimen is probably from a more posterior position in the maxilla because no sutures are visible on the medial or ventral surfaces, the alveoli diameters increase and the generally concave shape suggests an opening within the palatal area.

The fragment of the right premaxilla that is preserved is 67 mm anteroposteriorly, 26 mm dorsoventrally and 17 mm mediolaterally (Fig. 4I). This fragment is a semi-cylinder of bone that has been warped so that it is laterally convex. Thin grooves run anteroposteriorly on the lateral side, whereas there is a rounded bar medial and ventral of the tooth row. Five alveoli are present, but no teeth. Sutural "ribbing" covers the medial surface of the fragment.

NMMNH P-37283 is an incomplete skull of a juvenile *P. buceros* that includes a portion of the skull deck, the right and left jugals, a fragment of the left maxilla, the occipital condyle and the right squamosal (Fig. 5). The skull deck includes portions of the frontal, the right postfrontal, the parietals, the left posterior orbit rim, the left postfrontal, the left squamosal and the anterior margins of both supratemporal fenestrae (Fig. 5A). The skull deck from its anteriormost point to the posterior edge of the parietals is 87 mm long. The frontal-parietal sutures are not visible. The frontal, as preserved, is 15 mm wide, but very fragmentary. The right postfrontal is 24 mm mediolaterally and 22 mm anteroposteriorly. The parietals are approximately 35 mm mediolaterally, though they are incomplete. The left postfrontal is not well enough defined to be measured. The left squamosal region is 92 mm long from orbit rim to the posterior edge of the squamosal. The squamosal itself is 35 mm mediolaterally. The right supratemporal fenestra is 16 mm mediolaterally and the left is 0.9 mm mediolaterally.

The right jugal is similar to previously described jugals in that it is an arcuate bone fragment with two branches at an acute angle that form the ventral and anterior rims of the lateral temporal fenestra (Fig. 5B). The ventral branch is a flattened rod that is smooth and is 10 mm dorsoventrally, 56 mm anteroposteriorly and 5 mm mediolaterally. The anterior branch is fractured, has a moderately sculptured surface, and is 55 mm anteroventrally to posterodorsally and 10 mm mediolaterally. Medially, the anterior branch has a projecting ridge, 10 to 12 mm mediolaterally, that is part of a sutural zone between the jugal and the palatal bones. This suture runs along the anteroventral rim of the lateral temporal fenestra, creating a horizontal shelf. Anterior and somewhat ventral to this shelf is a shallow concavity. The left jugal is similar in morphology to the right (Fig. 5C), though it has a portion of the posterior maxilla joined to the anterior edge. The ventral branch is 49 mm anteroposteriorly, 18 mm dorsoventrally and 5 mm mediolaterally. The anterior branch is 46 mm anteroventrally to posterodorsally and is 13 mm mediolaterally. The medial shelf is also 13 mm mediolaterally. The fragment of maxilla attached to the anterior portion of the left jugal is 30 mm dorsoventrally, 28 mm anteroposteriorly and 9 mm mediolaterally. It is too poorly preserved to determine if there is sculp-
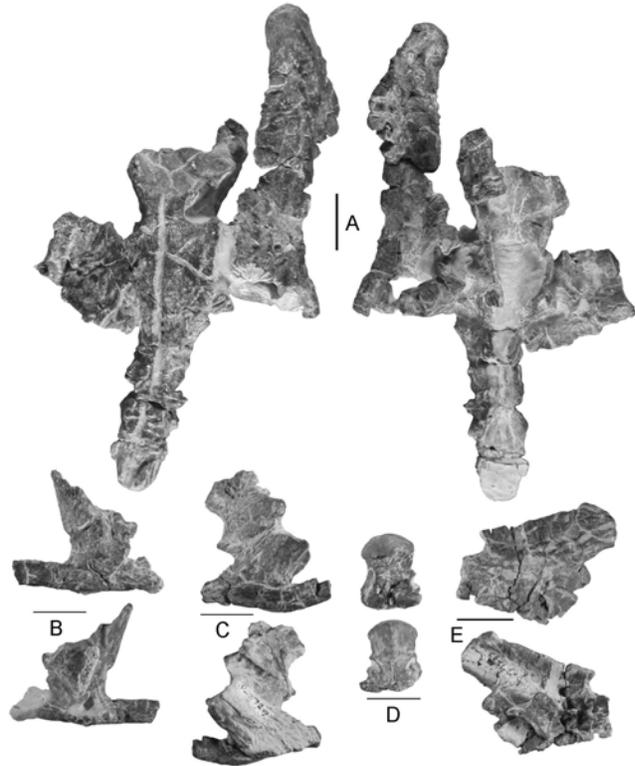
FIGURE 5. NMMNH P-37283, a partial juvenile skull of *Pseudopalatus buceros* from the Snyder quarry. **A**, Partial skull deck fragment in dorsal (top) and ventral (bottom) views. **B**, Right jugal in lateral (top) and medial (bottom) views. **C**, Left jugal in lateral (top) and medial (bottom) views. **D**, Occipital condyle in dorsal (top) and ventral (bottom) views. **E**, Right squamosal in dorsal (top) and ventral (bottom) views. Scale bars = 2 cm.

turing present, and the suture between the jugal and maxilla is not entirely clear.

The occipital condyle is a cylinder of bone that flares both anteriorly and posteriorly (Fig. 5D). Anteriorly, it flares out to meet the basioccipital, whereas posteriorly it flares out into the articular surface for the axis vertebra. The occipital condyle itself is 30 mm anteroposteriorly, 19 mm dorsoventrally, 22 mm mediolaterally in the center and 23 mm mediolaterally across the articular surface. Both the ventral and dorsal surface have a well-developed ridge than runs anteroposteriorly, with slight concavities on either side. The right squamosal is fragmentary, but does show the characteristic wrinkled texture on the dorsal surface, as well as retaining remnants of the ventral squamosal bar (Fig. 5E). This fragment is 62 mm anteroposteriorly, 11 mm dorsoventrally and 42 mm mediolaterally.

Isolated Cranial Elements

There are also several individual, identifiable skull fragments that have come from different parts of the bonebed (Fig. 6). They include a left distal premaxillary fragment, a right distal premaxillary fragment, a nearly complete right premaxilla, a right maxillary fragment, possible premaxillary or dentary fragments (not described), and a right quadrate and portion of a quadratojugal preserved together.

NMMNH P-33846 is a fragment of a subadult *Pseudopalatus* distal left premaxilla, consisting almost entirely of the tip of the rostrum (Fig. 6A). It is 35 mm anteroposteriorly, 23 mm dorsoventrally at the anterior edge, 15 mm dorsoventrally at the posterior edge and 13 mm mediolaterally. Four teeth are present in the preserved alveoli, though all are incomplete. There are small circular pits in a random pattern on the rostrum, and they become fewer in number along the lateral side. The medial side displays sutural "ribbing" of the premax-
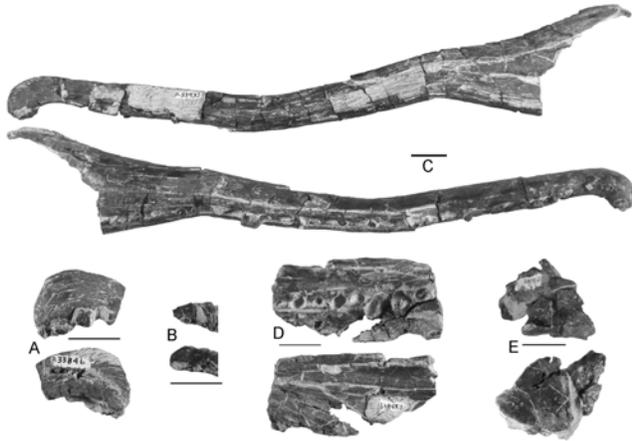
FIGURE 6. Isolated cranial elements of *Pseudopalatus buceros* from the Snyder quarry. **A**, NMMNH P-33846, left distal premaxilla fragment in lateral (top) and medial (bottom) views. **B**, NMMNH P-37894, right distal premaxilla fragment in lateral (top) and medial (bottom) views. **C**, NMMNH P-33935, nearly complete right premaxilla in medial (top) and lateral (bottom) views. **D**, NMMNH P-33849, right maxilla fragment in lateral (top) and medial (bottom) views. **E**, NMMNH P-36829, right quadrate (top) and quadratojugal fragment (bottom). Scale bars = 2 cm.

illary suture. At the anterior end, the rostrum curves strongly ventrally.

NMMNH P-37894 is a right distal premaxillary fragment that represents the rostrum of a juvenile (possibly hatchling) *Pseudopalatus* (Fig. 6B). This fragment is 24 mm anteroposteriorly, 9 mm dorsoventrally at the anterior end and 6 mm mediolaterally. It curves gently ventrally at the anterior end. There are four alveoli, two with teeth present. The lateral surface is broken away, revealing the internal cavities of two alveoli, of which the anterior one has a partial tooth still present. As with NMMNH P-33846, small pits cover the anterior surface of the rostrum. The suture is not distinct, which raises the possibility that the sutures were not well developed in very young phytosaurs.

A nearly complete right premaxilla (NMMNH P-33935) is from a juvenile to subadult phytosaur, and it is broken just anterior to the narial crest (Fig. 6C). It is 330 mm anteroposteriorly, 23 mm dorsoventrally at the rostrum, 50 mm dorsoventrally at the posterior end and ranges from 9 mm to 15 mm mediolaterally. Because the inflection point where the narial crest would begin to rise from the premaxilla is only a quarter of the length of the entire premaxilla, this premaxilla is probably from a female individual. There are 32 alveoli preserved, 19 of which contain teeth or tooth fragments. The rostrum is strongly curved ventrally, and the premaxilla itself is flexed at the midpoint, creating a concave outline. There is a longitudinal groove just above the tooth row on the lateral side that starts as a few shallow pits along the lateral side of the rostrum, then develops into a moderately deep groove before ending abruptly near the 29th alveolus. The tip of the rostrum has small round pits on the anterior side, similar to other premaxillary fragments. On the medial side, the premaxillary sutures are quite visible, though a concavity develops near the 30th alveolus, where the premaxilla begins to flare slightly laterally. This concavity probably corresponds to the beginning of the nasal cavity. The posterior end is mostly missing, but the dorsal portion rises quickly up towards the narial crest.

NMMNH P-33849 is a fragment of a right maxilla from an adult phytosaur that is badly fragmented, but quite large (Fig. 6D). It is 79 mm anteroposteriorly, 21 mm dorsoventrally at the tallest point and 21 mm mediolaterally at the widest point. There are eight alveoli present, three of which contain teeth. This fragment is a moderately thin bone that forms the lateral wall of the maxilla, with a right angle turn at the tooth row into a thin ventral plate that forms part of the palate. There is a poorly defined sulcus just above the tooth row on the lateral side and a well developed sulcus on the medial side of the tooth row. The me-

dial surfaces are all smooth and flat, with no evidence of sutures, indicating that this fragment is probably from the posterior portion of the maxilla.

NMMNH P-36829 is a right quadrate and fragment of a right quadratojugal from a juvenile *Pseudopalatus* (Fig. 6E). The quadrate is mostly complete and is trapezoidal in outline. It is 32 mm mediolaterally across the base, 25 mm dorsoventrally, 10 mm anteroposteriorly at the base and 7 mm anteroposteriorly in the middle. There is a small process halfway up the medial surface that is broken, and the ventral surface is a smooth rod that articulates with the mandible. The anterior and posterior faces of the quadrate are smooth and flat. The quadrate is separated from the attached quadratojugal by a thin infilling of matrix anterior of the quadrate-quadratojugal suture. The quadratojugal is a very fragmentary, thin plate of bone that is triangular in outline. It is 37 mm anteroposteriorly, 32 mm dorsoventrally and 5 mm mediolaterally. There are no markings or sculpturing on the exterior surface, and the interior surface is very slightly concave.

MANDIBLES

Among the bones removed from the Snyder quarry, a complete right mandible as well as three fragments of right mandibles and two of left mandibles have been recovered.

A complete right mandible from the Snyder quarry (NMMNH P-36051; Fig. 7) is long and slender, and is 695 mm anteroposteriorly, 58 mm mediolaterally at the articular process, and 22 mm mediolaterally at the rostral tip. The jaw is mediolaterally thin, but flares just anterior to the articulation point for the quadrate on the skull. There is also a distinct lateral flare at the rostrum's tip to accommodate the much larger rostral teeth. The symphysis is a little less than half of the jaw's complete length. At the point where the mandibles separate, a cup-like hollow is developed on the medial surface of each mandible. The jaw swells dorsoventrally towards the posterior third of the mandible, around the mandibular fenestra. The ventral surface is moderately wide, to accommodate the tooth row, then compresses mediolaterally halfway beneath the fenestra. The ventral surface does not show as pronounced a swelling as the posterior surface, and angles back up to the posterior-most process of the jaw.

There is a moderately deep fossa directed posteriorly on the posterior end of the medial side, which is overhung by a hook-like process that is directed medially and anteriorly. The articular surface for the quadrate is 250 mm anterior of the posterior-most process of the jaw, and rises up from a concavity that defines the posterior surface of the jaw. The articular surface itself is dorsally directed and is deeply concave, matching the shape of the quadrate. All structures posterior and medial of the quadrate's articulation point are not visible from the lateral side, except the posterior-most projection. Anterior of the articular surface, the dorsal surface drops off rapidly into the mandibular fenestra. The mandibular fenestra is mediolaterally wide at its posterior margin, with two walls. Towards the anterior margin of the fenestra, the medial and lateral surfaces of the mandible close. The fenestra itself is ellipsoid in outline. The lateral side of the medial bone surface is visible through the fenestra, except in the posterior quarter of the fenestra. On the lateral surface of the mandible, thin, longitudinal

FIGURE 7. NMMNH P-36051, complete subadult mandible of *Pseudopalatus buceros* from the Snyder quarry. Scale bar = 5 cm.
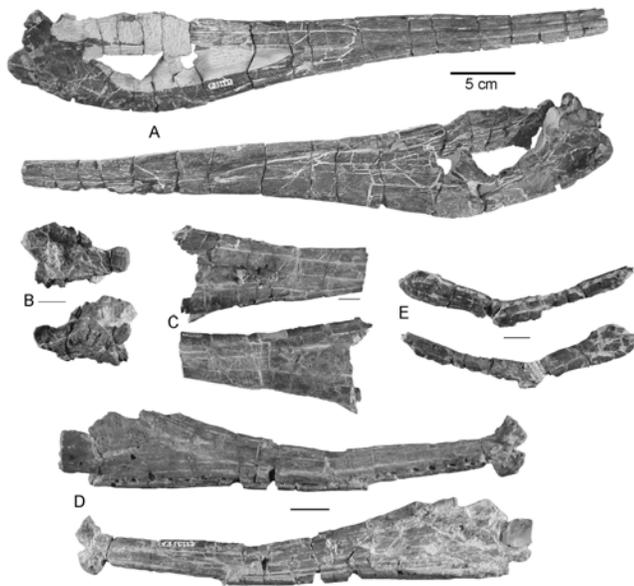
FIGURE 8. Isolated mandible fragments of *Pseudopalatus buceros* from the Snyder quarry. **A**, NMMNH P-33667, an incomplete right mandible in lateral (top) and medial (bottom) views. **B**, NMMNH P-35982, a fragment of the posterior of a right mandible in medial (top) and lateral (bottom) views. **C**, NMMNH P-33662, right mandible fragment in lateral (top) and medial (bottom) views. **D**, NMMNH P-35444, left mandible fragment in lateral (top) and medial (bottom) views. **E**, NMMNH P-35366, a left mandible fragment in lateral (top) and medial (bottom) views. Scale bars are 2 cm unless otherwise noted.

grooves run from the rostrum to the anterior margin of the fenestra. There are 42 alveoli, but no teeth were preserved in the mandible. The alveoli show little indication of heterodonty, although the three rostral alveoli indicate larger teeth (type C of Hunt, 1994; "tip of snout" teeth of Hungerbühler, 1998).

NMMNH P-33667 is a nearly complete right mandible of a subadult phytosaur (Fig. 8A). It is 422 mm anteroposteriorly, 19 mm dorsoventrally at the anterior end, 50 mm dorsoventrally at the posterior end, 14 mm mediolaterally at the anterior end and 44 mm mediolaterally at the widest part of the posterior end. There are approximately 22 alveoli present, with several of them apparently interconnected. The mandible is missing the anterior portion. The splenial is 145 mm posterior of the preserved anterior end and is well developed. The tooth row ends posteriorly in a very deep, thin groove that continues halfway over the mandibular fenestra. The fenestra is 79 mm anteroposteriorly, 17 mm dorsoventrally and 18 mm mediolaterally. The ventral and dorsal borders of the mandible become gently convex just below the fenestra. The posterior end is very narrow when compared to NMMNH P-36051, and the posterior concavity behind the articulation point is narrow and not well developed. The posterior process is a rounded blade rather than the distinct, separated prong on P-36051. There is a deep concavity on the medial side anterior of the process that is overhung by a shelf of bone that leads anteriorly to the articulation point.

NMMNH P-35982 is the posterior part of a right mandible that probably represents a subadult *Pseudopalatus* (Fig. 8B). This fragment is 75 mm anteroposteriorly, 17 mm dorsoventrally at the anterior end, 45 mm dorsoventrally at the posterior end, 10 mm mediolaterally at the anterior end and 34 mm mediolaterally at the posterior end. This fragment preserves half of the posterior concavity, all of the posterior process and the beginning of the gap at the posterior end of the fenestra. The articular facet for the quadrate is not well-defined and somewhat damaged. The posterior process is a robust peg or prong, much like that of P-36051, and not at all like the thin blade of P-33667. There is a deep concavity on the medial side anterior of the process that is over-

hung by a shelf of bone that leads anteriorly to the articulation point.

NMMNH P-33662 is a fragment of a large right mandible that is 176 mm anteroposteriorly, 42 mm dorsoventrally at the anterior end, 90 mm dorsoventrally at the posterior end, 22 mm mediolaterally at the anterior end and 25 mm mediolaterally at the posterior end (Fig. 8C). This fragment includes the anterior half of the fenestra, which is 84 mm anteroposteriorly, 6 mm dorsoventrally at the anterior end, 30 mm dorsoventrally at the posterior end and 12 mm mediolaterally. Ten alveoli are present, though none have teeth preserved within them. The alveoli have been completely cleaned of matrix in this specimen and are 15 mm deep The medial surface of the alveolar row appears to be delaminating from the alveoli and the interalveolus walls. The medial side of the bone is flat, with no grooves or other sculpturing. The lateral side has a moderately deep groove that twists from the ventral half of the lateral face onto the ventral surface just below the fenestra.

NMMNH P-35444 is a partially complete left mandible that is missing approximately a third of the anterior end and everything posterior of the anterior rim of the intermandibular fenestra (Fig. 8D). It is 241 mm anteroposteriorly, 16 mm dorsoventrally at the anterior end, 40 mm dorsoventrally at the posterior end, 10 mm mediolaterally at the anterior end and 15 mm mediolaterally at the posterior end. No portion of the fenestra is preserved. The medial surface is badly fractured, so that the splenial could not be clearly identified. There is a slight concavity in the posterior third of the bone that may be related to the splenial, but this could also be a preservational feature.

NMMNH P-35366 is the anterior end of a subadult to adult left mandible that is badly fractured, so that it has a sharp angle in the midsection of the bone (Fig. 8E). Its reconstructed length would be 186 mm anteroposteriorly, and it is 23 mm dorsoventrally at the anterior end, 13 mm dorsoventrally at the posterior end, 22 mm mediolaterally at the anterior end and 18 mm mediolaterally at the posterior end. There are 17 alveoli, but no teeth preserved. There is no splenial present, as the mandible is broken anterior of the sutural split. The rostrum is quite bulbous, especially in comparison to P-36051.

DISCUSSION

Pseudopalatus pristinus, the commonly used name for a gracile phytosaur species in Norian-age rocks of the American Southwest, is distinctive in having a "volcano"-like nares and a very long, thin rostrum (Mehl, 1928; Long and Murry, 1995). In 1881, Cope described a skull, *Belodon buceros*, collected from Chinle deposits in Arroyo Seco, near Ghost Ranch, New Mexico (Cope, 1881; Lucas et al., 2002). The holotype skull of *"Belodon" buceros* strongly resembles at least two of the skulls recovered from the Snyder quarry, with narial crests that are tall and very narrow, and that extend halfway along the length of the snout (Figs. 2, 3). Because there is little difference between the two complete Snyder quarry phytosaur skulls and the skull described by Cope, we recognize these skulls as belonging to *Pseudopalatus buceros*.

There is also evidence that phytosaurs were sexually dimorphic, which has important implications for phytosaur taxonomy (Zeigler et al., 2002b). An examination of 11 phytosaur skulls from the Canjilon quarry, which is stratigraphically equivalent to the Snyder quarry, revealed two strikingly different morphotypes that are different only in terms of the length and relative robustness of the premaxillae (Zeigler et al., 2002b) (Fig. 9). The premaxillae define the shape and the length of the rostral crest, and it is apparent that the dimensions of the crest are independent of the overall skull length. In one morphotype, traditionally assigned to *"Pseudopalatus pristinus,"* (Ballew, 1989; Long and Murry, 1995), the premaxillae are long and thin, and lead to an abrupt, volcano-like narial crest. In the other morphotype, typically referred to as "*P. andersoni*" (Ballew, 1989; Hunt, 1994; Long and Murry, 1995), the premaxillae are of the same length as in the first morphotype, but are dorsoventrally expanded halfway along their lengths (Zeigler et al., 2002b). This expansion leads to a longer and taller crest, which is possibly a display feature. Cope's "*Belodon*" *buceros*, as well as two of
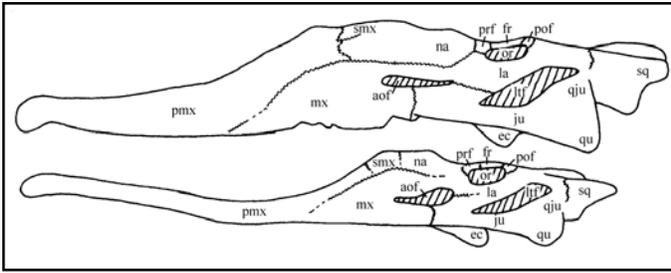
FIGURE 9. Sexual dimorphs of the phytosaur *Pseudopalatus* from the Canjilon quarry. **A**, Line drawing of UCMP 34250 (male) in left lateral view; **B**, Line drawing of UCMP 34249 (female) in left lateral view. Scale bar = 10 cm.

the Snyder quarry phytosaur skulls, are examples of the second morphotype. Therefore, we recognize only one valid species of *Pseudopalatus*, *P. buceros* (Cope) (Lucas et al., 2002).

Despite the clear dimorphism in the cranial anatomy of *P. buceros*, the individual postcranial elements show no obvious dimorphic variation (Zeigler et al., 2003). All of the ulnae, for example, are proportionately identical to one another and cannot be assigned to either a male or a female morphotype. Thus, all of the variation in the anatomy of these animals is occurring within the narrow region of the narial crest. This lack of postcranial variation is further evidence that these phytosaurs are a single taxon, as the dimorphism is more likely a display feature, and not related to ecological niche, for example.

It is of further interest to note that most of the isolated cranial material represents juvenile or subadult animals. Very few fragments are large enough to represent older, and thus larger, animals. There are also few very small elements that could represent hatchlings. Thus, the majority of the phytosaurs represented by the material in the Snyder quarry assemblage are subadult or young adult animals. These individuals would presumably be the strongest and healthiest members of the population and thus the least susceptible to disease or predation. The predominance of these younger, stronger animals provides additional support for a catastrophic mass mortality event (see also Zeigler, this volume).

We would contend that taphonomic distortion of cranial material can lead to erroneous assumptions related to the taxonomy of the phytosaurs (i.e., lead to the recognition of "taphotaxa": Lucas, 2001). For example, the elevation of the skull deck in relation to the nares is used by some authors as one of a suite of distinguishing features of various phytosaur genera (e.g., Ballew, 1986, 1989; Hunt, 1994). However, the narial crest is a relatively solid mass of bone, whereas the skull deck has fenestrae and vacuities that make it a much more open structure. The addition of a mass of sediment on to the top of a phytosaur skull will lead to a greater degree of dorso-ventral compression of the skull deck than of the more solid narial crest, leading to the appearance of elevated external nares in relation to the skull deck. In examining the phytosaur population sample from the Canjilon quarry, the female morphs were usually in much poorer condition than the male morphs, especially in the narial region. The more gracile premaxillae of the females is more susceptible to crushing and lateral distortion than the much more robust crest of the male morphs. A second example, and one that is perhaps more pertinent, is the distortion of the supratemporal fenestra. The shape and degree of visibility in dorsal view of the supratemporal fenestrae is a critical feature for distinguishing among grades of phytosaurs (Hunt, 1994; Long and Murry, 1995). However, dorso-ventral compression or lateral crushing of the skull's posterior region can lead to supratemporal fenestrae that are splayed open or crushed shut. It is not always easy to assess the degree of post-mortem distortion in any given phytosaur skull, especially in the cases of isolated crania from different localities. Thus, we urge caution in relying heavily upon these features for developing the taxonomy of phytosaurs.

CONCLUSIONS

Presently, the Snyder quarry is second only to the Canjilon quarry in terms of the number of phytosaur skulls available for study from a single population. Because the Snyder quarry and the Canjilon quarry are stratigraphically equivalent, and relatively close together, they may represent a single catastrophic event (Zeigler, 2002, 2003; see also Martz, 2002a,b). Consequently, the combined populations of the two quarries may provide an even larger sample of the phytosaur population at this time. We believe that further preparation of the Snyder quarry skulls will yield additional information on the variation (or lack thereof) in the skulls of *Pseudopalatus*. Presently, the population sample from the Snyder quarry supports Zeigler et al.'s (2002b) hypothesis that *P. buceros* was sexually dimorphic, with preserved females having more gracile snouts and smaller narial crests than the males.

Taphonomic data has not been incorporated fully into phytosaur systematics. Recognition of the Snyder and Canjilon quarries as mass death assemblages, presumably of a single population, facilitates identification of sexual dimorphism as a source of variation in *Pseudopalatus*. Furthermore, analysis of the taphonomic effects on phytosaur skulls highlights the need for caution in interpreting the systematic value of features such as the relative positions of the skull deck and nares.

ACKNOWLEDGMENTS

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