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A PHYTOSAUR SKULL FROM THE UPPER TRIASSIC SNYDER QUARRY (PETRIFIED FOREST FORMATION, CHINLE GROUP) OF NORTH-CENTRAL NEW MEXICO

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Abstract—We describe the skull of a subadult pseudopalatine phytosaur from the Late Triassic Snyder quarry, in the Petrified Forest Formation of the Chinle Group, north-central New Mexico. The specimen is complete with minimal distortion. The squamosal bars are moderately wide, and the occipital complex is u-shaped in occipital view. The supratemporal fenestrae are laterally compressed and short in dorsal view. The skull is nearly identical in proportions to the holotype of *Belodon buceros* Cope. Based upon the shape and proportions of the narial crest and upon the suture patterns, we refer this skull to *Pseudopalatus*, not *Nicrosaurus*, and therfore utilize the combination *Pseudopalatus buceros; Arribasuchus* is thus a junior subjective synonym of *Pseudopalatus*.

Keywords: phytosaur, skull; Petrified Forest Formation, sexual dimorphism

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. In three summers of excavation, the following tetrapod taxa have been recovered from the quarry: the primitive theropod *Eucoelophysis* sp., the aetosaurs *Typothorax coccinarum* and *Desmatosuchus chamaensis*, and the phytosaur *Pseudopalatus buceros* (Heckert et al., 2000; Zeigler et al., 2002). Phytosaurs dominate the Snyder quarry assemblage, with 11 skulls discovered so far. These skulls range from a hatchling (estimated skull length of 0.3 m) to a full adult (estimated skull length of one meter). The majority of the skulls appear to be from individuals of subadult age. Of the skulls recovered, one subadult specimen has been fully prepared. Here, we describe this skull and discuss the taxonomy of North American phytosaurs.

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 Rock Point Formation of the Chinle Group (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 of Lucas and Hunt (1993; Lucas, 1998a,b).

DESCRIPTION

NMMNH P-31292 (Figs. 2-3) is a complete skull of a subadult *Pseudopalatus*-grade phytosaur. The skull was found upright near the southwestern edge of the quarry excavations during the 2000 field season. The rostrum of the skull was pointing N11°E in grid square 6S2E of the original excavation.

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

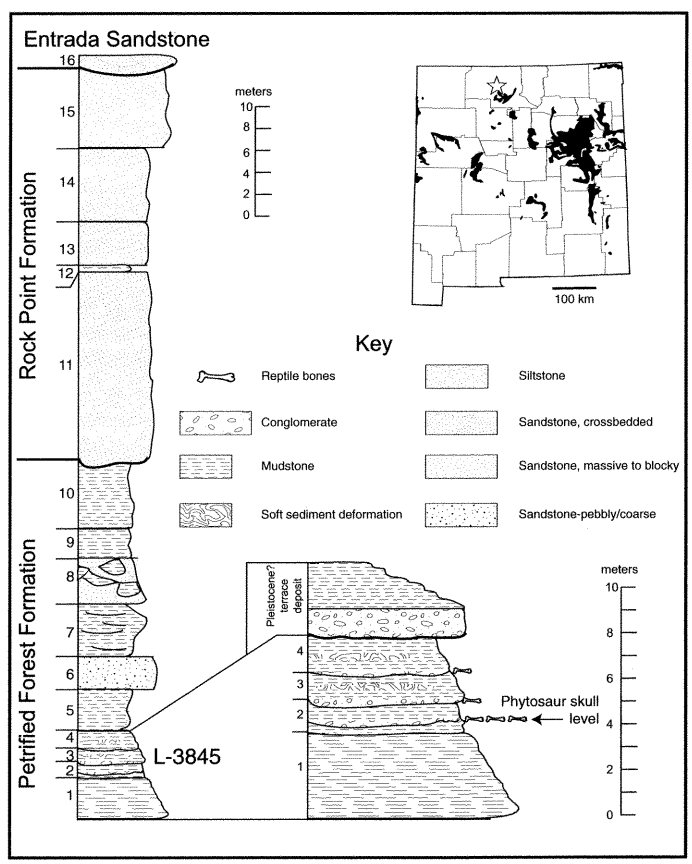

FIGURE 1. Index map and stratigraphic section showing the location of the Snyder quarry (NMMNH locality 3845) and the stratigraphic position of the phytosaur skull described here.

directly ventral to 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 *Belodon buceros* Cope (Huene, 1915; Lucas et al., 2002; Fig. 4). 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).

Dorsal Aspect

Rostrum/Premaxillae

The premaxillae are long, thin rectangular bones that are 362 mm in length, comprising approximately half of the total length of the skull (Fig. 3). The anterior third of the premaxillae are highly pitted on the bone surface, though the pitting tapers off toward the narial crest. The pits are fairly regular in size, small (3-4 mm diameter), and are evenly distributed, especially near the ventral edge. A thin sulcus runs from the rostrum to the end of the tooth row along the lateral edge of the premaxilla and maxilla. The sulcus is more strongly defined on the maxilla and is obscured in places by the pitting along the premaxilla. On the ventral aspect of the specimen, the premaxilla-maxilla suture falls approximately halfway along the tooth row (234 mm from the anterior tip of the snout). In this specimen, the posterior half of the premaxillae are more robust in their dorsoventral and lateral aspects, leading to a longer, taller crest than is normally seen in *Pseudopalatus pristinus* (Fig. 4; Mehl, 1928). There are 20-21 tooth positions on each premaxilla.

Septomaxillae

The septomaxillae are narrow, approximately rectangular bones that are 91 mm long, and these bones define the topmost portion of the narial crest. The sutures between the septomaxillae and maxillae are partially obscured on NMMNH P-31292.

Maxillae

The maxillae are clearly defined along their anterior border with the premaxillae by sutures, but the maxilla-lacrimal and maxilla-nasal boundaries are not clear. The sutures are partly obscured by adhering matrix and conservation materials. The maxillae are 300 mm long and 50 mm wide and rise to join with the septomaxillae and nasals to create the lateral sides of the narial crest. In the ventral aspect, the maxillae contact the palatines and the ectopterygoids medial to the tooth rows. There are 21-22 tooth positions on each maxilla.

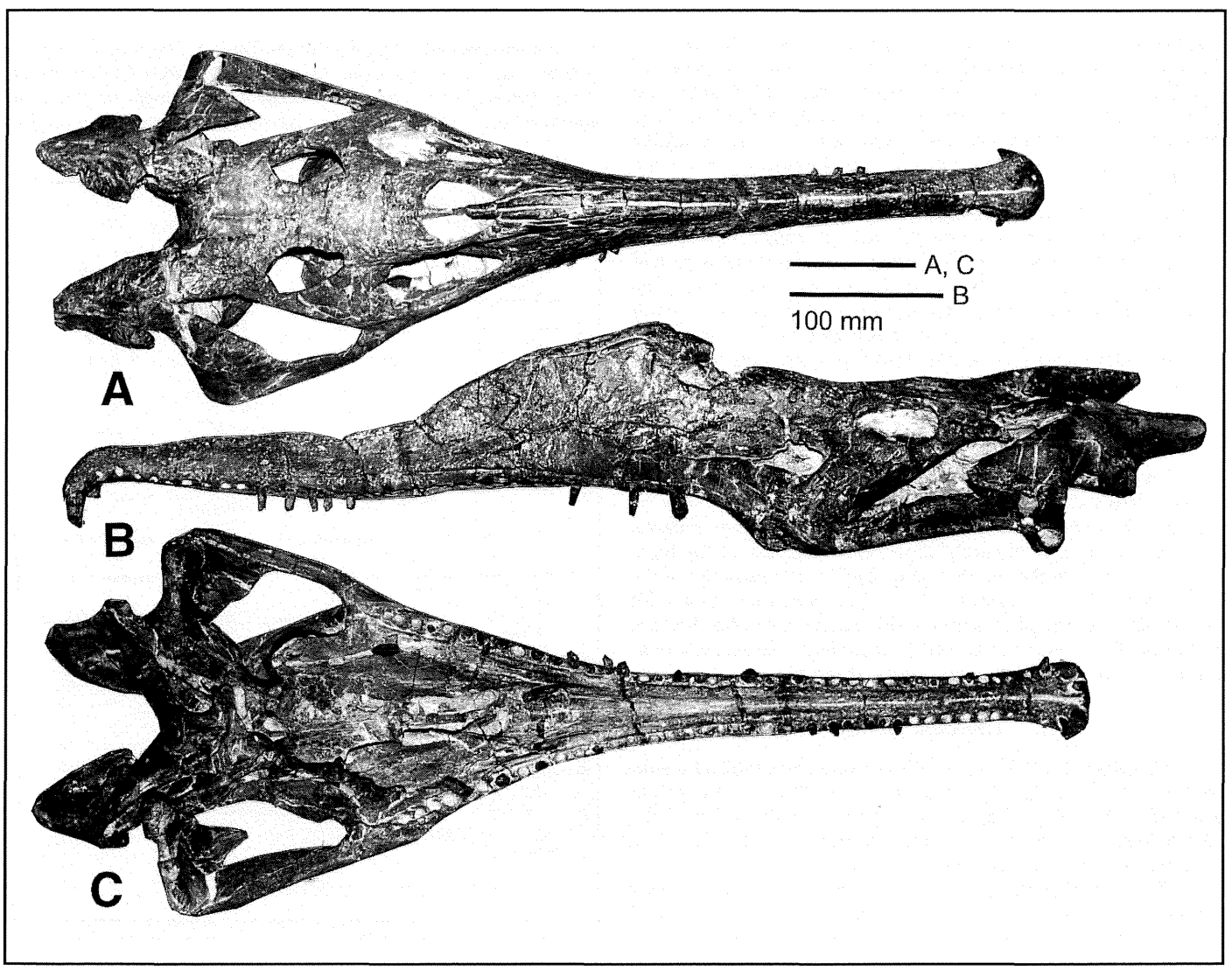

FIGURE 2. NMMNH P-31292, skull of *Pseudopalatus* in **A**, dorsal, **B**, left lateral, and **C**, ventral views.

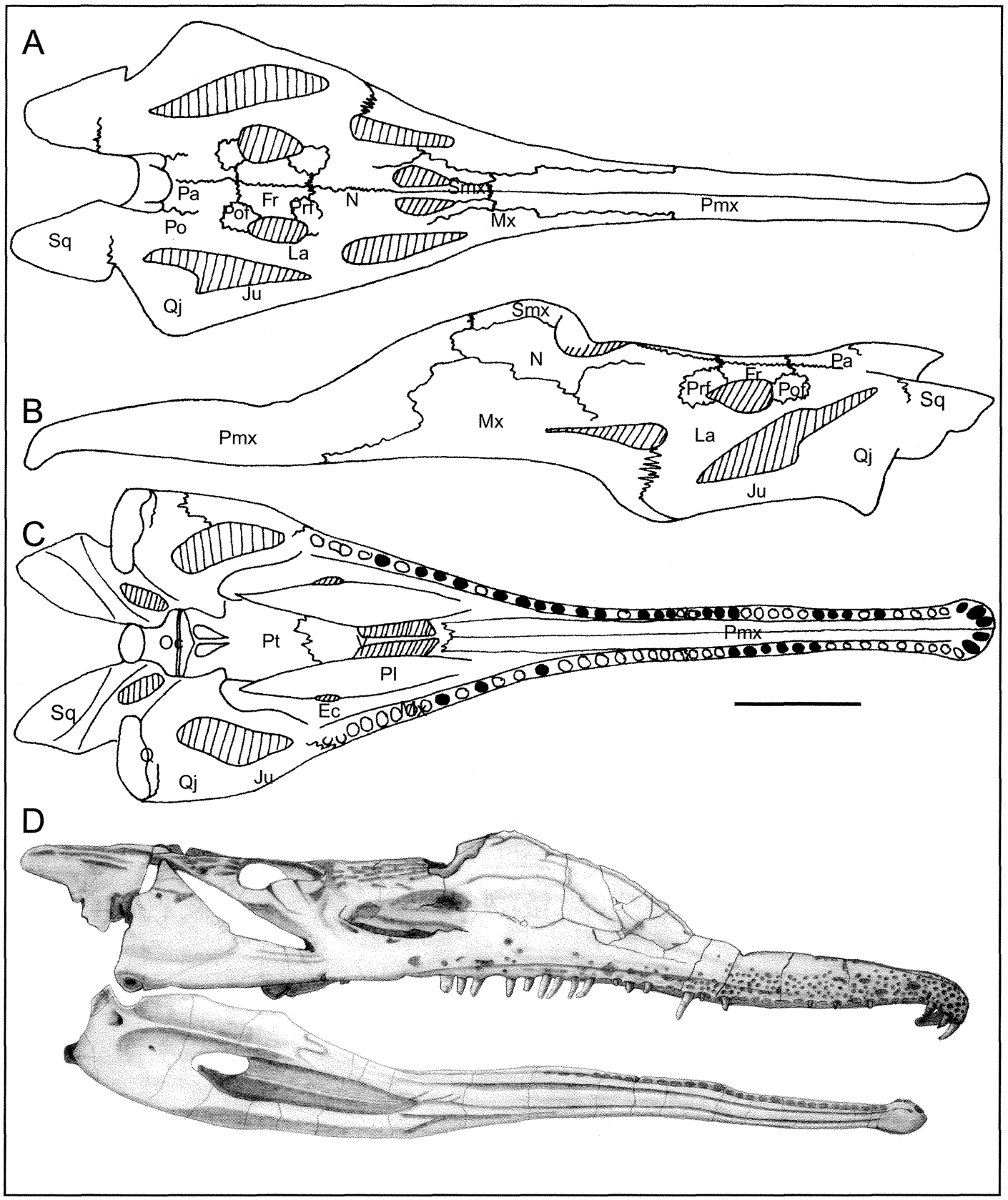

FIGURE 3. Line drawings (A-C) and detailed sketch (D) of NMMNH P-31292. **A-C**, NMMNH P-31292 in **A**, dorsal; **B**, left lateral; and **C**, ventral (reconstructed) views. **D**, Detailed sketch of NMMNH P-31292 (skull) and NMMNH P-36057 (lower jaw) in right lateral view, jaw scaled to match skull. Ec = Ectopterygoid, Fr = Frontal, Ju = Jugal, La = Lachrymal, Mx = Maxilla, N = Nasal, Oc = Occipital, Pa = Parietal, Pl = Palatine, Pmx = Premaxilla, Po = Postorbital, Pof = Postfrontal, Prf = Prefrontal, Pt = Pterygoid, Q = Quadrate, Qj = Quadratojugal, Smx = Septomaxilla, Sq = Squamosal, V = Vomer. Open tooth sockets are vacant. Scale bars = 10 cm.

TABLE 1. Selected measurements of 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 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 measured)	30 mm
Width of supratemporal fenestrae (right fenestra measured)	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 taken only on right side)	
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

Narial crest and nares

The narial crest is composed of portions of the maxillae, the septomaxillae, and the nasals. It rises 50 mm above the level of the skull deck, even with postmortem distortion taken into account. The crest is 110 mm at its maximum height and consists of two separate humps separated by a small groove. The anterior portion of the crest is broad and rises more gently from the premaxillae. The posterior portion of the crest is narrower and rises steeply before dropping off precipitously at the nares. The nares are 60 mm long, 20 mm wide, and sit at the same level of the skull deck, whereas the anterior margin of the nares sweeps up to meet the top of the narial crest.

Nasals

The nasals are long, rectangular bones that house the nares and form the posterior portion of the narial crest. They are 180 mm long and 30 mm wide. The anterior half of the nasals is sharply angled medially to form the crest, whereas the posterior portion of the nasals is nearly horizontal, forming the anterior-most portion of the skull roof. The sutural borders between the nasals and the maxillae and the nasals and the lachrymal are not clearly defined and were approximated in the drawings of the skull (Fig. 3). The lateral edge of the right nasal is crushed medially just above the antorbital fenestra.

Frontals and parietals

The prefrontals, frontals and postfrontals form the medial borders of the orbits as well as the central portion of the skull roof. The prefrontals and postfrontals are small, generally square bones that are, on average, 25 mm long and wide. The frontals together form a rough cross-shape in the center of the skull roof and are 65 mm long and 10 mm wide at their minimum width. The maximum width of each frontal is half of the minimum interorbital distance, which is 23 mm. Sutural contacts for the frontals and the medial edges of both the prefrontals and postfrontals are clear. There was some difficulty in identifying the lateral margins of the pre- and the postfrontals. The parietals form the posterior half of the skull roof and are 38 mm long and 24 mm wide. The parietal sutures are clearly defined.

Orbits

The orbits are approximately ovoid in outline, though the right orbit appears to be larger than the left due to distortion of the skull. On average, the orbits are 63 mm long and 40 mm wide. They are set high on the skull roof, with their lateral margins depressed ventrally relative to the medial margins. They lie on a vertical plane between the antorbital and lateral temporal fenestrae and on a perpendicular vertical plane between the nares and the antorbital fenestrae.

Lachrymals

The lachrymals are difficult to measure because the lachrymal-maxilla and lachrymal-nasal margins are not visible. The lachrymals are generally rhombohedral, and, at their longest, are approximately 160 mm long and approximately 40 mm wide (measured at the dorsal end of each lachrymal). The lachrymal forms the posterior margin of the antorbital fenestra, the medial margin of the lateral temporal fenestra and the lateral margin of the orbit.

Jugals and quadratojugals

The jugals and quadratojugals form one continuous L-shaped structure that defines the posterolateral margins of the skull. This is where the skull is widest. The jugals are 93 mm long and 30 mm wide on average. The quadratojugal is 103 mm long and 76 mm wide on the right side. The left quadratojugal has been broken, and a portion of the bone juts out into the lateral temporal fenestra. The contacts of the jugals with the maxillae are not clear.

Squamosals

The postorbital squamosal bars are 100 mm long (average) and approximately rod-like. Both are slightly splayed out, though it is not immediately apparent if the widening of the squamosals is natural or due to postmortem distortion. The distance from the middle of one squamosal to the middle of the other is 130 mm. Both squamosals are widest at their anterior borders and are 70 mm wide on average. The squamosals are strongly ornamented, with a series of ridges and grooves running along their length.

Fenestrae

The anterior margins of the antorbital fenestrae are in line with the anterior margins of the nares. These fenestrae are 110 mm long (measurement based on the left fenestra), 33 mm wide and ovoid. The right fenestra's medial wall has been crushed in until it is nearly beneath the midline of the right nares. Thus, the right fenestra appears much wider and deeper than the relatively undistorted left antorbital fenestra. The lateral temporal fenestrae are much larger than the antorbital fenestrae, rhombohedral, and strongly backswept posteriorly in outline. These fenestrae are 150 mm across the long axis and 50 mm long across the short axis. The left lateral temporal fenestrae has a portion of the quadratojugal protruding into it where the quadratojugal separated from the jugal and was displaced medially and dorsally. This distortion is probably due to postmortem and postburial

damage. The supratemporal fenestrae are very narrow and generally ovoid in shape. They are 30 mm long and 10 mm wide (measurements based solely on the right fenestra). They are visible both from posterior and dorsal views. The left fenestra is crushed almost completely shut by distortion of the left squamosal, which is broken at the suture along its anterior edge and displaced ventro-medially into the fenestra.

Ventral Aspect

All measurements on the ventral aspect of this specimen were taken from the right side due to postmortem distortion of the left side (Table 1).

Palatine

The palatines are long, rhombohedral bones that drop down from the level of the maxillae and premaxillae. They are 100 mm long and 30 mm wide. Sutural contacts with the maxillae, the ectopterygoids and the pterygoid are all distinct. The palatines are spread apart so that the choanae are clearly visible, similar to Camp's (1930, pl. 6) illustration, but not illustrated in *P. pristinus* as described by Mehl (1928).

Ectopterygoids and pterygoid

The ectopterygoids are small, generally rectangular bones with distinct sutural contacts with the pterygoids and the palatines. The distance between the ectopterygoid flanges is 85 mm. The pterygoid is a wide, rectangular plate of bone that sits dorsal to the ectopterygoid flanges and is partially hidden above the palatines.

Quadrates

The quadrates consist of two thick, cylindrical bars that are perpendicular to the long axis of the skull. They are 80 mm wide on average and 20 mm long, though the left quadrate is broken in the middle, so that it appears to be wider than usual. The lateral edge of the left quadrate is also displaced dorsally whereas the right is still nearly horizontal. The quadrates drop down below the horizontal plane of the palatines and pterygoids.

Occipital complex

The occipital complex is very clearly defined on this specimen, and it consists of the basioccipital, occipital condyle, and the basisphenoid. The length of the entire complex is 60 mm, whereas the width of the basioccipital and the basisphenoid is 61 mm, and the width of the condyle is 32 mm. Strong bars of bone extend along the ventral surfaces from the posterolateral corner of each squamosal toward the occipital complex. The right supratemporal fenestra is readily visible along the lateral margin of the complex.

Occipital Aspect

When viewed from the occipital aspect, the squamosal bars project posteriorly and slightly laterally, forming the u-shaped occipital complex *sensu* Ballew (1989). The quadrates are both visible anterior and lateral to the squamosals. The basioccipital and occipital condyle are also visible, ventral of the center of the posterior margin of the skull deck. The rostral crest and the anterior margin of the exterior nares rises above the skull deck.

Dentition

There are 42 tooth sockets in each tooth row in the premaxillae and maxillae. Only 11 teeth remain on the left side and 22 on the right. There were also three loose teeth preserved with the skull. The posterior teeth are weakly blade-like (type B teeth of Hunt, 1994; maxillary teeth of Hungerbühler, 2000), and the medial and anterior teeth are more caniniform (type U and type I teeth of Hunt, 1994; premaxillary teeth of Hungerbühler, 2000). The rostral teeth are very large, laterally compressed and more sharply recurved than the other teeth (Type C teeth of Hunt, 1994; tip-of-snout teeth of Hungerbühler, 2000). Thus, this skull has a heterodont dentition, as compared to the apparent homodont dentition seen in *P. pristinus* and *Mystriosuchus* (Hunt, 1994; Long and Murry, 1995).

COMPARISON

Current taxonomic schemes

There are several different taxonomic schemes that have been proposed for the phytosaurs (Gregory, 1962; Westphal, 1976; Ballew, 1989; Hunt, 1994; Long and Murry, 1995). Although we generally favor Ballew (1989), she did not discuss European phytosaurs in detail, so we utilize the scheme proposed by Long and Murry (1995) but note relevant information from the other taxonomic schemes. We have focused our comparisons on the pseudopalatines due to the similarities between *Pseudopalatus* skulls and NMMNH P-31292. We rely primarily upon Long and Murry (1995) for comparison to *Pseudopalatus*, Hunt (1994), and, to a lesser extent, Hungerbühler and Hunt (2000), for comparison of the specimen to *Nicrosaurus kapffi* and *Mystriosuchus planirostris*. Note here that we do not accept the species-level taxonomy of *Nicrosaurus* proposed by Hungerbühler and Hunt (2000).

Pseudopalatus

Specimens of *Pseudopalatus* possess moderately wide squamosal bars that are usually prominently sculptured. The supratemporal fenestrae are short and narrow in dorsal view with narrow anterior margins. A medial expansion of the squamosal bar narrows the transverse diameter of the supratemporal fenestrae (Long and Murry, 1995). The parietal-occipital complex in *Pseudopalatus* is an inverted U-shape. The area around the orbits is usually strongly sculptured, with less ornamentation on the rest of the skull roof. The external nares are elevated just above or even with the skull roof and sit on an abrupt and distinct prominence (Long and Murry, 1995). These phytosaurs do not possess the massive, full-crested rostrum seen in some other phytosaurs, and many completely lack a rostral crest. The dentition in *Pseudopalatus* is weakly heterodont to homodont, with specimens having 40 to 42 teeth in the tooth row (Gregory, 1962). The anterior end of the snout is bulbous and gently down-turned with a constriction just posterior to the anterior margin. A careful comparison of illustrations (Fig. 4; Mehl, 1928) demonstrates that premaxillary length is nearly 75% of the total skull length in *Pseudopalatus*, a measurement similar to *"Belodon" buceros*.

Nicrosaurus

In comparison to *Pseudopalatus*, *Nicrosaurus* also has moderately wide squamosal bars and supratemporal fenestrae that are short and moderately wide in dorsal view. The squamosals are more laterally compressed and cylindrical, and the parietal-occipital complex is an inverted V-shape. The external nares are at the level of the skull roof, rather than elevated above it as is in *Pseudopalatus*. Specimens of *Nicrosaurus* usually have a very robust rostral crest that may extend nearly the full length of the rostrum. The dentition in *Nicrosaurus* is strongly heterodont, with tooth shapes ranging from wide, laterally compressed blade teeth to cylindrical, recurved caniniform teeth (Hungerbühler, 2000). Specimens usually have 40 to 45 teeth in the tooth row (Hungerbühler, 2000). The snout constricts just posterior to the bulbous rostral end, then turns sharply downwards.

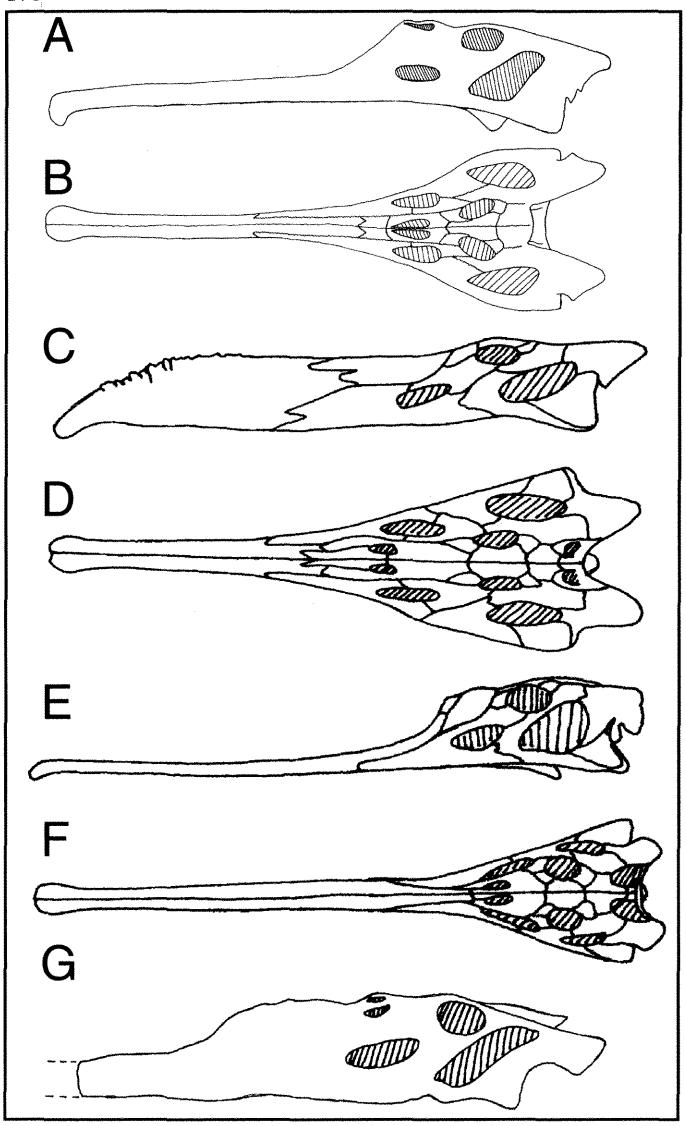

FIGURE 4. Line drawings of phytosaur skulls. **A-B**, *Pseudopalatus pristinus* in **A**, lateral and **B**, dorsal views (after Mehl, 1928); **C-D**, *Nicrosaurus* in **C**, lateral, and **D**, dorsal views (after Westphal, 1976); **E-F**, *Mystriosuchus* in **E**, lateral and **F**, dorsal views (after Westphal, 1976); **G**, *"Belodon" buceros* Cope in lateral view (after Hunt, 1994).

Mystriosuchus

Specimens of *Mystriosuchus* possess short squamosal bars that end abruptly with a hook-like process. The supratemporal fenestrae are visible in dorsal view and are broader than in *Pseudopalatus* and *Nicrosaurus*. The parietal-occipital complex is a shallow U-shape. The external nares are set more posteriorly, relatively close to the orbits and are elevated just above the level of the skull roof (Gregory, 1962), though they do not sit as high in *Mystriosuchus* as they do in *Pseudopalatus*. The rise to the nares in *Mystriosuchus* is also less prominent. The snout is long and very slender with a slight constriction just posterior of the rostrum which is gently down-turned and weakly bulbous. *Mystriosuchus* skulls have as many as 50 teeth in the tooth row and a homodont dentition (Gregory, 1962).

"Belodon" buceros

The first phytosaur taxon from New Mexico, *"Belodon" buceros*, was named from a skull collected by Cope in 1881 from the Chinle deposits in Arroyo Seco, near Ghost Ranch, New Mexico (Lucas et al., 2002; Fig. 4g). As noted above, the holotype skull of *"Belodon" buceros* strongly resembles NMMNH P-31292. In both skulls, the narial crest is tall and very narrow and extends only halfway along the length of the snout. The snout itself in both of these specimens is relatively thin, especially in comparison to *Nicrosaurus kapffi*. In specimens of *N. kapffi*, the narial crest is robust in all dimensions and extends to the tip of the snout. The snout itself is also much wider and more robust than in *"B." buceros*. Thus, we refer Cope's skull to *Pseudopalatus buceros*.

All recent authors agree that the genoholotype specimen of *"Belodon" kapffi* is an indeterminate phytosaur tooth that is now lost (Ballew, 1989; Hunt and Lucas, 1989; Hunt, 1994; Long and Murry, 1995; Hungerbühler and Hunt, 2000). Long and Murry (1995) considered the holotype of Cope's *Belodon buceros* generically distinct from *Nicrosaurus*. Given that *"Belodon"* is a *nomen dubium*, they erected the new genus *Arribasuchus* for Cope's skull. We note here that there is little difference in the skull proportions and suture patterns between Cope's skull and the holotype of *Pseudopalatus pristinus*. Indeed, the most significant differences between the two skulls are in the relative proportions of the rostral crest (and thus the septomaxillae). Accordingly, we recognize Cope's skull as a species of *Pseudopalatus*, *P. buceros* (Cope). *"Arribasuchus"* is thus a junior subjective synonym of *Pseudopalatus*, which we recognize as constituting a single species, *P. buceros*.

TABLE 2. Osteological characteristics of skulls of *Pseudopalatus*, *Nicrosaurus*, and *Mystriosuchus*. (Modified from Gregory, 1962).

	Pseudopalatus	*Nicrosaurus*	*Mystriosuchus*
Position of external nares (relative to aofe)	Posterior	Posterior	Posterior
Posttemporal bar	depressed	depressed	very depressed
Posterior squamosal process	rounded	rounded	absent
Post. squamosal process shape	elongate	short, deep	absent
Upper temporal bar	rounded	rounded	sharp ridge
Teeth on 1/2 upper jaw	39-50	35-49	39-57
Degree of heterodonty	mod. to strong	strong	homodont

aofe=antorbital fenestra

Rostral crest:

Pseudopalatus: Size dependent, confined to posterior half of rostrum
Nicrosaurus (*sensu stricto*): Massive, running the length of the rostrum
Mystriosuchus (*sensu stricto*): Absent

CONCLUSIONS

NMMNH P-31292 is an extremely well-preserved phytosaur skull from the Upper Triassic (Revueltian) Snyder quarry. The skull is similar to *P. pristinus* in that the squamosal bars are moderately wide and the supratemporal fenestrae are short and narrow in dorsal view. The parietal-occipital complex in this specimen is a broad, inverted U-shape. However, NMMNH P-31292 differs significantly from specimens of *P. pristinus* by the presence of a robust narial crest that extends halfway along the snout. However, because the suture patterns are very similar to those of *P. pristinus*, we refer P-31292 to *Pseudopalatus*, specifically to *P. buceros*.

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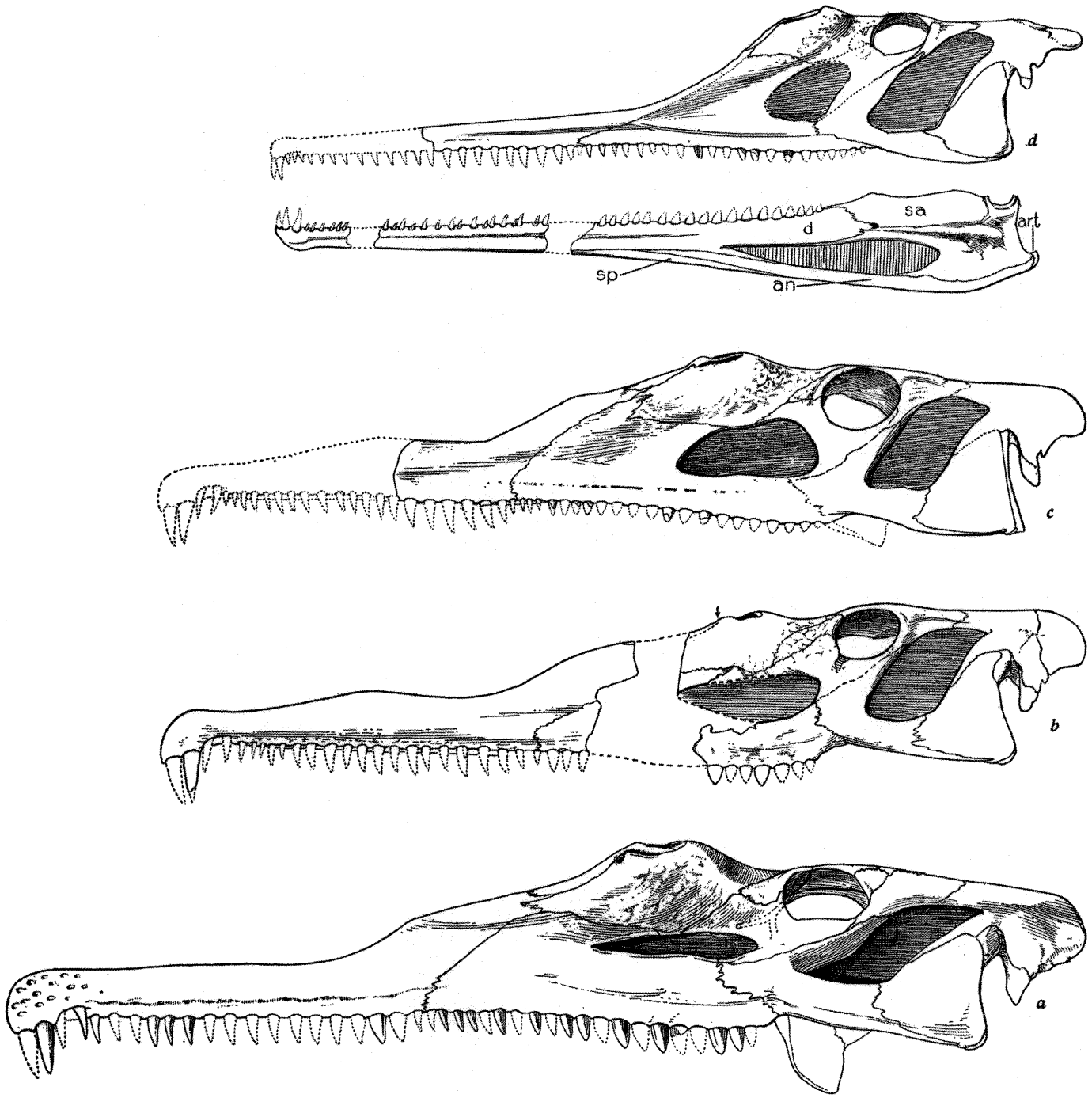

Series of skulls of Machaeroprosopus from a sequence of horizons in the Lower Chinle. *a. M. adamanensis* (type), 7038/26699, 209 feet above Moenkopi-Chinle contact. *b. M. adamanensis*, 7040/27007, 262-foot level. *c. M. lithodendrorum*, 7034/26719, 346-foot level. *d. M. tenuis* (type), 7043/27018, 375-foot interval. x1/6 (from Camp, 1930, fig. 4, p. 24).