INTRODUCTION

Phytosaurs are extinct archosaurs with a fossil record from across Late Triassic Pangea. Among the first Triassic tetrapods described in the early 1800s, an extensive knowledge of phytosaur anatomy is available in their prolific fossil record, particularly from North America and Europe (e.g., McGregor, 1906; Camp, 1930; Westphal, 1976). Despite this, fossils of juvenile phytosaurs are very rare, so the ontogeny of these archosaurs remains poorly understood. Indeed, the only juvenile phytosaur skulls discussed in the literature are the holotype (and only known specimen) of Paleoichthyosaurus (= Arganarhinus) of Long and Murry, 1995) magnoculus, which was originally named as a distinct species by Dutuit (1977), but is a juvenile example of Parasuchus (= Paleorhinus) (Fara and Hungerbuhler, 2000), and another juvenile skull of Parasuchus from Poland (e.g., Dzik, 2001)

Here, we add to the sparse fossil record of juvenile phytosaurs a nearly complete juvenile skull (Figs. 1-5) from the Upper Triassic Whitaker (= Ghost Ranch Coelophysis) quarry at Ghost Ranch near Abiquiu, New Mexico. Our purpose is to describe and illustrate this important fossil specimen to Redondasaurus sp. Spielmann and Lucas (2012, p. 36, figs. 45, 47) also illustrated the unprepared skull and referred it to R. gregorii. Here, we describe the prepared skull and also refer it to R. gregorii.

DESCRIPTION

Overview

The skull and lower jaws are nearly complete, only missing the snout and anterior end (symphyseal tip) of the lower jaw (Figs. 1-5). The right lateral view of the skull is virtually undistorted, but the right side of the mandible has been pushed up and partly obscures the postorbital region, which grows in negative allometry as opposed to the positive allometry seen in other phytosaurs. Although based on a small sample, the data thus imply that this is an important ontogeny-based diagnostic character of Redondasaurus.

JUVENILE SKULL OF THE PHYTOSAUR REDONDASAURUS FROM THE UPPER TRIASSIC OF NEW MEXICO, AND PHYTOSAUR ONTOGENY

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Abstract—Redondasaurus is the geologically youngest known North American phytosaur and an index fossil of the Apachean land-vertebrate faunachron. In the Rock Point Formation (Chinle Group) at the Whitaker quarry, Ghost Ranch, New Mexico, a nearly complete juvenile skull of Redondasaurus was preserved among the many skeletons of the dinosaur Coelophysis. Approximately 220 mm total length, it is the best preserved and most complete juvenile phytosaur skull of its ontogenetic stage known. The skull and lower jaws are nearly complete, missing only the anterior snout tip and anterior end (symphyseal tip) of the lower jaw. This skull shows that many of the diagnostic cranial features of Redondasaurus are present in small specimens, including septomaxillae that wrap around the outer margin of the external narial opening, thickened orbital margins, and inflated posterior nasal behind the external narial opening, and thus not subject to ontogenetic change. However, the juvenile skull does not possess some features that diagnose adult Redondasaurus, including supratemporal fenestrae concealed in dorsal view and reduced antorbital fenestrae. These differences are attributable to differential growth of selected parts of the skull, particularly the great expansion of the squamosal bars to conceal the supratemporal fenestrae in the adult. Thus, the juvenile skull of Redondasaurus demonstrates that juvenile phytosaurs can be diagnosed and assigned to taxa based on some adult characters. We assembled a growth series of five Redondasaurus skulls from which we assessed skull metrics and allometry. Relative growth (log-transformed) data for these Redondasaurus skulls, which range in length from 220 to 1205 mm, better fit a linear regression than a polynomial, which indicates that shape changes during ontogeny occurred along a single, constant trajectory. The allometry of the Redondasaurus skull is similar to that of numerous other phytosaur species, except in the postorbital region, which grows in negative allometry as opposed to the positive allometry seen in other phytosaurs. Although based on a small sample, the data thus imply that this is an important ontogeny-based diagnostic character of Redondasaurus.

PROVENANCE

The juvenile phytosaur skull described here, NMMNH P-44920, is from the Whitaker quarry, the world famous Coelophysis bonebed at Ghost Ranch, New Mexico. The quarry is in the Apachean (late Norian-Rhaetian) interval of the Rock Point Formation (Rinehart et al., 2009; Spielmann and Lucas, 2012). Rinehart et al. (2009, p. 36, fig. 41A) illustrated this skull in left lateral view and briefly described some features of the fossil and reported some measurements. They assigned the specimen to Redondasaurus sp. Spielmann and Lucas (2012, p. 36, figs. 45, 47) also illustrated the unprepared skull and referred it to R. gregorii. Here, we describe the prepared skull and also refer it to R. gregorii.

Dorsal View (Figs. 1B, 2)

The skull has a long, relatively thin snout anterior to the nares composed primarily of the premaxillae. This snout has a trihedral cross section and shows no evidence of anterior expansion into a “bulb” (note,
FIGURE 1. *Redondasaurus gregorii*, NMMNH P-44920, stereopairs of juvenile skull in A, right lateral, B, dorsal, C, left lateral and D, occipital view. In A–C anterior is towards top of the page.
FIGURE 2. *Redondasaurus gregorii*, NMMNH P-44920, **A**, photograph and **B**, line drawing of juvenile skull in dorsal view. **Abbreviations:** *aof*, antorbital fenestra; *d*, dentary; *f*, frontal; *j*, jugal; *mx*, maxilla; *n*, nasal; *o*, orbit; *p*, parietal; *pf*, prefrontal; *pmx*, premaxilla; *prf*, prefrontal; *q*, quadrate; *qj*, quadratojugal; *smx*, septomaxilla.

though, this “bulb” may have been present but is now missing). The suture between the premaxillaries and maxillaries is well anterior to the nares, and separates the premaxillaries from the septomaxillaries, which surround and make up the dorsal edge of the narial opening.

The septomaxillaries extend posteriorly to form the postero-dorsal rim of the external nares, where they are overlapped dorsally by the nasals. The nasals interdigitate posteriorly with the prefrontals (laterally) and the frontals (medially). The frontals form the medial portion of the dorsal skull roof between the orbits, and suture posteriorly to the postfrontals (laterally) and the parietals (medially). The postfrontals are broadly triangular and make up the postero-dorsal orbital rim. They meet the postorbitals dorso-laterally, and the postorbitals form part of the postero-lateral margin of the orbits. Just posterior to the lateral temporal fenestra, each postorbital is sutured to the squamosal, but also dorsally overlaps the squamosal to extend posteriorly onto the dorsal surface of each “squamosal bar.”

The supratemporal fenestrae are well defined and visible in dorsal view, medial to the squamosal horns. These fenestrae are antero-posteriorly elongate ovals medial to the narrow “squamosal bars.” Medial to the fenestrae are the parietals and the occiput.

**Right Lateral View (Figs. 1A, 3)**

The long, thin snout rises over a short distance to the narial region, where the external nares form a raised, dorsally-directed pair of openings just above the anterior portion of the antorbital foramen. This foramen is an antero-posteriorly-oriented “teardrop” with the point directed anteriorly.

The skull roof rises posterior to the nares, and the orbit is relatively large and nearly circular. The prefrontal and a posteriorly-directed lamina of the lacrimal form the anterior edge of the orbit. The lacrimal also forms the dorsal edge of the antorbital foramen, separating it from an anterior lamina of the nasal. Most of the antorbital foramen (its anterior and ventral edges) is encased by the maxillary.

The jugal is largely obscured by the lower jaw on the right side of the skull. However, on the left side, part of it is well exposed, forming much of the anterior margin of the lateral temporal fenestra. The quadratojugal and quadrate make up the postero-ventral portion of the skull, and form the jaw joint.

The “squamosal bars” project posteriorly as a slightly concave plate of bone (in lateral view) with a rounded, right angle dorso-posterior end.

**Ventral View (Figs. 1C, 4)**

The palate is a very long and narrow triangle, with the main point directed anteriorly. There are 28 small, slightly oval maxillary alveoli. One preserved tooth is a long, pointed cone that is striated and very slightly recurved. The palatines are long, thin, paired bones that cover the roof of the palate medial to the tooth rows.

Just ventral to the antorbital foramen, the palatal vacuity extends anteriorly as a long narrow fossa between the palatines. Some osteoderms on the ventral right edge of the specimen obscure the pterygoid region on the left side, but the small ectopterygoid is evident, just anteroventral to the pterygoid. The basicranium is largely obscured.
FIGURE 3. *Redondasaurus gregorii*, NMMNH P-44920, **A**, photograph and **B**, line drawing of juvenile skull in right lateral view. Abbreviations as in Fig. 2.
FIGURE 4. Redondasaurus gregorii, NMMNH P-44920, A, photograph and B, line drawing of juvenile skull in left oblique ventrolateral view. Abbreviations: od, osteoderm, all other as in Figure 2.
FIGURE 5. Redondasaurus gregorii, NMMNH P-44920, A, photograph and B, line drawing of juvenile skull in occipital view. Abbreviations as in Figure 2.
Most of the occiput is not discernable because of damage, distortion or some remaining matrix cover. There is a distinct “pocket” formed by the parietals and upper part of the occipital between the supratemporal fenestrae. The occipital, including the condyle, is displaced and attached to the medial side of the left lower jaw ramus, near its articular end. The occipital condyle is gently convex and not as wide as the ventrally concave main body of the occipital.

**Lower Jaw (Figs. 1A, C, 2–4)**

The lower jaw is long and slender. The anterior portion is mostly the dentary bones divided, in part, medially by the splenials (cf. Kischlat and Lucas, 2003). Posteriorly, a long, ovoid mandibular fenestra is present. The surangular borders much of the dorsal aspect of this fenestra, and the angular forms its postero-ventral edge. The articular surface for the quadrates is a low, broad, concave surface at the posterior end of the jaw.

**SKULL METRICS AND ALLOMETRY**

We assembled a growth series comprising five *Redondasaurus gregorii* skulls from which we assess skull metrics and allometry (Table 2). Note that in some cases the sum of the skull segment lengths is a few percent different than the total length. This is because of slight taphonomic distortion of the skulls. The best-preserved side was measured for each skull segment, but because the preservation was slightly different between the two sides, the sum of the segments was often not exactly the same as the total length. Three of the skull lengths were estimated (“e” in Table 2) because the snout tips were missing. Estimates were made based on 23 average-sized (for the particular skull) tooth sockets being present anterior to the premaxillary-maxillary suture.

**Metrics**

The *Redondasaurus* skulls in our metrics database (Table 2) vary in length from 220 mm to 1205 mm, encompassing the range of very small juvenile to very large adult. Previous to the discovery of NMMNH P-44920, the smallest nearly complete *R. gregorii* skull was the estimated 840 mm-long female morph, NMMNH P-31095 (see Spielmann and Lucas, 2012 for a discussion of inferred sexual dimorphism in *Redondasaurus*). The addition of the 220 mm-long juvenile skull to the database, NMMNH P-44920, greatly extends the growth series, thus enabling accurate assessment of skull metrics and relative growth throughout ontogeny.

We show selected skull metrics as a function of skull length (Fig. 6A, Table 3). Linear regressions provided the best curve fits to the data as judged by their Pearson correlation coefficients (R²). We compare the skull metrics of *Redondasaurus gregorii* to those of numerous other phytosaurs (Fig. 7A). The database used in this comparison includes 39 individuals representing 11 genera accumulated by the authors. Generally, the *R. gregorii* data points (filled points in the plot) are contained within the scatter of the overall population, the one exception being the postorbital skull segment. The postorbital region of adult *R. gregorii* is significantly shorter than the corresponding region of other phytosaur skulls, whereas the postorbital region of the juvenile is similar to or slightly longer than others.

**TABLE 2. *Redondasaurus gregorii* growth series database. “e” = estimated skull length, “m” = measured skull length, M/F indicates gender, A-P = anteroposterior. All measurements in mm.**

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<th>Skull length</th>
<th>M/F</th>
<th>A-P orbit diameter</th>
<th>Preorbital length</th>
<th>Premaxillary length</th>
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</table>

### Occipital View (Figs. 1D, 5)

In occipital view, both quadrates are apparent and are nearly parallel to each other but form an acute angle with the sagittal plane, indicative of distortion of the fossil. The articular surface of the jaw and the distal end of each quadrate are a medio-laterally long and antero-posterolrly short ginglymus that is ventrally and posteriorly slightly convex, but anteriorly concave. Each quadrate is a nearly triangular bone in occipital view that widens distally.
FIGURE 6. Metrics and allometrics of the skull of *Redondasaurus gregorii*. **A**, Bivariate plot of selected skull metrics with linear regressions. **B**, Bivariate allometry plot of selected skull metrics with linear regressions. Natural log transforms of the data are plotted. The slope of the linear regressions equals the allometric constant.
Within the limits of our database, of moving the orbits posteriorly as the animal grows larger. In this re-
exhibits negative allometry (allometric constant = 0.89), which indicates
metric behavior in this region.
Comparison to other phytosaur skulls (Fig. 7B) shows virtually identi-
ial growth of the snout to the total skull length does not change throughout ontogeny.
respectively), showing that these regions grow in isometry with respect
constant = 1.3, Fig. 7B), which would effectively move the orbits ante-
see the postorbital data in Figure 7B. A linear regression is better fit by
Allometrics
Allometric study defines shape change throughout the ontoge-
etic growth of an animal. Relative growth of various skull regions is
shown by plotting the natural log transforms of the metrics and then
fitting linear regressions (slope-intercept form) to the data (Fig. 6B). The
allelic constants that indicate the rate of growth of y (the pertinent skull region or segment) with respect to x (the total length of the skull) (Fig. 6B, Table 3). Allom-
eters <1 show negative allometry, where y grows at a lower rate than x; an allometric constant = 1 indicates isometry, where x and y grow at the same rate (no shape change); and a constant >1 shows positive allometry, where y grows at a higher rate than x (Gould, 1966).

The allometric constants (Fig. 6B, Table 3) of the postorbital and prenarial segments of Redondasaurus essentially = 1 (1.00 and 0.98, respectively), showing that these regions grow in isometry with respect to overall length. That is to say that the proportion of the long preorbital snout to the total skull length does not change throughout ontogeny. Comparison to other phytosaur skulls (Fig. 7B) shows virtually identi-
behavior in this region.

In contrast, the postorbital portion of the Redondasaurus skull exhibits negative allometry (allometric constant = 0.89), which indicates that it becomes relatively shorter throughout growth. This has the effect of moving the orbits posteriorly as the animal grows larger. In this re-
pect, within the limits of our database, R. gregorii appears to be unique among phytosaurs (Fig. 7B, Table 4). The postorbital area of the great majority of these animals shows positive allometry (collective allometric constant = 1.3, Fig. 7B), which would effectively move the orbits ante-
riorly throughout growth. Note that in the postorbital data in Figure 7B the data points of adult R. gregorii are all below the corresponding data points of other phytosaurs, whereas the postorbital data point of the juvenile is somewhat above the regression line. The result is that the R. gregorii data show a much lower slope (much more negative allometry). These data suggest that negative allometry of the postorbital region of the skull is diagnostic of Redondasaurus. The functional significance of this negative allometry merits study, as it likely indicates a unique shift in the jaw musculature of this phytosaur during ontogeny.

The anteroposterior orbit diameter of Redondasaurus shows strong negative allometry (allometric constant = 0.69). Thus, the orbits of juve-
niles are relatively quite large and they grow relatively little throughout life. The relative growth of the orbit is essentially identical to that of other phytosaurs (Fig. 7B).

The maximum width of the skull of Redondasaurus occurs at, or immediately anterior to, the quadrates. Maximum skull width grows in positive allometry (allometric constant = 1.25) (Fig. 7B, Table 3). The skull of R. gregorii is thus relatively slender in youth and grows proportionately wider throughout ontogeny. R. gregorii is similar to other phytosaurs in its skull width allometry, having a slightly higher allometric constant, even though its data points fall within the scatter of those of other species (Fig. 7B).

Discussion
All of the relative growth data for Redondasaurus are better fit by a linear regression than by a polynomial. This indicates that shape changes, where they occur, are along a single trajectory throughout life (McKinney and McNamara, 1991).

The allometry of the Redondasaurus gregorii skull is similar to that of numerous other phytosaur species, except in the postorbital region (Fig. 7B, Table 4). Within the limits of our database, this segment of the skull grows in negative allometry in R. gregorii as opposed to the positive allometry seen in other phytosaurs. The data thus imply that this is an important ontogeny-based diagnostic character of Redondasaurus. We calculated the postorbital length allometric constant of three other genera (Parasuchus, Rutiodon, and Pseudopalatus) for comparison to Redondasaurus (Table 4) and found that each of these showed positive allometry. However, several other genera (e.g., Leptosuchus, Anghistorhinus, Mystriosuchus) are not represented by large enough samples to make reliable calculations. The limited data representing these genera appear to indicate positive allometry in their postorbital regions, but a larger sample is required to confirm this. A regression analysis (Appendix) showed that the postorbital allometry of Redondasaurus is distinct from all other genera (P<.01) at the 99% probability level.

NMMNH P-44920 exhibits the slender-snouted female morphology of Redondasaurus gregorii (Spielmann and Lucas, 2012), but because it is certainly younger than the age of sexual maturity, we hesitate to assign a gender to this specimen. The other members of the growth series include three male morphs and one female morph (Table 2). While there is some scatter of the data points above and below the regression lines (Fig. 6), the position of any individual data point above or below the line does not correspond to the assigned gender of the specimens. We see no tendency toward different relative growth in the male and female skull morphs except in the narial crest.

TAXONOMY
Spielmann and Lucas (2012) provided a comprehensive revision of all the specimens of Redondasaurus and considered it to consist of a single species, R. gregorii (= R. bermani). Based on more than a dozen adult skulls and skull fragments they identified the following features as diagnostic of R. gregorii among phytosaurs: (1) supratemporal fenestrae concealed in dorsal view; (2) reduced antorbital fenestrae; (3) prominent pre-infratemporal shelf at the anterodorsal margin of the lateral tempora-
fenestra; (4) septomaxillae wrap around the outer margin of the external
opalatus buceros) have supratemporal fenestrae visible in dorsal view as well, however, they are more slit-like and proportionately are not as mediolaterally

<table>
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</tr>
<tr>
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FIGURE 7. Metrics and allometrics of 39 phytosaur skulls assigned to 11 genera. Datapoints representing the five *Redondasaurus gregorii* study skulls are filled. **A**, Bivariate plot of selected skull metrics with linear regressions. **B**, Bivariate allometry plot of selected skull metrics with linear regressions. Natural log transforms of the data are plotted. The slope of the linear regressions equals the allometric constant.
wide as the fenestrae of NMMNH P-44920. All adult specimens of *R. gregorii* have concealed supratemporal fenestrae and this suggests that as this taxon grows the supratemporal fenestrae shift from a dorsal-ventral orientation to an anterior-posterior orientation during ontogeny, likely due to an increase in the height of the basicranium or posterior expansion of the skull or a combination of these processes.

2. The antorbital fenestrae of NMMNH P-44920 are not reduced. The adult *Redondasaurus gregorii* skulls studied by Spielmann and Lucas (2012) possess antorbital fenestrae that are approximately as long, antero-posteriorly, as the narial opening. In NMMNH P-44920 the antorbital fenestrae are approximately twice as long as the narial openings. This suggests that during ontogeny the narial opening increases in size disproportionate to the size increase of the antorbital fenestrae.

3. A prominent pre-infratemporal shelf at the anteroverentral margin of the lateral temporal fenestrae cannot be evaluated in NMMNH P-44920. The right lateral temporal fenestra is obscured from view by the dislocation of the mandible, and the left lateral temporal fenestra is partially disarticulated and does not provide clear morphology of its anteroverentral margin.

4. The septomaxillae of NMMNH P-44920 do wrap around the outer margin of the external narial opening; thus, providing an unambiguous link between this specimen and other examples of *Redondasaurus gregorii*. In this juvenile specimen the septomaxillae form approximately two thirds of the lateral margin of the external nares, which is comparable to sub-adult and adult specimens of *R. gregorii* (e.g., Spielmann and Lucas, 2012, figs. 30-38), suggesting that the narial opening proportions were maintained throughout growth.

5. Adult examples of *Redondasaurus gregorii* have thickened orbital margins that consist of prominent rings of bone, at least one cm thick, that surround the orbit. NMMNH P-44920 does not possess thickened orbital margins on the same scale as adult specimens, but does have a distinct ring around its orbit that is raised above the level of the surrounding bone. Thus, NMMNH P-44920 does possess this diagnostic character, but its expression suggests that during growth this ring continues to thicken.

6. NMMNH P-44920 shares with adult specimens of *Redondasaurus gregorii* an inflated posterior nasal behind the external narial opening. Indeed, in NMMNH P-44920 this region forms a distinct subrectangular shelf immediately behind the narial openings. Thus, throughout the growth of *R. gregorii* the proportions of the nasals are maintained.

7. The thickened osteoderms diagnostic of *Redondasaurus gregorii* cannot be evaluated in NMMNH P-44920. The osteoderms associated with the specimen are fragmentary and visible only in ventral view, so we cannot confidently assess their relative thickness.

Two of the seven diagnostic characters identified by Spielmann and Lucas (2012) are not present in the juvenile *Redondasaurus gregorii* specimen, NMMNH P-44920: supratemporal fenestrae concealed in dorsal view and reduced antorbital fenestrae. Three diagnostic features are unambiguously present: septomaxillae wrap around the outer margin of the external narial opening; thickened orbital margin; and inflated posterior nasal behind external narial opening. Two diagnostic features could not be evaluated: prominent pre-infratemporal shelf at the anteroverentral margin of the lateral temporal fenestra and thickened dorsal osteoderms. Thus, it is possible to diagnose relatively young phytosaur specimens using at least some of the diagnostic features recognized in adult specimens. This is also the case in *Parasuchus* (Lucas et al., 2007) and is likely the case in all phytosaur genera.

Acknowledgments

David Berman oversaw excavation of the Whitaker quarry that yield the NMMNH block that contained the *Redondasaurus* juvenile skull described here. Pedro Toledo executed the drawings in Figures 2-5. Adrian Hunt, Julien Kimmig, Phillip Murry, Silvio Renesto and Robert Sullivan provided helpful reviews that improved the manuscript. Andrew Heckert made the measurements of several phytosaur skulls used in this study.

References


APPENDIX

COMPARE TWO REGRESSIONS

Null hypothesis: The data are better fit by a single regression line than by two regression lines, meaning that the postorbital allometry of Redondasaurus is not significantly different from that of other phytosaurs.

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OVERALL TEST OF COINCIDENCE

\[ F_{\text{observed}} = 11.355 \text{ with } 2 \text{ numerator and } 33 \text{ denominator degrees of freedom.} \]

\[ F_{\text{critical}} = 5.32 \text{ with } 2 \text{ numerator and } 33 \text{ denominator degrees of freedom.} \]

\[ F_{\text{observed}} > F_{\text{critical}} \text{ therefore the data are better fit by two regression lines than by one. The null hypothesis is rejected (P < .01) with greater than 99% probability (Glantz, 2005).} \]

Comparison of slopes: \[ t = 3.564 \text{ with } 33 \text{ degrees of freedom; } P = 0.001 \]

Comparison of intercepts: \[ t = 3.303 \text{ with } 33 \text{ degrees of freedom; } \]

\[ P = 0.002 \]