



A giant phytosaur (Reptilia: Archosauria) skull from the Redonda Formation (Upper Triassic: Apachean) of east-central New Mexico

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A GIANT PHYTOSAUR (REPTILIA: ARCHOSAURIA) SKULL FROM THE REDONDA FORMATION (UPPER TRIASSIC: APACHEAN) OF EAST-CENTRAL NEW MEXICO

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Abstract.—In the Summer of 1994, a field party of the New Mexico Museum of Natural History and Science (NMMNH) collected a giant, incomplete phytosaur skull from a bonebed discovered by Paul Sealey in east-central New Mexico. This bonebed lies in a narrow channel deposit of intraformational conglomerate in the Redonda Formation. Stratigraphically, this specimen comes from strata identical to the type Apachean land-vertebrate faunachron and thus of Apachean (latest Triassic: late Norian-Rhaetian) age. The skull lacks most of the snout but is otherwise complete and in excellent condition. As preserved, the skull measures 780 mm long, and was probably 1200 mm or longer in life, making it nearly as large as the holotype of *Rutiodon* (= *Machaeroprosoopus*, = *Smilosuchus*) *gregorii*, and one of the largest published phytosaur skulls. The diagnostic features of *Redondasaurus* present in the skull include robust squamosal bars extending posteriorly well beyond the occiput and supratemporal fenestrae that are completely concealed in dorsal view.

The specimen was originally encased in a plaster jacket only marginally larger than the preserved skull. Still, the contents of the jacket reveal one of the densest accumulations of disarticulated bones in the Chinle Group, including a total of 275 other teeth, bones, and bone fragments, including a smaller phytosaur skull. The smaller skull is poorly ossified, distorted, and slightly disarticulated due to lack of fusion. We suspect that this specimen represents a subadult *Redondasaurus*, but it lacks the temporal region and is thus not identifiable at the genus level. Aetosaur scutes associated with the phytosaurs may represent the first record of *Neoaetosauroides* in North America and suggest correlation of the Apachean Redonda Formation with the Los Colorados Formation of Argentina.

INTRODUCTION

Phytosaurs were large, semiaquatic, carnivorous reptiles known from Upper Triassic strata in North America, Europe, Brazil, India, Thailand, North Africa, and Madagascar. The Chinle Group in eastern New Mexico yields numerous fossils, particularly skulls, of phytosaurs, including a skull from the Travesser Formation described by Stovall and Savage (1939) and a skull from the Redonda Formation described by Gregory (1957, 1972) named *Redondasaurus gregorii* by Hunt and Lucas (1993). Here, we describe a giant phytosaur skull and associated fossils collected from the Redonda Formation by parties of the New Mexico Museum of Natural History and Science in 1994 and briefly comment on its biostratigraphic and taphonomic importance. In this paper, NMMNH = New Mexico Museum of Natural History and Science, Albuquerque.

STRATIGRAPHY AND AGE

The fossils described here were collected from a single locality, NMMNH locality 4211, discovered by Paul Sealey stratigraphically high in the Redonda Formation in Apache Canyon, Quay County, New Mexico (Fig. 1). The fossils occur in a narrow (<3 m wide) channel deposit consisting of an intraformational conglomerate fining upward into a bentonitic mudstone. Clasts in the conglomerate are principally reworked clay pebbles and fossil reptile bones. This deposit is approximately 2.3 m below a prominent, ledge-forming sandstone, the "Redonda Bench," that serves as a marker bed locally. This is the Redonda Ledge marker bed of Gregory (1972).

Hester (1988) studied the Redonda Formation here and at the type locality (Mesa Redonda) and determined that it represents a series of lakes (fine-grained clastics and occasional carbonates) fed

by numerous small streams and rivers (coarser-grained clastics). NMMNH locality 4211 appears to represent a relatively small-scale stream channel draining into one of the Redonda lakes.

Lucas and Hunt (1993; also see Lucas, 1998) established four land-vertebrate faunachrons (LVF) for the chronological intervals represented by successive faunas in the Chinle. The type fauna of the youngest of these intervals, the Apachean, was named for the fauna of the Redonda Formation in Apache Canyon. Index taxa that characterize the Apachean LVF are the phytosaur *Redondasaurus*, especially *Redondasaurus gregorii* Hunt and Lucas, 1993, and the aetosaur *Redondasuchus reseri* Hunt and Lucas, 1991. Other tetrapod taxa from the type fauna include the diminutive metoposaurid temnospondyl *Apachesaurus gregorii* Hunt (1993), a sphenodontian, a procolophonid, a rauisuchian, a large aetosaur, theropods, indeterminate cynodonts, and a giant, undescribed sphenosuchian (Hunt and Lucas, 1997; Lucas, 1998; Lucas et al., 1999). Occurrences of the phytosaur *Redondasaurus* correlate the Redonda Formation with the Travesser Formation in northeastern New Mexico, the Rock Point Formation in north-central New Mexico, including the famous Whitaker quarry (*Coelophysis*) bonebed at Ghost Ranch, and the basal Wingate Sandstone in southern Utah (Lucas et al., 1997a,b).

PALEONTOLOGY

Two jackets were collected from NMMNH locality 4211. The first was a small jacket containing a phytosaur ischium, although this jacket is apparently lost. The second jacket weighed several hundred pounds (200+ kg), and was known to contain a large, incomplete phytosaur skull and numerous other elements at the time of collection. Subsequent preparation of this jacket yielded the giant phytosaur skull described here (NMMNH P-31094; Fig. 2) as well as a "fauna" consisting of approximately 275 other ele-

DESCRIPTION OF THE GIANT SKULL

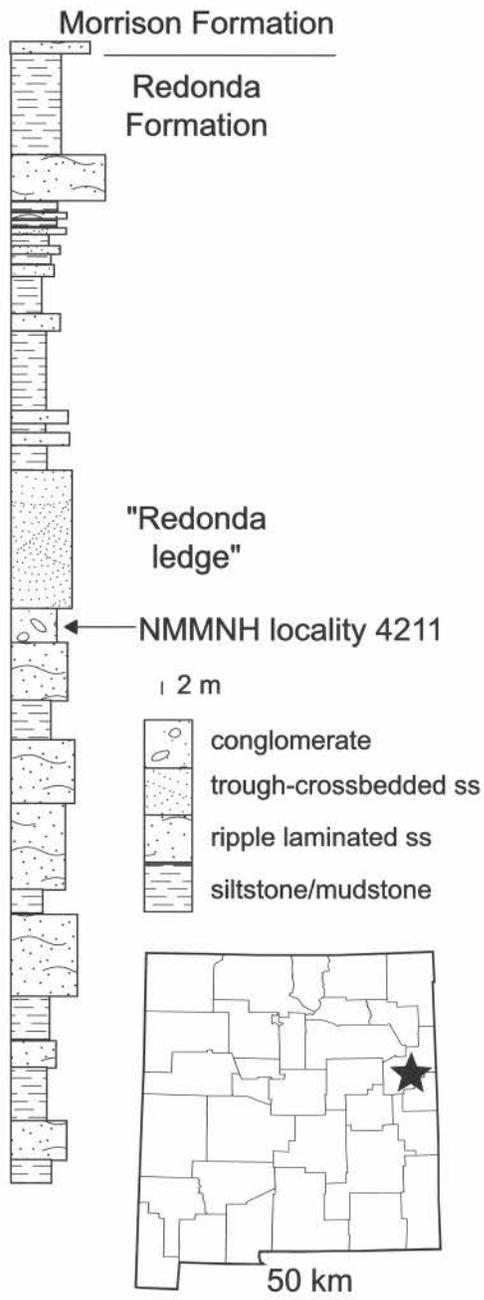


FIGURE 1. Index map and stratigraphic column showing the location of NMMNH locality 4211.

ments, principally teeth and bones of phytosaurs but also including bones of at least one aetosaur and scales of semionotid fish (Fig. 3). Perhaps the most surprising discovery was of a second, smaller, incomplete phytosaur skull (NMMNH P-34095) lying on the palate of the larger specimen (Figs. 2, 3C, 4). In this section we briefly describe the skulls (Figs. 2, 3C) and associated elements. The description of the larger skull, NMMNH P-31094 is the most detailed, yet is still preliminary pending more detailed comparisons with other phytosaurs.

NMMNH P-31094 is a well-preserved phytosaur skull lacking only the anterior portion of the maxillae, much of the premaxillae, and any *in situ* teeth (Fig. 2; Table 1). The skull is very slightly crushed dorsally, with some shearing from left to right (Fig. 2D). The skull is robust, and measures nearly 560 mm across at the quadrates (89 mm interorbital width). The postnarial length of this specimen is approximately 440 mm (540 mm from the anterior margin of the naris). Using Gregory's (1962) calculation that most robust phytosaurs have a prenarial: postnarial length ratio of approximately 1.20-1.25:1, we very conservatively estimate that the complete skull was 1170 mm long. Although many older and more primitive phytosaurs, particularly numerous specimens of *Rutiodon* and *Angistorhinus* reached this length (see Gregory, 1962, fig. 4 for comparison), few phytosaur skulls are as broad and heavily constructed as NMMNH P-31094. Both the sutural arrangements and the rugose surface texture of the bones are clear. Here we focus on the exterior skull bones and their taxonomic significance.

The only remnants of the premaxillae are their elongate dorsal processes, which lie medial to the maxillae and anterior to the septomaxillae. They slope gently from the rim of the nares anteriorly and lack a well-developed, bulbous crest. However, in lateral profile they match the "crested" outline of *Redondasaurus bermani* and are more inclined than those of *R. gregorii*.

The preserved portions of the maxillae are broad in dorso-lateral view, but lack the pronounced lateral bulge seen in the holotypes of *Nicrosaurus kapffii* or *Rutiodon gregorii*, although this character appears to vary within these and other species (Hunt, 1994a; Hungerbühler and Hunt, 2000). The left preserves 14 alveoli and the right 17. The maxillae almost surround the relatively small antorbital fenestrae, which are medio-laterally narrow and antero-posteriorly elongate (Table 1).

The nasals are broad and surround the external nares except for the anterior border, which is comprised of the septomaxillae. At the anterior margin of the external nares, the nasals each form a slightly bulbous process, and the nares are slightly elevated by a narial rim. The nasals terminate shortly behind the posterior edge of the external nares and well anterior to the orbital region.

The elongate septomaxillae extend from their junction with the premaxillae and nasals posteriorly into the external nares. They are widest anterior to the projections of the nasals, and taper posteriorly.

The lacrimal forms the dorsal margin of the antorbital fenestra and extends posteriorly to the orbit. It contributes to the anterior margin of the orbit, but is not as extensively involved as those of smaller species of *Rutiodon* (= *Leptosuchus* of Long and Murry, 1995).

The prefrontals are broad anteriorly, and they taper posteriorly. Narrow lateral extensions of the prefrontals stretch posteriorly to the anterodorsal corner of the orbital rim.

The frontals are small and antero-posteriorly approximately the same length as the orbit. Like most of the skull bones, they are coarsely pitted, but they also possess finer pitting adjacent to the orbit.

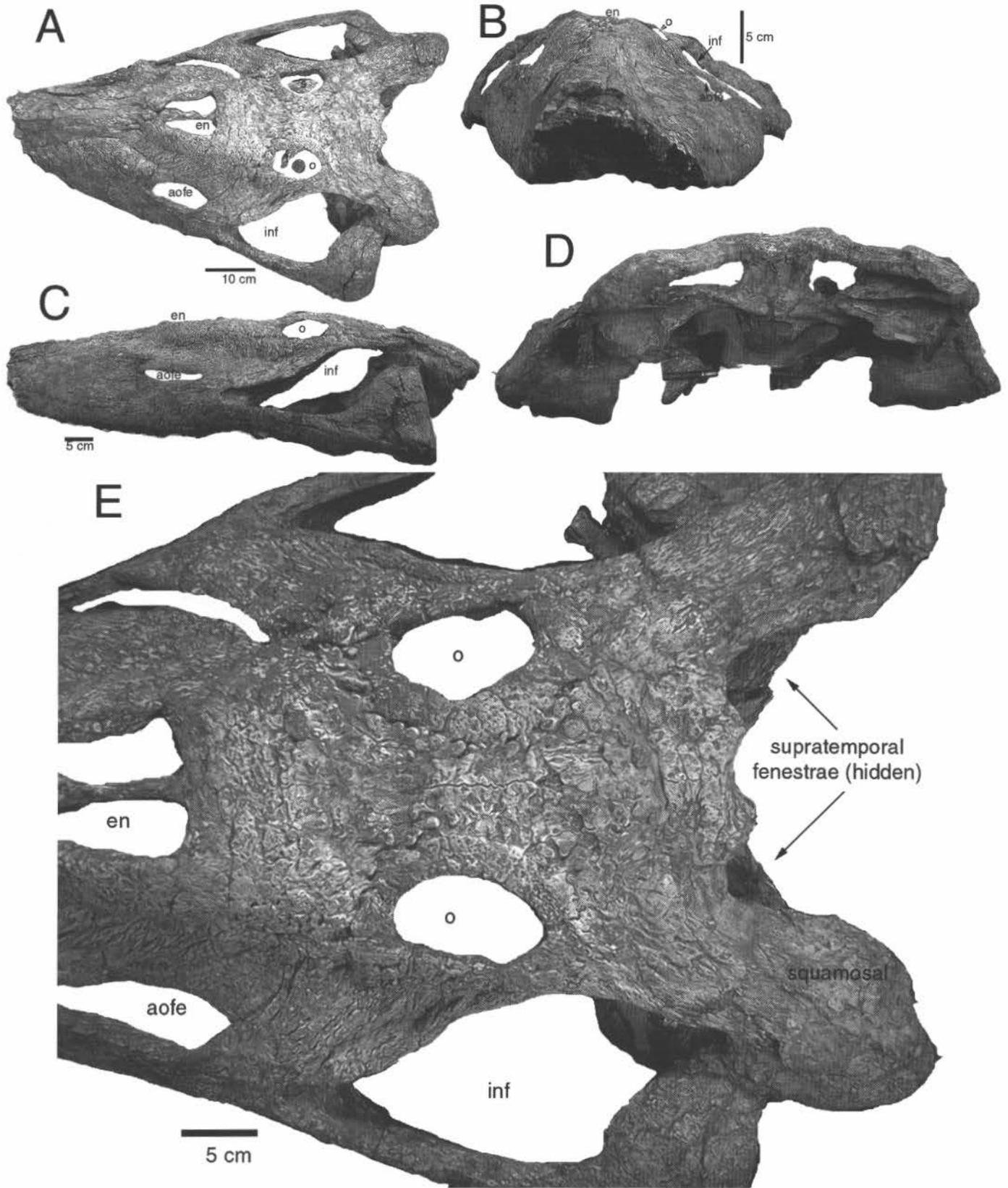


FIGURE 2. Photographs of the giant, incomplete phytosaur skull, NMMNH P-31094. A. Dorsal view showing elements remaining in orbits; B. Anterior view; C. Lateral view, D. Posterior view, metal is brackets of mount; E. Close-up of dorsal view with tooth and scute removed from orbits. Scale bars are 5 cm. Abbreviations: aofe = antorbital fenestra; en = external nares; inf = infratemporal fenestra; o = orbit; s = scute; t = tooth.

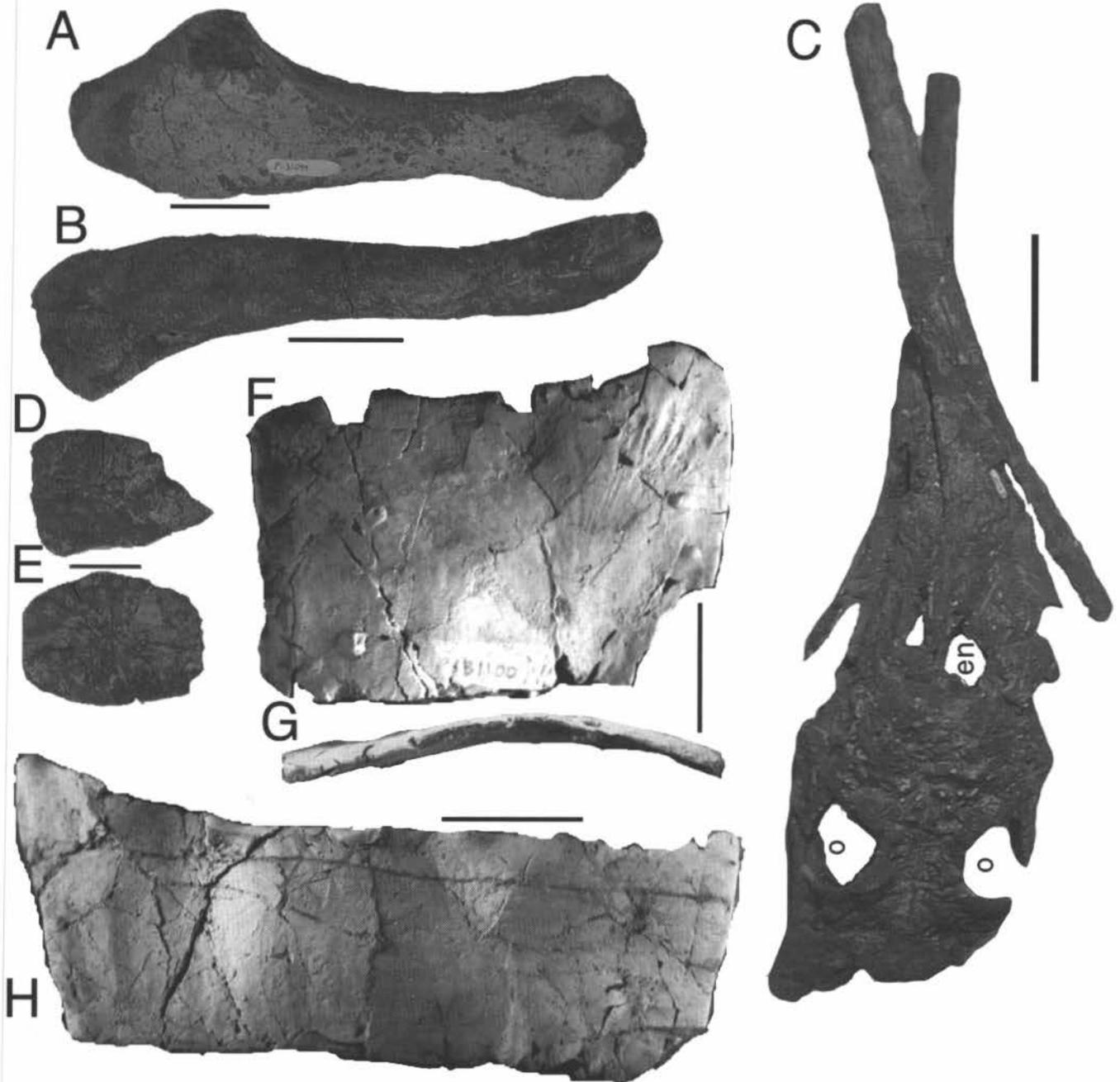


FIGURE 3. A small sample of the fossils found in the jacket with the giant phytosaur skull. A. NMMNH P-31099, large phytosaur right ulna in lateral view; B. NMMNH P-31098, small phytosaur right femur in posterior view; C. NMMNH P-31095, juvenile phytosaur skull in dorsal view; D-E. NMMNH P-31096, representative phytosaur scutes; F-G. NMMNH P-31100, small aetosaur paramedian? scute similar to *Neoaetosauroides* in dorsal (F) and anterior (G) views; H. NMMNH P-31100, larger aetosaur dorsal paramedian scute similar to *Neoaetosauroides* in dorsal view. Scale bars are 5 cm (A-B, D-E), 10 cm (C), and 2 cm (F-H).

Similarly, the relatively small postfrontals contribute to the posterior dorsal margin of the orbit. They also possess finer pitting adjacent to the orbit and coarser pitting posteriorly.

The parietals are relatively broad and flare posteriorly. Each has a slight posterior projection in the middle of its posterior margin. The parietals fully overlap the occiput and associated elements of the braincase, completely covering them in dorsal view.

The squamosals are broad and robust, extending posteriorly

and laterally from the parietals. The posterior process of the squamosal is a thick, heavy flange of bone that does not taper posteriorly and is strongly downturned, extending ventrally below the upper extent of the quadratojugal, although some of this may be the result of postmortem crushing. The supratemporal fenestrae are depressed well below the level of the skull roof and are completely hidden in dorsal view by the squamosals and, to a lesser extent, the parietals.

The quadratojugals are broad in lateral view and taper slightly dorsally. They form the bulk of the posterior margin of the infratemporal fenestra and extend anteriorly across the posterior third of its ventral margin. The quadrates are massive and more than 400 mm apart. Each bears a broad articular surface marked by two condyles for the articulation with the lower jaw.

Anteriorly, the jugals are rectilinear and form the posterior margin of the antorbital fenestra and the ventral margin of the orbit. The dorsal process slants posteriorly and dorsally, forming a sharply acute angle around the anterior edge of the infratemporal fenestra. Posteriorly they are relatively slender across the anterior two-thirds of the ventral margin of the infratemporal fenestra.

SYSTEMATICS OF THE GIANT SKULL

Recent phytosaur classifications include Ballew (1989), Hunt (1994a,b), Long and Murry (1995), and Hungerbühler (1998). All are fraught with difficulties. Ballew (1989) is the only cladistic treatment, but she only examined phytosaurs from the American Southwest. Hunt's (1994a,b) treatment is the most comprehensive, but lacks a cladistic analysis and remains essentially unpublished. Long and Murry's (1995) taxonomy is not based on phylogenetic analysis and only superficially examines numerous issues of taxonomy and non-American specimens. Hungerbühler (1998) provides exhaustive descriptions of Norian phytosaur skulls from southwestern Germany, but is limited in its treatment of other forms and, like Hunt (1994a), remains unpublished. Consequently, it is difficult to assign generic, let alone specific, names with confidence to phytosaurs, in spite of more than 150 years of phytosaur collecting and perhaps 100 well-preserved skulls in Europe and North America alone. Here, we rely principally on Hunt's (1994a) description and comparison of phytosaur skulls, with reference to Ballew (1989) and older classifications, including Westphal (1976) and Gregory (1962). We rely on Long and Murry (1995) only for comparison to specimens they illustrate, as we find their approach to taxonomy at best problematic and, in cases, (e.g., the new genus *Arribasuchus buceros*), arbitrary.

Most workers since Gregory (1962) concur that primitive phytosaurs (*Paleorhinus* and *Angistorhinus* of most recent classifications) had broad supratemporal fenestrae at the level of the skull roof that are visible in dorsal view. The most derived phytosaurs have relatively smaller, depressed supratemporal fenestrae. These fenestra also tend to become partially to completely obscured by the squamosals and parietals in dorsal view. NMMNH P-31094 clearly fits into the derived phytosaurs based on its depressed supratemporal fenestrae that are completely concealed in dorsal view.

Named phytosaur taxa with depressed, concealed supratemporal fenestrae include *Coburgosuchus goeckeli* Heller, 1954,

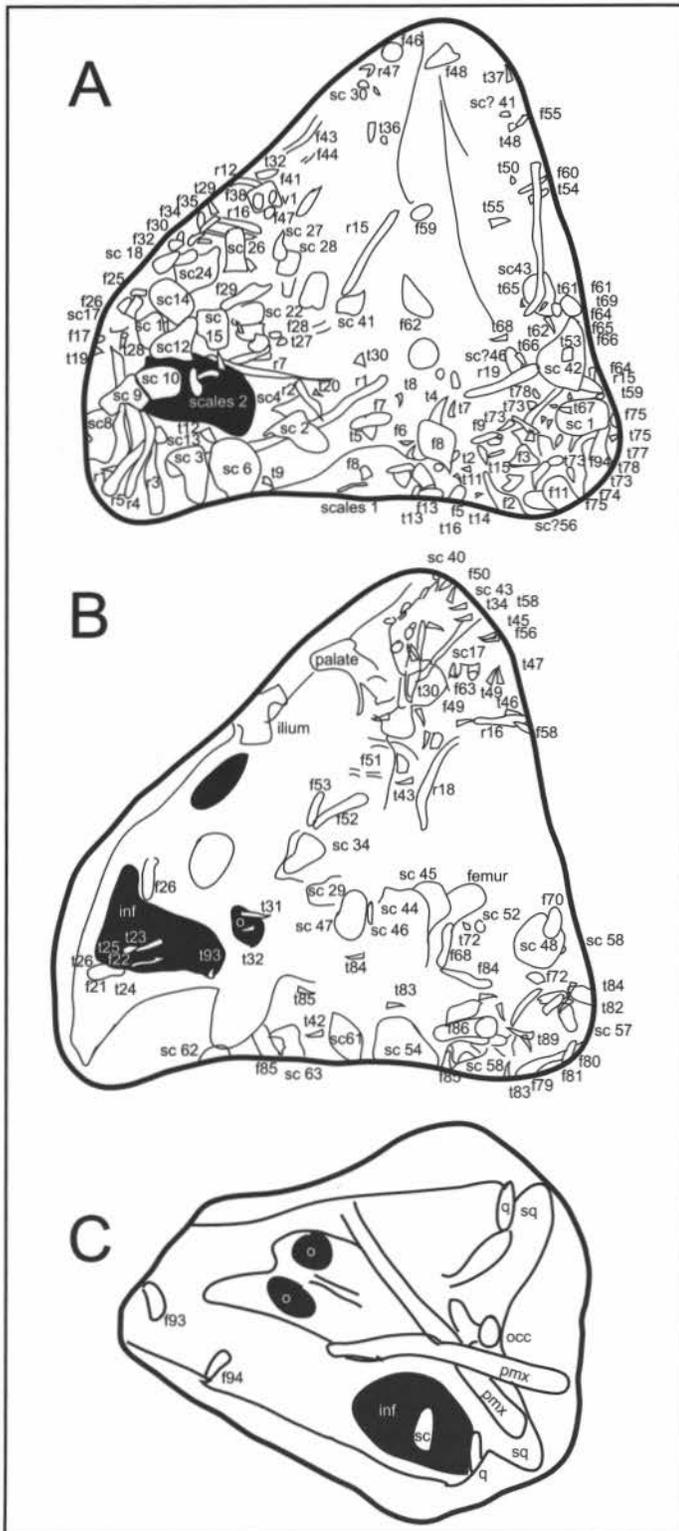


FIGURE 4: Three simplified, schematic sketches showing the distribution of bones found during preparation of the skull. A. Bones encountered dorsal to (stratigraphically below) the giant skull; B. Bones encountered adjacent to the skull on the dorsal surface; C. The position of the subadult phytosaur skull lying on the palate of the (upside-down) giant skull. Two patches of scales indicated. Shading indicates skull fenestra. Complete sketches on file at NMMNH. Abbreviations include: f = fragment, inf = infratemporal fenestra; o = orbit; occ = occipital condyle; pmx = premaxilla; q = quadrate; r = rib; sc = scute, sq = squamosal; t = tooth; v = vertebra. All elements numbered in the order of discovery (scute 1, 2, 3...etc).

Redondasaurus gregorii Hunt and Lucas, 1993, and *R. bermani* Hunt and Lucas, 1993. Additionally, Hunt (1994a) recognized another, robust morph from the Redonda Formation (NMMNH P-4983) with these characters. NMMNH P-31094 differs from all of these in that it possesses a relatively tiny antorbital fenestra. Indeed, no phytosaur illustrated by Gregory (1962), Westphal (1976) or Long and Murry (1995) has an antorbital fenestra as small relative to the nares in dorsal view as NMMNH P-31094. NMMNH P-31094 differs from *Coburgosuchus* in possessing squamosals that do not extend as far posteriorly and are proportionately broader, which we interpret as generally robust. NMMNH P-31094 is considerably more robust than the narrow-snouted (dolichorostral) *R. gregorii*, yet may not be as robust (brachyrostral) as Hunt's (1994a) robust morph exemplified by NMMNH P-4256 if the latter were scaled to the length of NMMNH P-31094. A true rostral crest is not as prominent as in many taxa, although the snout does taper from the nares anteriorly, as in *R. bermani*. Therefore, because we remain uncertain of its exact affinities, we refer this specimen to *Redondasaurus* sp. NMMNH P-31094 is most similar to *R. bermani* but possesses sufficient diagnostic features (autapomorphies), particularly regarding the reduction of the antorbital fenestra and breadth of the postorbital skull, to justify erection of a new specific name in most phytosaur classifications.

OTHER ELEMENTS FROM NMMNH LOCALITY 4211

NMMNH P-31094 was merely the largest element in an extraordinarily dense bonebed. Contents of the field jacket, aside from the giant skull, included another palatal skull element (P-31097), a large right ulna (P-31099; Fig. 3A), a small right femur (P-31098; Fig. 3B), an incomplete large right ilium (P-31101), a small incomplete interclavicle, (P-31102), two vertebrae, 27 ribs or rib fragments, 50 scutes, including three aetosaur scutes (P-31100; Fig. 3F-G) and a possible sphenosuchian

scute, 93 phytosaur teeth, 94 other bones or bone fragments, and, most surprisingly, a second, smaller phytosaur skull (P-31095; Fig. 3C) wedged in the palate of the larger specimen.

The smaller skull (650 mm preserved length) is slightly disarticulated, and consists of most of the snout, including a short narial crest, and the orbital region of the skull roof (50 mm interorbital width). In gross morphology, the preserved portion of the skull resembles phytosaur skulls from the stratigraphically lower Canjilon and Snyder quarries in north-central New Mexico in possessing a prominent narial crest immediately anterior to the nares. We suspect that this specimen represents a subadult, or at least less mature, *Redondasaurus*, but it lacks the temporal region and is thus not identifiable at the generic level.

Most of the elements found in the jacket are phytosaurian, including the ulna, femur, ilium, interclavicle, vertebrae, and teeth. Others, including many of the ribs and fragments are not diagnostic below the level of Reptilia. Three of the 50 scutes are not phytosaurian, and instead represent a relatively rare occurrence of an aetosaur in the Redonda Formation. These scutes are wider than long, possess anterior bars, a very faint pattern of elongate pits and grooves, and very little if any dorsal boss (Fig. 3F-H). The longest scute (Fig. 3F-G) is particularly narrow, and has a width:length (W:L) ratio of less than 1.2:1. We interpret this scute as a right cervical? paramedian scute. A shorter scute (Fig. 3H) is approximately 2.5 times wider than long, with less distinct patterning and a very low dorsal boss near the posterior margin medial to the middle of the scute. We interpret this scute as a left dorsal paramedian scute. A third scute is smaller, but similar in most respects to the wider scute.

Aetosaurs characterized by very faint ornamentation include *Coahomasuchus kahleorum* Heckert and Lucas 1999, *Aetosaurus arcuatus* (Marsh, 1896), and *Neoaetosauroides engaeus* Bonaparte, 1967 (Heckert and Lucas, 1999, 2000). The scutes described here are more robust than those of *Coahomasuchus* and possess a more radial pattern of grooves and ridges. Scutes of *A.*

Table 1. Measurements of NMMNH P-31094

Feature	Measurement (in mm)
Length preserved skull (tip broken snout to posterior end squamosal)	782
Length preserved skull (tip broken snout to posterior edge occipital condyle)	649
Maximum width of skull (across quadratojugals)	560
Length post-snout (anterior border nares to poster edge squamosal)	539
Maximum length of naris	102
Maximum width of naris	66
Maximum length left orbit	83
Maximum width left orbit	59
Minimum interorbital width	89
Width cranial table between infratemporal fenestrae	238
Maximum length supratemporal fenestrae	55
Maximum width supratemporal fenestrae	39
Interfenestral width	70
Length ventral border left infratemporal fenestra	170
Length anterior border left infratemporal fenestra	180
Length posterior border left infratemporal fenestra	145
Length left antorbital fenestra	122
Maximum width left antorbital fenestra	41
Maximum width palate between tooth rows	290

arcuatus differ from these in being slightly smaller and lacking dorsal bosses. Additionally, many paramedian scutes of *Aetosaurus* have W:L ratios of 3.0 or higher. Scutes of *Neoaetosauroides* are not well-preserved in the holotype material but in general shape and morphology conform to those described here. Specifically, scutes of *Neoaetosauroides* have a faint radial pattern of pits and grooves and are relatively narrow (W:L < 3.0). Some scutes of *Neoaetosauroides* possess a low dorsal boss similar in shape and position to that illustrated here. Therefore, we tentatively assign these scutes to cf. *Neoaetosauroides* sp.

During preparation of the specimen we also recovered several clusters of fish scales. These scales are loosely articulated to associated. They are somewhat rhomboid and elongate, and in most respects conform to semionotid fish, which are relatively common in the Redonda Formation (Huber et al., 1993).

TAPHONOMY

This assemblage, with approximately 276 known teeth, bones, or bone fragments, all from an area of less than 1 m², represents one of the densest accumulations of bone in the Chinle Group. All elements are disarticulated, and they appear hydrodynamically sorted as the bulk of the elements represented are long bones, principally ribs and limb bones. However, even with extensive mapping of the bones as they were uncovered (Fig. 4), there is no obvious preferential orientation other than that the giant skull, the smaller skull, several ribs and the large ulna were all oriented roughly parallel to each other, although the ulna was resting against the giant snout.

There is absolutely no indication of articulation of any of the remains described here. Furthermore, the condition of the phytosaur skulls indicates that the animals were deceased and nearly completely desiccated and/or rotted prior to burial. Every aperture of the giant skull contained at least one allochthonous element, including but not limited to the femur in the left infratemporal fenestra, a scute in the right orbit, and several teeth (some

removed during preparation) in the left orbit. Although many bones are broken, the assemblage was probably not transported very far before burial. There is no evidence of abrasion, and many of the broken or incomplete bones were damaged during collection, not deposition (note the large proportion of fragments adjacent to jacket walls in Figure 4). The break in the giant snout is fresh and probably was a result of Recent weathering, and the smaller snout was accidentally truncated while trenching around the jacket. Therefore, we suspect that the assemblage represents a short-term accumulation of dead and disarticulated individuals subsequently entrained and rapidly buried in a channel cut into floodplain mudstones. This accumulation thus well matches descriptions of channel lag deposits as characterized by Behrensmeyer et al. (1992).

The preserved elements indicate the presence of at least three individual phytosaurs, based on the giant skull, the subadult skull, and a tiny snout or jaw fragment too small to belong to either of the first two. In all probability, the minimum number of individual (MNI) phytosaurs was still higher, as even the largest limb and girdle elements appear too small for the giant skull, but are too large for the smaller one, and the unidentified palatal? element (NMMNH P-31097) likely represents another phytosaur. However, articulated phytosaur skeletons are rare and skull size:limb length ratios are essentially unknown.

Hunt et al. (1995) recognized six vertebrate taphofacies in the Redonda Formation. These included (1) nearshore clastic lacustrine; (2) carbonate lacustrine-margin; (3) beach conglomerate; (4) fluvial channels; (5) floodplain taphofacies; and (6) paleosol taphofacies. (Table 2). Of these, NMMNH locality 4211 clearly well-matches the fluvial channels, which Hunt et al. (1995, p. 32) describe as "intraformational conglomerates and lenticular sandstones, representing fluvial channel deposits, contain fragmentary and abraded bones; locally, small channels are full of well-preserved bones that are dominantly phytosaurian but also include ?poposaur and aetosaur specimens." These localities, while not areally extensive, are clearly an important source of fossil vertebrates.

Table 2. Taphofacies of the Redonda Formation

Taphofacies	Lithologic characteristics	Fossils
Nearshore lacustrine	Tabular sandstones and mudstones	Complete to disarticulated fish
Lacustrine margin	Carbonates, principally calcarenites	Vertebrate tracks, including <i>Brachychirotherium</i> <i>Pseudotetrasauropus</i> <i>Tetrasauropus</i> <i>Rhynchosauroides</i> <i>Grallator</i>
Beach	Tabular intraformational conglomerate	Fish scales, ichthyoliths, phytosaur teeth, rarely other tetrapods
Fluvial channel	Lenticular intraformational conglomerate and sandstone	Generally fragmentary and abraded bones, locally well-preserved material
Floodplain (proximal)	Mudrocks	Isolated phytosaur postcrania and skulls
Paleosol (distal floodplain)	Mottled mudrocks with calcareous nodules	Small tetrapods

CONCLUSIONS

The giant phytosaur here, which we refer to *Redondasuchus* sp., is another Apachean (latest Triassic) record of the genus from east-central New Mexico. Although phytosaur classification remains problematic, this skull is readily diagnosed as a highly derived phytosaur based on the presence of depressed supratemporal fenestrae that are completely concealed in dorsal view. Possible records of the aetosaur *Neoaetosauroides* from NMMNH locality 4211 are the first occurrence of that taxon outside the type area in the Los Colorados Formation (Ischigualasto basin) of Argentina and support cross-correlation of the type Apachean fauna with the Los Colorados, as suggested by Lucas (1998). Bonebeds such as NMMNH locality 4211 probably represent localized channel deposits near the margins of the Redonda Formation lakes.

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