

A GIANT SKULL, ONTOGENETIC VARIATION AND TAXONOMIC VALIDITY OF THE LATE TRIASSIC PHYTOSAUR *PARASUCHUS*

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Abstract—*Parasuchus* (= *Paleorhinus*) is the most primitive known phytosaur, and its fossils define a Carnian biochron recognizable across much of Pangea. The largest known specimen of this primitive taxon, an incomplete skull from the Popo Agie Formation in northwestern Wyoming, demonstrates that the nares remain anterior to the antorbital fenestra throughout the ontogeny of *Parasuchus*, an observation confirmed by an analysis of a broad database. The fact that this character is not variable through the ontogeny of this phytosaur genus, as some previous authors have speculated, helps to cement the taxonomic validity of *Parasuchus*. For the past century, systematists have attempted to establish a classification of organisms rooted in some form of a biological species concept. Cladotaxonomy, on the other hand, is the recognition of cladotaxa, which are low-level taxa (genera and species) that correspond to clades in a cladistic analysis. Cladotaxonomic relegation of all primitive phytosaurs to a metataxon is based on a posteriori evaluation of character polarity that fails to acknowledge the existence of a biotaxon regardless of how a cladist evaluates character polarities millions of years later. We reject assignment of primitive phytosaurs to a metataxon as uninformative, and recognize *Parasuchus* as a diagnosable phytosaur genus.

INTRODUCTION

Phytosaurs are an extinct group of primitive archosaurs whose body fossils are known from Upper Triassic strata in North and South America, Europe, Africa, Madagascar, India, and Thailand (e.g., Hunt, 1994; Hungerbühler, 1998, 2002, and references cited therein). The most primitive known phytosaur is *Parasuchus* (= *Paleorhinus*), which has an essentially Pangean distribution, including an occurrence in marine strata in Austria that reliably calibrates occurrences of *Parasuchus* as Carnian in age (Hunt and Lucas, 1991; Lucas, 1998; Lucas and Heckert, 2000). Indeed, *Parasuchus* is the primary index taxon of the Otischalkian land-vertebrate faunachron (lvf) (Lucas and Hunt, 1993; Lucas, 1998). Because of its widespread distribution and relative abundance, including articulated skeletons from India (Chatterjee, 1978), *Parasuchus* is one of the best-known phytosaurs. In this paper, we describe a specimen collected nearly 50 years ago that is the largest known skull of *Parasuchus*. This specimen is important because it provides insight into the growth of the skull of *Parasuchus*, which we analyze metrically with a preliminary data set. This analysis and the desirability of informative taxonomy lead us to reject cladotaxonomic relegation of all primitive phytosaurs to a metataxon.

In this paper we consider *Parasuchus* to be a subjective senior synonym of *Paleorhinus*, even though *Paleorhinus* was the widely used name by the 1990s. This is because a little advertised application by Chatterjee (2001) to the International Commission on Zoological Nomenclature (only one comment was published on this application: Hungerbühler, 2001a) requested a neotype designation for *Parasuchus hislopi*, the oldest name for a primitive phytosaur genus and a *nomen dubium* based on an undiagnostic holotype (Hunt and Lucas, 1991). The Commission (Opinion 2045) ruled in favor of the application, so *Parasuchus* is a diagnosable taxon that we consider a senior synonym of *Paleorhinus* (and the other synonyms of *Paleorhinus* listed by Hunt and Lucas, 1991, p. 488).

PROVENANCE

The specimen described here, FMNH (Field Museum of Natural History, Chicago) PR 130 (field number PA-75-48) (Fig. 1), was collected in Wyoming by a FMNH party led by G. Snyder in 1948, apparently as an incidental part of an expedition to collect younger fossils. The

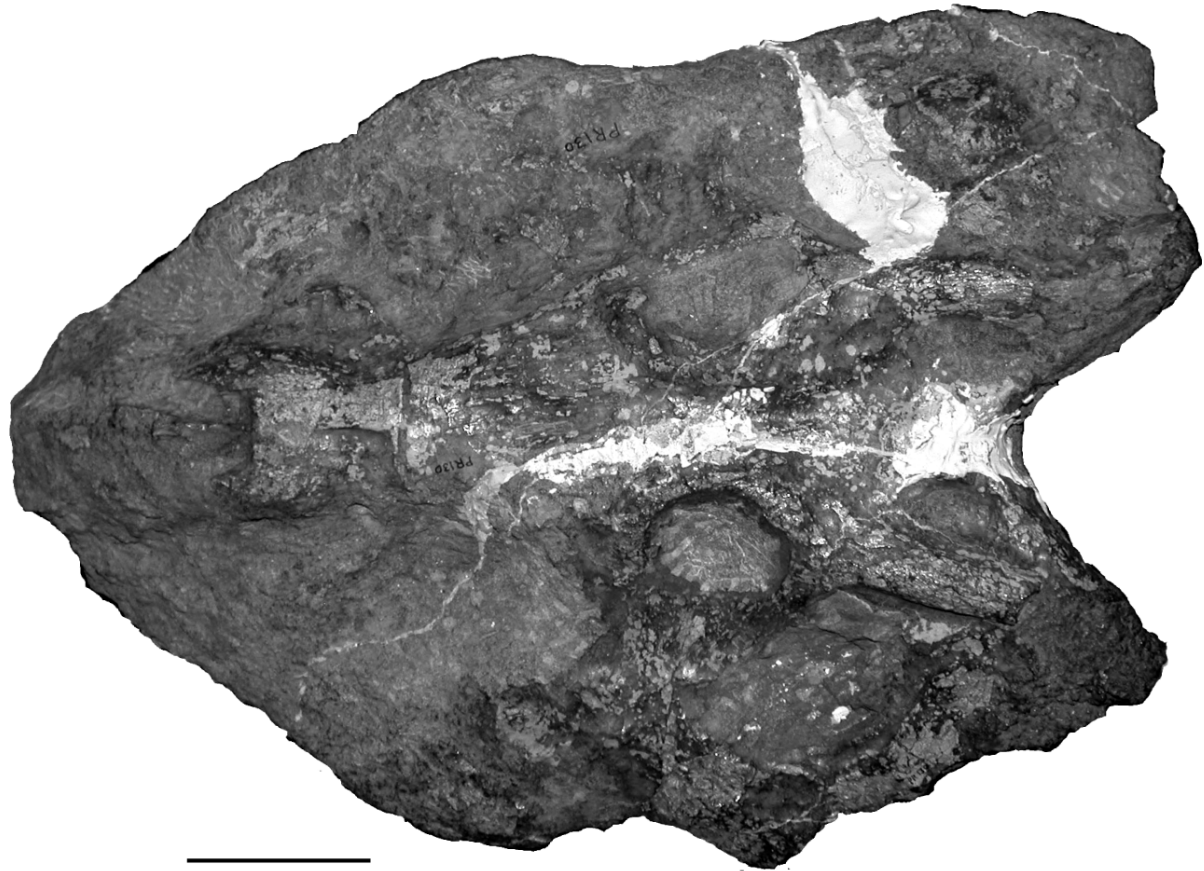
locality is recorded as the south banks of the river by “Ochre Hill,” approximately 1 mile southeast of Dubois in Fremont County, Wyoming. Presumably “the river” refers to the Wind River. The specimen’s matrix is a brownish red mudstone containing abundant flecks of whitish analcime, a typical lithology of the Popo Agie Formation in Wyoming (Lucas, 1993).

The Popo Agie Formation in Wyoming yields a relatively sparse, but important, tetrapod assemblage of Otischalkian age. That assemblage includes the metoposaurid temnospondyl *Buettneria*, the dicynodont *Placerias*, the rhynchosaur *Hyperodapedon*, the phytosaurs *Parasuchus* and *Angistorhinus*, the rauisuchian *Heptasuchus*, and the poposaurid *Poposaurus* as well as probable (but fragmentary) dinosaurs and other tetrapods (Williston, 1904; Mehl, 1913, 1915a,b, 1928; Branson and Mehl, 1928, 1929; Branson, 1948; Dawley et al., 1979; Lucas, 1994, 1998; Lucas and Heckert, 2002; Lucas et al., 2002).

DESCRIPTION

FMNH PR 130 is a very large, incomplete phytosaur skull exposed in dorsal view (Fig. 1). Preserved, identifiable portions of the skull include the bones immediately surrounding the external nares, remnants of the septomaxillae, the medial and posterior margins of the antorbital fenestrae, all of the bones surrounding the orbits, and the left lateral temporal fenestra, postfrontals, parietals, and right squamosal. It appears that the entire block broke into at least three pieces and was rather poorly (hastily?) repaired with plaster. Another block with the same catalog number is even more poorly preserved, with a few plates of bone visible on the surface. This block was also “restored” (repaired?) with plaster. No identifiable elements are visible on the second block, although some vertebrae or part of the snout may be present.

The skull has been only partially prepared. As preserved, it measures 590 mm long from immediately anterior to the nares posteriorly to the squamosals. Thus, the skull length of 590 mm includes little of the snout, which usually comprises much of the length of a phytosaur skull (Gregory, 1962; Chatterjee, 1978). At its widest, FMNH PR 130 is approximately 415 mm wide in the vicinity of the quadratojugals, although the lateral margins of the skull are generally missing, poorly preserved if present, and the whole skull appears to have been dorsoventrally crushed. Using the allometric regression for skull width, A-P orbital diameter and postorbital length versus length that we develop



10 cm

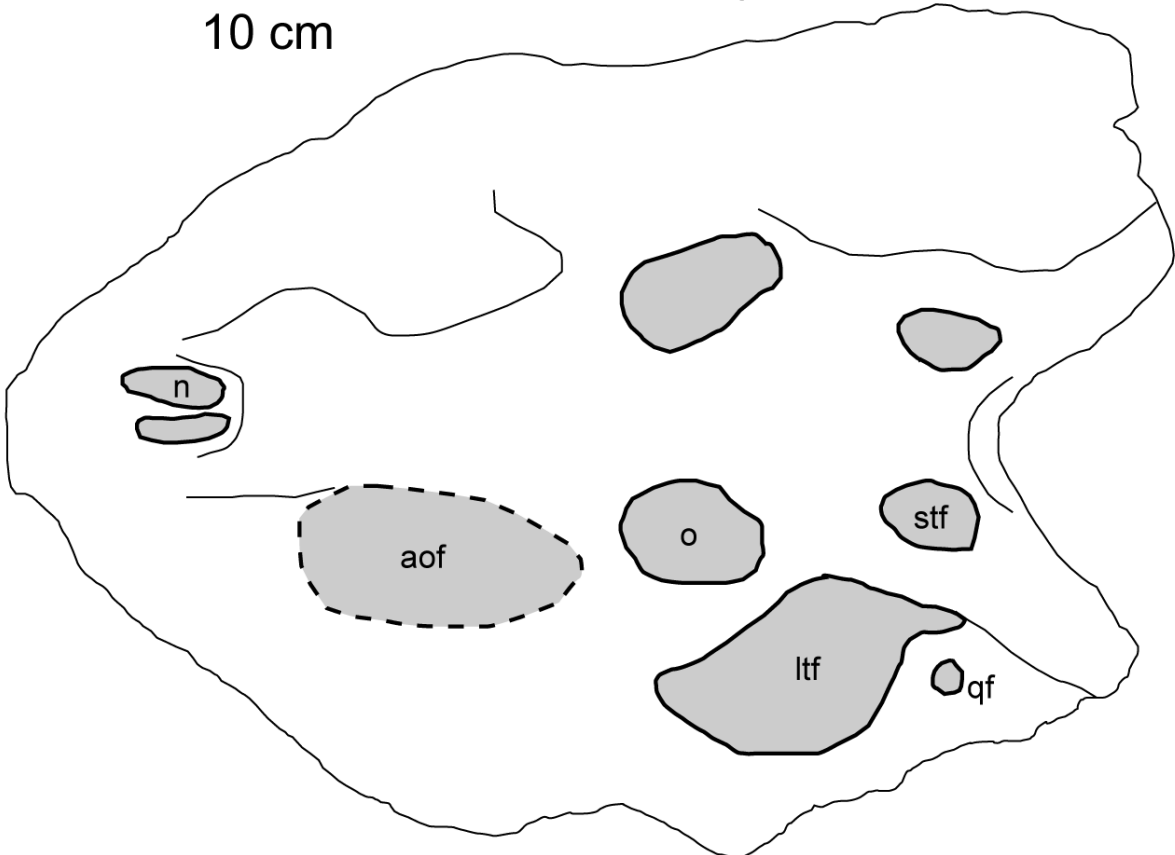


FIGURE 1. Photograph and line drawing of dorsal view of FMNH PR 130, skull of *Parasuchus* sp. from the Popo Agie Formation of Wyoming. Abbreviations are: aof = antorbital fenestra, ltf = lateral temporal fenestra; o = orbit; qf = quadratic foramen; stf = supratemporal fenestra.

later, we calculate that this skull would have been slightly over 1.5 m in length. This is, by far, the largest known skull of *Parasuchus*.

The nares are little, if at all, elevated above the skull roof and their dorsal margins are inclined anteriorly. There is very little bone preserved anterior to the nares, but the 6–7 cm of matrix block preserves no indication of a narial crest. The nares are located almost entirely anterior to the antorbital fenestrae, the primitive condition for archosaurs and one of the diagnostic traits of *Parasuchus* (Hunt and Lucas, 1991; Hunt, 1994; Long and Murry, 1995). In addition, the dorsal margin of the external nares is inclined anteriorly, the orbits are dorsally oriented and a large quadratic foramen is present, all characteristic features of *Parasuchus* (Hunt and Lucas, 1991).

The left orbit is the better-preserved and is ~65 mm long and ~58 mm across. The antorbital fenestrae are poorly preserved, but the left is ~120–140 mm long. The right is 100 mm long (minimum) and more likely 140 mm long. The left lateral temporal fenestra is a rhombus with the following dimensions: base ~75 mm, top ~65 mm, anterior margin ~100 mm, posterior margin ~110–130 mm (across curve), with diagonals of 140 and 90 mm. The supratemporal fenestrae are well-preserved, filled with matrix, and essentially at the level of the skull roof and fully exposed as two ovals in dorsal view. The left is ovoid and approximately 35 mm wide by 50 mm long. The right appears to be 30 mm wide by 55 mm long. The right squamosal is thin and rod-like, approximately 30 mm wide and 140 mm long and almost entirely at the level of the skull roof. There is very little, if any, descending process. A quadratic foramen appears to be present on the left side of the skull at the quadratoquadratojugal juncture.

ONTOGENY AND SIZE OF *PARASUCHUS*

Relatively little is known about the ontogeny of phytosaurs, and this has allowed some speculation about ontogenetic changes in key diagnostic features of the phytosaur skull. With regard to *Parasuchus*, this speculation began with comments by Padian (1994) on an incomplete rostrum (with external nares anterior to the antorbital fenestrae) from the Adamanian *Placerias* quarry of Arizona that Ballew (1989), Hunt and Lucas (1991), Long and Murry (1995) and Lucas et al. (1997) identified as *Paleorhinus*. Padian (1994, p. 405) suggested that this might be a fragment of a juvenile skull based on its small size and the possibility that juvenile phytosaurs may have retained the “plesiomorphic condition” of external nares that are anterior to the antorbital fenestrae with the former “migrating posteriorly and dorsally (through ontogeny) as they do in fact phylogenetically.” Nevertheless, as Lucas et al. (1997) noted, no data support this inference of ontogeny recapitulating phylogeny.

Subsequently, Fara and Hungerbühler (2000) correctly recognized that the holotype skull of *Paleorhinus magnoculus*, from the Upper Triassic of Morocco, is that of a juvenile (Fig. 2). Dutuit (1977) originally described this skull as a distinct species of *Paleorhinus*, and Long and Murry (1995) made it the type of a new genus, *Arganarhinus*. However, Fara and Hungerbühler (2000) argued that the relatively large orbits, relatively short snout and overall small size of the holotype of *P. magnoculus* indicate that it is a juvenile specimen, and we concur. Fara and Hungerbühler (2000, p. 836) went on to conclude that “no other characteristics than those deemed here ontogenetically variable have been presented to substantiate the assignment [of the holotype skull of *P. magnoculus*] to *Paleorhinus*,” even though they did not in any way demonstrate ontogenetic variation in the diagnostic characters of *Paleorhinus* (such as the nares located anterior to the antorbital fenestrae) that are evident in the holotype skull of *P. magnoculus*.

We have assembled a preliminary metric database from our own data and published information (Appendix) with which to evaluate relative growth of some aspects of the skull of *Parasuchus* across the various species. In an allometry plot (Huxley, 1932) we fit linear equations (slope-intercept form) to the \log_{10} -transformed data (Fig. 3). In such a plot, the relative growth of a sector or feature is indicated by the slope of

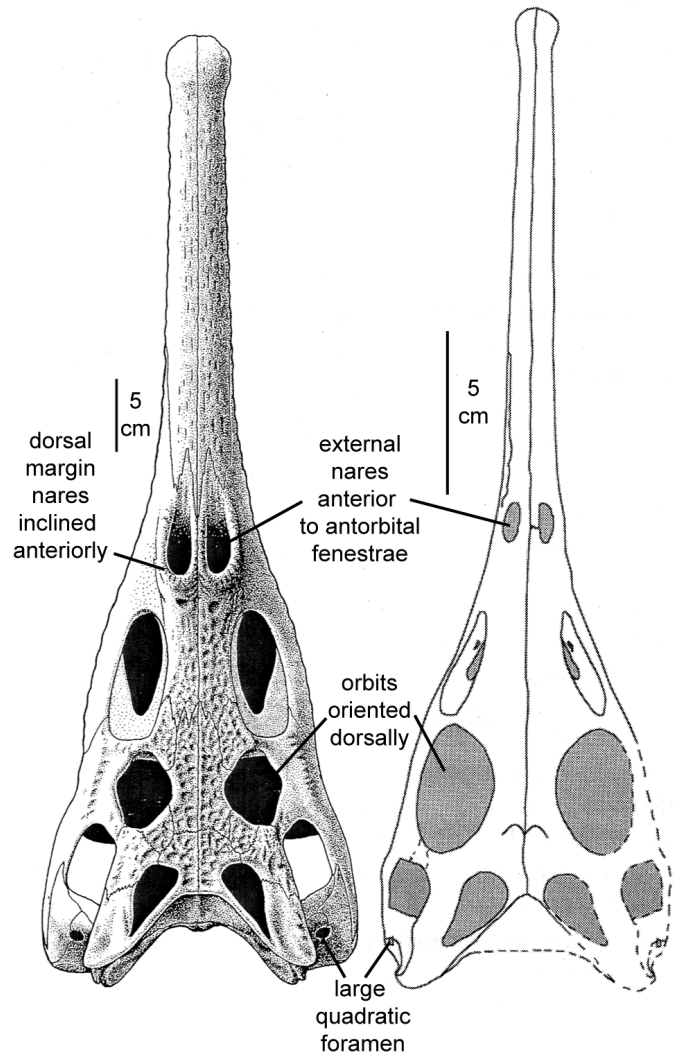


FIGURE 2. Diagnostic features of the skull of *Parasuchus*; adult skull from Poland (after Dzik, 2001) and the holotype juvenile skull of *P. magnoculus* (after Fara and Hungerbühler, 2000).

the curve fit line, which is the allometric growth constant, k . If $k = 1$, isometric growth is indicated, whereas positive and negative allometry are indicated by $k > 1$ and $k < 1$, respectively (Gould, 1966).

These data (Fig. 3) show that as the skull length of *Parasuchus* increased, the orbits grew relatively little (strong negative allometry, $k = 0.4$), whereas prenarial length grew relatively more than skull length (weak positive allometry, $k = 1.14$). Both preorbital and postorbital lengths increased in very slight positive allometry ($k = 1.06$ and $k = 1.07$, respectively). Given the small sample size, it is possible that isometric growth is present in these sectors. Skull width grew relatively less than length (negative allometry, $k = 0.83$).

Most significantly, there was essentially no growth (extreme negative allometry, $k \sim 0.06$) in the part of the rostrum between the antorbital fenestrae and external nares (postnaris-aof in the plot). In other words, the absolute distance between the external nares and the antorbital fenestrae remains approximately constant throughout ontogeny in *Parasuchus*. These data show very wide scatter, and the correlation coefficient, R^2 , is extremely low (0.001). The data points, however, definitely form a prolate grouping whose poles are essentially horizontal (zero growth). Additionally, the preantorbital fenestra length (pre aof L) shows slight negative allometry ($k = 0.95$) in spite of the fact that most of its length is made up of the prenarial length, which shows positive allometry. The allometric difference between the prenarial length and preantorbital length

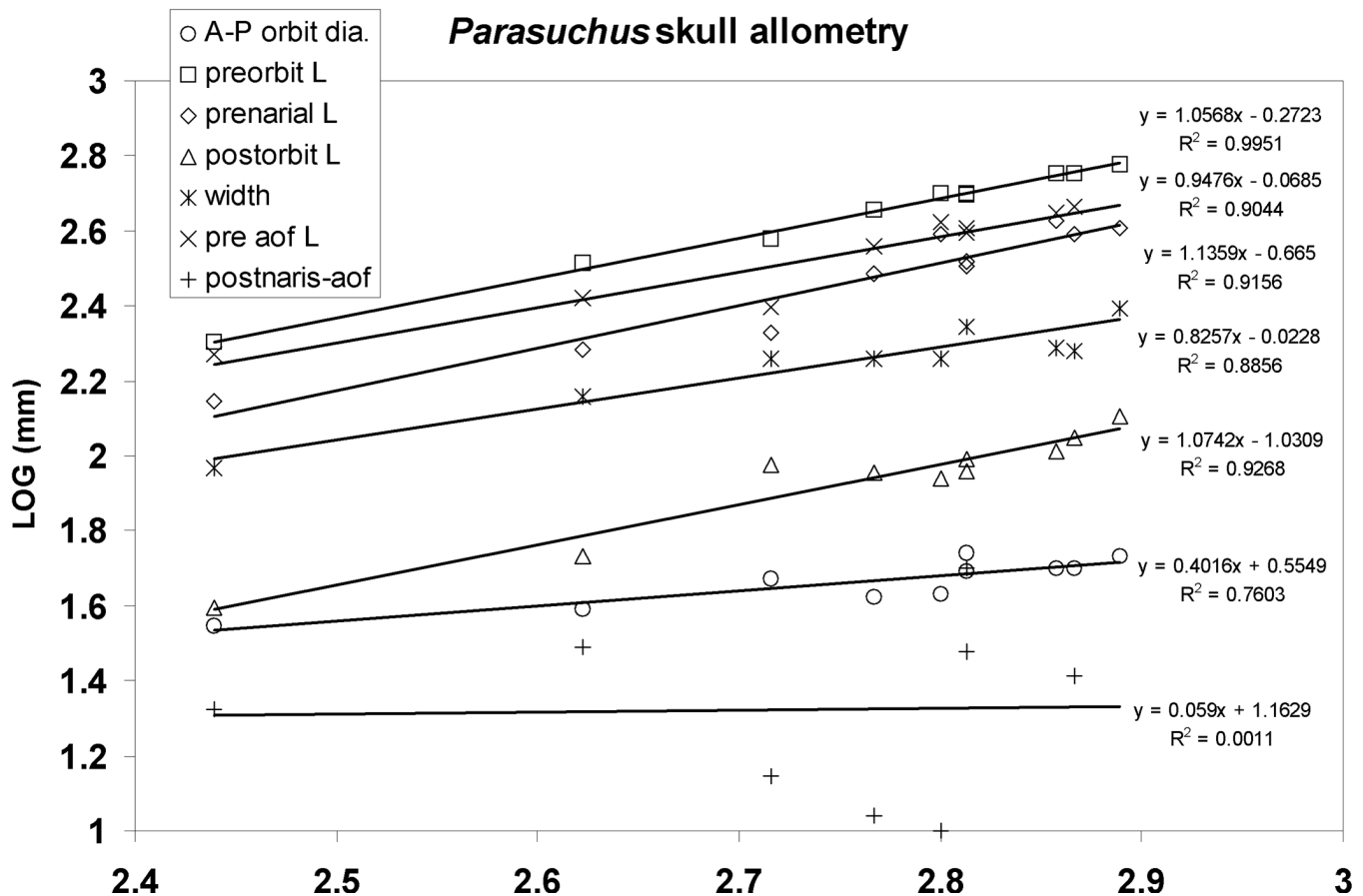


FIGURE 3. Cranial allometry of *Parasuchus* based on metric data listed in the Appendix.

definitely reinforces the idea that the sector between the nares and antorbital fenestra is one of extreme negative allometry. Obviously, at some point very early in ontogeny there must be some growth in this region, but over the span of skull lengths in our database (275 mm to 775 mm) there is practically none. The fact that the area between the nares and antorbital fenestra shows essentially no growth refutes previous suggestions that this key diagnostic character of *Parasuchus* is ontogenetically variable.

Therefore, the skull we document here, while nearly twice the length of any previously described specimen of *Parasuchus*, is certainly congeneric with other published specimens. Importantly, all of the characteristics used by Hunt and Lucas (1991) to diagnose *Parasuchus* (= *Paleorhinus*) are present on this specimen.

The estimated skull length of this specimen places it among the largest known phytosaur skulls. Some of the largest phytosaur skulls documented to date include:

1. The holotype of *Machaeroprotopus gregorii* Camp, 1930, (= *Rutiodon gregorii* of our usage).
2. The holotype of *Brachysuchus megalodon* Case, 1929 (= *Angistorhinus megalodon* of our usage).
3. A large *Rutiodon* (= *Machaeroprotopus*) skull described by Colbert (1947).
4. A large skull of *Redondasaurus* skull described by Heckert et al. (2001).

The first three of these comprise the longest specimens documented by Colbert (1947, table 3) or Gregory (1962, fig. 4) in their analyses of phytosaurs and are based on relatively complete skulls. The

fourth specimen was very conservatively estimated to be ~1.17 m long by Heckert et al. (2001) and is based on a skull lacking the snout, as is the specimen here. All of these specimens are robust, as well. If our analyses are correct, the skull we describe here, if it were complete, would probably be the longest known phytosaur skull, as only the gigantic skull described by Colbert (1947) exceeds 1.4 m in length.

CLADOTAXONOMY OF PRIMITIVE PHYTOSAURS

Lucas and Kondrashov (2004) coined the term cladotaxonomy, and defined a cladotaxon as a low-level taxon (genus or species) that corresponds to a clade in a cladistic analysis. We generally reject a cladotaxonomic approach (also see Lucas, 2005) to the alpha taxonomy of fossil vertebrates for four reasons:

1. No attempt at gauging the amount of, and the significance of, variation is incorporated into the cladistic analysis. Instead, the variation, such as it is determined, is assumed to be of phylogenetic significance only. Thus, the possibility of populational variation in characters deemed to be of phylogenetic significance is not addressed. This is of particular concern in phytosaurs, as some characters used in previous cladistic analyses, such as the presence of a rostral crest, are now known to be sexually dimorphic in at least some taxa (Zeigler et al., 2002, 2003).

2. The cladotaxonomy names nearly every branch, stem, and node on the cladogram, and thus results in taxonomic hypersplitting. Because the cladogram artificially imposes a cladogenetic pattern on this splitting, any genus currently considered speciose will be split into multiple genera by the cladotaxonomic approach, and anagenetic evolution within

a lineage cannot be recognized.

3. Cladotaxa only convey the topology of a cladogram and thus are taxa devoid of other biological significance. The cladogram is based on a character atomization that takes discrete characteristics of biological import and divides them into many smaller characters, all deemed to be of equal phylogenetic significance. Thus, any biological significance of the characters is removed from the analysis at the outset.

4. Finally, there is the “cladogram du jour factor.” Cladistic analysis has proven highly useful in constructing phylogenetic hypotheses that can be subjected to rigorous evaluation. But, when such hypotheses are instantly turned into new taxonomic names, the taxonomic nomenclature becomes burdened with numerous names based on little-tested hypotheses. In effect, the cladogram of the moment, even if it is the only published cladogram (the “cladogram du jour”), becomes the basis for new taxonomy. New alpha taxonomy based on such a cladogram is premature.

Another aspect of cladotaxonomy that has not been discussed can be called the metataxon problem. To many cladists, a taxon recognized as primitive in a cladistic analysis, and that lacks any supposed autapomorphies, cannot be identified as a taxon, and instead becomes a metataxon. Such metataxa are typically seen as taxonomic garbage cans (“grades”) that encompass specimens that defy precise identification. However, in reality, such metataxa are simply an artifact of a posteriori reasoning process—all cladistic hypotheses must have a symplesiomorphic sister taxon, and if that taxon lacks autapomorphies according to the analysis, it is deemed a metataxon. In reality, the taxon as a biological entity existed, regardless of how a cladist judges character polarities.

Parasuchus provides a good example. Cladistic a posteriori reasoning terms it a metataxon because it is the most primitive phytosaur and lacks autapomorphies in the analysis (e.g., Hungerbühler, 2001b,

2002). However, primitive phytosaurs lived during the Late Triassic and were unaware of subsequent a posteriori cladistic reasoning more than 200 million years later. Those primitive phytosaurs constituted a biological entity that merits a Linnaean name, as do all other diagnosable biotaxa, and that name is *Parasuchus*.

Indeed, *Parasuchus* (= *Paleorhinus*) is one of the best known and longest-recognized phytosaurs (e.g., Williston, 1904; Lees, 1907; Ballew, 1986, 1989; Hunt, 1989; Hunt and Lucas, 1991; Long and Murry, 1995). Furthermore, prior to cladistic a posteriori reasoning and Chatterjee’s (2001) unadvertised petition to the ICZN, the name *Paleorhinus* had one of the most stable taxonomic histories of phytosaurs (compare genus-level synonymies in Hunt [1994] and Long and Murry [1995]). Hunt and Lucas (1991) identified four diagnostic characters of *Parasuchus* that distinguish it (and its obvious synonyms: see Hunt and Lucas, 1991, p. 488) from all other phytosaurs: external nares anterior to antorbital fenestrae, dorsal margin of external nares inclined anteriorly, dorsally-oriented orbits and large quadratic foramina (Fig. 2). Referring to this genus as “*Parasuchus*-grade” phytosaurs (phytosaurs with nares clearly anterior to the antorbital fenestra, the primitive archosaurian condition) or “non-phytosaurid phytosaurs” (e.g., Fara and Hungerbühler, 2000; Hungerbühler, 2001b, 2002) simply ignores useful morphological information and thus produces an uninformative taxonomy. We prefer a taxonomy with maximum information that recognizes discrete morphological clusters as taxa, and continue to apply the generic name *Parasuchus* to the most primitive phytosaurs.

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APPENDIX

Parasuchus skull metrics; various species from various sources.

Taxon	Reference	skull L	A-P orbit		preorbital		prenarial		postorbital		width		pre aof L		postnaris-aof		
			dia	skull L	L	L	L	L	L	L	L	L	L	L	L	L	
<i>Paleorhinus magnoculus</i>	Fara & Hungerbuhler, 2000	275	35.1	200.4	140	39.5	92.4	186	21	2.4393327	1.54530712	2.301898	2.146128	1.596597	1.965672	2.269513	1.322221929
<i>Promyristosuchus ehlersi</i> *	Case, 1922	720	50	567	426	103	193	444	-15	2.8573325	1.69897	2.753583	2.62941	2.012837	2.285557	2.647383	
<i>Paleorhinus bransoni</i>	Fara & Hungerbuhler, 2000	775	54	599	404	127.5	248			2.8893017	1.73239376	2.777427	2.606381	2.10551	2.394452		
<i>Paleorhinus</i> sp.	Dzik, 2001	650	55	495	330	98	220	405	50	2.8129134	1.74036269	2.694605	2.518514	1.991226	2.342423	2.607455	1.69897
<i>Francosuchus broiji</i> *	Kuhn, 1932	520	47	378	212	95	181	250	14	2.7160033	1.67209786	2.577492	2.326336	1.977724	2.257679	2.39794	1.14612804
<i>Parasuchus hislopi</i> *	Chatterjee, 1978	565	42	453	305	90	182	362	11	2.7671559	1.62324929	2.656098	2.4843	1.954243	2.260071	2.558709	1.04139269
<i>Ebrachosuchus neukami</i> *	Kuhn, 1936	631	43	501	389	87	182	420	10	2.8000294	1.63346846	2.699838	2.569995	1.939519	2.260071	2.623249	1
<i>Paleorhinus bransoni</i>	Williston, 1904	735	50	565	390	112	190	461	26	2.8662873	1.69887	2.752048	2.591065	2.049218	2.278754	2.663701	1.41497335
<i>Paleorhinus</i> AbIII/112	SGL	419	39	326	192	54	144	264	31	2.622214	1.59106461	2.513218	2.283301	1.732394	2.156362	2.421604	1.49136169
<i>Paleorhinus</i> AbIII/200	SGL	650	49.1	502	322	91.5	221	393	30	2.8129134	1.69108149	2.700704	2.507856	1.961421	2.344392	2.594393	1.47712125

*Synonymized with *Paleorhinus* (Hunt, 1991)