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BODY MASS ESTIMATES OF PHYTOSAURS (ARCHOSAURIA: PARASUCHIDAE) FROM THE PETRIFIED FOREST FORMATION (CHINLE GROUP: REVUELTIAN) BASED ON SKULL AND LIMB BONE MEASUREMENTS

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Abstract—Phytosaurs were the largest and most common semi-aquatic predators of the Late Triassic. Although their skulls are relatively common in the fossil record, articulated, or even associated skeletons are extremely rare, so it has always been difficult to gauge just how large (mass or length) an individual phytosaur may have been. Body mass in particular is an important physiological variable, often used for the scaling of organs, biomass determination, biomechanics, and locomotion. We take advantage of phytosaurs' general similarity to extant crocodilians to attempt to reconstruct body mass and length based on measurements of the skulls and limbs of phytosaurs from the Upper Triassic Snyder and Canjilon quarries in north-central New Mexico. These quarries, in the Painted Desert Member of the Petrified Forest Formation (Revueltian: early-mid Norian) preserve catastrophic death assemblages that appear to well-represent discrete populations of phytosaurs. We also utilize a snout-vent measurement based on an articulated skeleton from the Canjilon quarry to compare the accuracy of different equations based on discrete limb elements. Body mass estimates for Snyder quarry phytosaurs range between 25 and 500 kg, with most specimens yielding estimates of approximately 200-350 kg. The Canjilon quarry sample encompasses fewer juveniles and more robust adults, including one individual that may have weighed as much as 535 kg. From equations based on nine extant crocodilian genera, these Revueltian phytosaurs appear to have approached 4.5 m total body length for a ~ 400 kg phytosaur. The prevalence of subadult to adult phytosaurs in both quarries based on body mass estimates corroborates qualitative estimates of the population structure based on skull sizes alone, thereby reinforcing the hypothesis that both quarries are catastrophic assemblages.

Keywords: Parasuchidae, phytosaur, body mass, size, analogue

INTRODUCTION

Phytosaurs are an extinct clade of primitive crurotarsan archosaurs known from Upper Triassic strata on most modern continents (Gregory, 1962; Westphal, 1976; Hunt, 1994; Long and Murry, 1995; Hungerbühler, 1998, 2002) (Fig. 1). Superficially similar to crocodiles in their elongate snout and tooth-filled mouths, phytosaurs have typically been regarded as filling a similar niche as semi-aquatic predator, although detailed studies of their paleoecology are few (Hunt, 1989). Although phytosaur skulls are relatively common in the fossil record, articulated, or even associated, skeletons are extremely rare, and seldom described (e.g., Camp, 1930; Renesto and Lombardo, 1999; Lucas et al., 2002a). Consequently, it has always been difficult to gauge just how large an individual phytosaur may have been. We take advantage of phytosaurs' general similarity to extant garials (crocodiles) to attempt to reconstruct body mass based on skull measurements. We also utilize length and mass estimates obtained from equations based on living crocodilians (principally *Alligator mississippiensis*) to obtain estimates of phytosaurian body mass.

Body mass (MBd) is an important physiological variable, and it is often used for the scaling of organs, biomass determination, biomechanics, and locomotion. Relationships between body mass and skeletal dimensions in modern amniotes are often used to estimate the body mass of extinct amniotes (Anderson et al., 1985; Gingerich, 1990; Hurlburt, 1999). Crocodilian body mass has therefore been estimated from total length (TL) (Dodson, 1975), TL and tail girth (TG) (Chabrek and Joanen, 1979), and multiple regression equations using TL and TG (Woodward et al., 1992, 1995). TG taken at the base of the tail, varies with fat deposited, whereas TL does not vary depending on fat level. A multiple regression equation estimating MBd from TL and TG (Woodward et al., 1992) gave more accurate estimates of MBd than equations using TL alone, in alligators of known TL (Hurlburt, 1999).

A

B

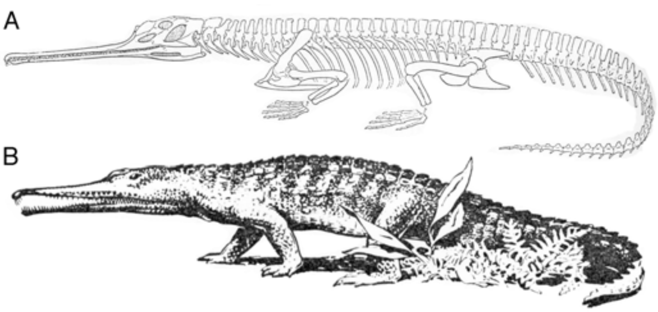

FIGURE 1. Generalized reconstructions of phytosaurs. **A**, skeletal reconstruction, after Colbert (1972); **B**, flesh reconstruction, after Colbert (1955).

Body mass (MBd) and total body length (TL) of fossil crocodilians and crocodiliform vertebrates have been estimated from equations predicting either from skull length or TL in recent crocodilians (e.g., Sereno et al., 2001). The usefulness of such techniques is hampered by two factors—variable rostal (snout) length among and within crocodilian taxa, and variable tail length among species. Equations predicting snout-anterior vent length (SVLA) and body mass (MBd) from orbito-cranial length (ODCL) and orbito-vent length (OVLA) in alligators are used to estimate these in phytosaurs.

Alligators (Alligatoridae: *Alligator mississippiensis*) are widely studied and available for study in the U.S. Use of alligator skull length to estimate body mass is hampered by the fact that snout length is more variable than "braincase length" among both Recent and fossil crocodilians, and the primitive crurotarsan archosaurian phytosaurs (Benton and Clark, 1988; Sereno, 1991; Brochu, 2001). Alligators in particular have the shortest snouts among crocodilians (Rowe et al., 1999; Sereno et al., 2001). Predictions from orbitocranial length (ODCL), which approximates braincase length, can evade this confounding factor and make alligator-based equations applicable to crocodilians and vertebrates of crocodilian body form with varying snout length (Fig. 2) (for abbreviations, see Table 1).

A major challenge of this study is the difference between skull morphology in crocodilians and phytosaurs. Specifically, the retracted nares of the phytosaurs confound measurements based on their position. Furthermore, it has long been apparent that phytosaurian taxa exhibited strikingly different snouts, presumably correlated to specific feeding habits (e.g., Chatterjee, 1978, fig. 16; Hunt, 1989). Thus, we suspect that estimates based on skull length alone may be erroneous, as the phytosaurs with the proportionately longest skulls (e.g., *Mystriosuchus*) tend to be the most gracile, whereas the more robust taxa have less elongate snouts (Hungerbühler, 2002).

Institutional abbreviations: NMMNH = New Mexico Museum of Natural History and Science, Albuquerque; ROM = Royal Ontario Museum, Paleobiology Department, Toronto; UCMP = University of California, Berkeley; U. Mo. = University of Missouri, Columbia, Missouri.

TABLE 1. Abbreviations used in this paper

ANDCL = narial-cranial length from anterior narial limit to posterior mid-sagittal skull limit
ANDCL = anterior dorso-cranial length (narial-cranial length from anterior narial limit to posterior mid-sagittal skull limit)
ANVLA = anterior nares-vent length (anterior narial -vent length from anterior narial limit to anterior vent limit)
AP = antero-posterior
DCL = dorsal cranial length
DV = dorso-ventral
MBd = body mass
MFL = maximum femur length
ML = medio-lateral
ODCL = orbito-cranial length
OVLA = orbito-vent length
SL = snout length
SVL = snout-vent length
SVLA = snout-vent length (to anterior limit)
SVLP = snout-vent length (to posterior limit)
TG = tail girth
TL = tail length

MATERIALS AND METHODS

Equations new to this paper relating cranial dimensions to crocodilian body mass, total length, and snout-vent length are based on a sample of wild and pen-raised alligators from Florida and Louisiana. In both states, pen-raised alligators were raised from eggs in water-filled environmental chambers until reaching four feet TL in Florida and three years of age in Louisiana, at which point they were released to pens. In Louisiana, the chambers held 530 liters with 10.4 m^2 surface area; in Florida the chambers were about half this size. These enclosures were approximately two meters wide and two or more meters long. In Louisiana, pens were fenced areas of two acres that contained rectangular ponds 5-18 m wide, 30-53 m long, and 2 m deep, with additional small ponds and natural vegetation (Joanen and McNease, 1987). Penned alligators could and did catch and eat birds and other wild creatures, and were also fed ground nutria and fish weekly in the spring and summer. The Florida pen-raised alligators (Hill-top Farms) were raised and released to pens in similar conditions in central Florida: they were fed chicken (rejects from restaurants; young alligators were fed ground chicken). Wild alligators were obtained from licensed trappers of nuisance animals in northern Florida, and on the Louisiana Rockefeller Wildlife Refuge. Alligators were measured where caught. Skulls and skeletons were defleshed on site and at one of the author's (JOF) home institution by dermestid beetles or maceration. The ALLMASS programs use relationships among fifteen pen-raised and three wild alligators from Florida, and the MFL (maximum femur length) sample includes wild and pen-raised alligators.

For purposes of this paper we focus primarily on the fossil record of phytosaurs from the Chama basin in north-central New Mexico. This includes the UCMP sample from the Canjilon quarry (Gregory, 1962; Lawler, 1974; Long et al., 1989; Zeigler et al., 2002a) and the Snyder quarry (Zeigler et al., 2002b, 2003a,b). All of these specimens pertain to the species *Pseudopalatus buceros* (Lucas et al., 2002; Zeigler et al., 2002a,b). These fossils were recovered from the Painted Desert Member of the Petrified Forest Formation. Specifically, we studied skulls of *Pseudopalatus* in the New Mexico Museum of Natural History, Albuquerque (NMMNH), humeri, ulnae, femora, and tibiae of *Pseudopalatus* (NMMNH), and UCMP V2816/27235, an articulated fossil skeleton of *Pseudopalatus pristinus* lacking only the tail in the collection of the UCMP. All specimens were measured directly except UCMP V2816/27235 (*Pseudopalatus*), which was measured from figure 42 in Long and Murry (1995). UCMP V2816/27235 is a preserved complete fossil skeleton except the tail, facilitating estimation of MBd, TL, and SVLA from skull dimensions, the axial skeleton, and limb bones. Skull dimensions for UCMP V2816/27235 were measured from the dorsal view of the skull of U. Mo. 525VP, the holotype of *P. pristinus*, figured in Long and Murry (1995), and enlarged 123% to match the length of the skull of UCMP V2816/27235. These measurements were also compared to NMMNH skulls (especially NMMNH P-31292) and lower jaws (e.g., NMMNH P-36051).

In this paper, the posterior limit of the ischium is used as a skeletal correlate of the anterior vent limit in alligators, thus facilitating snout-vent length (SVLA) and orbito-vent length (OVLA) measurement in fossil crocodilians and phytosaurs, the "A" indicating anterior vent limit. It is useful to estimate MBd from SVL instead of or in addition to TL for the following reasons. First, tail length is often less accurately measured than SVL on living crocodilians, due to accidental loss of terminal tail segments. Second, the number of trunk vertebrae is more constant than the number of caudal vertebrae, due to tail length differences, among Recent and fossil crocodilian and crocodiliform vertebrates. For example, in the phytosaur ?*Mystriosuchus*, the tail is much longer than the body (Renesto and Lombardo, 1999), whereas alligator SVL approximates one-half TL (Woodward et al. 1992). The ?*Mystriosuchus* specimen possesses 70-75 caudal vertebrae, but only an estimated 25 presacral vertebrae (Camp, 1930; Renesto and Lombardo, 1999). By way of contrast, *Alligator mississippiensis* possesses 23 presacral vertebrae (plus the proatlas) and 34 caudals in (examination of three complete adult skeletons—ROM R4406, R4410, and R4414). Third, terminal caudal elements are often absent from otherwise relatively complete fossil specimens, due to their small size, so that a missing meter of TL can greatly affect body mass estimates even though terminal tail segments often contribute little to body mass in crocodilians and other non-avian reptiles. Use of SVL circumvents these limitations.

In this study, MBd, TL, and SVL are estimated separately from different skeletal elements, with the expectation that similar estimates from different elements are more reliable than a single estimate from one element or dimension. Use of a largely complete articulated phytosaur, *Pseudopalatus pristinus*, UCMP V2816/27235 (Long and Murry, 1995, fig. 42), will permit assessment of the accuracy of several equations.

Equations predicting body mass (MBd), total length (TL) and snout-vent length (SVL) from cranial dimensions were calculated us-

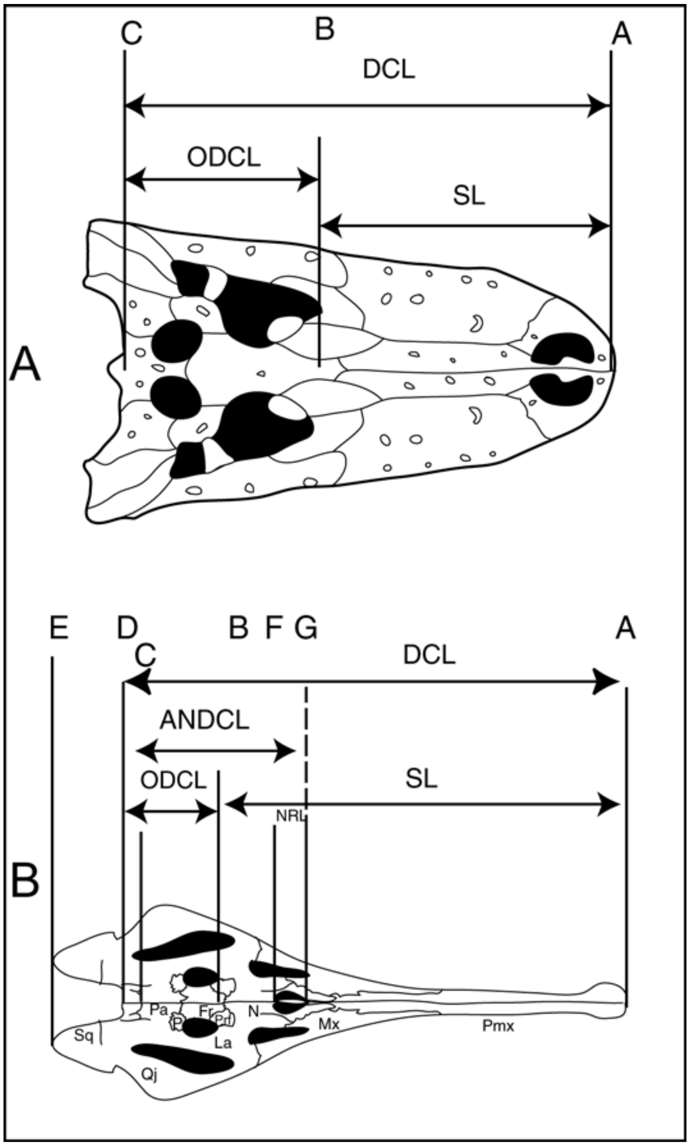

FIGURE 2. Measuring protocols used here on **A**, alligator, and **B**, phytosaur skulls. **A**, dorsal view of skull of a wild female *Alligator missippiensis* from northern Florida (DCL, 246 mm; SVLA 905 mm; TL, 1913 mm), FL01-06 in private collection of GRH. **B**, idealized dorsal view of NMMNH P-31292 (DCL, 685 mm), a phytosaur skull assigned to *P. buceros* (modified from Zeigler et al., 2002b). Drawings not to scale. Abbreviations: A, anterior snout-tip; B, anteriormost inner rim of orbit; C, posteriormost dorsal midpoint of parietals; D, posteriormost dorsal midpoint of supraoccipital; E, posteriormost limit of squamosals; F, posterior limit of inner rim of nares; G, anterior limit of inner rim of nares. Points B, C, F, and G are the intersection of the sagittal midline with transverse lines determined by the right and left points and limits described above. ANDCL, anterior narial dorsal cranial length between anterior nares and posteriormost dorsal midpoint of skull; DCL, dorsal cranial length between snout tip (A) and posteriormost dorsal midpoint of skull (C or D); ODCL, orbitocranial length between anteriormost inner rim of orbit and posterior dorsal skull limit; NRL, narial length; SL, snout length from snout tip to anteriormost inner rim of orbit. Fr, frontal; Mx, maxilla; N, nasal, P, postorbital; Pa, parietal; Pmx, premaxilla; Qj, quadratojugal; Sq, squamosal.

ing a sample of combined wild and farmed alligators. The cranial dimensions included dorsal cranial length (DCL), measured from the snout tip to the posterior dorsal midpoint of the skull, which was on the parietals in alligators but often the supraoccipital in phytosaurs (Fig. 2). This marked the point at which the skull met the vertebral column. Orbito-cranial length (ODCL) extends from the internal anterior limit of the orbit to the posterior dorsal skull limit (Fig. 2), and orbito-vent length (OVLA) from the internal anterior orbital limit to the anterior vent limit. The anterior ODCL point was a point where the skull midsagittal line crossed a transverse line joining the internal anterior limit of the orbit. ODCL can be approximated by DCL minus snout length (SL), where SL is the distance between the most rostral snout tip and the anteriormost internal rim of the orbit. SL and DCL resemble similar measurements in Iordansky (1973). The anterior vent limit was approximated by the posterior limit of the ischium. Dissection showed the anterior vent limit was 15 to 25 mm posterior to the ischium in a wild female alligator in Florida with the following dimensions: TL, 2470 mm; SVLA, 1350 mm; MBd, 60 kg and vent length 36.05 mm (specimen FL01-01, collection of GRH). This positioning in archosaurs is supported by the presence of a vent-like structure in the articulated type skeleton of *Coahomasuchus* (Heckert and Lucas, 1999, fig. 4), located about 30 mm caudal to the broken and incomplete caudal end of the ischium.

Equations predicting alligator MBd from various variables (ODCL, DCL, TL, SVL_{Def}, and OVL_{Def}) were calculated for a mixed sample including all specimens for which SVLA was known (N=32) and a second mixed sample using SVLA when available (32 cases), and SVL_P (SVL to posterior limit) otherwise (5 cases). This second, mixed sample (N=37)was designated as SVL_{Def}. SVLA was known for all pen-raised and all but five wild alligators. SVL_{Def} equations are used to predict SVLA in fossil specimens.

Due to the differences between braincase form in alligators and phytosaurs, the measurements ANDCL and ANVLA were taken on phytosaurs, extending from the anterior interior narial limit to the posterior skull limit (ANDCL, fig. 2) and the posteriormost point visible on the pelvic region of UCMP V2816/27235. This dimension was entered in the equations with ODCL and OVLA as independent variables. This relationship was investigated to test the hypothesis that braincase length in alligators, measured as ODCL, is functionally equivalent to braincase length measured from the anterior narial limit. Phytosaur SVLA was estimated by subtracting estimated (from SVLA) alligator skull length (DCL) from the calculated SVLA, then adding the actual phytosaur DCL.

Body mass was also estimated from ALLMASSC18 and ALLMASSD18, Microsoft Excel® programs using equations for relationships in alligators (N=18). Similar ALLMASS programs in QBASIC are described in Hurlburt (1999). These equations essentially modify the approach for mammals of Gingerich (1990). ALLMASSD is based on 12 equations predicting body mass from bone length and two parasagittal midshaft diameters from each of humerus, ulna, femur, and tibia. Entering any of these dimensions in the program yields a prediction of body mass with upper and lower 95% confidence limits. Where two or more dimensions are entered, the program also calculates the geometric mean of the predictions and the 95% confidence limits. In this calculation, individual predications are weighted by the coefficient of determination (r^2) corresponding to each equation. In ALLMASSD, body mass was also calculated by obtaining the geometric mean of two estimates, one from bone lengths and the second from both diameters, so as to equally weight estimates obtained from lengths and midshaft diameters (Hurlburt, 1999). ALLMASSC is similar, using equations predicting body mass from length and midshaft circumference of the same bones. Lengths of all bones were measured as in Dodson (1975). Midshaft was one-half length. The humerus and femur were measured as extending laterally from the body, whereas the ulna and tibia were measured as vertically upright. This resulted in dorsoventral (DV) and anteroposterior (AP) diameters measured on the humerus and femur, and mediolateral (ML) and AP diameters measured on the ulna and tibia. MBd, TL, and SVLA were also estimated from maximum femur length (MFL) in alligators and crocodilians using equations in Farlow et al. (in prep.). MFL was the maximum distance from the lateral condyle of the distal end to the most proximal end of the femur head.

RESULTS

Equations predicting MBd, TL, SVLA, and SVL_{Def} from cranial or axial skeletal dimensions were based on samples combining wild and pen-raised alligators (Tables 2-3). "Def" (default SVL) indicates measurements were to anterior vent limit (SVLA) except in the four cases where only SVL_P was available. Where N=37 or 38, the MBd range is 1.15-232.27 kg, TL range of 805-3836 mm, and SVL range of 385-1913 mm. Where N=51, the MBd range is 1.15 -237.9 kg; and the TL and SVL range the same as for N=38. Wild alligators (N=20) were generally smaller, with mean TL and MBd of 1890 mm and 36.7 kg respectively, and only one specimen exceeding 68 kg (232 kg and 2700 mm). In contrast, pen-raised alligators (N=18) had a mean TL and MBd of 2340 mm and 63 kg respectively, with an MBd range of 12.9-124.7 kg and TL range of 1664-2870 mm (Appendix 1, table 2).

SVL_{Def} equations were calculated to produce equations based on larger sample sizes. Comparisons of 95% confidence interval of slopes indicates that the slopes of SVLA and SVL_{Def} samples were not significantly statistically different for equations predicting MBd from skull dimensions, SVL and TL (Appendix 1, table 1), nor were equations predicting TL from ODCL and DCL (Appendix 1, table 3). Slopes predicting SVL from ODCL and DCL were significantly statistically different between the small and larger mixed samples, perhaps due to the effect of the frequency of alligators with truncated tails (Appendix 1, table 3). TL predicted for phytosaurs using alligators is less dependable than SVL or MBd in any case due to differences between phytosaurs and alligators. Slopes were statistically indistinguishable for equations predicting SVL_{Def} from DCL and ODCL (Appendix 1, table 4). These results legitimize the use of all equations based on the larger mixed sample (equations using SVL_{Def}), with the possible exception of those predicting TL from OVLA and SVL.

All slopes of equations predicting MBd using the larger common sample (N=37, 38, or 51) were within the 95% confidence interval of the wild and pen-raised samples, (Appendix 1, tables 1-2). Of all equations predicting MBd, only the slopes relating MBd and OVL_{Def} of the smaller mixed sample (N=32) and the pen-raised sample had statistically distinct slopes, and the smaller mixed sample slope was not used in this study. For equations predicting TL from ODCL, DCL, OVLA, and SVL, all slopes of the maximum mixed samples (N=37 or 51) were within the 95% confidence interval of the wild and pen-raised samples, except that the TL=DCL slope was outside the 95% confidence interval of the wild sample, but the wild slope was within the maximum sample's slope (Appendix 1, table 3). For equations predicting SVL_{Def} from ODCL and DCL, the slopes of the mixed, pen-raised, and wild samples were all within each other's confidence interval (Appendix 1, table 4).

Table 3 (see appendix) lists slopes (*b*), intercepts (*a*), N, 95% confidence limits, and correlation coefficients (R) for least squares equations predicting MBd, TL, and SVL_{Def} from the independent variables ODCL, DCL, OVLA, ODCL, and maximum femur length (MFL). Note that correlation coefficients (r) relating MBd, TL, and SVL_{Def} to ODCL and OVL_{Def} are very close to those relating MBd, TL, and SVL_{Def} to DCL and $SVL_{Def,}$ differing by 0.016 or less (Table 3). Figures 3-5 are scattergrams of raw data showing point scatters and power functions relating MBd and ODCL and DCL, SVL_{Def} and ODCL and DCL, and MBd and OVL_{Def} and SVL_{Def} for the mixed samples. Raw data are plotted to show shapes of the point distributions; the plotted power functions, of the form $Y= aX^b$, are equivalent to the $\log_{10}$-transformation of the least squares regression equations, of the form $\text{Log}Y = \text{Log}a + b\text{Log}X$, used to predict size.

Table 4 (see appendix) shows estimates from various equations of MBd, TL, and SVLA for UCMP V2816/27235 from skull dimensions, the axial skeleton, and limb bones. Importantly, MFL estimates resulted in a trunk length estimate and phytosaur SVLA that were

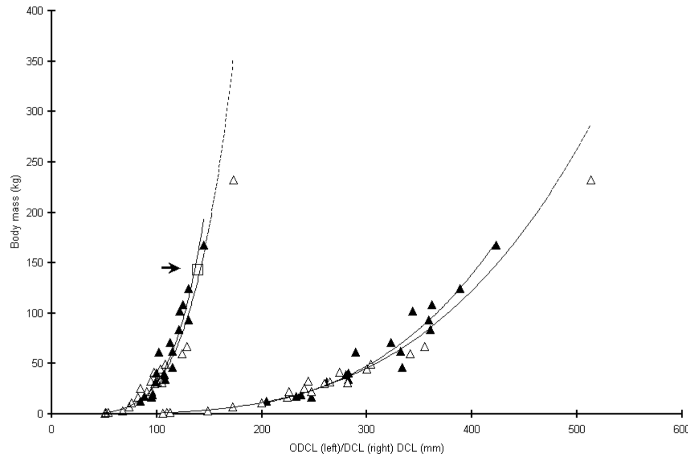

FIGURE 3. Raw data power functions ($Y=aX^b$) predicting body mass from ODCL (left) and DCL (right), for pen-raised alligators (solid symbols) and wild alligators (open symbols and dashed line). Arrow shows open square indicating predicted body mass (142.9 kg) from ODCL for phytosaur UCMP V2816/27235. Predicted body mass was 2034 kg from DCL. Raw data power functions used to show raw data distribution and shape of raw data curves. Predictions were made from corresponding $\log_{10}$ least squares equations. DCL, dorsal cranial length; ODCL, orbitocranial length (see text and tables).

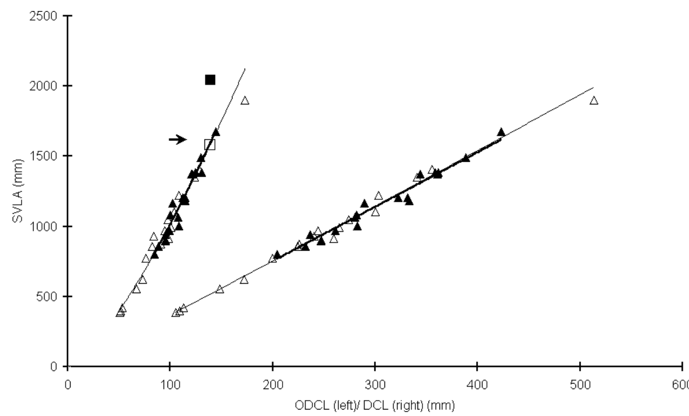

FIGURE 4. Raw data power functions ($Y=aX^b$) predicting SLVA from ODCL (left) and DCL (right), for pen-raised alligators (solid symbols) and wild alligators (open symbols and dashed line). Arrow shows open square indicating SVLA (1583 mm) predicted for an alligator with the ODCL of phytosaur UCMP V2816/27235. Upper solid square indicates ODCL and predicted SVLA (2047.7 mm; 81.6 % of actual) for UMCP V2816/27235 incorporating actual phytosaur DCL (see text) . The SVLA prediction from DCL was 137% of actual SVLA (table 3). SVLA, snout-vent length to the anterior vent limit. Other abbreviations as in Fig. 3.

100.4% and 100.3% respectively of the actual trunk length and SVLA measured on figure 42 of Long and Murry (1995). ODCL produced the next nearest estimate at 81.6% of actual phytosaur SVLA, but only 71.7% of trunk length (atlas-vent length, or AtVLA). Other estimates were 37% or more away from actual phytosaur SVLA, and more from trunk length. This gives reason for confidence in the MFL-based estimate of MBd (377 kg), and similar results were obtained from ALLMASSD (389 kg) and OVLA (416 kg), all converging on a range of 380-416 kg. The estimate from ODCL (142 kg) was less than half the average value, whereas that from phytosaur SVLA was nearly double the actual estimate, and only the lower 95% prediction limit (PL) was above the range. Both DCL and ANCL gave estimates about five times the most reasonable estimate. Presumably because of the differences in skull morphology between alligators and phytosaurs, phytosaur skull length (DCL) gives totally unreliable results for body mass. The inac-

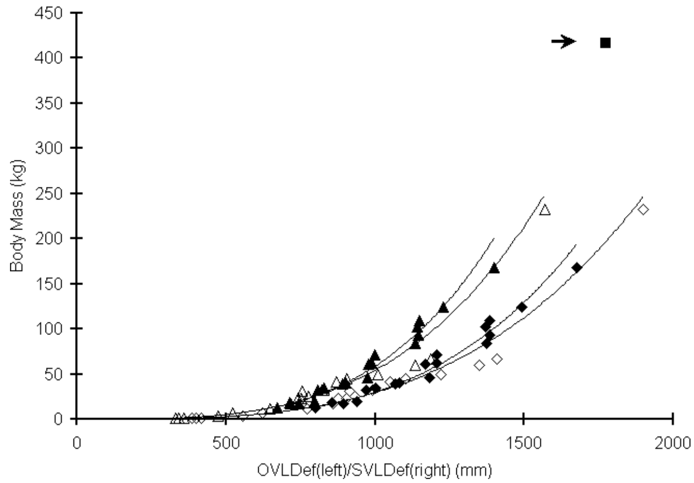

FIGURE 5. Raw data power functions (Y=aX^b) predicting body mass from OVLA (left) and SVLA (right), for pen-raised alligators (solid symbols) and wild alligators (open symbols and dashed line). Arrow shows solid square indicating predicted body mass (416.4 kg) from OVLA, within 40 kg of predictions from leg bone dimensions (table 3). The predicted MBd from SVLA (691.4 kg) considerably exceeded leg bone-based estimates. Although the equations relate MBd to SVL_{Def} and OVL_{Def}, MBd is predicted from SVLA and OVLA. Abbreviations: OVLA, orbito-vent length to anterior vent length. Other abbreviations as in Figs. 3 and 4.

curate results from skull and axial skeleton dimensions measured from the anterior nares, using equations predicting from ODCL and OVLA, are reason to abandon use of these measurements. Although DCL predicts an SVLA within 40% of the actual figure, it is less accurate than the 81% result from ODCL (Table 4). Estimates of phytosaur TL are given, but their accuracy cannot be assessed because UCMP V2816/27235 lacks a tail. Table 4 gives estimates of MBd, TL, and phytosaur SVLA from ODCL and DCL. Estimates of SVLA from ODCLA are most likely to be accurate. No estimates were made from dimensions measured from the anterior narial limit due to the results for UCMP V2816/27235. Tables 5 and 6 give similar estimates for individual bones from ALLMASS and MFL. Table 7 shows ALLMASSD output for UCMP 2816/27235.

DISCUSSION

This is the first study known to the authors to use orbitocranial length and snout-vent length to predict MBd in fossil amniotes, the first known to predict snout-vent length, and one of the few to use several uncorrelated dimensions to estimate MBd. This was done under the assumption that similar estimates from different methods would converge on a more accurate result than any single method. The close similarity of r-values relating the predicted variables MBd, TL and SVL_{Def} to ODCL and OVL_{Def} (0.991) to those relating these predicted variables DCL and SVL_{Def}, some different only at the third decimal place, gives confidence in their use in predictive equations.

Estimates of MBd, SVLA, and TL for Phytosaurs.

The accuracy of the MFL estimate of SVLA (discussed below) suggests that the MBd estimate computed from MFL is likely accurate as well. Further support is provided by the fact that estimates from two other sources (ALLMASS and OVLA), one uncorrelated and the other only partly correlated with MFL, resemble those from MFL. This suggests a MBd of approximately 390 kg for UCMP V2816/27235, if it has a alligator-shaped tail (Tables 4 and 5). Although ALLMASS results may be partly correlated with MFL due to inclusion of femur length in ALLMASS, estimates from other dimensions (diameter) and other elements in ALLMASS gave similar results (Table 5). Because MFL and ODCL underestimated SVLA until a phytosaur skull was added, MBd may similarly have been underestimated by an amount equivalent to the difference between phytosaur and alligator skull mass. The ALLMASS estimates from femora and humeri may be more accurate than those from tibiae and ulnae, as in Hurlburt (1999). The MBd estimate from ODCL was about 50% of that from the other sources, but was of the same order of magnitude. In contrast, estimates from ANCL and DCL were an order of magnitude higher, and not useful at all. Although the estimate from ANVLA (140%) was of the same order of magnitude of the MFL estimate, the OVLA estimate approximated the MFL result much more closely.

MFL estimated trunk length and "phytosaur" SVLA (when actual phytosaur skull length was included) with nearly 100% accuracy (Table 4). The method of subtracting estimated (from SVL) alligator skull length, and adding actual phytosaur skull length gave a much more accurate estimate of SVLA (81.6% of actual SVLA) than an estimate that retained alligator skull length (63%). This result not only recommends this method, but also indicates strong similarity between trunk proportions of alligators and phytosaurs, at least based on one specimen.

Our estimates of the mass and length of the Chama basin phytosaurs are thus as follows. ODCL-derived estimates yielded masses of 91-476 kg and SVLA lengths of 1400-2260 mm (Table 5). ALLMASS-derived MBd estimates, based on hind limb measurements, range from 50-350 kg (Table 6). MFL-derived MBd estimates range from 126-377 kg, and yield SVLA estimates of 1600-2200 mm depending on the specimen. We also provide estimates of total length, but as discussed earlier, these are much more speculative due to the difference in caudal vertebral counts in phytosaurs and alligators. In alligators, SVLA equals approximately one-half TL, but the relationship is not known for phytosaurs presently. We do not believe that this greatly affects MBd estimates, as using an alligator as a model for a phytosaur should yield a similar mass, as the apparently more elongate, gracile tail of a phytosaur (Renesto and Lombardi, 1999) would add relatively little mass to the animal.

Utility of Anterior Orbital Limit and Snout-vent Length

Measuring from the anterior orbital limit provides useful information from incomplete skulls, as does SVL for incomplete skeletons. The results indicate the utility of these methods, as ODCL produced acceptable estimates, whereas equations using skull length and ANCL both overestimated MBd by a factor of 10. Skull and axial skeleton measurements from the anterior narial opening were not useful, nor were estimates of SVL or TL from dorsal cranial length. The hypothesis that "braincase length" is more conservative in the group including crocodilians and phytosaurs is supported, despite the specializations of the phytosaur skull, providing a theoretical explanation for the empirically determined results. It is possible that other dimensions from the phytosaur skull may provide better accuracy. The results generally suggest that most variation between phytosaurs and crocodilians is in skull and tail length. Estimates of SVL are more dependable than estimates of TL, because trunk length is similar in phytosaurs and alligators, but tail length differs according to available evidence. It is encouraging that ODCL and therefore "braincase" length can be used to estimate phytosaur size, as this allows the measurement of incomplete skulls.

Usefulness of maximum femoral length

These results also suggest that estimates from ALLMASS, MFL and OVLA are more accurate than those from DCL, SVLA, or the distance from the anterior narial limit to the posterior skull limit. The extremely accurate result from MFL for SVLA is particularly useful, and further indicates proportional similarities between phytosaurs and crocodilians in leg dimensions and trunk size.

CONCLUSION

The results of this study are encouraging. It may be possible to associate separate elements from the same deposit based on similar associated body size estimates

Body size in the form of body mass (MBd), snout-vent length to the anterior vent limit (SVLA), and total length (TL) was estimated in phytosaurs using several methods, some of which appear for the first time in this paper. Accuracy of methods was assessed using UCMP V2816/27235, a fossil phytosaur skeleton missing only the tail. SVLA, measuring to the posterior ischial limit, is used here for the first time and shown useful on crocodiliform archosaurs of conservative body form, allowing comparisons to Recent non-avian reptilians in whom SVLA is commonly used, and circumvents problems of missing tail elements and differences in relative tail length among taxa. The paper also introduces body size estimates from orbital cranial length (ODCL) and orbito-vent length (OVLA), measured from the anterior orbital limit. ODCL estimated 80% of actual SVLA and 50% of probable MBd of UCMP V2816/27235, a fossil phytosaur skeleton missing only the tail, whereas OVLA estimated an MBd near estimates from leg bones. Approximately 100% of both actual trunk length and actual SVLA of UCMP V2816/27235 was estimated from maximum femur length (MFL) relations in Recent crocodilians, by replacing estimated alligator skull length (DCL) by actual phytosaur skull length. Similar MBd estimates were produced by MFL, ALLMASS, which estimates body mass from long bone dimensions (Hurlburt, 1999), and from OVLA. ODCL estimated half this body mass. In contrast, estimates of MBd using alligator equations from DCL or ANCL (anterior phytosaur nares to posterior skull limit) were an order of magnitude higher for MBd and 40% to 50% too large for SVLA.

ODCL gave an estimate that was 80% of actual phytosaur SVLA. Use of ODCL and OVLA allowed use of alligator-based equations to make reasonably accurate estimates of phytosaur mass and SVL from the phytosaur skull, which would not be possible using DCL or SVLA, despite many differences in skull morphology between phytosaurs and crocodiles. Cranial and ALLMASS equations provided 95% confidence limits. These and use of estimates from several uncorrelated dimensions may allow convergence on accurate values.

In general, phytosaurs appear to have comparable trunk and leg bone proportions to alligators, suggesting these regions and elements are conservative within crocodiliform archosaurs, whereas the greatest skeletal differences are in skull dimensions and morphology. Mbd estimates for Snyder quarry phytosaurs range between 25 and 500 kg, with most specimens yielding estimates of approximately 200-350 kg. The Canjilon quarry sample includes fewer juveniles and more robust adults, including one individual that may have weighed as much as 535 kg. From equations based on nine extant crocodilian genera, these Revueltian phytosaurs appear to have approached 4.5 m total body length for a ~ 400 kg phytosaur. The prevalence of subadult to adult phytosaurs in both quarries based on body mass estimates corroborates qualitative estimates of the population structure based on skull sizes alone, thereby reinforcing the hypothesis that both quarries are catastrophic assemblages (Zeigler, 2002, 2003).

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APPENDIX—TABLES

TABLE 2. Mean SD, and CV of alligator skull and body linear measurements and body mass. SVLA (Snout-vent length) to anterior vent margin known for 32 alligators (MBd known for 31). SVL_{Def} known for 38 alligators (MBd known for 37). SVL_{Def} (Default) is SVLA when known, otherwise SVL_P (SVL to posterior vent limit). SVLA known for all pen-raised alligators, and all but five wild alligators. MBd was unknown for one wild alligator with a TL of 3836 mm and SVLA of 1913 mm. Abbreviations: CV, coefficient of variation (=SD x 100/Mn); CW, cranial width at quadrates; DCL, dorsal cranial length from snout to posterior dorsal midpoint of skull; MBd, body mass; Mn, mean; ODCL, orbital dorsal cranial length from interior anterior orbital limit to posterior dorsal midpoint of skull; OVLA, P; orbitovent length from interior anterior orbital limit to anterior or posterior vent limit; SL, snout length from snout to interior anterior orbital limit; TG, maximum tail girth posterior to vent; TL, total length from snout to tail tip.

Sample Alligators	Parameter	TL (mm)	MBd (kg)	SVLA (mm)	SVLDef (mm)	OVLDef (mm)	DCL (mm)	ODCL (mm)
known SLVA	SD	432.97	37.11	242.45	242.45	199.82	60.07	17.29
(N=32 but 31 for	Mean	2205.43	49.96	1094.72	1094.72	910.81	286.99	104.47
31 for MBd)	CV	19.63	74.28	22.15	22.15	21.94	20.93	16.55
SVLA or SVLP	SD	626.43	48.08		338.18	277.19	85.75	25.09
(N=38 but 37 for	Mean	2103.24	49.19		1045.65	870.74	275.07	101.12
31 for MBd)	CV	29.78	97.75		32.34	31.83	31.17	24.81
Pen-raised	SD	438.91	43.10	240.89	240.89	197.72	59.69	16.09
(N=18)	Mean	2340.13	63.04	1169.94	1169.94	971.37	307.51	110.54
	CV	18.76	68.37	20.59	20.59	20.35	19.41	14.56
	Range	MBd, 12.9-124.7 kg; TL, 1664-2870 mm; plus one at 167.8 kg and 3302 mm.						
Wild (N=20 but	SD	700.57	49.95	215.37	3792.37	311.49	96.12	33.30
19 for MBd)	Mean	1890.05	36.72	998.00	927.89	320.33	245.88	96.53
(N=15 for SVLA)	CV	37.07	136.03	21.58	408.71	97.24	39.09	34.49
	Range	MBd, 1.15-67.3 kg; TL, 805-2700mm; plus one at 232.3 kg and 3700 mm.						

TABLE 3. (MBd); body length (TL), and snout-vent length to anterior vent limit (SVLA) predicted from cranial dimensions, orbitovent length, SVLA, and maximum vent length. For all femur-based equations, p<0.001. Most wild and domestic alligators in skull sample also included in femur sample. Interspecific equation consists of 1 individual of each of *Alligator mississippiensis*, *A. sinensis*, *Paleosuchus trigonatus*, *Caiman crocodilus*, *Melanosuchus niger*, *Tomistoma schlegelii*, *Crocodylus acutus*, a *C. porosus-C. siamensis* hybrid, and *Gavialis gangeticus*. All lengths in mm unless otherwise indicated, MBd in kg. Abbreviations: FLM, maximum femur length; Log_{10}, logarithm to base 10; N, sample size; ODCL, orbitocranial length measured from anterior internal limit of orbit to posterior skull limit; OVL_{Def}, default orbitovent length from anterior internal orbit limit to default vent limit ("default" indicates measurements were to anterior vent limit except in four specimens in which only the posterior vent limit was used in the contributing sample); R, correlation coefficient; Sample, sample on which equations based; SVLA, snout-vent length measured to the anterior vent limit. All samples from Farlow et al. except those where (Hurlburt) indicated.

Predicted Variable	Independent Variable	Slope (*b*)	Intercept (*a*)	R	N	Sample
$Log_{10}MBd$	$Log_{10}ODCL$	4.573	-7.642	0.9759	38	Wild and domestic Alligators (Hurlburt)
$Log_{10}MBd$	$Log_{10}DCL$	3.522	-7.054	0.9919	51	Wild and domestic Alligators (Hurlburt)
$Log_{10}MBd$	$Log_{10}OVL_{Def}$	3.471	-8.659	0.9909	37	Wild and domestic Alligators (Hurlburt)
$Log_{10}MBd$	$Log_{10}SVL_{Def}$	3.395	-8.704	0.9920	37	Wild and domestic Alligators (Hurlburt)
$Log_{10}TL$	$Log_{10}ODCL$	1.259	0.793	0.9817	39	Wild and domestic Alligators (Hurlburt)
$Log_{10}TL$	$Log_{10}DCL$	0.970	0.954	0.9941	52	Wild and domestic Alligators (Hurlburt)
$Log_{10}TL$	$Log_{10}OVL_{Def}$	0.964	0.489	0.9922	37	Wild and domestic Alligators (Hurlburt)
$Log_{10}TL$	$Log_{10}SVL_{Def}$	0.944	0.475	0.9941	37	Wild and domestic Alligators (Hurlburt)
$Log_{10}SVL_{Def}$	$Log_{10}ODCL$	1.351	0.306	0.9857	37	Wild and domestic Alligators (Hurlburt)
$Log_{10}SVL_{Def}$	$Log_{10}DCL$	1.026	0.515	0.9952	37	Wild and domestic Alligators (Hurlburt)
TL	FLM	14.448	16.454	0.9960	98	Wild and domestic Alligators
TL	FLM	15.361	-102.039	0.9860	9	Interspecific regression equation
Log_{10} MBd	Log_{10} FLM	3.335	-5.720	0.9940	36	Wild alligators
SVLA	FLM	7.167	5.828	0.9920	43	Wild and domestic alligators
$Log_{10}DCL$	$Log_{10}SVL_{Def}$	0.965	-0.473	0.9952	37	Wild and domestic alligators (Hurlburt)

TABLE 4. Estimates of Body Mass (MBd); Snout-vent length to anterior vent limit (SVLA) and trunk length ($ATVL_{Def}$) from skull, other axial skeleton, and long bone dimensions for the phytosaur UCMP V2816/27235, a largely complete specimen of *Pseudopalatus pristinus* lacking the tail. Equations estimate alligator SVLA. Phytosaur SVLA calculated by subtracting estimated alligator skull length (DCL) for a given SVLA, and adding DCL (below) of UCMP V2816/27235. V2816/27235 ALLMASS based on anteroposterior (AP) diameter of femur and humerus, mediolateral (ML) diameter of tibia and fibula, and lengths of all four elements. All measurements from figures in Long and Murry (1995) are provisional. Abbreviations: ANDCL, narial-cranial length from anterior narial limit to posterior mid-sagittal skull limit; ANVLA, anterior narial -vent length from anterior narial limit to anterior vent limit; DCL, dorsal cranial length from snout tip to posterior dorsal mid-sagittal limit of skull; MFL, maximum femur length (see text) ODCL, orbitocranial length, anterior orbital limit to posterior midsagittal skull limit; OVLA, orbitovent distance from interior anterior orbital limit to anterior vent limit (posterior ischial limit in skeletons); TL, total body length. Phytosaur TL is essentially the phytosaur skull (DCL) added to an estimated alligator TL from which estimated alligator DCL (from SVLA) has been subtracted, i.e., a phytosaur skull on an alligator body. For TL from OVLA, DCL values for ANCL estimates were used, because the TL values from ANCL were similar. UCMP V2816/27235 dimensions: ANCL=268.242 mm; ANVLA=1903.6 mm; DCL=875.32; Trunk L. (AtVLA)=1635.335 mm; ODCL=138.83 mm; OVLA =1774.2 mm; and SVLA=2510.7 mm.

Source of Estimate	MBd (kg)	Est. allig. SVLA (mm)	Est.allg. DCL fr.SVLA (mm)	Trunk L. (AtVLA) =est.SVLA -est. DCL	Percent of actual phytos Trunk L.	Phytosaur SVLA (mm) =AtVLA + phyto. DCL	Percent of actual phytos. SVLA	Phytosaur TL (w/allig DCL) (mm)	Phytosaur TL (w/phyto DCL) (mm)
MFL (mm)	377.092	2208.9	566.3	1642.6	*100.4*	2517.9	100.3	4457.6	4766.6
ODCL (mm)	142.856	1583.0	410.6	1172.4	*71.7*	2047.7	81.6	3095.2	3559.9
(PL_1)	126.620	1539.5	399.7	1139.7	*69.7*	2015.1	80.3	3012.0	3487.6
(PL_2)	161.175	1627.7	421.8	1205.9	*73.7*	2081.2	82.9	3180.7	3634.2
ANCL (mm)	2903.246	3853.3	968.7	2884.5	*176.4*	3759.8	149.8	7094.2	7000.8
(PL1)	2049.838	3556.6	896.7	2659.9	*162.7*	3535.2	140.8	6543.0	6521.7
(PL_2)	4111.954	4174.7	1046.6	3128.1	*191.3*	4003.4	159.5	7691.8	7520.6
DCL (mm)	2033.997	3426.9	865.1	2561.8	*156.7*	3437.1	136.9	6437.9	6448.1
	1744.276	3285.3	830.6	2454.7	*150.1*	3330.0	132.6	6215.9	7091.2
	2371.841	3574.7	901.1	2673.6	*163.5*	3549.0	141.4	6667.9	7543.3
OVLA (mm)	416.412		968.7					4190.6	4097.2
	367.6070004		896.7					4058.4	4037.1
	471.697		1046.6					4327.2	4155.9
SVLA (mm)	691.4541063								
	603.3271004								
	792.4536803								
ANVLA (mm)	531.681		968.7					4485.0	4391.6
(PL_1)	464.040		896.7					4330.8	4309.5
(PL_2)	609.182		1046.6					4644.8	4473.5
ALLMASSD	389.323 PL_1, PL_2=(310.1, 488.8)								

TABLE 5. Estimates of body mass (MBd), snout-tail tip total length (TL) and snout-vent length to anterior vent limit (SVLA) from cranial dimensions using alligator-based equations. Anterior vent limit approximates the posterior ischial limit in alligators and presumably phytosaurs. Abbreviations: ANDCL, narial-cranial length from anterior narial limit to posterior mid-sagittal skull limit; ANVLA, anterior narial -vent length from anterior narial limit to anterior vent limit; DCL, dorsal cranial length from snout tip to posterior mid-sagittal limit of skull; dorsal ODCL, orbito-cranial length from interior anterior orbital limit to posterior midsagittal skull limit; OVLA, orbitovent distance from interior anterior orbital limit to anterior vent limit PL_1 and PL_2, upper and lower 95% confidence limits. DCL and ODCL measured to posterior edge of parietal (P) or Supraoccipital (Su), as indicated in P/Su column, depending on which corresponded to the contact between the skull and vertebral column. For UCMP V2816/27235, OBVLA=1774.2 mm; ANSVLA=1903.6 mm. TL and SVLA with phytosaur skulls calculated as in Table 2.

Specimen	Identification	P/ Su	ODCL (mm)	DCL (mm)	Ratio DCL/ ODCL	MBd (fr. ODCL) (PL1, PL2)	MBd (fr. (DCL) (PL1, PL2)	TL (fr. ODCL) (mm)	TL (fr. ODCL) phyto skll	TL (fr. DCL) (mm)	TL (fr. DCL) phyto skll	SVLA (fr. ODCL) (PL1, PL2)	SVLA (fr. ODCL) phyto skll	SVLA (fr. DCL) (PL1, PL2)	SVLA (fr. DCL) phyto skll	Est. allig. DCL from SVLA (mm)
1. P-31292	*Pseudopalatus*	Su	125.867	685.317	5.445	91.260	859.148	2735.854	3059.779	5077.439	5401.363	1386.719	1710.643	2665.762	2989.686	361.393
		(PL1)	(calc.)			83.671	760.537	2683.640	3014.501	4938.413	5269.274	1359.140	1690.001	2577.393	2908.254	354.456
		(PL2)				99.536	970.546	2789.085	3105.937	5220.379	5537.231	1414.857	1731.709	2757.161	3074.013	368.465
2. P-7140	*Pseudopalatus*	P	155.650	901.000	5.789	241.013	2252.085	3574.734	3999.110	6621.122	7045.498	1847.428	2271.804	3530.199	3954.575	476.624
		(PL1)				205.348	1924.067	3446.393	3887.456	6387.193	6828.256	1780.430	2221.494	3380.864	3821.928	459.937
		(PL2)				282.872	2636.025	3707.856	4114.938	6863.620	7270.702	1916.947	2324.029	3686.130	4093.212	493.918
3. CM69727. Type	Type of *Redondosaurus bermani*	Su	152.000	799.000	5.257	216.231	1475.096	3469.496	3806.385	5892.653	6229.542	1789.157	2126.046	3120.618	3457.506	462.112
		(PL1)				185.749	1280.044	3351.402	3703.659	5704.982	6057.240	1727.522	2079.779	3001.117	3353.374	446.743
		(PL2)				251.715	1699.870	3591.752	3912.743	6086.497	6407.488	1852.991	2173.982	3244.877	3565.868	478.009
4 P-31094	*Redondosaurus*	Su	180.650	N/A	N/A	476.247	N/A	4312.250	N/A	N/A	N/A	2259.117		N/A		578.728
		(PL1)				385.431		4107.313				2151.610				552.133
4 P-31094	*Redondosaurus*	(PL2)	180.650			588.460		4527.413				2371.995				606 603
5 P-31095	*Redondosaurus*	P	132.717	N/A	N/A	116.282	N/A	2924.645	N/A	N/A	N/A	1489.606		N/A		387.230
		(PL1)				104.680		2856.475				1453.856				378.260
		(PL2)				129.170		2994.441				1526.235				396.413
6. P-4983	*Pseudopalatus*	P	155.867	960.000	6.159	242.551	2815.788	3581.002	4063.513	7041.350	7523.861	1850.902	2333.413	3767.684	4250.195	477.489
		(PL1)				206.559	2385.951	3452.044	3951.322	6779.663	7278.941	1783.582	2282.860	3600.357	4099.635	460.722
6. P-4983	*Pseudopalatus*	(PL2)	155.867			284.814	3323.062	3714.777	4179.911	7313.138	6818.271	1920.764	2385.897	3942.788	4407.922	494.866
7 P-4256	*Pseudopalatus*	P	166.683	1051.000	6.305	329.638	3873.651	3896.700	4426.584	7688.003	8217.887	2026.462	2556.346	4134.725	4664.610	521.116
		(PL1)				274.296	3243.988	3735.909	4286.668	7382.204	7932.963	1942.388	2493.147	3938.679	4489.438	500.241
		(PL2)				396.147	4625.532	4064.412	4572.550	8006.470	8514.608	2114.174	2622.312	4340.530	4848.668	542.862
8. UCMP V2816/ Su			138.83	875.316		142.856	2033.997	416.412	3095.207	6437.934	4190.649	1582.976	3426.943			
27235 using U. Mo.			ODCL	DCL		126 620	1744 276	367 607	3012.003	6215 866	4058 433	1539.477	3285.278			
525 VP blw. up 123%			OBVLA=1774.2			161.175	2371.841	471.697	3180.710	6667.936	4327.172	1627.704	3574.718			
Figs.40, 42, L.&M. Pseudopel.pristinus PROVISIONAL Feb.1/03.			ANVLA=1903.6 SVLA=2510 7 ANCL=268.242			MBd (fr. ODCL) (PL_1, PL_2)	MBd (fr. (DCL) (PL_1, PL_2)	MBd (fr. OVLA)	TL (fr. ODCL) (mm)	TL (fr. DCL) (mm)	TL (fr. OVLA) (mm)	SVLA (fr. ODCL) (PL1, PL2)	SVLA (fr. DCL) (PL1, PL2)			

TABLE 6. Body mass (MBd) estimates from leg bone dimensions in phytosaurs, using ALLMASSD and ALLMASSC (see text). All four ALLMASSC measurements (length, circumference, and two orthogonal diameters) were taken on each phytosaur element. Also calculated was the geometric mean (GM) of the ALLMASSD estimate from length and the estimate from the two diameters, to equally weight the estimates from length and diameters. Estimates from skull dimensions provided for selected skulls possibly associated with limb bone elements. Abbreviations: D, diameter; Elem, element; F, femur; H, humerus; L, left; R, right; T, tibia; and U, ulna.

Specimen	Elem. ($PL_{1,2}$)	ALL-MASSD (kg)	ALL-MASSC (kg)	ALLMASS GM L&D= mass(kg)
NMMNH P-34731	R. H.	47.974	51.030	50.135
Pseudopalatus	(PL_1)	44.091	46.367	46.274
	(PL_2)	52.199	56.162	54.318
NMMNH P-34733	L. H.	28.024	30.690	29.869
Pseudopalatus	(PL_1)	25.586	27.681	27.443
	(PL_2)	30.693	34.025	32.508
3. NMMNH P-34732	L. F.	300.163	340.287	324.712
Pseudopalatus	(PL_1)	245.723	279.376	267.666
	(PL_2)	366.663	414.477	393.917
P-34733 & P-34732	LH&LF	91.431	102.791	98.254
	(PL_1)	79.058	88.435	85.518
	(PL_2)	105.741	119.477	112.888
NMMNH P-31297	R. H.	65.061	74.055	70.391
Pseudopaltus	(PL_1)	59.355	66.593	64.400
	(PL_2)	71.316	82.353	76.939
NMMNH PREP. Lab	R. H.	306.479	388.566	348.932
Project 12A51	(PL_1)	254.814	310.248	290.793
(probably aetosaur)	(PL_2)	368.620	486.656	418.696
NMMNH P-33663	L. F.	131.649	144.422	138.788
Pseudopalatus	(PL_1)	114.694	126.238	121.582
	(PL_2)	151.110	165.225	158.430
2. NMMNH P-33670	L. F.	330.296	368.351	350.257
Pseudopalatus	(PL_1)	268.107	300.377	286.867
	(PL_2)	406.910	451.707	427.655
3. NMMNH P-34732	L. F.	300.163	340.287	322.176
Pseudopalatus	(PL_1)	245.723	279.376	265.753
	(PL_2)	366.663	414.477	390.579
4. NMMNH P-35999	L. F.	321.319	400.333	349.418
Pseudopalatus	(PL_1)	261.158	324.272	286.128
	(PL_2)	395.338	494.235	426.707
5. NMMNH P-30843	L. F.	309.972	358.330	343.160
Pseudopalatus	(PL_1)	253.454	293.502	282.121
	(PL_2)	379.093	437.478	417.405
NMMNH P-35785	L. T.	222.654	139.201	133.565
Pseudopalatus	(PL_1)	180.208	119.691	114.165
	(PL_2)	275.096	161.893	156.262
UCMP V2816/27235	R.H.	356.776	N/A	N/A
P. pristinus	(PL_1)	293.721		
	(PL_2)	433.367		
UCMP V2816/27235	R.U.	407.522	N/A	N/A
P. pristinus	(PL_1)	310.602		
	(PL_2)	534.686		
UCMP V2816/27235	R. F.	445.343	N/A	N/A
Pseudopal. pristinus	(PL_1)	360.855		
	(PL_2)	549.614		
UCMP V2816/27235	RT	354.687	N/A	N/A
P. pristinus	(PL_1)	280.457		
	(PL_2)	448.564		
UCMP V2816/27235	RH,U,F,T	389.323	N/A	N/A
P. pristinus		310.078		
		488.821		

TABLE 7. Estimates of body mass (MBd), total length (TL), and SVLA (see below) in phytosaurs from maximum femur length (MFL) based on relationships in alligators and nine crocodilian genera (Farlow et al., in prep.). Abbreviations: D, diameter; Elem, element; F, femur; H, humerus; L, left; R, right; SVLA, snout-vent length to the anterior vent limit; T, tibia; and U, ulna.

Specimen	Elem.	LogMBd =LogMFL (kg)	TL=MFL (mm)	TL=MFL Intersp. 9spp (mm)	SVLA= MFL (mm)
NMMNH P- Ctars, Phdae. *Nicrosaurus*? *buceros*. (L-3845)	L. F. L. Tr.	125.851	3212.352	3295.814	1591.168
NMMNH P Ctars, Phdae. *Pseudopalatus* ?buceros.	L. F.	303.617	4178.200	4322.697	2070.282
3. NMMNH Ctars, Phdae. *Pseudopalatus*	L. F.	294.802	4141.599	4283.783	2052.126
4. NMMNH Ctars, Phdae. L. femur	L. F.	314.111	4220.822	4368.012	2091.425
5. NMMNH Ctars, Parasuchidae. (sic) (Phytosaur)	L. F.	339.835	4321.236	4474.771	2141.236
UCMP V281 *Pseudopal. pristinus*	R. F.	377.092	4457.632	4619.786	2208.896

TABLE 8. ALLMASSD output for UCMP V2816/27235, *Pseudopalatus pristinus* Output gives body mass and 95% prediction limits for each dimension, and calculates geometric mean of all predictions and 95% PL, weighted by the coefficient of determination (r^2) associated with each equation. Original equations based on 18 specimens of *Alligator missippiensis*.

Dimension	Enter Dimension (mm)	N	Predicted Body Mass (kg)	95% Prediction Limits Min (kg)	Max (kg)
Humerus length	281.5		485.420	409.127	575.941
Ulna length	187.2		409.051	332.683	502.949
Femur length	311.1		549.354	454.816	663.545
Tibia length	198.0		329.744	271.110	401.059
Humerus DV diameter			0.000	0.000	0.000
Ulna ML diameter	35.1		405.935	289.139	569.909
Femur DV diameter			0.000	0.000	0.000
Tibia ML diameter	29.0		382.069	290.322	502.811
Humerus AP diameter	33.3		260.206	209.122	323.768
Ulna AP diameter			0.000	0.000	0.000
Femur AP diameter	33.3		359.518	284.988	453.539
Tibia AP diameter			0.000	0.000	0.000
N, GM of prediction, PL_1, & PL_2.		8	389.323	310.078	488.821

The crew of September 1999 pulling jacket 37 out of the western end of the Snyder quarry.