

FEMORAL DIMENSIONS AND BODY SIZE OF *ALLIGATOR MISSISSIPPIENSIS*: ESTIMATING THE SIZE OF EXTINCT MESOEUCROCODYLIANS

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ABSTRACT—Total length, snout-vent length, and body mass are tightly correlated with length and other dimensions of the femur in *Alligator mississippiensis*. American alligator-based equations relating total length and body mass to femoral dimensions predict the sizes of other extant crocodylian species reasonably well, suggesting that alligator-based relationships should also work for extinct crocodylians and their close relatives. Size estimates from different femoral dimensions are most consistent when extinct forms have femora similar in size and shape to those of alligators. For many extinct mesoeucrocodylians, alligator femur-based total length estimates are close to length estimates based on reasonably complete skeletons or estimates made from osteological parameters other than femoral dimensions. However, the total length estimated for *Pristichampsus* is much larger than the length of the skeleton, indicating a relatively longer femur in this form, perhaps reflecting a more terrestrial lifestyle. In contrast, femur-based size estimates of a large individual of *Deinosuchus* are considerably less than an estimate based on mandible length. Femur size may be reduced relative to body size in *Deinosuchus*, which may be associated with more strictly aquatic habits than in alligators.

INTRODUCTION

Mesoeucrocodylian crocodyliforms (Fig. 1) have been prominent components of aquatic communities since the Mesozoic Era. Many extinct mesoeucrocodylians reached enormous sizes (Campbell and Frailey, 1991; Erickson and Brochu, 1999; Sereno et al., 2001; Head, 2001; Schwimmer, 2002; Storrs, 2003). Body size is closely linked with numerous physiological and ecological features (Peters, 1983; Calder, 1984; Paladino et al., 1990; Seebacher et al., 1999; Grigg and Seebacher, 2000; McNab, 2002), and so estimating the size of extinct mesoeucrocodylians is helpful for understanding the role of these reptiles in ancient aquatic communities.

For mesoeucrocodylians known on the basis of incomplete skeletal remains, body size is generally estimated from skull length-total length relationships in extant crocodylians (Webb and Messel, 1978; Woodward et al., 1995; Sereno et al., 2001). Here we report different size estimators, the relationship between body size (body length or mass) and several femoral dimensions in *Alligator mississippiensis*. Because mesoeucrocodylian femora are stout bones often found as fossils, our equations can be used to verify estimates based on skull length, and as size estimators for taxa for which good skulls are unknown.

We emphasize linear dimensions of body size of extinct mesoeucrocodylians, rather than body mass, because length estimates can potentially be evaluated by direct measurements of complete fossil material. Mass will likely vary considerably among individuals of a given length due to variability in body

condition (amount of fat deposits, muscle development, and [in females] egg load). Nevertheless, for many paleobiological considerations, body mass is more important than length, so we also consider estimators of this parameter.

MATERIALS AND METHODS

Specimens and Measurements

We measured captive and wild alligators sacrificed in Louisiana and Florida (Appendix 1; Farlow and Britton, 2000; Hurlburt, 2001). Total length (TL) was usually measured along the dorsal midline (in a few cases we had to measure TL along the ventral midline) from snout to tail tip; we corrected TL for “bob-tailed” individuals for which a reasonable estimate of the missing portion of the tail could be made. Alligators were weighed by attaching their carcasses with rope to a large scale suspended from a truck hoist. Specimen measurements used in this study, and details about the precision of our measurements, are posted on the Society of Vertebrate Paleontology website.

Snout-vent length was measured to both the anterior (aSVL) and the posterior (pSVL) edge of the vent. SVL is routinely measured by herpetologists, and so regression equations for estimating SVL are reported here. However, our detailed analyses of crocodylian linear dimensions are restricted to TL, because TL can be estimated for complete fossil skeletons (and therefore compared with femur-based TL estimates), while SVL is a soft-tissue feature (but see Hurlburt et al., 2003). We report TL estimates of extinct crocodyliforms to the nearest mm, but these should be taken seriously only at a coarser level of precision; for an animal the size of an adult alligator (ca. 3–4 m TL), we would be happy if our estimates were accurate to the nearest 100 mm.

In addition to our alligator measurements, TL and body mass (M) data were obtained for alligators and other extant crocodyl-

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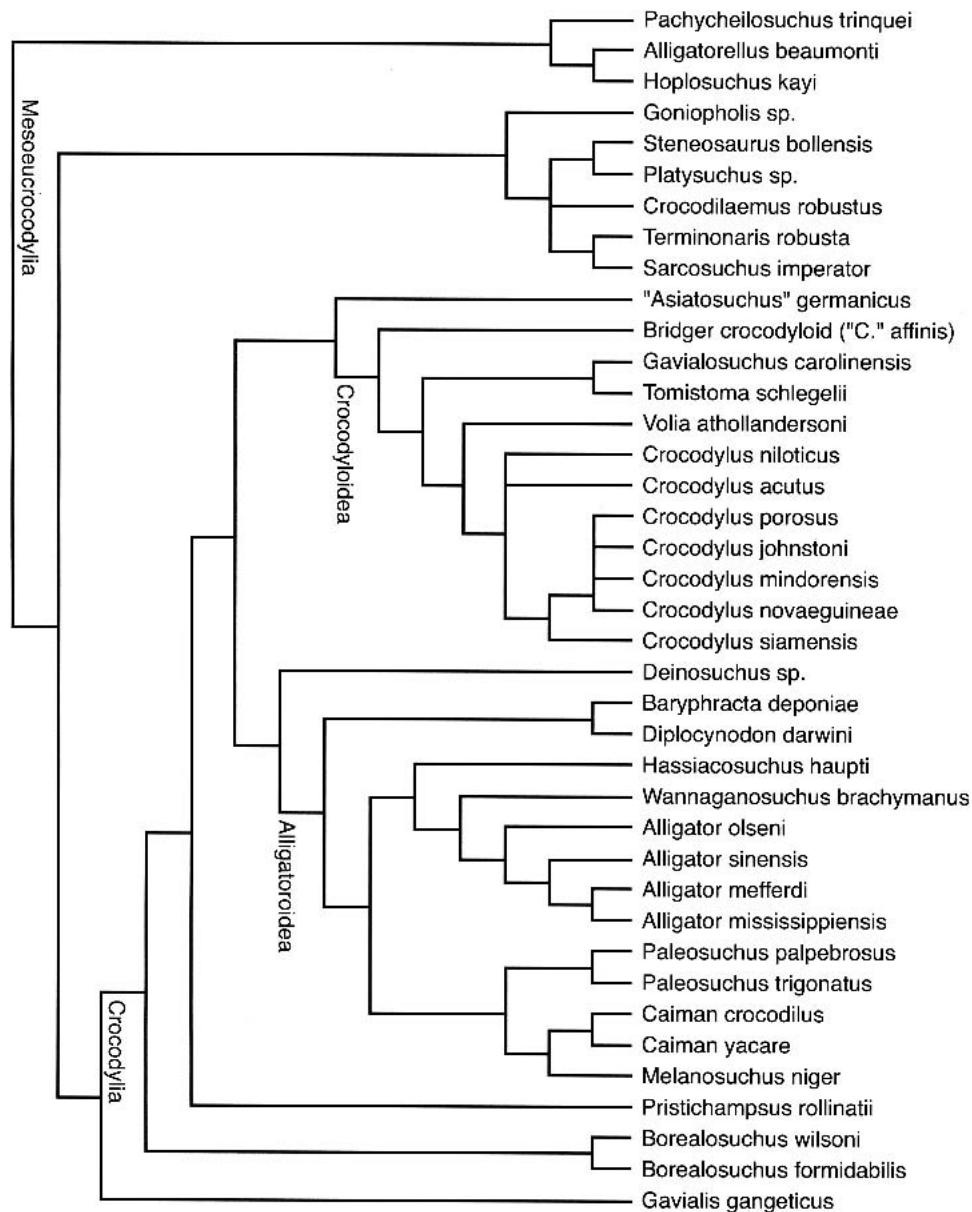


FIGURE 1. Diagram of phylogenetic relationships among the mesoeucrocodylian taxa considered in this paper; compiled from information in Brochu (1999, 2000, and pers. comm. 2003), Sereno et al. (2001), Wu et al. (2001), Molnar et al. (2002), and Rogers (2003). The phylogenetic position of *Gavialis* with respect to other crocodylians (particularly *Tomistoma*) is controversial; placement here follows morphological as opposed to molecular evidence (Brochu and Densmore, 2000).

ian species from museum records, the literature (Banks, 1930; Cott, 1961; Greer, 1974; Coulson and Hernandez, 1983; Woodward et al., 1995), and unpublished measurements of *Crocodylus johnstoni* and *C. porosus* made by us and others. Estimates of TL were also made on reasonably complete skeletons of fossil forms; measurements were made using both actual material and casts of specimens. In most cases, TL estimates of fossil skeletons were made by extending string along the vertebral column of specimens as preserved in situ. Obviously postmortem disruption of the skeleton can affect the accuracy of such estimates. Some TL measurements were made on mounted skeletons of fossil forms, which are also subject to some uncertainty. For a few extinct forms (*Baryphracta deponiae*, *Platysuchus* sp., and *Alligatorellus beaumonti*), TL and femur length were estimated from photographs.

Femora were removed from our alligator carcasses, cleaned, and dried; where possible, the following measurements (Fig. 2) were made on one femur of each animal:

- Length (**FL**): distance from the most proximal point on the proximal articular surface of the bone to the most distal point on the lateral distal condyle;
- Distal width (**Fdw**): greatest transverse width of the distal articular surface of the bone;
- Distal height (**Fdh**): greatest dimension across the distal articular surface, perpendicular to distal width, across the lateral condyle;
- Maximum proximal diameter (**Fpmx**): greatest dimension across the proximal articular surface;
- Minimum proximal diameter (**Fpmn**): greatest dimension across

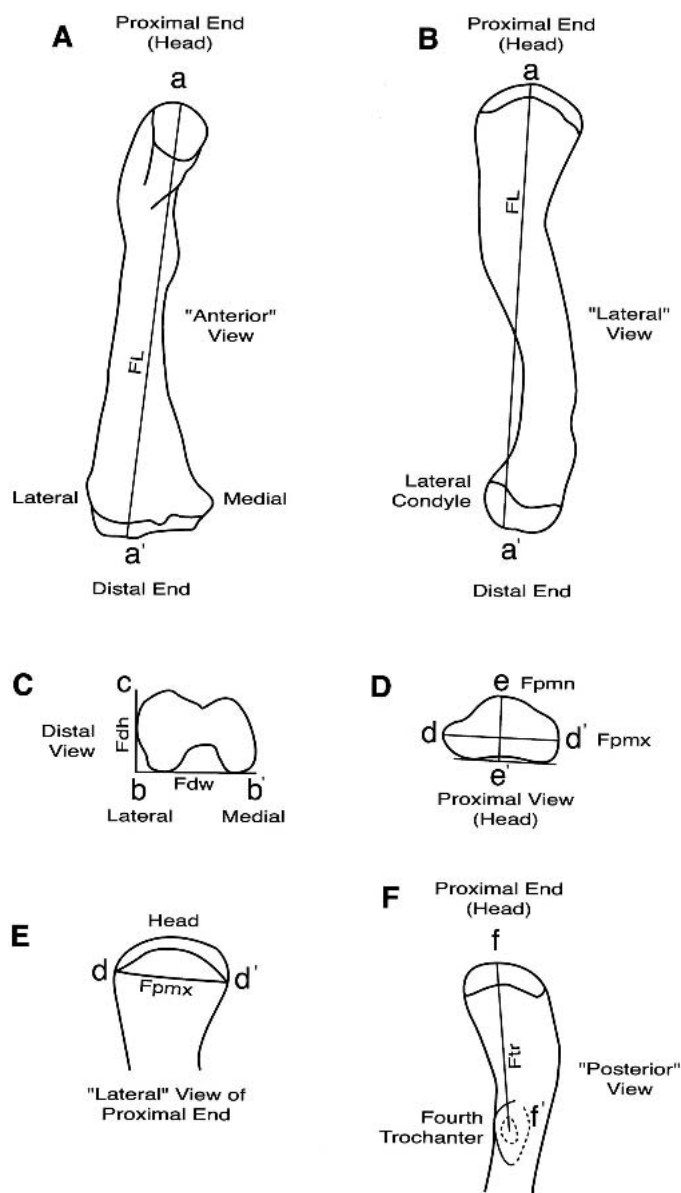


FIGURE 2. Measurements of crocodylian femora. **A–B**, femur in ‘anterior’ and ‘lateral’ view, showing measurement of length (**FL**: a-a’) in two views; **C**, distal articular end of femur, showing measurement of distal width (**Fdw**: b-b’) and distal height (**Fdh**: b-c); **D–E**, proximal articular end of femur, showing measurement of maximum (**Fpmx**: d-d’) and minimum (**Fpmn**: e-e’) diameter; and **F**, ‘posterior’ view of proximal half of femur, showing measurement of distance from proximal articular end of bone to fourth trochanter (**Ftr**: f-f’).

the proximal articular surface perpendicular to the maximum proximal diameter;

Minimum midshaft circumference (**Fc** [not illustrated in Fig. 2]): measured with string distal to the fourth trochanter, and proximal to where the bone flares outward toward the distal condyles;

Distance from the most proximal point on the proximal articular surface of the bone to the fourth trochanter (**Ftr**): the point on the fourth trochanter used in making the measurement was somewhat subjective, due to the highly variable configuration of the scar. In some cases the central part of the scar was used, but where the trochanter had a large prong projecting outward from the bone this spot was used, re-

gardless of where the prong was located with respect to the rest of the scar

Femoral measurements were also made on specimens of alligators and other extant and extinct mesoeucrocodylians in museum herpetological and paleontological collections. In estimating alligator size from femoral measurements, we regressed TL and M against all femoral dimensions. For aSVL and pSVL we only examined the relationship with FL, because of the lesser value of SVL than TL as a size estimate for fossil mesoeucrocodylians. For a subset of our alligators, we measured skull length (to the nearest mm), taken from the snout to the most posterior point on the medial surface of the occipital table, for use in regressing TL and M against skull length.

One large male alligator (RWR 13) was a clear outlier in all plots of animal size vs. femoral dimensions. With a recorded TL of 3759 mm, a body mass of 237.9 kg, and a femur length of 204 mm, this animal seemingly had a very small femur for its body size. We suspect a mismatch between the femur and the body size measurements associated with it, but cannot verify this. We excluded RWR 13 from our data analyses, but cannot exclude the possibility that this alligator had an unusually small femur.

Nomenclature and Institutional Abbreviations

The taxonomic names applied to specimens were generally those by which they were identified in museum collections. Where we were aware of more current names, however, we used these identifications.

Institutional Acronyms—**ChM**, Charleston Museum, Charleston, SC, USA; **CM**, Carnegie Museum of Natural History, Pittsburgh; **FMNH**, Field Museum of Natural History, Chicago; **FL**, Florida specimen collected during this study; **GM**, Geiseltalmuseum, Halle, Germany; **GMNH**, Gunma Museum of Natural History, Tokyo; **HLMD**, Hessisches Landesmuseum, Darmstadt, Germany; **MNN**, Musée National du Niger, Niamey; **MNZ**, Museum of New Zealand Te Papa Tongarewa, Wellington; **ROM**, Royal Ontario Museum, Toronto; **RWR**, Rockefeller Wildlife Refuge (Louisiana) specimen; **SMF**, Senckenbergmuseum, Frankfurt, Germany; **SMM**, Science Museum of Minnesota, Saint Paul; **SMNH**, Royal Saskatchewan Museum, Regina; **SMU**, Southern Methodist University, Dallas; **TMM**, Texas Memorial Museum, Austin; **UA**, University of Alabama, Tuscaloosa; **UF**, Florida Museum of Natural History, Gainesville; **USNM**, National Museum of Natural History (Smithsonian Institution), Washington, DC; **WDC**, Wyoming Dinosaur Center, Thermopolis.

Data Analysis

Possible Effects of Captivity and Sex—Because many of our alligators (particularly the larger individuals) were captives, the possibility that life in captivity altered morphometric relationships from the natural state had to be considered (Meers, 2002). We also attempted to identify possible sexual differences.

Analyses of covariance (ANCOVA), with TL as the dependent variable, animal status (captive vs. wild, female vs. male) the test variable, and femoral dimensions as covariates, are summarized in Tables 1 and 2. In some ANCOVAs, violations of assumptions of the procedure (inequality of variances of the two test populations, lack of fit) occurred; efforts to counteract this problem by log-transforming the data were in some cases successful. In some tests involving wild alligators, goodness-of-fit tests could not be carried out; as long as the assumption of equality of variances of the test populations was not violated, we assumed that the inability to test goodness of fit was not a problem with the ANCOVA procedure.

Relationships of TL with FL, Ftr, and Fpmn give no indication of differences between wild and captive populations. Relation-

TABLE 1. Effects of animal status (captive vs. wild) on morphometric relationships in *Alligator mississippiensis*. **Anatomical abbreviations:** **Fc**, minimum midshaft circumference of femur; **Fdh**, height of distal articular end of femur; **Fdw**, width of distal articular end of femur; **FL**, femur length; **Fpmn**, minimum diameter of proximal articular end of femur; **Fpmx**, maximum diameter of proximal articular end of femur; **Ftr**, length from proximal articular end of femur to fourth trochanter; **M**, body mass; **TL**, total length.

| Dependent variable | Covariate | Probability Associated with F Test: | | | | N of Alligators (captive:wild) |
|--------------------|-----------|--|------------------|---------------------|-------------------------|--------------------------------|
| | | Levene's test of equality of error variances | Lack of fit test | Effect of covariate | Effect of animal status | |
| TL | FL | 0.179 | 0.857 | <0.001 | 0.359 | 52:46 |
| TL | Fdw | 0.266 | 0.514 | <0.001 | <0.001 | 52:46 |
| TL | Fdh | 0.313 | 0.008 | <0.001 | <0.001 | 53:46 |
| log TL | log Fdh | 0.195 | 0.001 | <0.001 | <0.001 | 53:46 |
| TL | Fpmx | 0.716 | 0.005 | <0.001 | 0.117 | 53:46 |
| log TL | log Fpmx | 0.090 | <0.001 | <0.001 | 0.035 | 53:46 |
| TL | Fpmn | 0.807 | <0.001 | <0.001 | 0.173 | 51:46 |
| log TL | log Fpmn | 0.507 | <0.001 | <0.001 | 0.063 | 51:46 |
| TL | Fc | 0.021 | 0.180 | <0.001 | <0.001 | 52:46 |
| log TL | log Fc | 0.679 | 0.262 | <0.001 | <0.001 | 52:46 |
| TL | Ftr | 0.237 | 0.716 | <0.001 | 0.564 | 51:45 |
| log M | log FL | 0.193 | 0.179 | <0.001 | <0.001 | 52:36 |
| log M | log Fdw | 0.520 | 0.729 | <0.001 | 0.062 | 52:36 |
| log M | log Fdh | 0.365 | <0.001 | <0.001 | 0.010 | 53:35 |
| log M | log Fpmx | 0.601 | 0.009 | <0.001 | 0.952 | 53:36 |
| log M | log Fpmn | 0.065 | <0.001 | <0.001 | 0.833 | 51:36 |
| log M | log Fc | 0.954 | 0.103 | <0.001 | 0.021 | 52:36 |
| log M | log Ftr | 0.485 | 0.321 | <0.001 | 0.087 | 51:35 |
| log M | log TL | 0.400 | 0.335 | <0.001 | <0.001 | 58:58 |

ships of TL with Fdw and Fc, and possibly Fdh and Fpmx, in contrast, show differences between captive and wild alligators.

For wild alligators, none of the TL vs. femoral ANCOVAs shows a difference between the sexes (Table 2). However, captive alligators show possible sexual differences in ANCOVAs involving TL vs. Fdw, Fdh, Fpmx, and Fpmn, again indicating the possibility that captive and wild animals differ in morphometric relationships involving TL and diameters across the articular ends of the femur.

Because mass is approximately proportional to volume, and volume is in turn proportional to the cube of linear dimensions, analysis of alligator mass-length relationships requires log-transformed data. Captivity had a significant effect on the relationship between M and FL, Fdh, and Fc, but not between M and Ftr, Fpmn, Fpmx, and Fdw; captivity also affected the relationship between M and TL (Table 1). Captive animals were heavier than wild animals of the same linear dimensions. Sex did not affect most M:linear dimension relationships (Table 2).

Regression Equations—The 95% confidence intervals of slopes of reduced major axis (RMA) relationships between log-transformed TL and log-transformed femoral dimensions were calculated following Leduc (1987). Where the confidence interval of the slope included 1, the bivariate relationship was assumed to be linear rather than allometric, and we calculated a regression equation using untransformed data; where the confidence interval of the slope did not include 1, we used log-transformed data to calculate the regression equation (Table 3). Log-transformed data were used to calculate all relationships between alligator M and linear dimensions. Where allometric equations were used to predict TL or M, the quasi-maximum likelihood estimator (cf. Smith, 1993) was applied to the detransformed predicted value; the difference between this corrected estimate and the uncorrected detransformed prediction was, however, minor in all cases.

For femoral dimensions whose impact on TL differs between captive and wild animals, caution would dictate using regression equations for wild animals only. However, this would eliminate all of the biggest alligators in our sample, exacerbating an already unavoidable problem of extrapolating beyond the range of data when we apply our regression equations to very large ex-

tinct species. In an attempt to circumvent these problems, we used both all-alligator and wild-alligator-only equations.

For comparison with TL predictions of our *A. mississippiensis* TL:FL regression equation, we also did an interspecific regression of TL against FL, using species (the biggest individual of each, with TL at least 1000 mm) for which data were available: *A. mississippiensis*, *A. sinensis*, *Paleosuchus trigonatus*, *Caiman crocodilus*, *Melanosuchus niger*, *Tomistoma schlegelii*, *Crocodylus acutus*, a *C. porosus*-*C. siamensis* hybrid, and *Gavialis gangeticus* (Table 3).

For comparison with TL lengths based on femoral dimensions, we did a regression of TL against skull length in alligators (Table 3). In estimating TL for some extinct forms we also used TL:skull length regressions from Sereno et al. (2001) for *Gavialis gangeticus* (TL = [7.4 * skull length] - 69.369) and *Crocodylus porosus* (TL = [7.717 * skull length] - 20.224); TL and skull length are given in centimeters in both equations.

In assessing how accurately American alligator femoral dimension:TL relationships predict TLs of other species, we used several criteria: (1) consistency among length estimates based on different femoral dimensions; (2) consistency of femur-based length estimates with estimates based on skull length; and (3) consistency of femur-based estimates with either known TLs (of extant species) or TLs estimated from fossil material, whether preserved in situ or as skeletal mounts. Because FL is the single best femoral dimension for predicting TL (see below), we placed more emphasis on TLs estimated from FL than on TLs estimated from other femoral dimensions.

We evaluated consistency among different femur-based TL estimates by calculating the ratio of the largest to the smallest TL estimate; maximum/minimum ratios of no more than 1.2 (indicating that the larger value was no more than 20% greater than the smaller value) were judged to indicate very consistent results. We also determined whether various femur-based and skull-based estimates fell within the 95% individual prediction interval of TL predicted from FL. Known TLs of extant crocodylian species and TLs of extinct forms estimated from skeletons were judged to be consistent with estimates based on FL if they fell within the 95% PI of the latter, and/or were no more than 20% larger or smaller than the estimate based on FL.

TABLE 2. Effects of sex on morphometric relationships in *Alligator mississippiensis*. Parameter acronyms as in Table 1. **Abbreviations:** **Cov**, covariate; **DV**, dependent variable. Treatments: all sexed alligators, wild sexed alligators, and captive sexed alligators; treatments flagged with an asterisk (*) were done with log-transformed variables.

| DV | Cov | Treatment | Probability associated with F test: | | | | N of alligators (females:males) |
|-------|----------|-----------|--|---------------------|------------------------|------------------|------------------------------------|
| | | | Levene's test of equality of error variances | Lack of fit test | Effect of covariant | Effect of sex | |
| TL | FL | all | 0.188 | 0.983 | <0.001 | 0.133 | 55:39 |
| | | wild | 0.028 | — | <0.001 | 0.398 | 22:21 |
| | | wild* | 0.026 | — | <0.001 | 0.970 | 22:21 |
| TL | Fdw | captive | 0.794 | 0.831 | <0.001 | 0.051 | 33:18 |
| | | all | 0.183 | 0.125 | <0.001 | 0.347 | 54:40 |
| | | wild | 0.705 | 0.203 | <0.001 | 0.802 | 22:21 |
| TL | Fdh | captive | 0.085 | 0.403 | <0.001 | 0.018 | 32:19 |
| | | all | 0.228 | 0.003 | <0.001 | 0.140 | 55:40 |
| | | wild | 0.829 | 0.487 | <0.001 | 0.855 | 22:21 |
| TL | Fpmx | captive | 0.848 | 0.014 | <0.001 | 0.009 | 33:19 |
| | | all | 0.025 | 0.006 | <0.001 | 0.531 | 56:39 |
| | | all* | 0.176 | <0.001 | <0.001 | 0.405 | 56:39 |
| TL | Fpmn | wild | 0.652 | 0.231 | <0.001 | 0.418 | 22:21 |
| | | captive | 0.287 | 0.038 | <0.001 | 0.026 | 34:18 |
| | | all | 0.074 | <0.001 | <0.001 | 0.621 | 56:37 |
| TL | Fc | wild | 0.988 | 0.240 | <0.001 | 0.599 | 22:21 |
| | | captive | 0.480 | 0.006 | <0.001 | 0.003 | 34:16 |
| | | all | 0.817 | 0.313 | <0.001 | 0.989 | 55:39 |
| TL | Ftr | wild | 0.770 | 0.223 | <0.001 | 0.937 | 22:21 |
| | | captive | 0.246 | 0.408 | <0.001 | 0.871 | 33:18 |
| | | all | 0.033 | 0.736 | <0.001 | 0.406 | 55:37 |
| log M | log FL | all* | 0.257 | 0.120 | <0.001 | 0.747 | 55:37 |
| | | wild | 0.514 | — | <0.001 | 0.628 | 22:20 |
| | | captive | 0.821 | 0.826 | <0.001 | 0.627 | 33:17 |
| log M | log Fdw | all | 0.970 | 0.093 | <0.001 | 0.758 | 47:39 |
| | | wild | 0.337 | — | <0.001 | 0.347 | 14:20 |
| | | captive | 0.198 | 0.350 | <0.001 | 0.462 | 33:18 |
| log M | log Fdh | all | 0.173 | 0.016 | <0.001 | 0.088 | 46:40 |
| | | wild | 0.280 | 0.733 | <0.001 | 0.613 | 14:20 |
| | | captive | 0.182 | 0.007 | <0.001 | 0.093 | 32:19 |
| log M | log Fpmx | all | 0.671 | <0.001 | <0.001 | 0.035 | 47:39 |
| | | wild | 0.522 | 0.562 | <0.001 | 0.575 | 14:19 |
| | | captive | 0.980 | <0.001 | <0.001 | 0.045 | 33:19 |
| log M | log Fpmn | all | 0.757 | 0.021 | <0.001 | 0.236 | 48:39 |
| | | wild | 0.354 | 0.331 | <0.001 | 0.498 | 14:20 |
| | | captive | 0.913 | 0.030 | <0.001 | 0.136 | 34:18 |
| log M | log Fc | all | 0.879 | <0.001 | <0.001 | 0.545 | 48:37 |
| | | wild | 0.636 | 0.555 | <0.001 | 0.086 | 14:20 |
| | | captive | 0.315 | <0.001 | <0.001 | 0.024 | 34:16 |
| log M | log Ftr | all | 0.401 | 0.092 | <0.001 | 0.171 | 47:39 |
| | | wild | 0.416 | 0.827 | <0.001 | 0.533 | 14:20 |
| | | captive | 0.259 | 0.096 | <0.001 | 0.707 | 33:18 |
| log M | log TL | all | 0.317 | 0.534 | <0.001 | 0.586 | 47:37 |
| | | wild | 0.551 | 0.627 | <0.001 | 0.761 | 14:19 |
| | | captive | 0.230 | 0.661 | <0.001 | 0.992 | 33:17 |
| log M | log TL | all | 0.332 | 0.375 | <0.001 | 0.320 | 57:47 |
| | | wild | 0.587 | 0.479 | <0.001 | 0.702 | 22:28 |
| | | captive | 0.120 | 0.471 | <0.001 | 0.323 | 35:19 |

For M:femoral dimension relationships in which captivity did not have a significant effect, we calculated all-alligator regression equations. For those relationships in which captivity did have a significant effect, we calculated regression equations for wild alligators only. As already noted, however, this eliminated the largest alligators in our sample. Consequently, in addition to M estimates based directly on femoral measurements, we also estimated M via a two-step procedure in which we first estimated TL of animals from femur length, and then employed a regression equation (Table 3) of wild *A. mississippiensis* M against TL that used our data and also data from the literature (Coulson and Hernandez, 1983; Woodward et al., 1995).

For comparison with M estimates based on femoral dimensions we regressed M against skull length (Table 3) for our alligators, using data for both captive and wild animals. Even though captive alligators tend to be heavier than wild alligators of the same linear dimensions, the regression equation for M

against skull length changed little if captive individuals were excluded.

We also estimated M from skull length using data for *Crocodylus porosus* via a second two-step procedure. We first estimated SVL from skull length (Webb and Messel, 1978:appendix 1, equation 49; $SVL [cm] = [3.60 * \text{head length [cm]}] - 4.30$). We then estimated M from SVL (Webb and Messel, 1978:appendix 2, equation 122; $\log M [g] = [3.2613 * \log SVL [cm]] - 2.0894$).

RESULTS

Alligator Size and Femoral Dimensions

Unsurprisingly, all femoral dimensions are highly correlated with total length and with each other; in all bivariate comparisons of untransformed variables, Pearson's *r* is at least 0.97. The relationship between alligator TL and FL is linear (Fig. 3; cf.

TABLE 3. Regression equations for predicting alligator body lengths and mass from skeletal measurements; all measurements in millimeters. **Anatomical abbreviations** as in Table 1; **SKULL**, skull length. **Abbreviations:** **DV**, dependent variable; **intcpt**, intercept; **IV**, independent variable; **N**, number of cases; **p**, probability associated with F test; **r**, correlation coefficient; **SEE**, regression standard error of estimate; **Treat**, treatment (**wild**, equation determined for wild alligators only; **all**, equation based on captive and wild alligators; **interspp**, interspecific equation).

| DV | IV | Treat | Slope | Intcpt | r | SEE | p | N |
|---|---------|----------|-------|---------|-------|--------|--------|----|
| TL | FL | all | 14.45 | 16.45 | 0.996 | 75.47 | <0.001 | 98 |
| TL | FL | interspp | 15.36 | -102.04 | 0.986 | 210.99 | <0.001 | 9 |
| log TL | log Fdw | all | 0.82 | 2.06 | 0.990 | 0.0293 | <0.001 | 98 |
| log TL | log FDW | wild | 0.87 | 2.00 | 0.985 | 0.0343 | <0.001 | 46 |
| log TL | log Fdh | all | 0.79 | 2.24 | 0.987 | 0.0329 | <0.001 | 99 |
| log TL | log Fdh | wild | 0.85 | 2.18 | 0.985 | 0.0349 | <0.001 | 46 |
| log TL | log | all | 0.83 | 2.07 | 0.987 | 0.0327 | <0.001 | 99 |
| TL | Fpmx | wild | 59.83 | 194.53 | 0.987 | 105.91 | <0.001 | 46 |
| log TL | log | all | 0.79 | 2.33 | 0.983 | 0.0373 | <0.001 | 97 |
| log TL | Fpmn | wild | 0.85 | 2.27 | 0.981 | 0.0385 | <0.001 | 46 |
| log TL | Fpmm | all | 0.83 | 1.92 | 0.987 | 0.0330 | <0.001 | 98 |
| TL | Fc | wild | 41.98 | 164.37 | 0.990 | 94.10 | <0.001 | 46 |
| log TL | log Ftr | all | 0.88 | 1.81 | 0.993 | 0.0246 | <0.001 | 96 |
| Multivariate (all alligators): log TL = (0.81 * log FL) + (0.15 * log Fdh) + 1.37 | | | | | 0.995 | 0.0216 | <0.001 | 93 |
| TL | SKULL | all | 7.13 | 130.31 | 0.990 | 97.92 | <0.001 | 51 |
| aSVL | FL | all | 7.17 | 5.83 | 0.992 | 47.31 | <0.001 | 43 |
| pSVL | FL | all | 7.52 | -18.80 | 0.989 | 61.11 | <0.001 | 36 |
| log M | log FL | wild | 3.33 | -5.72 | 0.994 | 0.0681 | <0.001 | 36 |
| log M | log Fdw | all | 2.80 | -2.78 | 0.995 | 0.0685 | <0.001 | 89 |
| log M | log Fdh | wild | 2.78 | -2.23 | 0.992 | 0.0794 | <0.001 | 35 |
| log M | log | all | 2.80 | -2.72 | 0.989 | 0.0979 | <0.001 | 90 |
| log M | log | all | 2.65 | -1.83 | 0.987 | 0.1071 | <0.001 | 88 |
| log M | Fpmm | wild | 2.85 | -3.25 | 0.991 | 0.0815 | <0.001 | 36 |
| log M | log Fc | all | 3.01 | -3.66 | 0.994 | 0.0749 | <0.001 | 87 |
| log M | log Ftr | wild | 3.47 | -10.03 | 0.997 | 0.0553 | <0.001 | 58 |
| Multivariate (wild alligators): log M = (1.47 * log Fdw) + (1.61 * log FL) - 4.21 | | | | | 0.995 | 0.0634 | <0.001 | 34 |
| log M | log | all | 3.48 | -6.97 | 0.996 | 0.0581 | <0.001 | 27 |
| | SKULL | | | | | | | |

Dodson, 1975). The relationships between TL and Fdw, Fdh, Fpmm, and Ftr are allometric (Fig. 4), and the relationship between TL and Fpmx and Fc is allometric or linear depending on whether captive animals are included (Fig. 4; Table 3).

For wild alligators, partial correlation analysis using log-transformed variables indicates no significant relationships be-

tween TL and Fdw, Fdh, Fpmx, Fpmm, Fc, or Ftr after controlling for the effects of FL, and stepwise multiple regression analysis rejects all but FL as a predictor of TL. Including captive as well as wild alligators changes these results. Again employing log-transformed data, Fdh, Fpmx, and Ftr now have statistically significant correlations with TL after controlling for the effects of

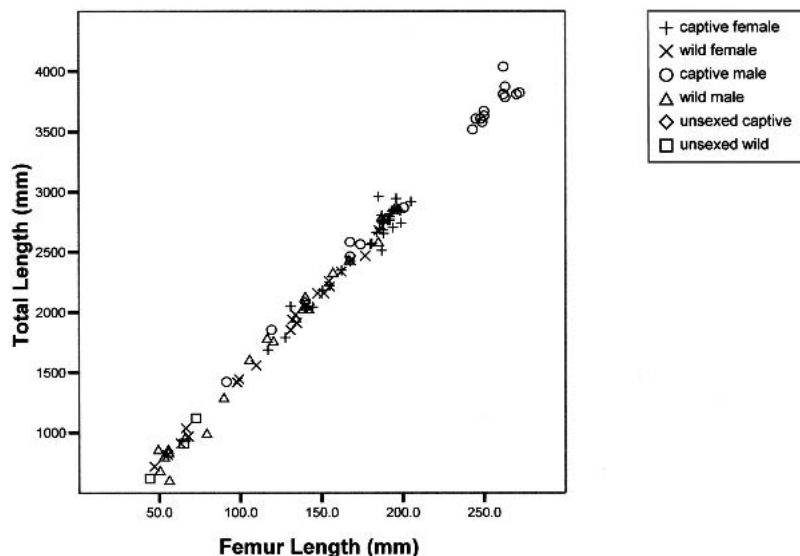


FIGURE 3. Total animal length vs. femur length in *Alligator mississippiensis*; regression equation for this relationship, as well as those in Figs. 4-7, given in Table 3.

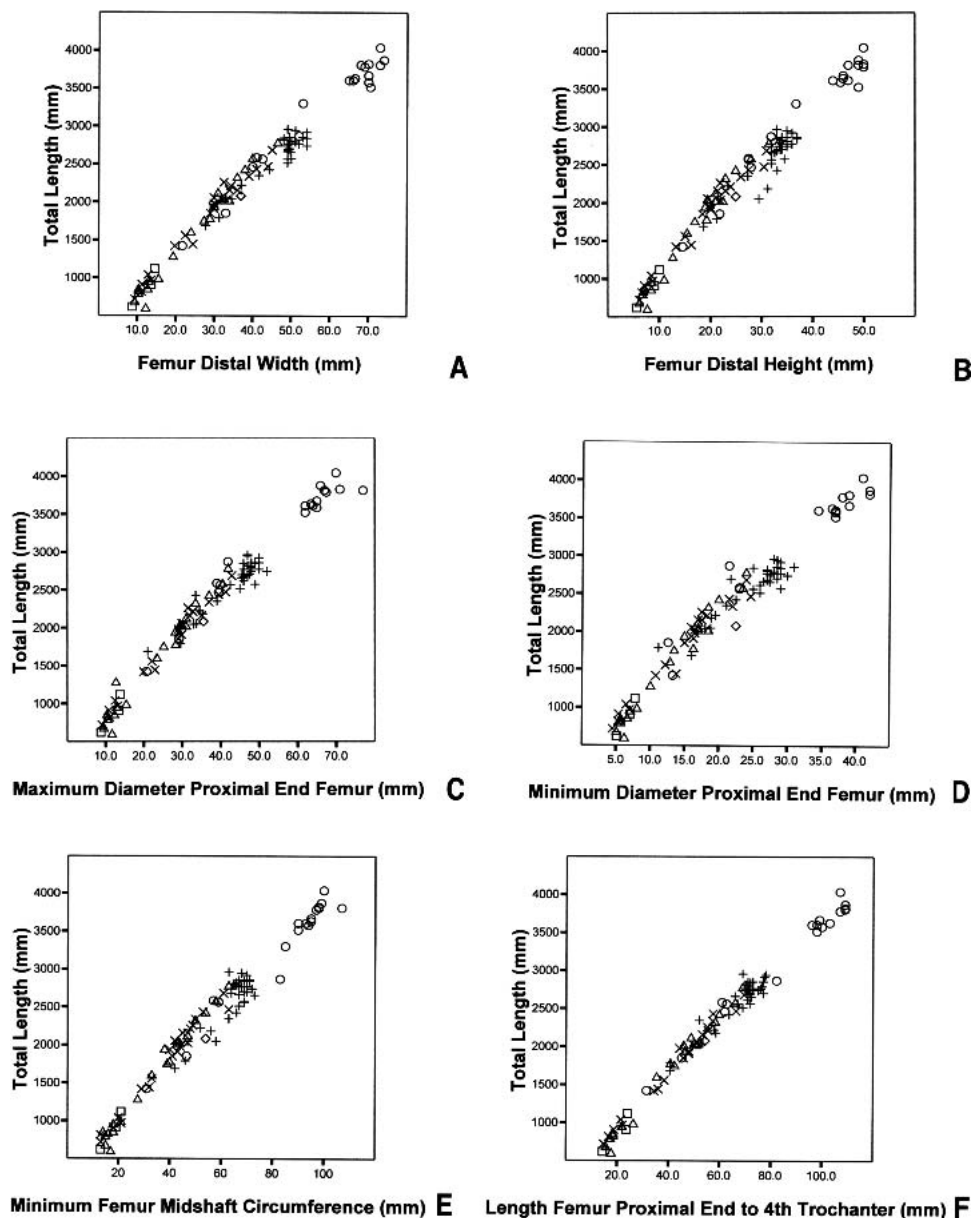


FIGURE 4. Total length as a function of various femoral dimensions in *A. mississippiensis*. Legend symbols as in Fig. 3.

FL. Stepwise multiple regression analysis includes Fdh as well as FL as a predictor of TL (Table 3).

Relationships of aSVL and pSVL with FL are linear ($r = 0.99$; Table 3).

All femoral dimensions are highly correlated with M (r at least 0.98). Stepwise multiple regression (using log-transformed data for wild alligators) first selects Fdw as a predictor of M, followed by FL (Table 3).

Size Estimates of Other Species

Total Length—Although there is no a priori reason for expecting intraspecific alligator size-femoral dimension relationships to provide good size estimates across crocodylian species (cf. Currie, 1978), alligator femoral dimensions nonetheless predict TL reasonably well for those extant species for which data (museum records) are available (Figs. 5, 6). TL measurements for most species fall within or near the 95% individual prediction

interval for American alligator equations, and 20 of 23 specimens of extant crocodylians have TLs within 20% of the TL predicted from the alligator TL:FL relationship. This suggests that alligator TL:femoral measurement relationships should also be useful for estimating the sizes of extinct crocodylians, and perhaps other mesoeucrocodylians as well (Table 4; Figs. 5, 6).

The greatest consistency among size estimates based on different measurements of the same femur is for taxa with femora comparable in size to modern *A. mississippiensis*, for which the ratio of the largest/smallest TL estimate (including the TL-interspecific and multivariate estimates) is 1.1–1.3. For the biggest crocodylians (*Deinosuchus* sp., *Terminonaris robusta*), in contrast, the largest/smallest TL estimate ratio is as much as 1.4.

For many species close in size to modern *A. mississippiensis*, some or all of the TL estimates are within the 95% prediction interval (PI) for the estimate based on FL alone. For the gigantic extinct forms, in contrast, few of the other estimates are within the 95% PI for the FL-based estimate.

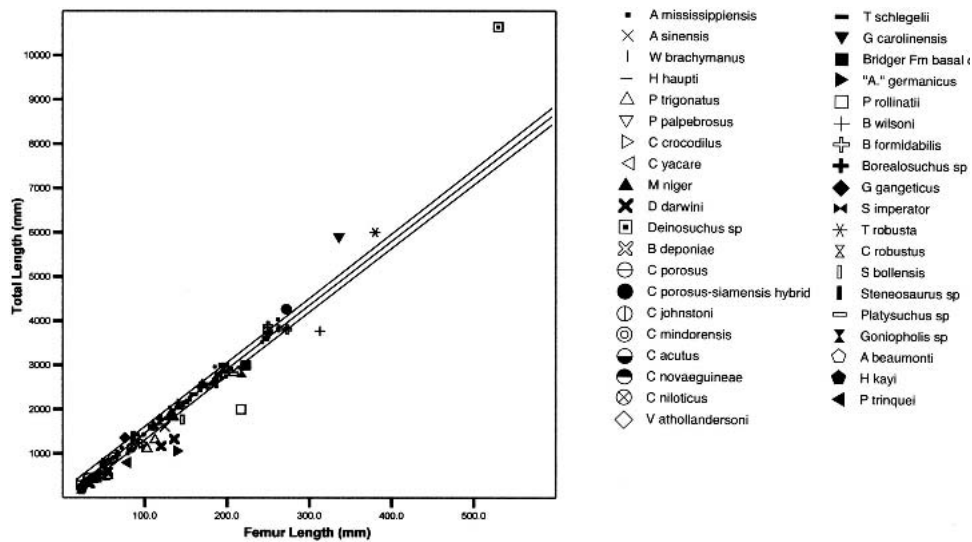


FIGURE 5. Total length as a function of femur length in living and fossil mesoeucrocodylians. Regression line and 95% individual prediction interval are for *A. mississippiensis* (including both wild and captive individuals; Table 3). For American alligators and other extant species, total length was measured on intact specimens. For fossil forms, total length estimates are based on specimens as preserved in situ or on mounted skeletons, or are predictions based on criteria other than the femoral dimensions considered in this paper (see Table 4 for details and caveats). Symbol legend is for this and the following figures (see Fig. 1 for full species names); data for all species do not occur in every graph.

The femoral dimension that predicts the largest size varies, but the smallest TL estimator is usually Fdw (using the all-alligator equation). For a given value, wild-alligator-only equations usually predict slightly larger TLs than do all-alligator equations. TL estimates made from FL using the interspecific equation (Table 3) are very close to those predicted by the intraspecific alligator equation.

TL estimates based on skull length are fairly close to estimates based on FL for a basal crocodyloid from the Bridger Formation and also for *Borealosuchus*, *Pristichampsus rollinatii*, *Wannaganosuchus brachymanus*, *Goniopholis* sp., and most *Diplocynodon* specimens (Table 4), lying either within the 95% PI for FL-based estimates, or close to them. For *Steneosaurus*, TLs estimated from the *G. gangeticus* TL:skull length equation (Serenio et al., 2001) are within the 95% PI of alligator FL-based estimates, but *C. porosus* and *A. mississippiensis* skull-based TL estimates are well outside the 95% PI of alligator FL-based estimates. None of the skull-based TL estimates for *Deinosuchus* sp., *T. robusta*, or *Gavialosuchus carolinensis* is within the 95% PI for FL-based estimates, although gharial skull-based TL estimates for the latter two species are only a little larger than the biggest values of the 95% PIs of alligator FL-based estimates.

For *Diplocynodon darwini*, *Hassiacosuchus haupti*, *Baryphracta deponiae*, “*Asiatosuchus*” *germanicus*, *Pristichampsus rollinatii*, *Goniopholis* sp., *Steneosaurus bollensis*, *Alligatorellus beaumonti*, *Crocodylaemus robustus*, and *Hoplosuchus kayi*, TL estimates based on FL are larger than estimates made from skeletons preserved in situ or skeletal mounts (Table 4), with the ratio of skeleton-based TL estimates of *H. kayi* and “*A.*” *germanicus* being 40–50% less than FL-based estimates. However, some of these TL estimates (particularly those of small individuals) made from entire skeletons are within, or close to, the 95% PI for the alligator-based FL equation (Fig. 5). TLs of *D. darwini* estimated from in situ skeletons are 25–35% less than FL-based TLs; skeleton-based TLs of the bigger individuals of this species, unlike those of smaller specimens, are some distance outside the 95% PIs of FL-based TL estimates. In contrast to the specimen of *S. bollensis*, the specimen of *Steneosaurus* sp. has a FL-based TL estimate that is slightly lower than the skeleton-based TL estimate.

For the Bridger Formation basal crocodyloid and *Goniopholis* sp., all femur-based length estimates are larger than the lengths of the mounted skeletons, but the skeleton lengths are only 7–10% less than the FL-based TL estimates; the lengths of the mounted skeletons are within, or just outside, the 95% PI of femur-based length estimates (Figs. 5, 6). The skeleton-based TL estimate of *Platysuchus* sp. is likewise very close to the FL-based estimate.

As preserved, the skeleton of *Borealosuchus wilsoni* is 17% less than the FL-based estimate (Table 4). The skeleton length is outside the 95% PI of the FL-based estimates (Fig. 5), but may have been artifactually shortened during preparation (Table 4). In contrast, the small specimen of *Borealosuchus* sp. has a skeleton-based TL estimate slightly larger than the FL-based TL estimate.

Rogers’ (2003) estimate of the length of a composite skeleton of *Pachycheilosuchus trinquei* is 30% less than the FL-based estimate, and the composite skeleton length (Table 4) is just outside the 95% PI of most femur-based TL estimates (Figs. 5, 6). However, because the specimen is a composite, the significance of these discrepancies is hard to assess.

Wu et al. (2001) and X.-C. Wu (pers. comm., July 2002) estimated the TL of a *Terminonaris robusta* by assuming skull length:body length proportions comparable to those of *A. sinensis*; their TL estimate was 1.1 times our FL-based estimate (Table 4). However, because of the slenderness of the femur of this species, Wu’s TL estimate is up to 1.5 times greater than other femur-based TL estimates. Of course, this begs the question of whether the Chinese alligator is a good model upon which to reconstruct the body proportions of *Terminonaris*.

Our only TL estimate of *Sarcosuchus imperator* is based on the circumference of a fragmentary femur of an immature (in size, but not necessarily in terms of reproductive status) individual (Table 4). Obtaining an independent TL estimate for comparison with the Fc-based estimate requires a rather attenuated chain of reasoning (Table 4). Even so, the larger independent TL estimate is only 1.2 times the smaller TL estimate based on Fc, and is within the 95% PI of the TL estimate based on Fc (wild alligator relationship; Fig. 6E).

TABLE 4. Total length estimates of fossil mesoeucrocodylians; all lengths in millimeters. Size estimates are based on regression equations in Table 3; parameter acronyms as in Table 1. Where equations were determined both for all alligators in our sample and for wild alligators only, both equations were used to make TL estimates; estimates based on wild alligators only are flagged with an asterisk (*). The 95% individual prediction intervals for estimates based on femur length are reported; 95% PIs for other TL estimates are not given, but some are shown graphically in Fig. 6. Where available, length estimates based on skeletons preserved in situ or in mounts, or length predictions based on parameters other than the femoral dimensions examined here, are reported; for TL predictions based on skull length, the value of skull length is given in parentheses before the TL estimate made from it.

| Specimen | Length parameter | Estimate based on: | | | | | | |
|--|---|---------------------|---------------|---------------|---------------|---------------|---------------|------|
| | | FL (95% PI) | Fdw | Fdh | Fpmx | Fpmn | Fc | Ftr |
| Crocodylians: | | | | | | | | |
| <i>A. mississippiensis</i> UF 68916, Irvingtonian, Florida | TL | 2429 (2278–2580) | 2364 2479* | 2437 2583* | 2415 2528* | 2326 2441* | 2378 2515* | 2407 |
| | TL interspp | 2463 | | | | | | |
| | TL multivariate | 2427 | | | | | | |
| <i>Alligator</i> cf. <i>A. mefferdi</i> UF 69929 | TL | 3484 (3332–3636) | 3297 3524* | — — | 3492 3844* | 3395 3672* | — — | 3435 |
| | TL interspp | 3585 | | | | | | |
| <i>A. olseni</i> UF 206760 | TL | 1822 (1671–1973) | 1785 1842* | 1940 2023* | 1837 1870* | 1795 1846* | 1945 2012* | 1692 |
| | TL interspp | 1818 | | | | | | |
| | TL multivariate | 1838 | | | | | | |
| <i>Wannaganosuchus brachymanus</i> SMM P76.28.247 | TL | 1416 (1265–1568) | 1306 1324* | 1571 1614* | 1426 1427* | 1459 1477* | 1413 1424* | 1340 |
| | TL interspp | 1386 | | | | | | |
| | TL multivariate | 1437 | | | | | | |
| | TL estimated from alligator skull length (145): TL relationship = 1163 | | | | | | | |
| <i>Hassiacosuchus haupti</i> HLMD ME 8008 | TL | 696 (542–849) | | | | | | |
| | TL interspp | 620 | | | | | | |
| | TL estimated from skeleton as preserved = 530 (Rauhe and Rossmann, 1995) (24% less than FL-based estimate) | | | | | | | |
| <i>Baryphracta deponiae</i> SMF ME 899; estimated FL = 47 | TL | 696 (542–849) | | | | | | |
| | TL interspp | 620 | | | | | | |
| | TL estimated from skeleton as preserved = 500 (Keller and Schaal, 1992: fig. 115) (28% less than FL-based estimate); FL estimated from the reported TL and the photograph of the specimen | | | | | | | |
| <i>Diplocynodon darwini</i> WDC Specimen A | TL | 479 (325–633) | | | | | | |
| | TL interspp | 390 | | | | | | |
| | TL estimated from alligator skull length (60): TL relationship = 558 TL estimated from skeleton as preserved = 337 (30% less than FL-based estimate) | | | | | | | |
| WDC Specimen B | TL | 479 (325–633) | | | | | | |
| | TL interspp | 390 | | | | | | |
| | TL estimated from skeleton as preserved = 330 (31% less than FL-based estimate) | | | | | | | |
| WDC Specimen C | TL | 493 (339–647) | | | | | | |
| | TL interspp | 405 | | | | | | |
| | TL estimated from alligator skull length (53): TL relationship = 508 TL estimated from skeleton as preserved = 327 (34% less than FL-based estimate) | | | | | | | |
| WDC Specimen D | TL | 609 (455–762) | | | | | | |
| | TL interspp | 528 | | | | | | |
| | TL estimated from alligator skull length (65): TL relationship = 593 TL estimated from skeleton as preserved = 460 (24% less than FL-based estimate) | | | | | | | |
| SMM P77.9.15 | TL | 1750 (1599–1901) | | | | | | |
| | TL interspp | 1741 | | | | | | |
| | TL estimated from alligator skull length (c.175): TL relationship = 1377 TL estimated from skeleton as preserved = 1170+ (33%) less than FL-based estimate) | | | | | | | |
| SMM P81.2.10 | TL | 1981 (1830–2132) | | | | | | |
| | TL interspp | 1987 | | | | | | |
| | TL estimated from alligator skull length (230): TL relationship = 1769 TL estimated from skeleton as preserved = 1330 (33% less than FL-based estimate) | | | | | | | |

TABLE 4. (Continued)

| Specimen | Length parameter | Estimate based on: | | | | | | |
|--|------------------|--|---------------|---------------|---------------|---------------|---------------|------|
| | | FL (95% PI) | Fdw | Fdh | Fpmx | Fpmn | Fc | Ftr |
| <i>Diplocynodon</i> sp. GM XXXVI433, 1963 | TL | 2530 (2380–2681) | 2413 2533* | 2642 2816* | 2415 2528* | 2326 2343* | 2519 2683* | 2362 |
| | TL interspp | 2571 | | | | | | |
| SMM | TL multivariate | 2547 | | | | | | |
| | TL | 615 (461–768) | | | | | | |
| P81.2.9 | TL interspp | 534 | | | | | | |
| | | TL estimated from alligator skull length (64); TL relationship = 586 TL estimated from skeleton as preserved = 465 (24% less than FL-based estimate) | | | | | | |
| <i>Deinosuchus</i> sp. UA specimen | TL | 4365 (4210–4521) | 3115 3319* | 3169 3422* | 3727 4144* | 3157 3395* | 4176 4782* | 3889 |
| | TL interspp | 4522 | | | | | | |
| TMM 43632-1 | TL multivariate | 4112 | | | | | | |
| | TL | 7674 (7495–7853) | 5939 6566* | 6151 6959* | 7175 8930* | 6711 7659* | 6645 8225* | 7432 |
| | TL interspp | 8039 | | | | | | |
| | TL multivariate | 7368 | | | | | | |
| | | Three linear measurements of a partial mandible of this individual are 114% to 141% of the same measurements of the mandible of a slightly smaller individual of <i>Deinosuchus</i> (TMM 43620-1) that has a skull with a length of 1180 mm. Assuming 1.25 to be the average ratio of the linear dimensions of the larger to the smaller individual, this gives an estimated skull length for TMM 43632-1 of about 1475 mm. Using our regression of TL on skull length (Table 3), this gives an estimated TL of 10,640 mm for TMM 43632-1. | | | | | | |
| <i>Volia athollandersoni</i> MNZ S38187 | TL | — | — | — | 2415 2528* | 1879 1939* | 2589 2767* | 1872 |
| | | TL estimated at 2000–3000 mm by comparison with the femur diameter: animal total length relationship of <i>Crocodylus porosus</i> (Molnar et al., 2002); note that this TL estimate, made as it is on a femoral measurement, is not really independent of the other femur-based estimates | | | | | | |
| <i>Gavialosuchus carolinensis</i> SMM P92.2.1c (cast of ChM PV 4279) | TL | 4871 (4713–5029) | 4002 4325* | 4460 4932* | 4278 4862* | 3857 4214* | 4584 5328* | 4807 |
| | TL interspp | 5059 | | | | | | |
| | TL multivariate | 4792 | | | | | | |
| | | TL estimated from alligator skull (805): TL relationship = 5866; from <i>C. porosus</i> skull length: TL relationship = 6010; from <i>G. gangeticus</i> skull length: TL relationship = 5263 | | | | | | |
| Basal crocodyloid, Bridger Formation (“ <i>Crocodylus</i> ” <i>affinis</i>) USNM 12719 | TL | 3239 (3087–3390) | 2908 3087* | — | 3037 3276* | — | 3068 3355* | 3073 |
| | TL interspp | 3323 | | | | | | |
| | | TL estimated from alligator skull length (418; Gilmore [1946]): TL relationship = 3109; from <i>C. porosus</i> skull length: TL relationship = 3023; TL estimated from mounted skeleton = 2997 (Gilmore [1946]) (7% less than FL-based estimate); although this is a fairly well-preserved skeleton, there was some reconstruction of the vertebral column | | | | | | |
| “ <i>Asiatosuchus</i> ” <i>germanicus</i> GM VI/347 | TL | 2054 (1903–2204) | | | | | | |
| | TL interspp | 2064 | | | | | | |
| | | TL estimated from skeleton as preserved = 1060 mm (Rauhe and Rossman, 1995) (48% less than FL-based estimate) | | | | | | |
| <i>Pristichampsus rollinatii</i> GM Leo X-8001 | TL | 3152 (3000–3303) | | | | | | |
| | TL interspp | 3231 | | | | | | |
| | | TL estimated from alligator skull length (395): TL relationship = 2945; from <i>C. porosus</i> skull length: TL relationship = 2846 TL estimated from skeleton as preserved = 2000 (37% less than FL-based estimate) | | | | | | |
| <i>Borealosuchus wilsoni</i> FMNH PR1674 | TL | 4539 (4383–4695) | | | | | | |
| | TL interspp | 4706 | | | | | | |
| | | TL estimated from alligator skull length (580): TL relationship = 4263 TL estimated from skeleton as displayed = 3770 (17% less than FL-based estimate), but the accuracy of this is uncertain. As preserved, the tail of the skeleton was folded across the trunk, and was straightened out during preparation. Possibly some posterior dorsal or proximal caudal vertebrae were lost during this; the tail looks rather short compared with the rest of the skeleton (Grande, 1994: fig. 8B; L. Grande, pers. comm., 2003). | | | | | | |

TABLE 4. (Continued)

| Specimen | Length parameter | Estimate based on: | | | | | | |
|---|---|---------------------|---------------|---------------|---------------|---------------|---------------|------|
| | | FL (95% PI) | Fdw | Fdh | Fpmx | Fpmn | Fc | Ftr |
| <i>Borealosuchus formidabilis</i> SMM P89.6.370 | TL | 3628 (3476–3781) | | | | | | |
| | TL interspp | 3738 | | | | | | |
| | TL estimated from alligator skull length (527 [skull 66]): TL relationship = 3885 mm | | | | | | | |
| SMM P92.2.16 | TL | 3961 (3807–4115) | — | — | 3445 3785* | 4230 4656* | 3598 4027* | 3566 |
| | TL interspp | 4092 | | | | | | |
| | TL estimated from alligator skull length (516 [skull 79]): TL relationship = 3807 mm | | | | | | | |
| <i>Borealosuchus</i> sp. FMNH PR1793 | TL | 753 (600–906) | | | | | | |
| | TL interspp | 681 | | | | | | |
| | TL estimated from alligator skull length (84): TL relationship = 729 | | | | | | | |
| | TL estimated from skeleton as preserved = 770+ (2% greater than FL-based estimate) | | | | | | | |
| Non-Crocodylian Crocodyliforms: | | | | | | | | |
| <i>Goniopholis</i> sp. GMNH 102 | TL | 3166 (3014–3318) | 2604 2746* | 2709 2893* | 3062 3306* | 2498 2637* | 2865 3103* | 2872 |
| | TL interspp | 3247 | | | | | | |
| | TL multivariate | 3073 | | | | | | |
| | TL estimated from alligator skull length (383): TL relationship = 2859 | | | | | | | |
| | TL of mounted skeleton = 2850 (C. Miles, pers. comm., 2004) (10% less than FL-based estimate) | | | | | | | |
| <i>Terminonaris robusta</i> SMNH P2411.1 | TL | 5507 (5345–5668) | — | — | 4004 4503* | 4082 4480* | 4365 5034* | 4494 |
| | TL interspp | 5735 | | | | | | |
| | TL estimated from alligator skull length (949 [Wu et al., 2001; fig. 2]): TL relationship = 6892; from <i>C. porosus</i> skull length: TL relationship = 7121; from <i>G. gangeticus</i> skull length: TL relationship = 6329 Wu et al. (2001) and Wu (pers. comm., 2002) estimated TL of this individual at ca. 6000 mm by using the body proportions of <i>Alligator sinensis</i> , in which TL is roughly twice the combined skull and trunk length, and trunk length is itself twice skull length | | | | | | | |
| <i>Sarcosuchus imperator</i> MNN G102–2 | TL | — | — | — | — | — | 7246 9107* | — |
| | Sereno (pers. comm., 2002) estimated that this individual was about 75% of the TL of a large <i>S. imperator</i> , based on the size of partial cervical centra as compared with those of another not fully grown individual that has a skull; Sereno et al. (2001) estimated TL of a full-sized individual (11.5–12 m) based on regression equations of TL against skull length in <i>G. gangeticus</i> and <i>C. porosus</i> . Thus the estimated size of the present individual would be 8625–9000 mm. | | | | | | | |
| <i>Steneosaurus bollensis</i> WDC specimen | TL | 2111 (1961–2262) | | | | | | |
| | TL interspp | 2125 | | | | | | |
| | TL estimated from alligator skull length (394): TL relationship = 2938; TL estimated from <i>C. porosus</i> skull length: TL relationship = 2838; TL estimated from <i>G. gangeticus</i> skull length: TL relationship = 2222 | | | | | | | |
| | TL estimated from skeleton as preserved = 1770 (16% less than FL-based estimate) | | | | | | | |
| <i>Steneosaurus</i> sp. SMM P77.11.22c | TL | 1255 (1103–1407) | | | | | | |
| | TL interspp | 1214 | | | | | | |
| | TL estimated from alligator skull length (278): TL relationship = 2111; TL estimated from <i>C. porosus</i> skull length: TL relationship = 1943; TL estimated from <i>G. gangeticus</i> skull length: TL relationship = 1364 | | | | | | | |
| | TL estimated from skeleton as preserved = ca. 1400 (12% greater than FL-based estimate) | | | | | | | |
| <i>Platysuchus</i> sp. Estimated FL = 208 | TL | 3022 (2870–3173) | | | | | | |
| | TL interspp | 3093 | | | | | | |
| | Actual TL = 2800 (Urlichs et al., 1979; fig. 16) (7% less than FL-based estimate); FL estimated from the reported TL and the photograph of the specimen | | | | | | | |
| <i>Crocodylaemus robustus</i> USNM 15828 (cast) | TL | 821 (668–974) | | | | | | |
| | TL interspp | 754 | | | | | | |
| | TL estimated from skeleton as preserved = 550 (33% less than FL-based estimate) | | | | | | | |
| <i>Pachycheilosuchus trinquei</i> SMU composite skeleton (Rogers, 2003) | TL | 1130 (978–1283) | 875 867* | 1025 1022* | 1092 1086* | 982 963* | 1214 1214* | 1136 |
| | TL interspp | 1082 | | | | | | |
| | TL multivariate | 1102 | | | | | | |
| | TL estimated from dentary length = 635 mm; estimated from composite skeleton = 800 mm (Rogers, 2003) (the larger LT estimate is 30% less than the FL-based estimate) | | | | | | | |

TABLE 4. (Continued)

| Specimen | Length parameter | Estimate based on: | | | | | | |
|---------------------------------|------------------|--|-----|-----|------|------|----|-----|
| | | FL (95% PI) | Fdw | Fdh | Fpmx | Fpmn | Fc | Ftr |
| <i>Alligatorellus beaumonti</i> | | | | | | | | |
| Estimated | TL | 363 (209–518) | | | | | | |
| FL = 24 | TL interspp | 267 | | | | | | |
| | | TL estimated from skeleton as preserved = 243 (33% less than FL-based estimate); both TL and FL estimated from Lortet (1892: plate 11) | | | | | | |
| <i>Hoplosuchus kayi</i> | | | | | | | | |
| CM 11361 | TL | 349 (194–503) | | | | | | |
| | TL interspp | 251 | | | | | | |
| | | TL estimated from skeleton as preserved = 200 (43% less than FL-based estimate) | | | | | | |

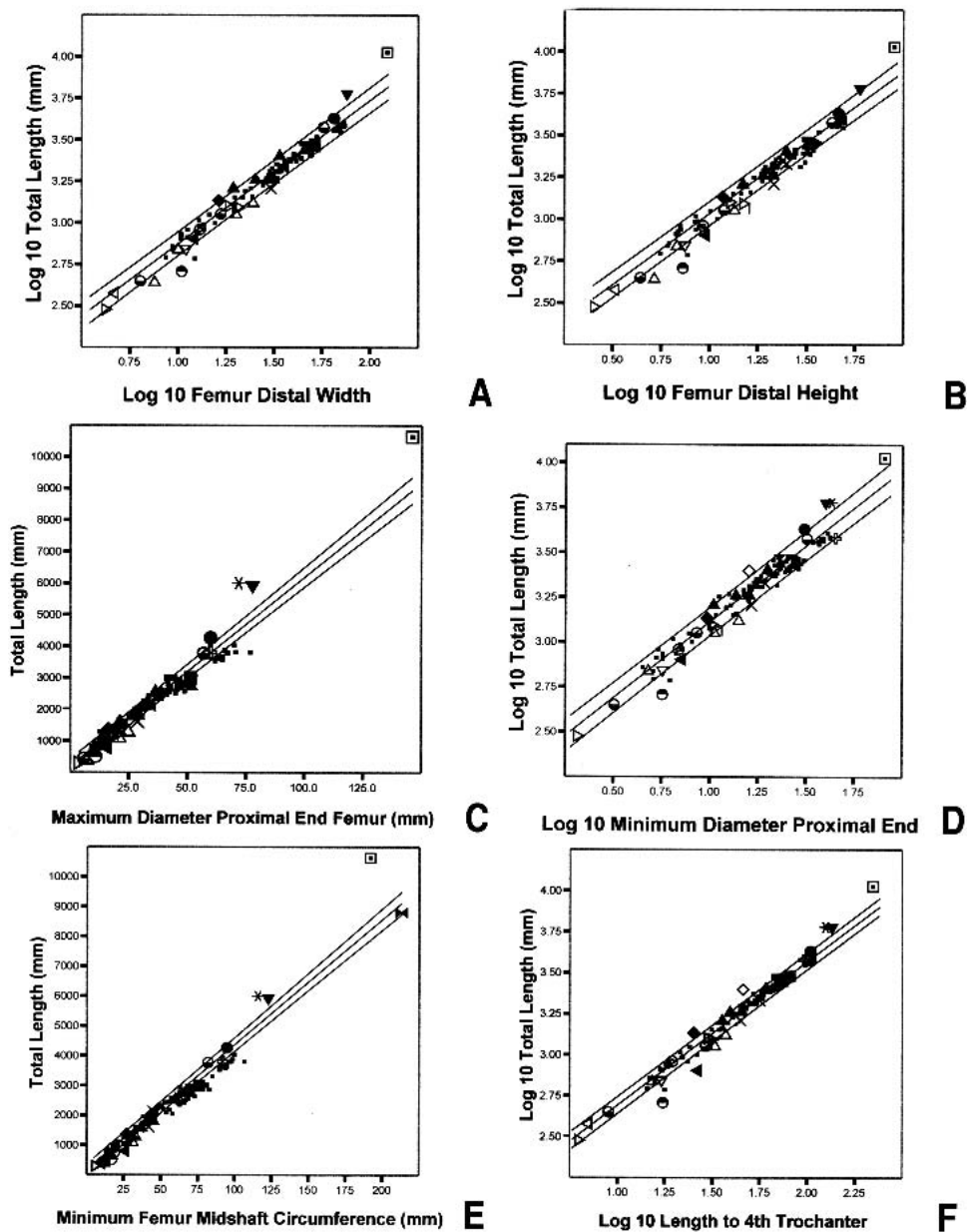


FIGURE 6. Total length as a function of various femoral dimensions in mesoeucrocodylians. Regression lines and 95% prediction intervals are for wild or all *A. mississippiensis*. Where wild and captive alligators do not differ in the graphed relationship, the regression line and 95% prediction interval are for all American alligators. For relationships in which separate regression equations are reported for wild as opposed to all American alligators (Table 3), the regression line and 95% prediction interval are for wild alligators. Legend symbols as in Fig. 5.

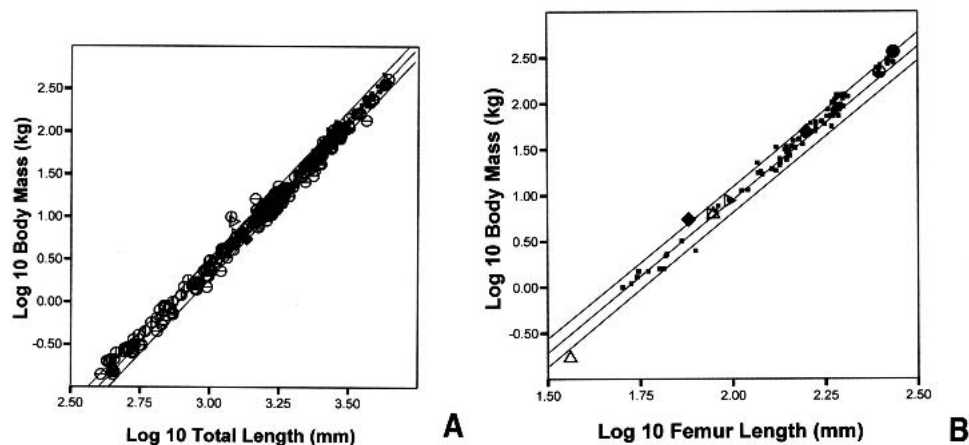


FIGURE 7. Body mass as a function of **A**, total length; and **B**, femur length in *A. mississippiensis* and other crocodylians. Legend symbols as in Fig. 5. Regression lines and 95% prediction intervals are for wild alligators (Table 3).

Body Mass—Although data are fewer than for TL:femoral dimension relationships, alligator-based M:femoral dimension relationships seem to work reasonably well for other extant crocodylian species (e.g., Fig. 7). Furthermore, the M:TL relationship for American alligators also works well for other crocodylian species (Fig. 7), suggesting that however a TL estimate for an extinct form is made, the alligator M:TL relationship can be used to estimate the animal's body mass from that TL.

Body mass estimates for selected crocodylians are summarized in Table 5. M estimates from different femoral dimensions of the same specimen are more variable than TL estimates, possibly in part because M is proportional to the cube of length, in consequence making masses estimated from these linear dimensions inherently more variable than TL estimates. This is particularly true for the biggest forms, animals whose femora are larger than those of the alligators used to construct the regression equations. M estimates based on dimensions across the articular ends of the femur are much less than estimates based on FL and Ftr. Fdw consistently predicts the smallest masses; in some cases these are so low as to be untenable—suggesting, for example, that the larger individual of *Deinosuchus* weighed only slightly more than a large *C. porosus* (Grigg and Seebacher, 2000). Despite the fact that Fdw seems to be the best single predictor of M in alligators, M estimates of very large extinct crocodylians based on FL intuitively seem more reasonable.

The relatively slender femur of *T. robusta* yields M estimates based on Fpmx, Fpmn, and Fc that are much less than those based on FL. Ftr likewise predicts a much lower M than does FL.

Independent M estimates based on skull length can be made for two of the fossil forms in Table 5. For the basal crocodyloid from the Bridger Formation, skull-based M estimates are close to femur-based estimates; the same is true for *Goniopholis* sp. (not reported in Table 5). For *T. robusta*, however, skull-based M estimates (Table 5) are much heavier than femur-based estimates.

DISCUSSION

In *Alligator mississippiensis*, femoral measurements are highly correlated with both TL and M (Table 3). Although all the femoral dimensions analyzed in this study are good predictors of alligator body size, FL is the best single predictor of TL, and Fdw of M. Femoral dimensions have also been found to correlate with body mass or length in other terrestrial vertebrates, both intraspecifically and interspecifically (cf. Anderson et al., 1985 [mid-shaft circumference {femur + circumference} used to estimate M]; Gingerich, 1990; Scott, 1990; Campbell and Marcus, 1992; Anyonge, 1993; Rosenberg and Dodson, 1996; Christiansen, 1999; Reynolds, 2002; Erickson et al., 2003). Our results provide further justification for using femoral measurements as proxies

TABLE 5. Body mass estimates of selected taxa of fossil crocodylians. Mass estimates are based on regression equations in Table 3. For parameters marked with a single asterisk (*), mass estimates were based on equations employing wild alligators only. For the two-step estimate from FL (marked with two asterisks), total length was estimated from femur length using an all-alligator equation, after which mass was estimated from a regression against total length using wild alligators only. For parameters without an asterisk, all-alligator equations were used.

| Specimen | Body mass estimate (kg) based on | | | | | | | |
|-------------------------------------|---|-----------------|------|------|------|------|------|------|
| | FL (95% PI)* | "Two-Step" FL** | Fdw | Fdh* | Fpmx | Fpmn | Fc* | Ftr |
| <i>Deinosuchus</i> sp. | | | | | | | | |
| UA Specimen | 356 (244–506) | 408 | 132 | 157 | 244 | 137 | 368 | 283 |
| | Multivariate*: 219 | | | | | | | |
| TMM 4362-1 | 2349 (1556–3458) | 2893 | 1194 | 1597 | 2250 | 1752 | 1794 | 2626 |
| | Multivariate*: 1724 | | | | | | | |
| Bridger Formation basal crocodyloid | | | | | | | | |
| USNM 12719 | 131 (91–184) | 145 | 104 | — | 122 | — | 128 | 126 |
| | Multivariate*: 120 | | | | | | | |
| | Estimates from skull length: 145 (<i>A. mississippiensis</i> equation [Table 3]); 94 (<i>C. porosus</i> two-step estimate) | | | | | | | |
| <i>Terminonaris robusta</i> | | | | | | | | |
| SMNH P2411.1 | 774 (525–1115) | 914 | — | 311 | 326 | 428 | 465 | — |
| | Estimates from skull length: 2522 (<i>A. mississippiensis</i> equation [Table 3]); 1438 (<i>C. porosus</i> two-step estimate) | | | | | | | |
| <i>Sarcosuchus imperator</i> | | | | | | | | |
| MNN G102-2 | — | — | — | — | — | — | 2411 | — |

for the body size of extinct tetrapods (e.g., Currie, 2003; Hurlburt et al., 2003).

For most living and extinct mesoeucrocodylians, alligator femur-based size estimates are at least good first approximations, and are as good as those based on skull lengths. However, Figures 5 and 6 suggest systematic departures of TLs of extinct mesoeucrocodylians estimated from femoral dimensions from TLs estimated on non-femoral bases. For smaller forms, when femur-based TLs are greatly different than non-femoral estimates, femur-based estimates are usually larger than non-femoral estimates. For enormous forms, in contrast, femur-based estimates are smaller than estimates based on other osteological criteria.

Accounting for these discrepancies is difficult, because more than one explanation is plausible. Most of the TL estimates of small-bodied forms are based on skeletons preserved in situ. Slight postmortem jumbling of the vertebrae, and the fact that these estimates are based on skeletons, rather than on intact animals, undoubtedly contribute to smaller TL estimates than those based on femoral dimensions, even if these factors do not account completely for the discrepancy. All of the non-femoral TL estimates of the biggest crocodyliforms, in contrast, are based on skull lengths, so one explanation for the pattern is that different kinds of TL estimates are being compared with femur-based TL estimates at the extreme ends of the size range.

Two fossil forms for which femur-based TL estimates show excellent agreement with independent TL estimates (Table 4) are the Bridger Fm basal crocodyloid and *Goniopholis* sp., neither of which is closely related to *A. mississippiensis* (Fig. 1), but both of which are similar in size to adult alligators. This suggests that some of the discrepancy between alligator femur-based TL estimates and the skull-based TL estimate for *Deinosuchus* may simply reflect problems of extrapolating too far beyond the range of data used to create the regression equations. On the other hand, there is better agreement between some FL-based TL estimates and skull-based TL estimates for other very large forms (*Sarcosuchus*, *Terminonaris*, and *Gavialosuchus*; Figs. 5, 6).

However, some of the discrepancy between alligator femur-based TL estimates and other estimates of TL undoubtedly reflects real differences in body proportions between American alligators and other species. Thus three specimens of a modern alligatoroid, *Caiman crocodylus*, had observed TLs ranging from 3–14% less than TLs predicted from FLs using our alligator equation, and four *Paleosuchus trigonatus* had observed TLs 5–23% less than predictions from the *A. mississippiensis* FL-based equation, suggesting that each species has a relatively longer femur in comparison with TL than in American alligators. Similarly, Brochu (1997, pers. comm., 2003) noted that particularly slender (and possibly relatively long) proximal limb elements constitute a synapomorphy for *Borealosuchus*.

In some cases, marked differences in the size of the femur relative to the rest of the skeleton between American alligators and extinct crocodylians may relate to adaptive differences. The TL of *P. rollinatii* estimated from FL is 1.6 times the TL measured on the specimen as preserved (Table 4). TLs estimated from skull length are also much larger than the length of the skeleton, and comparable to the TL estimated from FL. For *A. mississippiensis*, the ratio of TL/FL ranges 10.8–17.5 (mean = 14.6; $n = 98$), and the ratio of shoulder–hip length (measured along the dorsal midline of intact carcasses) to FL ranges 3.3–3.7 (mean = 3.5; $n = 23$). For the skeleton of *P. rollinatii*, estimated TL/FL is 9.2, and estimated shoulder–hip length/FL is 2.2. *Pristichampsus* clearly had a relatively longer femur than *Alligator*; conceivably this is related to a more terrestrial lifestyle on the part of the former genus (cf. Busbey, 1986; Rauhe, 1995; Rossman, 2000).

Similarly, TL of the basal crocodylomorph *Protosuchus*, as

reconstructed by Colbert and Mook (1951:fig. 4), is about 860 mm, but TL estimated from FL on the basis of our alligator equation is 1460 mm, about 70% greater. Colbert and Mook (1951:fig.14) noted that the hindlimb of *Protosuchus* was relatively longer, compared to the aggregate length of the presacral and sacral vertebrae, than in a young *C. porosus* of comparable size, and used this as one basis to argue for more terrestrial habits on the part of *Protosuchus* than in modern crocodylians. The sphenosuchian *Dromicosuchus* (Sues et al., 2003) likewise has a relatively long femur compared with TL (H.-D. Sues, pers. comm., 2004).

However, the discrepancy between the alligator FL-based TL estimate and the TL estimate made from the entire skeleton is even greater for “*A. germanicus* (Table 4), which is not viewed as an unusually terrestrial form, than it is for *P. rollinatii*. Although the hypothesis that a relatively long femur is associated with terrestrial habits in crocodylomorphs is attractive, it is somewhat problematic.

Femoral dimensions predict that the larger specimen of *Deinosuchus* (Table 4) had a TL of 6–8 m. In contrast, comparing the dimensions of an incomplete lower jaw of the larger specimen with the complete jaw and skull of a slightly smaller individual (TMM 43620–1) yields a TL estimate of 10–11 m for the larger specimen (Table 4). Erickson and Brochu (1999) estimated that *Deinosuchus* reached lengths of 8–10 m, and Schwimmer (2002) thought that the biggest individuals were as much as 12 m long. If the discrepancy between our two length estimates is not an artifact of applying regression equations to specimens much larger than those used to create the equations, and is not due to the unlikely (we believe) possibility that two individuals of different size are mixed in the larger specimen, then *Deinosuchus* must have reduced the size of its femur relative to overall body size, as compared with alligators. Reversing the argument about a relatively long femur and more terrestrial habits that we considered for *Pristichampsus*, a relative reduction of femur length in *Deinosuchus* might be related to a more strictly aquatic lifestyle than that of *Alligator*. The sheer size of the animal favors such a notion, as does the coastal context of most *Deinosuchus* burials.

Ghariales (*Gavialis gangeticus*) are among the most aquatic modern crocodylians, rarely going far from water; individuals larger than 2 m TL move on land only by sliding on their bellies (Singh and Bustard, 1976; Whitaker and Basu, 1983; Whitaker and Andrews, 1988). Indeed, ghariales are said to have “somewhat feeble front legs” (Whitaker and Andrews, 1988:621). The one gharial for which we had data (Fig. 5) seems to have a rather long TL for its FL, suggesting that a reduced femur might also be associated with the less terrestrial habits of this species.

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APPENDIX 1

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