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COMPARISON OF BODY MASS ESTIMATION TECHNIQUES, USING RECENT REPTILES AND THE PELYCOSAUR *EDAPHOSAURUS BOANERGES*

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ABSTRACT—Body mass estimation is important for the study of relative brain size, biomechanics, and other physiological and ecological aspects of extinct vertebrates. Body mass of *Edaphosaurus boanerges* (ROM 7985), a mounted skeleton with a fibreglass model built around the left side was estimated by various methods: (1) Graphic Double Integration (GDI) on the fibreglass model divided into measurable components; (2) regression equations using total body length (TL), snout–vent length, and TL and tail-girth (TG); (3) three QBASIC programs which predict body mass from leg bone dimensions (humerus, ulna, femur and tibia) using regression equations from Recent amniotes; specifically: lengths and parasagittal diameters in mammals; lengths and mediolateral and anteroposterior diameters in alligators; and lengths and circumferences in alligators; and (4) prediction from an equation relating body mass to femur and humerus circumferences.

GDI yielded 92.79 kg (including fin volume of 3.57 kg), within the body mass range of alligators on which leg-bone equations were based. The estimate from alligator-based TL and TG was 75.05 kg. Estimates from leg bone dimensions were 17.85 kg from lengths and diameters (mammal-based); 73.33 kg from lengths and diameters (alligator-based), although estimates from humerus and femur, humerus alone and femur alone bracketed the GDI result; and 61.70 kg from lengths and circumferences (alligator-based). The fin added 66% to body surface area and only 4% to total mass.

INTRODUCTION

Estimation of body mass in Recent and extinct vertebrates is important to studies of allometry including relative brain size, physiology, biomechanics and ecology. It is also useful for estimates of available flesh for dietary needs from archaeological faunal remains and dosage determination of tranquilizers and other pharmacological agents.

The body mass of extinct animals has been estimated by calculating and scaling up volumes of carefully constructed scale models, assuming a specific gravity between 0.9 (Colbert, 1962) and 1.0 (Alexander, 1985). Romer and Price (1940) used the volume of a half-size model of the pelycosaur *Dimetrodon limbatus,* to estimate a life mass of 9.7 kg, assuming a specific gravity of 1.025. They calculated body masses of other pelycosaurs, including *Edaphosaurus* (83 kg), using the *D. limbatus* body mass estimate, and an index of relative body mass which was the square of the mean transverse radius (r^2) of dorsal vertebral centra. Romer and Price suggested the pelycosaur estimates were within 10 to 20% of actual masses. Jerison (1973) estimated body mass in extinct mammals using a regression equation relating body mass (MBd) in grams to head and body length in centimetres (HBL) in Recent perissodactyls, artiodactyls and carnivores (see Methods).

Jerison also estimated volumes of endocasts from dorsal and lateral views, using graphic double integration (GDI, see Methods). He found GDI volumes were 5% or less of volumes he found by water displacement for the same endocasts, and gave an example of a GDI volume of 536 ml for a *Tyrannosaurus rex* endocast for which he determined a water displacement volume of 530 ml (Jerison, 1973). Anderson et al. (1985) estimated dinosaur body mass using regression equations which relate body mass (g) to femur circumference (cm) in birds, and to the sum of femur circumference and humerus circumference in quadrupedal mammals. Gingerich (1990) created the QBASIC BODYMASS program, which gives body mass estimates from leg bone dimensions. Woodward et al. (1991) calculated a multiple regression equation for wild alligators predicting body mass from body length and tail girth in *Alligator mississippiensis.*

This paper has three objectives: (1) to introduce three new methods of estimating body mass; (2) to compare the accuracy of these and other methods on Recent reptiles; and (3) to obtain a body mass estimate for *Edaphosaurus boanerges* using several methods.

METHODS AND MATERIALS

Body mass estimation methods used in this paper were tested on a sample of modern reptiles, consisting of three frozen specimens which had died in captivity: *Osteolaemus tetraspis* (African dwarf crocodile), *Cyclura cornuta* (Rhinoceros iguana), and *Varanus salvatore* (Malaysian water monitor); and four live specimens: *Caiman crocodylus* (Spectacled caiman), *Iguana iguana* (Green iguana), and two specimens of *Alligator mississippiensis* (American alligator). Methods were also tested on skeletal elements from alligators of known body mass.

These methods were then used to estimate body mass of a specimen of *Edaphosaurus boanerges,* a presumably herbivorous and slow-moving animal of the late Pennsylvanian and early Permian. Its laterally expanded ribs gave it a wide-bellied form, typical of Recent herbivorous reptiles (Modesto, 1991). The cutting edges of its marginal teeth resemble those of Recent herbivorous reptiles (Modesto, 1991), and toothed plates on much of the palate and lower jaw appear suited for crushing soft plant material (Romer and Price, 1940). *Edaphosaurus* had greatly elongated neural spines which, as in *Dimetrodon,* presumably supported a sail. Unlike *Dimetrodon,* the spines bear transverse crossbars or tubercles, which extend up to 4 cm laterally in another species, *Edaphosaurus pogonias* (Bennett, 1996), but no more than 1.7 cm in the specimen investigated here. The *Edaphosaurus boanerges* specimen, Royal Ontario Museum (ROM) 7985, consists of a mounted skeleton with a fibreglass model built around its left side at the Royal Ontario Museum, under the supervision of G. Edmund (Fig. 1). The fibreglass is close to or contacts the skeleton in most cases, excepting the limbs, but these elements are small portions of

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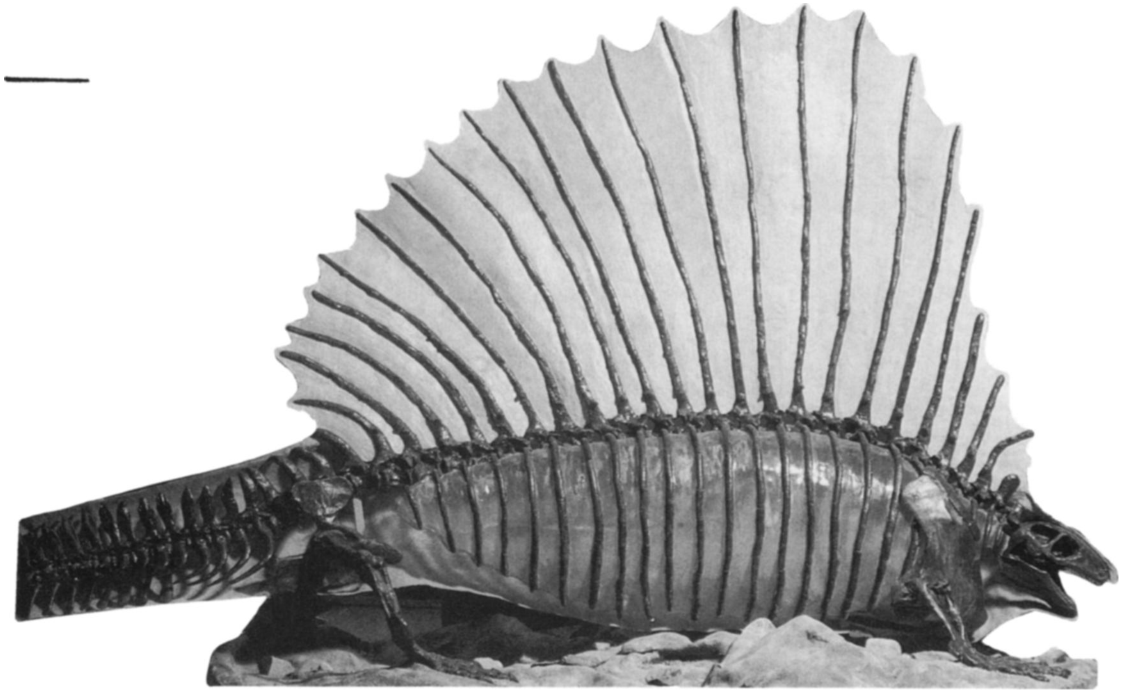

FIGURE 1. Photograph of right lateral view of *Edaphosaurus boanerges* (ROM 7985) showing the skeleton and the medial side of the fibreglass model. The thirteen caudal vertebrae visible represent 361.25 mm and 31.1% of tail length. Scale bar equals 10 cm.

total mass. The model, with the exposed skeleton, allows body mass estimates by several methods which can be compared. The available information with the specimen indicates collection in 1939 by a Harvard Museum of Comparative Zoology (MCZ) crew under A. S. Romer, in the Geraldine Quarry, Archer County, Texas, and that the pelvis was from another individual and the head modeled. All skeletal elements are painted dark brown and coated in gelva or a similar medium, and all appear to be casts of varying accuracy. The most accurate casts strongly resemble original fossils, reproducing fine details of morphology, cracks and slightly crushed areas, but all elements are relatively light-weight, and beneath the coating all elements investigated (femur, exposed edges of ribs and neural spines, and some vertebrae) are composed of a relatively soft, whitish plaster-like material, while genuine *Edaphosaurus* fossils from the same site (MCZ 1755, 1761, and 1762), are relatively heavy, dark-colored, and relatively hard. In the axial skeleton, the ribs, the 23 vertebrae between the second cervical ("axis") and sacrum, and their neural spines, are all very accurate casts, save the neural spine of #23, which was probably modelled. The two cervical, three sacral, and first six caudal vertebrae are also partly or completely molded, judging by their smooth and rounded appearance and lack of complex morphology and surface detail. The bodies and neural arches of caudal vertebrae 7 to 17 are good casts, but the neural spines, transverse processes, and chevrons are molded. Chevrons were unknown for *Edaphosaurus boanerges* and were modeled on the reconstruction of MCZ 1531 (*E. boanerges*) by Romer and Price (1940). All the remaining caudal vertebrae, from 18 to 54, and small terminal elements, are clearly casts or molds, possibly sculpted, and show little or no surface detail. In the appendicular skeleton, the shoulder girdle appears mostly or completely molded, but probably accurate since such elements are abundant in quarries, while the pelvis appears compatible with the size of the specimen. The femur, humerus, radius, ulna, tibia, and fibula appear very accurate and all six retain their original length, proximal and distal widths, and their original midshaft "roundness". Manus and pes elements appear to be casts or molded. Romer and Price (1940) note that no carpal elements and few tarsal elements definitely associated with *Edaphosaurus* had been found. Because no MCZ number was found associated with ROM 7985, measurements on the skeleton were compared to those of *E. boanerges* specimens in Romer and Price (1940) to assess the accuracy of the restoration.

Body Mass Estimation by Graphic Double Integration

In Graphic Double Integration (GDI), the body or body part under investigation is modelled as an elliptical cylinder to determine volume (Jerison, 1973). Following Alexander (1985), a specific gravity of 1 is assumed, so that volume (ml) is numerically equivalent to mass (g).

Body Volume and Mass Calculation—The body mass of the six reptiles and the *Edaphosaurus* model was estimated by calculating volume by GDI of the following body parts: head, trunk, tail, upper and lower elements of fore- and hindlimbs. Volume of manus and pes were calculated either by GDI or by modelling elements as rectanguloid blocks from determination of mean height, width and length, as for *Edaphosaurus*. The GDI procedure requires determination of two diameters, the second perpendicular to the first, for each body part, from photographs or illustrations. The method is more accurate if bodies or body parts are measured in sections of approximately the same diameter. Body parts of reptiles were photographed as in the following account for *Edaphosaurus*. The following views of the model of the left side, were photographed, with scale bars: lateral and dorsal views of the head, lateral and dorsal views of the trunk, dorsal and anterior views of the upper foreleg, lateral and anterior views of the lower foreleg, dorsal and posterior views of the upper hindleg, and lateral and posterior views of the lower hindleg. The volume of each part was obtained as in the following description of trunk volume calculation. The outline of the lateral side was traced on paper from the photograph, and 16 equally spaced vertical lines were drawn

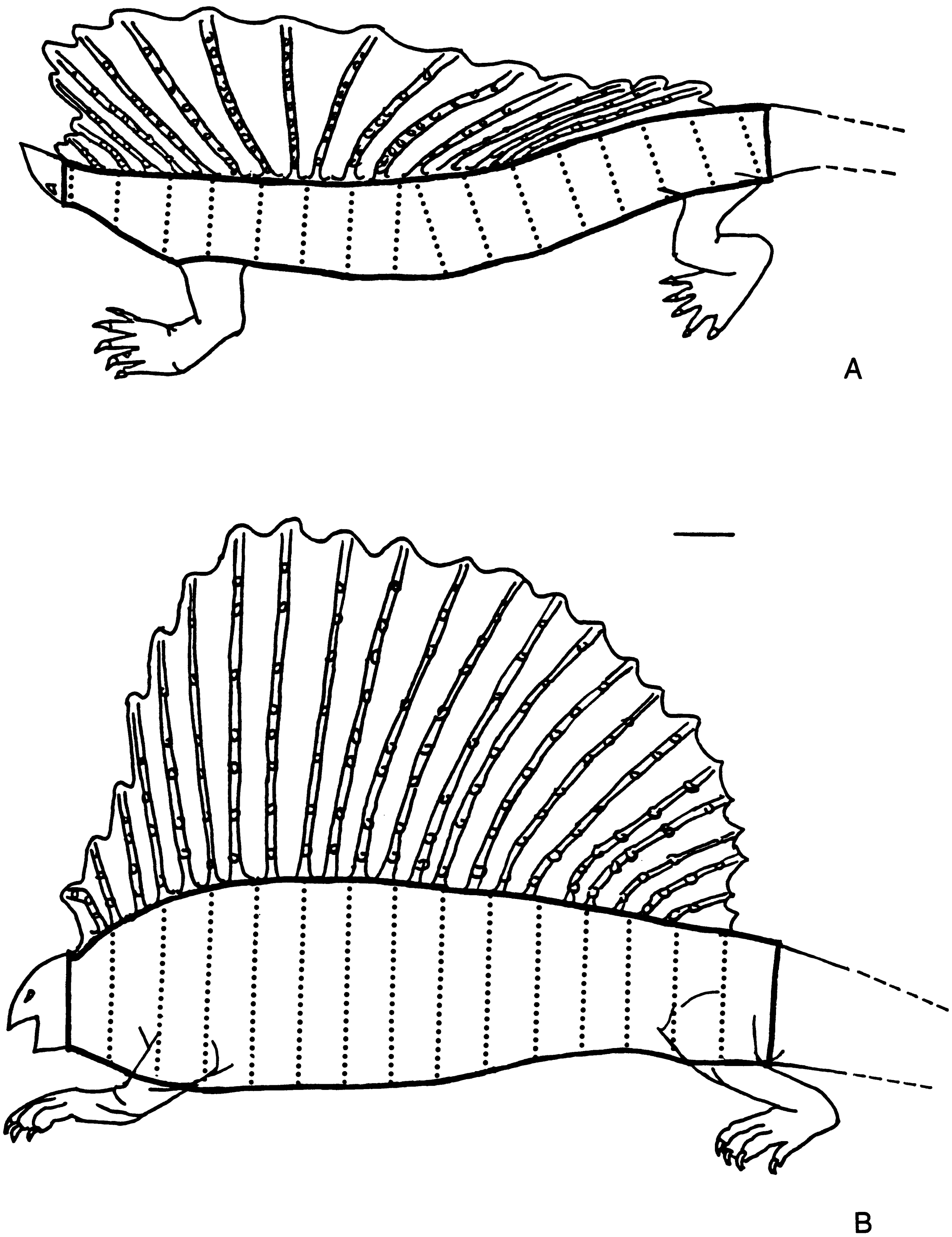

FIGURE 2. Dorsal (**A**) and left lateral (**B**) views of fiberglass *Edaphosaurus boanerges* model, traced from photographs, illustrating Graphic Double Integration volume calculation for trunk portion of body. Trunk areas used outlined in bold and equally-spaced dotted lines drawn across outlined areas. Tail continues to right on specimen but excluded from drawings. Tail length = 116.0 cm. Means of line lengths equal average transverse and dorsoventral diameters respectively (value for dorsal view doubled as it measures only left half of trunk). Body length measured from lateral view. Note that in dorsal view, body is curved, and line orientation correspondingly varied to obtain diameter. Trunk volume calculated using formula $V = \pi(r_1)(r_2)(L)$ (see text). Volumes of head, upper and lower fore and hind legs, and tail similarly calculated. Scale bar equals 10 cm.

across it. The mean length of the lines gave an average dorsoventral diameter (Fig. 2b). Transverse diameter was similarly obtained from a dorsal view (Fig. 2a) and doubled since only the left half was present. Length was measured, and life transverse diameter (D_t), dorsoventral diameter (D_{dv}), and length (L) in cm were obtained using the scale bar. These diameters were converted to radii, r_1 and r_2. Trunk mass in g ($Mass_g$) was considered numerically equivalent to volume in ml (Vol_{ml}), which was obtained from the formula for the volume of an elliptical cylinder:

$$Mass_g = VBd_{ml} = \pi(r_1)(r_2)(L) \tag{1}$$

This formula is equivalent to the product of the length of a cylinder and the area (A) of an ellipse, where:

$$A = \pi(r_1)(r2) \tag{2}$$

and r_1 and r_2 are the two radii of the ellipse. For *Varanus, Iguana* and *Cyclura,* tail masses were obtained by GDI for the first 20 cm (first 10 cm for *Iguana*) of the tail posterior to the vent. Past that point, direct measurements of transverse and dorsoventral diameters were taken at regular intervals. The volume of this posterior segment was relatively small, and direct measurement was easier than photography and photograph measurement. *Edaphosaurus* tail mass was also obtained by direct measurement on the actual model because tail circumference decreased regularly, and GDI of the tail would have been difficult as it was constructed in a sinuous curve.

Surface Area—Lateral surface area of the *Edaphosaurus* model was calculated from the product of length (L) of the cylinder and the perimeter (P) of the ellipse:

$$SA = LP \tag{3}$$

where P is approximated by the formula:

$$P = 2\pi\sqrt{(0.5)(r_1^2 + r_2^2)} \tag{4}$$

where again r_1 and r_2 are the two radii of the ellipse. Only lateral surface area was used as the faces of adjacent cylinders abut each other in the animal and are not exposed.

In *Edaphosaurus,* fin area was calculated by multiplying mean fin height and multiplying by the length. Mean fin height was calculated as in the GDI method for mean lateral diameter. Fin mass was calculated by taking the sum of the volume of the neural spines with crossbars when encased in a layer of fibreglass 0.15 cm thick and of the volume of the skin/flesh part of the fin between successive spines, which was assumed to be 0.30 cm, equivalent to a double layer of fibreglass. In ROM 7985, each spine bears a single large proximal tubercle, and several minor tubercles. The major tubercles were estimated to be 1.70 cm lateral width and 0.88 cm mean height, and the minor tubercles 0.45 cm width lateral and 0.38 cm mean height, excluding the fibreglass layer. Volume and lateral surface area of spines without fibreglass was also calculated. Mass (g) was estimated as numerically equivalent to volume (mm).

Body Mass Estimated from Body Length

The following formulae estimating body mass from total body length (TL: head, trunk, and tail length combined) were intended by their originators for alligators or mammals. In this paper, the accuracy of these methods will be investigated for body mass estimation in Recent reptiles and extinct tetrapods using *Edaphosaurus* as an example.

Body Mass Estimated from Body Length (Alligators)—Body mass was estimated from total body length using an equation relating these variables in *Alligator* (Dodson, 1975):

$$MBd_g = (0.00000097)(TL_{mm}^{3.18}) \tag{5}$$

where MBd_g is body mass in grams and TL_{mm} total body length (head, trunk and tail) in mm.

Body Mass Estimated from Total Body Length and Tail Girth (Alligators)—Body mass is estimated from TL_{cm} and tail girth in cm (TG_{cm}), using the alligator-based equation of Woodward et al. (1991):

$$MBd_{kg} = (7.198 \times 10^{-6})(TL_{cm}^{1.948})(TG_{cm}^{1.251}) \tag{6}$$

Alligator tail girth was measured two scale rows posterior to the vent. TG of the mounted *Edaphosaurus* was measured at the tip of the neural spine of the first caudal vertebrae (the vertebra anterior to it articulated with the ischium). This equation was intended for alligators, and was calculated from a sample of wild specimens ≥1220 mm total length, 70% of which were male, and the largest of which was a male 4230 mm long and 473 kg in mass.

Body Mass Estimated from Body Length (Mammals)—Body mass in grams (MBd_g) was estimated from snout–vent length (SVL), substituting SVL for head-body length (HBL) in an equation based on mammals (perissodactyls, artiodactyls and carnivores; Jerison, 1973):

$$MBd_g = 0.025\ (SVL_{cm})^3 \tag{7}$$

Edaphosaurus SVL was calculated as head length plus trunk length.

Body Mass Estimated from Leg Bone Dimensions

The next three procedures employ QBASIC programs using least squares regression equations to predict body mass from dimensions of four leg bones: humerus, ulna, femur and tibia. The dimensions are: total bone length, midshaft circumference, and two midshaft diameters, one perpendicular to the other. Midshaft is 50% of total bone length. The BODYMASS program, which uses equations derived from mammal data, uses lengths and midshaft parasagittal diameters of the four bones, excluding ulna diameter (Gingerich, 1990). It also uses metapodial lengths and diameters but those are not considered here. The two ALLMASS programs were made by substituting alligator equations and statistics, based on a sample of fourteen alligators, into the BODYMASS program code. The alligator body mass range was 6.35 to 167.83 kg. ALLMASSD uses lengths and two orthogonal diameters, and ALLMASSC uses lengths and circumferences of the four bones. For ALLMASSD, humerus and femur diameters are dorsoventral (DV) and anteroposterior (AP), while ulna and tibia diameters are mediolateral (ML) and AP. Any combination of measurements can be entered into each program, all of which produce a mass estimate and 95% prediction intervals for each measurement entered, and the geometric mean of all estimates, weighted by the coefficient of determination (R^2) of each equation. BODYMASS also lists the maximum minimum and minimum maximum 95% prediction intervals, differing from ALLMASS programs, which output weighted (by R^2) geometric means of minimum and maximum 95% prediction intervals.

Mammal leg bones move in a parasagittal plane; the humerus and femur project ventrally from the body and all four bones are vertically oriented in anterior view, although they can be angled in lateral view. In alligators and pelycosaurs such as *Edaphosaurus,* the humerus and femur project laterally from the body, while the epipodials are vertically oriented. The deltopectoral crest projects ventrally in alligators and early reptiles but projects anteriorly in dinosaurs. The dinosaur femur is also rotated as the hindlimb develops an upright position. In both the humerus and femur of dinosaurs, the DV diameter of alligators is AP and the former AP diameter is ML. Consequently in the mammal-based BODYMASS equation, DV diameters of the upper limb elements are used for parasagittal diameters. All anatomical directions are consistent with Romer (1956). Mass estimates from subsets of all bone measurements were inves-

TABLE 1. Body mass and volume, specific gravity, total length, snout–vent length, and tail girth of Recent reptile specimens. For ROM specimens, body mass obtained from weight before photography for GDI. Volume is the mean of two determinations obtained by water displacement two weeks after photography for GDI. Tail girth (TG) was measured two scale rows posterior to vent in crocodilians, and at the widest portion of tail posterior to vent, at the distance from posterior end of vent in mm given in parentheses below Tail Girth figure. Vent is 23 mm long in *Osteolaemus*. Abbreviations: SG, specific gravity of dead frozen specimen (MBd/VBd); MBd, body mass; MZ, live specimen from Metropolitan Toronto Zoo; R, frozen specimen from Royal Ontario Museum, Department of Biodiversity (Ichthyology and Herpetology); SG, specific gravity of dead frozen specimen (MBd/VBd); SVL, snout–vent length (mm); TG, tail girth; TL, total body length (head, trunk and tail); VBd, body volume; Z, live specimen from Department of Zoology, University of Toronto.

Specimen	MBd (kg)	VBd (SG) (l)	SG	TL (SVL) (mm)	SVL (mm)	TG (mm)
Iguana iguana$^{\mathrm{z}}$	1.8*	—	—	970	345	165
Cyclura cornuta$^{\mathrm{R}}$	2.435	2.165	1.125	895	395	171
Varanus salvatore$^{\mathrm{R}}$	2.605	2.152	1.21	1,860	585	142
Osteolaemus tetraspis$^{\mathrm{R}}$	2.745	2.951	0.93	940	495	224
Caiman crocodylus$^{\mathrm{Z}}$	4.4*	—	—	1,050	470	265
*Alligator mississippiensis*A$^{\mathrm{MZ}}$	44.2*	—	—	1,880	965	640
*Alligator mississippiensis*B$^{\mathrm{MZ}}$	64.9*	—	—	2,225	1,085	700

*Measured to nearest 0.1 kg.

tigated to determine if such subsets gave more accurate and repeatable results.

Edaphosaurus body mass was estimated by an additional method, which uses the sum of femur and humerus circumference (C_{h+f}) in mm, based on the following relationship in 14 species of 12 mammal genera (Anderson et al., 1985):

$$MBd_g = 0.078(C_{h+f}{}^{2.73\pm0.09}{}_{mm}) \qquad (8)$$

These equations were developed for estimating body mass in dinosaurs. The masses predicted by the four methods (GDI and length-based) used for the six Recent reptiles (excluding *Alligator* A) were regressed on the actual masses to compare the accuracy of the four methods.

(ALLMASSD and ALLMASSC programs can be obtained by sending a diskette to the author).

RESULTS

Mass Estimations of Recent Reptiles

Graphic Double Integration—Table 1 lists the actual mass of the Recent reptiles, volume, and other measurements used in length-based body mass determination methods. Table 2 gives mass estimates on Recent reptiles by GDI and three length-based methods, and also expresses these estimates as percents of the actual body mass. Body mass predictions were regressed on the actual body mass of six specimens in Table 2 (*Alligator* A not included). For TL Mass, SVL Mass, TL–TG Mass, and GDI Mass, the standard deviations of the residuals were 8.53, 1.34, 1.24, and 0.22, respectively. The standard errors of the Y estimate for the same mass estimates were 9.54, 1.50, 1.39 and 0.25 respectively (Smith, 1984; Zar, 1996). These statistics indicate that the estimates from GDI varied least and those from TL varied most from the actual masses. (Note: Although the SEE and SD of the residuals are generally considered equivalent (Smith, 1984), they differ at low values of N. Calculation of both involves division of the Residual Sum of Squares by the degrees of freedom (DF). For SEE, Residual S is divided by Error DF, equal to N-2, but for the SD of the residuals, DF = N-1. In this study, in each case the ratio of Residual SD to SEE was 0.89443, equal to the square root of 4/5 (N-2/N-1)). Table 3 lists means and ranges of masses expressed as percents for subsets and the complete set of the reptile results. Subsets are used to exclude extreme estimates from estimates based on total body length (TL) and to show differences between frozen and live animals. These subsets show that even with extreme estimates removed (e.g. the TL-based 928.9% for *Varanus*) methods other than G.D.I. are still less accurate. The range of mass estimates by GDI (87.1–120.8%) was smaller than the range of results of the three length-based methods, with one exception, and the mean estimate (104.6%) was closer to 100% than any of the other three methods, with one exception (Tables 2 and 3). In all sets and subsets of data, GDI gave both the smallest range and means closest to 100% of all methods, with two exceptions (Table 3). First, for live specimens (N=3) the TL–TG Mass range (84.3–100.0%) was slightly smaller than the GDI range (87.1–105.6%) but the TL–TG Mass mean percent (90.2%) was further from 100% than the GDI mean percent (97.6%). Secondly, for all specimens (N=6), the TL–TG Mass mean percent of 104.4% was nearer 100% than the GDI estimate (104.6%), but the GDI percent range (87.1–120.8%) was much less than the TL–TG mass range (65.4–201.2%). GDI masses were usually overestimates but all of the six estimates were within 20% of actual mass, five were within 17%, and three were within 5% of actual body mass (Table 2). The TL Mass and TL–TG Mass estimates each had only one estimate within 5% of actual body mass, and no SVL Mass estimates were within 5%. (None of the three additional TL Mass estimates for alligators discussed below were within 5% either).

The GDI mass estimates for the frozen specimens were high in two cases, particularly for *Osteolaemus* (120.8%). Estimates of volume for the frozen specimens were high (112.6–137.7%: Table 2). This is probably because the GDI method assumes that the body parts are structures with smooth, rounded walls,

TABLE 2. Body mass estimates for Recent reptile specimens from Table 1. Abbreviations: GDI Mass, body mass estimated by Graphic Double Integration; SVL Mass, body mass estimated from SVL ($MBd_g = 0.025(SVL_{cm}{}^3)$), substituting SVL for HBL in the mammal-based equation of Jerison (1973); TL Mass, body mass estimated from TL ($MBd_g = 0.00000097(TL_{mm}{}^{3.18})$, Dodson, 1975); TL–TG Mass, body mass estimated from TL and TG ($MBd_g = 0.007198(TL_{cm}{}^{1.948})(TB_{cm}{}^{1.251})$, Woodward, 1991); %MBd, estimated body mass as a percentage of actual body mass (from Table 1), in parentheses below each estimate; %VBd, estimated body mass as a percent of body volume, below %MBd in GDI column where available. Other abbreviations as in Table 1. For specimens originally weighted to 0.1 kg, the percentages are estimated from mass rounded to 0.1 kg.

Specimen	TL Mass (kg) (%MBd)	SVL Mass (kg) (%MBd)	TL-TG Mass (kg) (%MBd)	GDI Mass (kg) (%MBd) (%VBd)
Iguana iguana$^{\mathrm{z}}$	3.053	1.027	1.78	1.938
	(172.2)	(55.6)	(100.0)	(105.6)
Cyclura cornuta$^{\mathrm{R}}$	2.364	1.540	1.592	2.438
	(97.1)	(63.3)	(65.4)	(100.1)
				(112.6)
Varanus salvatore$^{\mathrm{R}}$	24.200	5.005	5.24	2.964
	(928.9)	(192.1)	(201.2)	(113.8)
				(137.7)
Osteolaemus tetraspis$^{\mathrm{R}}$	2.763	3.032	2.455	3.317
	(100.6)	(110.5)	(89.4)	(120.8)
				(112.4)
Caiman crocodylus$^{\mathrm{z}}$	3.928	2.595	3.758	4.393
	(88.6)	(59.1)	(86.4)	(100.0)
*Alligator mississippiensis*A$^{\mathrm{MZ}}$	25.038	22.466	35.22	—
	(56.6)	(50.9)	(79.6)	
*Alligator mississippiensis*B$^{\mathrm{MZ}}$	42.784	31.932	54.705	56.544
	(66.0)	(49.2)	(84.3)	(87.1)

TABLE 3. Summary statistics for body mass estimates as percentages of actual body mass (from Table 2). Only the second-last row includes the small *Alligator* (44.2 kg). Abbreviations: Mass (i.e., TL, SVL, or TL–TG), mass estimate as percentage of actual mass; SVL, snout–vent length; TG, tail-girth; TL, body length. Other abbreviations as in Table 1.

Sample	TL Mass Mean (Range)	SVL Mass Mean (Range)	TL-TG Mass Mean (Range)	GDI Mass Mean (Range)
Frozen specimens N = 3	375.5 (97.1–928.9)	122.0 (63.3–192.1)	118.7 (65.4–201.2)	111.6 (100.1–120.8)
Live specimens N = 3	108.9 (66.0–172.2)	54.6 (49.2–59.1)	90.2 (84.3–100.0)	97.6 (87.1–105.6)
Sample excluding *Varanus* N = 5	104.9 (66.0–172.2)	67.5 (49.2–110.5)	79.2 (65.4–100.0)	102.7 (87.1–120.8)
Frozen & live sample N = 6	242.2 (66.6–928.9)	88.3 (49.2–192.1)	104.4 (65.4–201.2)	104.6 (87.1–120.8)
Complete sample N = 7	215.9 (56.6–928.9)	82.9 (49.2–192.1)	96.7 (65.4–201.2)	—
Mass of frozen specimens as % of volume N = 3	—	—	—	115.7 (112.6–137.7)

and thus overestimates volumes of structures with concavities, grooves or depressions. The skin of all three frozen specimens was loose or in folds on the body, presumably due to weight loss. All three specimens had died in captivity, and weight loss probably owed to a combination of post-mortem water loss and failure to feed preceding death, as reptiles commonly react to stress, including disease, by failure to feed (Frye, 1995). The specimens were frozen, facilitating water loss during several freeze-thaw cycles as water in tissues crystallized out as ice, which was lost as free water, or through sublimation, on thawing. Each specimen gave off water while thawing, and specimen weights taken two weeks after a first weighing were 0.5–1.0% less than at the first weighing; they had been thawed, frozen and re-thawed in the interim. In *Varanus* and *Cyclura,* both with specific gravities exceeding 1.1, skin was visibly loose and wrinkled in folds. In the former several folds extended 5 mm from the body and 10 mm from the neck; in *Cyclura* several folds extended 14 mm from the body. In both there were loose skin folds on the posterior of the upper hind leg, and skin was loose on the tail of the latter. (In contrast, the skin was tight and filled out in the live specimens examined, and in live specimens observed in the wild and in captivity, and in photographs). Since the method involves photographing animals, diameters calculated from photographs recorded the maximum lateral extent of body walls including the skin folds and thus overestimated mass. *Osteolaemus* also had apparently lost mass compared to a healthy specimen. Like all crocodilians, its skin is stiffened, relative to other reptiles, due to scale-like forms in the epidermis and the presence of osteoderms in the skin (Grenard, 1991), preventing collapse into wrinkles. A single fold one cm wide extended along the left ventrolateral corner from the foreleg to the hindleg. The body was sunken in the dorsolateral areas of the neck and of the trunk anterior to the hind leg for about eight cm. The tail skin was noticeably depressed laterally on the left side for 20 cm posterior to the hind leg, and also ventrally. The belly was sunken between the sternal ribs and the pelvis. In all healthy crocodilians I have seen in life and photographs, the body "fills" the skin and outer contours are consistently round or flat but never sunken. That the specific gravity of *Osteolaemus* was less than one may be because the relatively rigid skin retained air spaces beneath it, while in the other two specimens the less rigid skins collapsed to the body. A healthy *Osteolaemus,* would have had about the same dimensions in photographs for GDI and yet had a greater mass and volume, accounting for the apparent overestimate of mass (120%).

For two live specimens (*Iguana* and *Caiman*), GDI body mass estimates were very close to 100%. The mass of the live *Alligator mississippiensis* was underestimated (87.1%), possibly because the picture of the dorsal trunk was taken at a slightly oblique angle, producing an view with less than the greatest possible transverse diameters. Positioning the camera for a perfect dorsal view was difficult due to safety considerations involving occasional rapid sudden movement of the alligator and the unsteadiness of the ladder and camera tripod beside and over the animal.

Body Mass from Body Length—The mass estimate from body length (TL Mass) for the *Varanus* specimen, which had an unusually long tail, was 928.9% of actual body mass. With the *Varanus* excluded from the sample (N=5), estimates ranged from 66.6–172.2% with a mean of 104.9 (Tables 2 and 3). Although TL produced the most aberrant estimate, half of the estimates were within 20% of actual mass. This alligator-based equation underestimated mass of two Metro Toronto Zoo alligators by 34% or more, although it gave estimates within 15% (84.8–92.0%) of three other alligators of which two were wild and one captive, from the Florida Museum of Natural History (FMNH, see below). By contrast, GDI estimates were within 17% of body mass with one exception. The unusually long tail of the *Varanus* gave a tail length:snout vent length (TailL:SVL) ratio of 2.18. This ratio is much greater than that of three *V. salvatore* specimens I have observed; than the ratio range of 0.54–0.84 in a sample of *V. bengalensis* of (SVL range 10–50 cm, N=120, Auffenberg, 1994); and than that of a larger *V. bengalensis* (TailL:SVL = 1.33, SVL 75 cm, Auffenberg, 1994).

Mass estimates from SVL (SVL Mass) ranged from 49.2–192.1% with a mean of 88.3% for the sample including the *Varanus* estimate of 192.1% (N=6, Table 3). With the *Varanus* excluded, the range was 49.2–110.5%, with a mean of 67.5%. The 96.7% mean for the complete sample (N=6) is misleadingly biased by the effect of the high *Varanus* estimate. The *Varanus* SVL Mass was an overestimate but much less so than the TL Mass; however, only one estimate was within 20% of actual body mass, and body mass generally was underestimated as suggested by the mean of 67.5% (N=5, Table 2 and 3). SVL Masses usually had the lowest mean estimate of all combinations of specimens (Table 3).

The Mass estimate from Total Length and Tail Girth (TL–TG Mass) was 201.2% for the *Varanus,* much better than the TL result. TL–TG Masses was more accurate and less erratic than the other length-based methods and gave estimates which were 80% or more of actual masses of crocodilians. For the sample excluding *Varanus* (N=5), estimates ranged from 65.45–100.0% with a mean of 79.2% (Tables 2 and 3). Four of six estimates were within 20% of actual body mass, as were

TABLE 4. Output of alligator-based ALLMASSD (lengths, parasagittal diameters and lateral diameters) program for Alligator specimen AMNH Z-3315. Body mass 124,850 g. Abbreviations: AP, Anterioposterior; DV, dorsoventral; geom. mean, geometric mean; gm min (and max), geometric mean of minimum (and maximum) prediction limits; max, minimum 95% prediction limit; min, minimum maximum 95% prediction limit; ML, mediolateral.

Element	Measurement (mm)	Predicted body mass (g)	95% Prediction limits Min	Max
Humerus length	185	121,711	83,276	177,885
Ulna length	138	137,433	97,124	194,473
Femur length	205	142,274	104,773	193,199
Tibia length	161	168,351	113,766	249,126
Humerus DV diameter	21.8	105,074	62,668	176,126
Ulna ML diameter	15.5	62,082	36,498	105,174
Femur DV diameter	21.8	72,830	43,749	121,242
Tibia ML diameter	15.6	72,766	46,903	112,890
Humerus AP diameter	20.8	78,062	46,310	131,585
Ulna AP diameter	9.3	48,545	26,835	87,819
Femur AP diameter	21.5	115,797	72,499	184,952
Tibia AP diameter	17.3	70,924	43,226	116,368
N, geom. mean, gm min, gm max	12	93,645	59,283	147,924
max and max			113,766	87,819

TABLE 5. Output of alligator-based ALLMASSC (lengths and circumferences) program for alligator specimen FMNH Z-3315 (124,850 g). Abbreviations as in Table 4.

Element	Measurement (mm)	Predicted body mass (g)	95% Prediction limits Min	Max
Humerus length	185	121,711	83,276	177,885
Ulna length	138	137,433	97,124	194,473
Femur length	205	142,274	104,773	193,199
Tibia length	161	168,351	113,766	249,126
Humerus circumference	66	78,701	45,460	136,250
Ulna circumference	44	58,592	31,614	108,594
Femur circumference	71	98,280	55,565	173,832
Tibia circumference	56	79,378	46,868	134,438
N, geom. mean, gm min, gm max	8	105,283	66,535	166,596
max, min			113,766	108,594

five of seven including the small alligator, which the TL method underestimated by 34% (Table 2). The alligator-based TL–TG method also estimated 100% of the *Iguana* body mass, but only 65.4% of the *Cyclura* body mass. TG responds to variation in cross-sectional area of the tail, and thus volume, and is not solely reliant on TL. Since most fat is stored in the pelvic area and tail in crocodilians and other reptiles, accounting for variation in this region is important for mass estimation. Nevertheless, it usually underestimated body mass, with only one estimate exceeding 100% and one other equalling 100%. Both TL and TL–TG based methods were closer to the *Osteolaemus* mass than GDI, although they were similar to the GDI volume estimate for *Osteolaemus*.

Body Mass Estimates from Leg Bone Dimensions—Tables 4 and 5 show ALLMASSD (lengths and diameters) and ALLMASSC (lengths and circumferences) calculations for Alligator FMNH Z-3315 (124.85 kg). Table 6 gives mass estimates for three FMNH alligators from TL and the three programs BODYMASS, ALLMASSD and ALLMASSC. The three TL-based estimates were within 15% of actual body mass (84.8–92.0%), better than TL estimates for the Metro Zoo alligators. This may be because Zoo alligators were obese, whereas two of the three FMNH alligators were wild and TL estimates do not respond to variation in girth. This range is better than the three length-based estimate ranges in Table 2 but still poorer than the GDI results, and no TL Mass estimates were within 5% of actual body mass. The BODYMASS program, (based on and intended for mammals) gave estimates of 20.6–34.3% of actual body mass for alligators which show that it is not suitable for these animals. ALLMASSD and ALLMASSC estimates, expressed as percents of weighed body mass, were, for a 20.5 kg alligator, 102.1% and 114.1%; for a 124.85 kg. alligator, 75.0% and 84.3%, and for a 199.95 kg alligator 135.2% and 138.7% (Table 6). The ALLMASS alligator sample was 6.350–167.83 kg with an arithmetic mean mass of 57.46 kg. The largest alligator (199.95 kg) was outside this range, so that it is not surprising that its mass estimate is less accurate. Tables 4 and 5 give ALLMASSD and ALLMASSC output for the 124.85 kg alligator. ALLMASSD and ALLMASSC estimates differed by about 10% for the two smaller alligators but were close for the 199.95 kg alligator. For the 20.5 kg and 124.85 kg alligators, estimates from length were high while estimates from either circumference or diameter were low; conversely, estimates from length, diameters and circumferences were all similar for the 199.95 kg specimen (Tables 4, 5 and 7).

For the two smaller alligators, ALLMASSD estimates were lower than ALLMASSC estimates because the eight diameters had a greater effect than the four ALLMASSC circumferences on the (geometric) mean estimates; in the ALLMASSC, lengths and midshaft measures are equally weighted. ALLMASSD estimates from the eight diameters only (i.e., without lengths) were similar to ALLMASSC estimates from the four circumferences only (without lengths, Table 7). Diameters and lengths were given equal weights by taking the geometric mean of two quantities: the ALLMASSD mass estimate from eight diameters alone and the estimate from four lengths alone. This requires two passes through the program (Table 7). With lengths and diameters equally weighted, the estimate for the 20.5 alligator was 111.4% of actual mass, and very close to the ALLMASSC estimate of 114.1%. Similarly, the estimate for the 124.85 kg specimen from equally weighted lengths and diameters was 83.0% of actual mass, very near the 84.3% estimate from lengths and circumferences (Table 7). Finally, for the 199.95 kg specimen, the estimate from equally weighted lengths and diameters, at 133.6%, was similar to both ALLMASSD and ALLMASSC estimates and was in fact closer to 100% than either (Table 7). Although use of the ALLMASSD method with eight diameters gave an estimate within 102.1% of actual body mass for one animal, this advantage was offset by the 75% estimate for the other. Use of equally weighted diameters and

TABLE 6. Mass estimates of Recent alligator FMNH specimens of known body mass from ALLMASSC ALLMASSD, BODYMASS, and body length ($MBd_g = 0.00000097TL_{mm}^{3.18}$). Abbreviations: Z-3535, found dead in lake; Z-3315, "nuisance alligator"; Z-3848 captive at St. Augustine Alligator Farm. C, captive; F, female; M, male; MBd, body mass; TL Mass, estimate from TL; TL, total body length; U, sex unknown; W, wild specimen.

Specimen	MBd (kg)	TL (cm)	Mass estimate (kg) from: TL Mass (%MBd)	ALLMASSD (%MBd)	ALLMASSC (%MBd)	BODYMASS (%MBd)
Z-3535	20.5	167.6	17.38	20.93	23.39	7.03
U W			(84.8)	(102.1)	(114.1)	(34.3)
Z-3315	124.85	297.18	107.39	93.64	105.28	25.66
M W			(86.0)	(75.0)	(84.3)	(20.6)
Z-3848	199.95	352.0	183.98	270.25	277.26	54.82
M C			(92.0)	(135.2)	(138.7)	(27.4)

TABLE 7. ALLMASSD and ALLMASSC output for subsets of bone dimensions of alligator specimens FMNH Z-3535 (20.5 kg), Z-3315 (124.85 kg), and Z-3848 (199.95 kg). The ALLMASSD and ALLMASSC produce the geometric mean (GM) of all predictions from single leg dimensions. Because ALLMASSD uses four lengths and eight diameters, estimates from the latter contribute more to the result. Lengths and diameters were equally weighted by taking the GM of the prediction from four lengths and the prediction from eight diameters. Abbreviations: % MBd, GM estimate expressed as a percentage of the specimens body mass; AP, anterioposterior; circumf., circumference; DV, dorsoventral; L and D, lengths and diameters.

	Z-3535 (20.5 kg)		Z-3315 (124.85 kg)		Z-3848 (199.95 kg)	
Measurement subsets	GM (kg)	% MBd	GM (kg)	% MBd	GM (kg)	% MBd
4 lengths	29.96	146.2	141.47	113.3	258.06	129.1
4 circumfs.	18.1	88.3	77.53	62.1	298.65	149.4
4 diameters (2 DV + 2 ML)	18.01	87.8	82.52	66.1	273.78	136.9
4 AP diameters	16.84	82.0	69.68	55.8	279.69	139.9
8 diameters	17.42	85.0	75.84	60.7	276.72	138.4
L and D equally weighted	22.84	111.4	103.58	83.0	267.23	133.6
All lengths and circumfs.	23.39	114.1	105.28	84.3	277.26	138.7
All lengths and diameters	20.93	102.1	93.64	75.0	270.25	135.2

lengths gave results within 17% of actual body mass for alligators in the ALLMASS sample range and slightly better results than ALLMASSC and ALLMASSD for the alligator outside the ALLMASS sample range. These results for the two small alligators suggest firstly, that both length and a measure of midshaft area should be used so that the estimate from one balances that from the other, and secondly, that equally weighting the estimates from lengths and diameters gives more consistent results, while no accuracy is lost by equally weighting diameters. Estimates from ALLMASSC and ALLMASSD were less often close to actual masses than GDI estimates. While all ALLMASS (C and D) estimates were within 17% of actual body mass, only one estimate was nearer than 10%, and that by a method that allowed an underestimate greater than 17% of another alligator. In comparison, while the range of GDI estimates resembled the range of ALLMASS estimates, 50% of GDI estimates were within 5% of actual body mass.

Mass Estimations of *Edaphosaurus boanerges*

Edaphosaurus specimens collected in Geraldine, Texas, and described by Romer and Price (1940) include MCZ 1531, consisting of remains of six partially articulated individuals found together. Both ROM 7985 and a composite reconstruction of MCZ 1531, figured in Romer and Price (1940), have 25 vertebrae between the head and sacrum, and three sacral vertebrae. ROM 7985 is mounted with the trunk vertebral column curved ventrally, and the tail curving sinuously laterally, whereas the trunk is straighter and the tail straight in MCZ 1531. The total length of ROM 7985 is 2482.5 mm (or 2543 mm measured along the curvature of the trunk) and is nearly identical to the 2500 mm length of MCZ 1531, also reported as the adult size for the species (Romer and Price 1940). Selected body dimensions, expressed as percentages of total length (2543) for ROM 7985, with those measured on the figure of MCZ 1531 in brackets are: skull length, 6.2% (5.8%); trunk length, 48.2% (44.1%); tail length, 45.4% (50.0%), and the 11th thoracic rib length 12.0% (10.9%), indicating similar but not identical proportions. The 11th rib is the longest and midway through the series, and the tail–trunk boundary was the junction of vertebral bodies of the last sacral and first caudal vertebrae. Dimensions of the modeled skull resemble those of WM 658, a reconstructed skull of *E. cruciger,* which was mounted on restorations of *E. boanerges* prior to 1940 (Romer and Price, 1940). Its dimensions in mm, followed by those of ROM 7985 in brackets are: length to quadrate, 157 (164); length to orbit 47 (53); anteroposterior diameter of orbit, 40 (39.5); length posterior to orbit, 70 (66.2); height at orbit 46 (48.3), width at quadrate, 105 (100); and jaw length, 150 (149.9). The discrepancies, which are greatest in total and rostrum length, are at most 7 mm, and may owe to differences in restoration of casts of the skull, and difficulties in measuring a mounted skull. If the skull is not WM 658, it is only 7 mm larger. The jaw length is 10 mm longer than reported for a jaw of MCZ 1531, so that the skull is probably 10 mm too long.

In the ROM 7985 pelvis, dimensions of the ilium in mm (length, 94.1; neck width, 34.7; and base width, 74.0), are nearly identical to those reported for one pelvis associated with MCZ 1531 (930, 350, and 700 respectively). Left side limb bone dimensions of ROM 7985 were similar to those for MCZ 1531 and to no other specimens in Romer and Price (1940). Length, proximal width, and distal width of the ROM 7985 humerus were 153.2, 53.0, and 88.95, and in the single MCZ 1531 humerus, 150, 52+, and 75, respectively. These dimensions in the ROM 7985 ulna were 88.6, 26.3, and 28.9; and in the single MCZ 1531 ulna, 92, 33, and 30; in the ROM 7985 femur, 176.25, 46.6, and 48.5, and in the single complete MCZ 1531 femur, 167, 50, and 55; in the ROM 7985 tibia, 96.8, 49.5, and 29.4, and in one MCZ femur, 98, 48, and missing, and in a second, 102, 50, 50, and missing. No MCZ elements bones had identical dimensions to any ROM 7985 element, and the ROM 7985 skeleton, if actually one individual, is more complete than any specimen in Romer and Price, 1940) suggesting that the original of ROM 7985 was recovered too late (1939) for inclusion in their account.

Dimensions of limb bones and all other body proportions of ROM 7985 are consistent with those of an *Edaphosaurus boanerges* of its size, so that all mass estimate methods in this paper are appropriate. Relative to total body mass, estimated tail and head mass were only 8.21% and 1.12%, and the total left and right manus and pes masses 0.90% and 0.73% respectively, so that possible inaccuracies in their reconstruction would little affect the total mass estimate.

Graphic Double Integration—The Graphic Double Integration (GDI) *Edaphosaurus* body mass estimates were 89.23 kg without the fin and 92.80 kg with the fin (Table 8). Both are close to the 83 kg estimate by Romer and Price (1940) which was 89.6% of the with-fin mass estimates respectively (Table 9). Table 8 gives masses and surface areas of individual body parts. The fin added 4.0% to the without-fin body mass and 65.9% to the surface area of the body.

The results for modern reptiles indicate that GDI estimates tend to be closest to actual mass; consequently results of all other methods for *Edaphosaurus* will be compared to the GDI estimate. Comparisons below are made to the with-fin estimate, since some methods depend on the relationship between leg bone and body mass, which includes that of the fin. Inaccuracies in the GDI result may owe to measurement of an insufficient number of diameters, or inaccuracies in the model, the most significant of which would be an incorrect rib articulation angle; the body may have been wider or narrower. The fiberglass model was placed fairly close to the ribs and to the tail vertebrae, and volume inaccuracies may be no more than occur with normal fluctuations in body mass. Leg mass may be least accurately estimated due to inaccurate limb musculature reconstruction, but limbs constitute less than 9% of total body mass in *Edaphosaurus* and thus little affect body mass (Table 8). Leg SA constitutes 21.6% of total (non-fin) SA, but leg mass would have to be markedly different to affect this figure.

TABLE 8. Mass and volume of body parts determined by Double Graphic Integration of model of *Edaphosaurus boanerges* (ROM 7985). Calculations for legs are for left side, multiplied by two (2) to give total value for both sides. Fin mass = fiberglass-encased spine mass + total interspine fiberglass fin mass = 2,288.27 + 1,286.03 ml = 3,574.30. Fin surface area of both sides = 2(Mn. Ht × Length) = 2(51.163 cm. × 115.653) = 11,834.3 cm^2. Abbreviations: L, left; MBd, body mass; SA, surface area.

Body Part	MBd (kg)	% wo.-fin MBd	Surface Area* (cm^2)	% wo.-fin SA.
1. Trunk Mass	73.84	82.76	10,526.74	58.63
2. Head Mass	1.00	1.12	410.13	2.28
3. L. Upp. foreleg 582.30 × 2	1.16	1.30	567.64	3.16
4. L. Low. foreleg 561.22 × 2	1.12	1.26	779.56	4.34
5. L. Upp. hindleg 1141.28 × 2	2.28	2.56	904.82	5.04
6. L. Low. hindleg 520.13 × 2	1.04	1.17	728.79	4.06
7. L. manus: 400 × 2	0.80	0.90	460.0	2.56
8. L. pes: 323.76 × 2	0.654	0.73	442.16	2.46
9. Tail	7.33	8.21	3,135.99	17.46
Subtotal (without fin)	89.22	100.0	17,955.52	99.99
10. Fin	3.57	4.0	11,834.3	65.9
Total (body + fin)	92.79		29,789.82	

*Body surface area excludes soles and inner sides of manus and pes, as these are not insolated.

Body Mass Estimated from Body Length—Table 9 lists estimates from several body mass estimation formulae (*Edaphosaurus* measurements are in the legend). Of the three length-based formulae, the 75.05 kg estimate from TL–TG is the highest and the closest (80.8%) to the with-fin GDI estimate. This percentage resembles the TL–TG Mass estimates for two alligators of 79.6–84.3% (Table 2). The 60.61 kg estimate from TL was 65.3% of the with-fin GDI result, again resembles the TL estimate for two live alligators on Table 2, but is much less than the percentage for FMNH alligators (Table 6). The estimate from SVL (based on HBL in mammals) of 57.8 kg was 62.3%, close to the alligator length-based estimate, and also resembled the SVL Mass results for modern alligators (56.6–66.0%). Because the *Edaphosaurus* length-based estimates have similar relationships with the *Edaphosaurus* GDI estimate to that between length-based estimates and actual body masses of Recent reptiles, this may be reason for confidence in the *Edaphosaurus* GDI estimate. These length-based estimates are slightly less than the ALLMASSC estimate (Tables 9 and 12).

***Edaphosaurus* Body Mass Estimated from Leg Bone Dimensions**—Measurements of leg bone dimensions are given in Tables 10–12. The BODYMASS estimate of 17.8 kg was 19.2% of the GDI estimate of 92.79 kg, although the estimate from femur diameter was close at 89.1% of the GDI estimate. Moreover, the mean 95% prediction intervals of 13.84 and 49.07 kg excluded the GDI estimate kg (Table 10). A mammal-based equation using the sum of femur and humerus circumference (Anderson et al., 1985) gave a body mass of 51.04 kg, 55.0% of the GDI estimate, the second lowest estimate in this study (Table 9). This was similar to the 48.93 kg BODYMASS estimate for diameters alone, 52.7%. of the GDI estimate. *Edaphosaurus* mass estimates from ALLMASSD and ALLMASSC were closer than body length-based estimates to the GDI estimate but were underestimates (Tables 11 and 12). The ALLMASSD estimate of 73.5 kg, was closer (79.2%) to the GDI estimate, than the ALLMASSC result of 61.7 kg (66.5%), which was slightly greater than the estimate from TL. Estimates from other combinations of measurements were investigated.

TABLE 9. Body Mass estimates for *Edaphosaurus boanerges* by various methods. 1, Graphic Integration; 2a, regression of body mass on snout–vent length in mammals (Jerison, 1973); 2b, regression of body mass on total body length in alligators (Dodson, 1975); 2c, multiple regression of body mass on total body length and tail girth in alligators (Woodward et al., 1991), with the intercept modified to produce Body Mass in grams, not kilograms. Tail girth was measured on fiberglass model (the left side) and doubled. Note length and circumference measurements in cm except in mm for Dodson (1975), to conform with original equations as reported. Fiberglass "skin" of model considered to overlap on the right ventrally and measurement accordingly modified. Abbreviations: TL, snout to tail-tip body length; C_{h+f}, sum of circumferences of humerus and femur; MBd, body mass; SVL, snout–vent length; TG, tail girth. For *Edaphosaurus*, TL = 248.25 cm; C_{h+f} = 135 mm; SVL = 132.25 cm; TG = 76.0 cm. (Lengths: Head + Body + Tail = 13.25 + 119.0 + 116.0 = 132.25 + 116.0 = 248.25 cm.)

Method	Body Mass (kg)	% of with-fin D.G.I. estimate
1. Graphic Double Integration (without fin)	89.22	96.2
1. Graphic Double Integration (with fin)	92.79	100.0
2a. $MBd_g = 0.00000097(TL_{mm}{}^{3.18})$ (Alligators, Dodson, 1975)	60.61	65.3
2b. $MBd_g = .007198(TL_{cm}{}^{1.948})(TG_{cm}{}^{1.251})$ (Alligators, Woodward, 1991)	75.05	80.9
2c. $MBd_g = 0.025(SVL_{cm}{}^{3})$ (Mammals, Jerison, 1973)	57.83	62.3
3a. BODYMASS (Gingerich, 1990)	17.85	19.2
3b. ALLMASSD	73.37	79.07
3c. ALLMASSC	61.70	66.5
4. $MBd_g = 0.078(C_{h+f}{}^{2.73\pm0.09}{}_{mm})$ (Mammals, Anderson et al., 1985)	51.04	55.0
5. Comparison to *Dimetrodon limbatus* using centrum transverse radius (Romer and Price, 1940)	83	89.4

For all four elements, the estimate from lengths only was 52.62 kg (56.7%); from diameters, 87.00 kg (93.8%); and from circumferences, 72.77 kg (78.4%). For all elements, lengths gave lower estimates than midshaft measures, of which diameters gave higher estimates. When lengths and diameters were equally weighted, as for the FMNH alligators, the estimate was 67.66 kg (72.9%, Table 13). Equally weighting the estimates from lengths and means gave more consistent results. Both ALLMASSC and ALLMASSD estimates were low largely due to

TABLE 10. Body mass estimates for *Edaphosaurus boanerges* ROM 7985 by mammal-based BODYMASS program (Gingerich, 1990). Program used parasagittal diameters (no equation for ulna diameter). *Edaphosaurus* parasagittal equivalents: DV for humerus and femur, AP for ulna and tibia; AP, anterioposterior; DV, dorsoventral.

Element	Measurement (mm)	Predicted body mass (g)	95% Prediction limits	
			Min	Max
Humerus length	153.2	19,414	5,738	65,685
Ulna length	118.0	6,050	1,919	19,076
Metacarpal length	—	—	—	—
Femur length	176.25	16,256	4,448	59,418
Tibia length	96.8	2,413	656	8,874
Metatarsal length	—	—	—	—
Humerus diameter	22.05	49,752	27,334	90,559
Ulna diameter	13.4	—	—	—
Metacarpal diameter	—	—	—	—
Femur diameter	25.45	82,664	43,204	158,163
Tibia diameter	16.4	28,319	11,080	72,384
Metatarsal diameter	—	—	—	—
N, geom. mean, max, min	7	17,852	43,204	8,874
gm min, gm max			13,843	49,069

TABLE 11. Output of ALLMASSD (lengths, parasaggittal diameters and lateral diameters) program for *Edaphosaurus boanerges* (ROM 7985). Abbreviations as in Table 4.

Element	Measurement (mm)	Predicted body mass (g)	95% Prediction limits	
			Min	Max
Humerus length	153.2	63,033	43,726	90,866
Ulna length	118.0	76,032	54,442	106,184
Femur length	176.25	81,322	60,770	108,823
Tibia length	96.8	19,573	13,521	28,334
Humerus DV diameter	22.05	108,212	64,472	181,629
Ulna ML diameter	16.35	70,603	41,395	120,419
Femur DV diameter	25.45	112,736	66,628	190,751
Tibia ML diameter	15.8	75,416	48,945	117,088
Humerus AP diameter	21.8	88,624	52,385	149,933
Ulna AP diameter	13.4	121,711	65,446	226,346
Femur AP diameter	18.75	77,282	48,945	122,027
Tibia AP diameter	16.4	61,103	37,348	99,968
N, geom. mean, gm min, gm max	12	73,373	46,558	115,634
max, min			66,628	28,334

TABLE 12. ALLMASSC (lengths and circumferences) body mass estimates for *Edaphosaurus boanerges* (ROM 7985).

Element	Measurement (mm)	Predicted body mass (g)	95% Prediction limits	
			Min	Max
Humerus length	153.2	63,033	43,726	90,866
Ulna length	118.0	76,032	54,442	106,184
Femur length	176.25	81,322	60,770	108,823
Tibia length	96.8	19,573	13,521	28,334
Humerus circumference	68.0	85,664	49,357	148,678
Ulna circumference	45.0	62,045	33,437	115,131
Femur circumference	67.0	82,103	46,702	144,340
Tibia circumference	52.0	64,133	38,056	108,077
N, geom. mean, gm min, gm max	8	61,705	398,348	96,766
max, min			60,770	28,334

the low mass estimates from tibia length; estimates from tibia midshaft dimensions were consistent with estimates from other elements (Table 10). The tibia is relatively long and slender in archosaurs (including crocodilians) but of generalized form in pelycosaurs (Romer, 1956). For example, the tibia:femur ratio is 55:100 in *Edaphosaurus* whereas it is 79:100 in the alligator sample (N=13), and the tibia:humerus ratio is 63:100 in *Edaphosaurus* but 86:100 in alligators (N=14). In contrast, the ulna:humerus ratio of 77:100 in *Edaphosaurus* is similar to the ratio of 74:100 in alligators (N=14).

With tibia length excluded, the ALLMASSD estimate was 82.1 kg, 88.5% of the GDI estimate, and the ALLMASSC estimate was 72.9 kg (78.6%). The ulna is flattened anteroposteriorly in both alligators and *Edaphosaurus* and appears to be more variable in form than the other bones. When both tibia and ulna were excluded from calculations so that only humerus and femur (propodial) dimensions were used, estimates were higher and closer to the GDI estimate. The ALLMASSD program yielded geometric means for humerus and femur of 90.6 kg (97.6%); for humerus alone, 86.4 kg (93.1%); and for femur alone, 94.9 kg (102.3%), results which bracket the GDI estimate. The ALLMASSC program also gave higher estimates from these two elements: humerus and femur, 77.4 kg (83.4%); humerus, 73.3 kg (79.0%); and femur 81.7 kg (88.0%), but these were lower than the ALLMASSD estimate. This method is consistent with alligator results. For the two smaller FMNH alligators, estimates from humerus and femur dimensions, resembled those from all four elements, and were within 18% of the actual mass of these specimens, whether they used all elements or equally weighted diameters and lengths (Table 13). For the largest alligator, ALLMASSD estimates differed little from estimates using all elements, but the ALLMASSC estimate were 10% higher.

Estimates for *Edaphosaurus* from humerus and femur only (propodials) were 71.63 kg from lengths alone, 95.60 kg from diameters alone, and 72.77 kg from circumferences alone. The estimate from lengths resembles that from circumferences because it was no longer decreased by the tibia length estimate. Diameters gave a higher estimate than those from the other two dimensions, which were similar. Estimates for *Edaphosaurus* from propodials were: for lengths and diameters, 90.6 kg (97.64% of GDI); for equally weighted lengths and diameters, 82.74 kg (89.17%); and for lengths and circumferences, 77.4 kg (83.41%). Estimates for FMNH alligators using propodials only, were also consistent with estimates from all four dimensions, They are within 18% of actual weight for alligators inside the ALLMASS sample range.

Fin Mass and Area—Fin area and mass are given in Table 8. Total body SA without the fin was 17955.5 cm^2, while total fin SA for both sides was 11834.3 cm^2. This is consistent with the area reported in Bennett (1996) of 0.60 m^2, presumably a measure of area of one side. The fin added 3.57 kg to body mass, increasing it by 4.0% while increasing surface area by 65.9% (Table 1). The spines and crossbars had an estimated volume of 1.50 kg; the total mass estimate for the fin assumes that the skin was 0.15 cm thick on spines, and 0.3 cm thick between spines, which was the thickness of the fiberglass.

DISCUSSION

Graphic Double Integration

The results for modern reptiles indicate that GDI estimates tend to be closest to actual mass of all methods tested here. When the four mass estimation methods were regressed on actual body mass for the six reptiles, GDI had the lowest standard deviation of the residuals (and lowest SEE), 20% of the next lowest standard deviation (and SEE). In Recent reptiles, five of six GDI estimates were within 15% of actual body mass, and three of six were within 5% of actual body mass. The most extreme GDI estimate was 120.8% of actual body mass. The less accurate GDI estimates could be explained either by un-

TABLE 13. ALLMASSD and ALLMASSC output for humerus and femur data of FMNH alligators Z-3535 (20.5 kg), Z-3315 (124.85 kg) and Z-3848 (199.95 kg) and *Edaphosaurus*. Results are given for equally weighted lengths and diameters (Table 6). Abbreviations: circumf., circumference; H&F, humerus and femur data only; L&D, lengths and diameters; % Mass, ALLMASS estimate expressed as a percent of weighed mass (GDI mass for *Edaphosaurus*).

Specimen (Mass)	Mass estimate (kg) from:		
	H and F: All lengths and diameters (% Mass)	H and F: L and D equally weighted (% Mass)	H and F: All lengths and circumfs. (% Mass)
Alligator Z-3535 (20.5 kg)	22.80 (111.2%)	20.16 (117.9%)	23.64 (115.3%)
Alligator Z-3315 (124.85 kg)	103.30 (82.7%)	109.80 (87.8%)	107.96 (86.5%)
Alligator Z-3848 (199.95 kg)	280.31 (140.2%)	276.63 (138.4%)	297.35 (148.7%)
Edaphosaurus (GDI: 92.79 kg)	86.68 (93.4%)	82.74 (89.2%)	77.41 (83.4%)

even body outlines of emaciated animals (due to skin folds), or imprecise camera angles. Overall, there seems good reason to trust the results of GDI for estimating body mass of healthy animals. It is a direct measurement of body volume, whereas other methods are based on regression equations on specific modern animals of a finite mass range, with problems related to extrapolations beyond the body mass range of the original sample. Estimating mass from body or skeletal dimensions requires structural similarity between the test animal and the initial sample. GDI is not vulnerable to these constraints. The advantages of GDI are that it approximates a direct measurement of the body, is specific to the specimen investigated, is unlikely to wildly under- or overestimate mass, allows comparisons among masses and surface areas of individual body parts, and permits investigations of relations between leg bone dimensions and body mass. A disadvantage of GDI is that it is somewhat laborious. This method could be made more efficient by determining diameters from digitized images, through dividing area by length. A second disadvantage is the requirement of a complete body, the restoration of which requires a restored skeleton for fossil forms. While such models are themselves estimates, it is possible that the variation of such reconstructions may be no more than annual fluctuations in life body mass. Since GDI takes diameters at regular intervals, it is sensitive to small changes in form. Nevertheless, where diameter of an object changes markedly, the object should be measured in parts of roughly similar diameter. The GDI *Edaphosaurus* estimate is used as a standard of comparison for results of other estimation methods in this study. The fin area of 11834.3 cm^2, for *Edaphosaurus* is approximately equal to twice the area given in Bennett (1996) of 0.60 m^2, presumably a measure of area of one side. The fin added 3.57 kg to body mass, increasing it by 4.0% while increasing surface area by 65.9% (Table 8), thus gaining a great increase in surface area for a slight increase in mass. Bennett (1996) reviewed the literature on thermoregulatory function of the fin in *Dimetrodon* and *Edaphosaurus* and investigated the topic using models of *Edaphosaurus.*

Body Mass Estimated from Body Length

Advantages of mass estimation from body length over using GDI include ease of measurement of body length and of use of formulas, but the method requires similarity of proportions between the animal investigated and those upon which the formula was based. A complete vertebral column is also required, while tail girth requires at least a pelvis, as well as relatively accurate assessment of location where tail girth is measured. The Recent reptile results indicated the vulnerability of length-based methods to unusual tail lengths. In extinct animals obtaining TL, inclusive of the tail, can be difficult. An SVL equation based on mammals was used to avoid problems associated with tail length, and although its mean estimates were 67.5% or more of actual body mass, and not prone to the extreme result given for the *Varanus* TL Mass, only one estimate was within 20% of actual body mass. It did perform better than other mammal-based equations using leg-bone dimensions. The TL–TG method was more accurate and less erratic than the other two length-based methods and estimates were approximately 80% or more of actual mass for crocodilians. It is not solely reliant on TL because TG responds to variation in cross-sectional area of the tail, and thus to volume. Nevertheless, it usually underestimated body mass, with only one estimate exceeding 100% and only one other equalling 100%.

Body Mass Estimated from Leg Bone Dimensions

The three programs, BODYMASS, ALLMASSD and ALLMASSC, have the advantage that users can easily obtain mass estimates, not only from single leg bone dimensions, but also from various combinations of leg bones and dimensions. Methods using regression equations between skeletal dimensions and actual body mass are less accurate when the investigated animal differs in structure from those on which the equations were based. Predictions from regression equations for animals outside the sample size range are not necessary justifiable, as shown by the ALLMASS estimates for the 199.95 kg FMNH alligator. The BODYMASS program, originally intended for mammals, is used here to test its utility for tetrapods with sprawling limb posture. Its results (20.6–34.3% of actual body mass for alligators, and 19.3% of the *Edaphosaurus* GDI estimate) show that it is not suitable for tetrapods with sprawling limb posture. That the mass estimate for *Edaphosaurus* from the mammal-based equation using femur and humerus circumference in mammals was 55.0% of the GDI result, the second lowest *Edaphosaurus* estimate, also indicates the unsuitability of mammal-based equations for tetrapods with sprawling limb posture (Table 9). Mammal leg bones are aligned parallel to the sagittal plane, especially in forms of *Edaphosaurus* size, and a mammal with similar leg bone proportions would have been much lighter (Tables 9 and 10). Body-mass estimation equations should be based on animals functionally similarly to the fossil animals investigated.

The similarity of the stance of pelycosaurs to that of many modern reptiles suggests pelycosaur locomotion included lateral undulations of trunk and tail (Romer and Price, 1940; Carroll, 1986). Therefore, Recent large reptiles such as alligators, would make good analogues, from whose proportions body mass could be estimated. Obligate large terrestrial reptiles such as varanids might make even better models. Alligators are amphibious animals in which fast aquatic locomotion consists of swimming by lateral tail motion and lateral body undulations, or on land in quick, short-term lunges. Younger, smaller alligators travel further on land than older animals in general (Dodson, 1975), and are more agile. In younger alligators, propodials are shorter relative to more distal elements than in older animals: these more "cursorial" proportions are consistent with more active locomotion (Dodson, 1975). Edaphosaurs were probably terrestrial at all ages (Romer and Price, 1940; Modesto, 1991). The two groups also differ in that both wrists and ankles of pelycosaurs were mosaics of bones, whereas both are hinges in modern lizards and crocodiles, allowing more efficient locomotion (Carroll, 1986). Carroll considers that this allows the pes to function as an additional propulsive unit: presumably this applies to the manus as well.

ALLMASSD and ALLMASSC results differed for two alligators within the ALLMASS sample range but were similar for the largest alligator, which was outside this range. Because ALLMASSD uses twice as many midshaft measures as lengths, but ALLMASSC uses equal numbers, ALLMASSD lengths and diameters were given equal weights by taking the geometric mean of the estimates from lengths and from diameters. This gave results which were consistent between ALLMASSD and ALLMASSC results for the two smaller alligators and little different from the original large alligator estimate. For ALLMASS programs to be useful, consistent results are necessary. For *Edaphosaurus* the estimate from ALLMASSD (all lengths and circumferences) was higher and closer to the GDI estimate than the ALLMASSC result. However, it is desirable to have consistent results for ALLMASSD and ALLMASSC to make the methods dependable, and also to have estimates closer to the GDI result. It is therefore of interest why the results of the two methods differed, and to seek subsets of measurements which both give results closer to the GDI result and are consistent with results for alligators. ALLMASSD results were higher because diameters alone gave a higher estimate than circumferences, which in turn gave a higher estimate than lengths. The low mass estimates from tibia length lowered the overall estimate from lengths (Tables 10 and 11). However, this is not a reason to use diameters alone for extinct tetrapods. The alligator results suggest it is advisable to have both midshaft and length estimates, since these balance each other when estimates differ. Moreover, in the FMNH alligators, circumference estimates exceeded those from diameter (Tables 4 and 7). For *Edaphosaurus,* tibia length biased the mean estimates downwards in both programs, and ulna estimates had a small effect as well. Both ALLMASSD and ALLMASSC estimates, using only humerus and femur measurements, gave higher results: 93.4% for ALLMASSD (i.e., four lengths and eight diameters), 82.7% for equally weighted lengths and diameters, and 83.4% for ALLMASSC. Use of humerus and femur alone for the FMNH alligators gave results similar to those from equally weighted lengths and diameters or ALLMASSC, except that the humerus and femur ALLMASSC estimate for the large alligator was 10% larger than with all four elements. This suggests that tibia and ulna may vary more in the measured dimensions than do propodials in tetrapods of sprawling posture, and that consistent results can be obtained by using humerus and femur data only for ALLMASSD and ALLMASSC to estimate body mass and femur only for extinct amniote tetrapods. This gave estimates which are closer to the GDI estimate for *Edaphosaurus* and results consistent with ALLMASS estimates from all four elements for alligators. Previous workers who estimated body mass from mid-shaft bone dimensions, (sometimes in combination with bone length), have used either circumference or diameter but have not compared the two (Anderson et al., 1985; Gingerich, 1990). The results here for both mammal-based and alligator-based equations suggest that estimates from either diameters or circumferences are equally accurate. However, two diameters for each bone may describe shape better than the single circumference available. While estimates from diameters were more consistent with the GDI estimate than those from circumferences, coefficients of determination (R^2) linking measures to body mass in alligators were nearly indistinguishable (all lengths, $R^2=0.98804$; all eight diameters, $R^2=0.99082$; all circumferences, $R^2=0.97813$; all lengths and circumferences, $R^2=0.99012$) so that these would be no guide as to which measure to choose. It does seem advisable to use equations using both lengths and a midshaft measurement from samples of animals structurally similar to the investigated subject. The humerus and femur appear to vary less among similar tetrapods than the tibia and ulna. For alligators, use of all four elements is advisable because multiple measurements may lessen the effect of outlying estimates (Tables 11 and 12). Estimates using humerus and femur only were also consistent for alligators, with estimates from all four dimensions falling within 18% of actual mass for alligators within the ALLMASS sample range. Estimates from humerus and femur alone were also within 18% of the GDI estimate for *Edaphosaurus.* That estimates from ALLMASSD and ALLMASSC were similar (when lengths and diameters were equally weighted) but different for *Edaphosaurus* illustrates that leg bones may have similar circumferences but different diameters. The differences probably reflect differences between *Edaphosaurus* and alligators in interrelationships among bone length, circumference, and diameter. ALLMASS estimates from propodials for *Edaphosaurus* were within 17% (83.4% to 93.4% or 77.41–86.68 kg) of the GDI estimate, closer than any other estimate except that of Romer and Price (1940). ALLMASS propodial estimates were also within 18% of actual body mass of the two smaller FMNH alligators (Table 13). The largest alligator specimen (199.95 kg) was outside the range of the alligators used for the ALLMASS equations, so it is not surprising its ALLMASS estimates are nearly 140% of actual mass; however, the ALLMASSD (but not ALLMASSC) estimates resemble those from all four elements.

Alligators might be assumed to have smaller legs for their body mass than obligate terrestrial animals more dependent on legs for support and locomotion. Since alligator-based equations might overestimate *Edaphosaurus* mass, the underestimates from ALLMASS programs using data for all four leg bones are surprising. Possibly the alligator sample size (N=14) is too small, but the *Edaphosaurus* GDI body mass estimate is within the range of the body mass of the contributing alligators, so that there is no danger of extrapolating beyond the data. If the GDI estimate is accurate, the underestimate of body mass from leg bone dimensions may be because *Edaphosaurus* may have retained the length and leg bone proportions of a slimmer carnivorous pelycosaur with an expanded abdominal cavity. Many Recent herbivorous reptiles have relatively larger and more elaborate colons than carnivorous reptiles. This may increase gut surface area and increase food retention in the gut, possibly facilitating digestion and nutrient absorption (Zimmerman and Tracy, 1989). This hypothesis could be tested by estimating mass of a carnivorous pelycosaur such as *Dimetrodon* by the several methods used in this paper.

CONCLUSION

Several methods of body mass estimation were tested on Recent reptiles and then used to estimate body mass of *Edaphosaurus boanerges.* The methods were of three types: graphic double integration (GDI), which models the body as a series of elliptical cylinders; allometric equations relating body mass to measures of body length; and allometric equations relating body mass to leg bone dimensions. GDI, originally devised for endocast volume estimation (Jerison, 1973), was applicable to a life-size three-dimensional model of *Edaphosaurus* built around a fossil skeleton (ROM 7985). The GDI method allows comparison of mass and surface area of the entire body and of its parts. On six Recent reptiles of known body mass, GDI gave estimates within 15% of body mass with one exception (120%) and had by far the smallest range of percents of actual body mass (87.1–120.8%). Half of the GDI estimates were within 5% of actual body mass. When estimates from three length-based equations and GDI were regressed against actual body mass for the Recent reptile sample, the standard deviation of the residuals of the GDI estimates were the lowest, and less than 20% of the next lowest SD of residuals. GDI estimates were least accurate for frozen dead animals which had lost weight ante- and/or postmortem and had loose or folded skin which gave overestimates of body mass by GDI. Body length equations used for the same Recent reptile sample gave estimates over a much wider range of percentages of actual body mass. Estimates using relations of total length (TL) and body mass in alligators had a range of 56.6–172.2%, excluding a 928.9% estimate for a *Varanus* specimen with an unusually long tail (estimates from TL for three additional alligators were 84.8–92.0% of actual body mass; Dodson, 1975). Estimates from an equation regressing body mass on snout-vent (SVL) in Recent mammal equation ranged from 49.2% to 192.1% of actual body mass: they were usually underestimates, and were within 20% of actual body mass in one of six specimens (Jerison, 1973). Estimates using equations predicting body mass from TL and tail girth (TG) in alligators, were the most accurate of length-based methods, probably because TG was sensitive to variations in cross-sectional body area (Woodward et al., 1991). The estimates ranged from 65.4% to 201.2%, with four of six estimates within 20% of actual body mass. GDI was not subject to the great extremes of error sometimes found with the other methods, nor to problems of extrapolations to animals beyond the body mass range of samples on which allometric equations were based. Body mass was also estimated from individual leg bone dimensions: length, midshaft circumference, and two orthogonal midshaft diameters of humerus, ulna, femur, and tibia, using three QBASIC programs. The programs also gave the geometric mean of all estimates from single dimensions. BODYMASS (Gingerich, 1990) uses equations for Recent mammals, while both ALLMASSD, which uses lengths and diameters, and ALLMASSC, which uses lengths and circumferences, are based on equations from a sample of 14 alligators. These programs were tested on skeletons of three Recent alligators of known body mass. The two smaller specimens were within the ALLMASS sample range and the largest specimen beyond it. The BODYMASS estimate program gave extremely low estimates for these alligators. ALLMASSD and ALLMASSC both gave estimates within 25% of body mass of the two smaller alligators, and within 40% of the largest alligator. When diameters were given equal weight to lengths (there were two diameters for each length), ALLMASSD estimates were similar to ALLMASSC estimates and both were within 17% of actual mass for the smaller alligators. The estimate for the largest alligator was within 33% of actual mass, even though this was extrapolating beyond the sample mass range.

Body mass of *Edaphosaurus boanerges* was estimated using ROM 7985, a fossil skeleton around half of which a model was built. Several methods were used to give the most probable estimate, introduce new techniques, and to compare several body mass estimation techniques. The mass estimates for *Edaphosaurus* were 89.22 kg without the fin and 92.79 kg including the fin mass. The fin increased body mass by 3.57 kg, thus adding 4% to body mass while increasing body surface area by 66%. Because of the relative accuracy of the GDI results for Recent reptiles, the *Edaphosaurus* GDI estimate was used as a standard of comparison for other estimates. Nearest to the GDI result was the 83 kg estimate (89.4%) of Romer and Price (1940), based on comparisons using transverse dorsal vertebral diameter, scaled from a *Dimetrodon* model of known volume. The next nearest was 75.05 kg, (81%), estimated from TL and TG. Two other formulas, using TL (alligator-based) and SVL (mammal-based) yielded less accurate results, which were similar to each other (65% from TL and 62% from SVL of the with-fin GDI estimate; Table 8). Circumferences and diameters gave similar estimates for both mammal-based and alligator-based equations.

Body mass was predicted from formulas relating body mass to leg bone dimensions in alligators and mammals. The mammal-based BODYMASS program gave an extremely low body estimate for *Edaphosaurus* (19.3% of the GDI). Estimates using equations based on relations in mammals, from either humerus and femur circumference (Anderson et al., 1985) and from leg bone diameters in BODYMASS programs were similar, slightly exceeding 50% of the GDI estimate. The inaccurate results from mammal-based equations emphasizes the need for equations based on structurally similar animals. When all dimensions were used in alligator-based equations, the ALLMASSD estimate was 80.9% of the GDI result and the ALLMASSC estimate was only 66.5%. However, when only humerus and femur dimensions were used, the estimates from ALLMASSC, ALLMASSD, and equally weighted lengths and diameters estimate (using ALLMASSD) were 83.4%, 96.6% and 89.2% of the GDI estimate. When the mass of Recent alligators was estimated from only humerus and femur, results were similar to those from all four bones, and within 18% of actual mass. This suggests that use of propodial dimensions alone may be recommended for body mass estimations of extinct tetrapods with sprawling leg posture. There are noticeable differences between crocodilians and pelycosaurs in tibia form, and possibly also in ulna form, while humerus and femur dimensions are more conservative. All estimates place *Edaphosaurus* within the body mass range of the ALLMASS sample, further reason for confidence in the results.

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