Material properties of mandibular cortical bone in the American alligator, *Alligator mississippiensis*

Uriel Zapata [a,b], Keith Metzger [c], Qian Wang [d], Ruth M. Elsey [e], Callum F. Ross [f], Paul C. Dechow [a,*]

[a] *Texas A&M Health Science Center, Baylor College of Dentistry, Dallas, TX, USA*
[b] *Eafit University, Mechanical Engineering Department, Medellín, Colombia*
[c] *Hofstra University, School of Medicine in partnership with North Shore-LIJ, Hempstead, NY, USA*
[d] *Mercer University School of Medicine, Macon, GA, USA*
[e] *Louisiana Department of Wildlife and Fisheries, LA, USA*
[f] *University of Chicago, IL, USA*

ABSTRACT

This study reports the elastic material properties of cortical bone in the mandible of juvenile *Alligator mississippiensis* obtained by using an ultrasonic wave technique. The elastic modulus, the shear modulus, and Poisson's ratio were measured on 42 cylindrical *Alligator* bone specimens obtained from the lingual and facial surfaces of 4 fresh *Alligator* mandibles. The data suggest that the elastic properties of alligator mandibular cortical bone are similar to those found in mammals and are orthotropic. The properties most resemble those found in the cortex of mammalian postcranial long bones where the bone is most stiff in one direction and much less stiff in the two remaining orthogonal directions. This is different from cortical bone found in the mandibles of humans and some monkeys, where the bone has greatest stiffness in one direction, much less stiffness in another direction, and an intermediate amount in the third orthogonal direction. This difference suggests a relationship between levels of orthotropy and bending stress. The comparability of these elastic moduli to those of other vertebrates suggest that the high bone strain magnitudes recorded from the alligator mandible in vivo are not attributable to a lower stiffness of alligator mandibular bone.

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Introduction

The sizes, shapes, and material properties of skeletal elements determine their biomechanical properties, such as strength, stiffness and the amount of energy needed to move them around, and these biomechanical properties in turn affect animal performance [1–7]. The American Alligator (*Alligator mississippiensis*) is an ideal model for the study of structure–function relationships in vertebrate musculo-skeletal systems. The ready accessibility of alligators makes them of practical utility; the wide size range traversed during ontogeny make them of interest for scaling studies [8–12]; and their phylogenetic relationships make them of interest to those interpreting the functional significance of some vertebrate fossilized skeletal remains, as closely related specimens may have similar patterns in cortical material properties [13,14]. The relationships between skull shape and feeding behavior of crocodilians are the focus of ongoing research on a number of fronts [15–21]. We are currently investigating the biomechanics of mandibular function in the American Alligator using *in vivo* bone strain, electromyographic and finite-element modeling techniques. Although it is of particular interest in biomechanical research as mentioned, the mandibles of some mammalian species have been the subject of detailed biomechanical analyses based on *in vivo* data [22–30], the same cannot be said of any nonmammalian vertebrates. This paper reports on the material properties of cortical bone from alligator mandibles of differing size and age, compares them with the data from mandibles of other vertebrates, and uses them to evaluate hypotheses regarding the functional significance of bone material properties.

Reptiles have been argued to have relatively constant bone material properties during growth and show little evidence of cortical remodeling [31–33]. It has been argued that their slow, indeterminate growth makes bone remodeling physiologically challenging. The high safety factors demonstrated for the alligator femur have been argued to be evidence that crocodilians adopt an alternate strategy of "over-building" the skeletal apparatus to avoid the necessity of remodeling damaged bone [34]. In contrast, high bone strain magnitudes recorded in alligator mandibles (>4000 $\mu\varepsilon$ in tension and compression) when compared with both human mandibles (1500 $\mu\varepsilon$) [35] and *Macaca fsacicularis* mandibles (755 $\mu\varepsilon$) [36] lead us to suggest that high safety factors do not characterize the feeding system in *Alligator* [37], arguing against hypotheses that invoke organism-level differences in physiology to explain the lack of remodeling in reptiles. Here we evaluate whether the high strain magnitudes in alligator mandibles

are attributable to low stiffness in bone matrix and compare the data from the mandible with data reported from the postcranial skeleton.

Studies of the material properties of primate mandibles have led to the development of hypotheses regarding the relationship between elastic properties and skeletal function. Dechow and colleagues reported that human mandibular corpus bone is denser, stiffer, and more anisotropic than that of supraorbital bone, and is stiffest along the long axis of the mandible [38–40]. Relatively high stiffness along the long axis of the mandible is plausibly linked to mandibular function as it provides increased resistance to deformation under bending. If relatively high stiffness along the mandibular long axis is an adaptation conferring increased resistance to bending in primates, even with their relatively short mandibles, it seems likely that the relatively longer mandibles of alligators would also exhibit stiffer mandibles along their long axes.

Elastic properties of bone are necessary for accurate estimates of stress to be calculated from strain measurements [41] or from finite-element modeling approaches to vertebrate function. The constitutive equations that relate stress and strain are fundamental components of finite element analysis (FEA). Elastic and other material property data for nonmammalian vertebrates are rare and such data are never going to be directly measurable in fossils. FEAs of the skulls of extinct reptiles, and dinosaurs, have in the past used data derived from the femurs of alligators or even mammals [13,42,43]. Clearly, then, data on elastic and other material properties of alligator mandibles are of interest, not only for improving our understanding of alligator musculoskeletal biomechanics, but potentially biomechanics of other vertebrates as well [43–46].

This paper presents the results of measurements of density and elastic properties of fresh cortical bone removed from four mandibles of wild-shot juvenile *Alligator mississippiensis*. These data were used to evaluate the extent to which elastic properties of alligator mandibular bone resemble those of alligator postcranial bones and mammalian mandibular bone. Assuming that alligator mandibles are subjected to significant bending moments during biting, we predicted that the bones of the alligator mandible would be stiffer in the direction of the long axis of the mandible than in other directions.

Materials and methods

Four freshly sacrificed juvenile male *Alligator mississippiensis* specimens were provided by Rockefeller Wildlife Refuge at the Louisiana Department of Wildlife and Fisheries. Although the age of sexual maturity in *Alligator* can vary greatly depending on ambient temperature [47], alligators typically reach sexual maturity at a length of 1.8 m. Based on the length of our specimens (Table 1), their age is estimated to be 2–3 years old and not yet sexually mature. Animal tissue acquisition and use conformed to all NIH, state, and federal standards. The skulls were obtained from alligators sacrificed for research projects unrelated with the present investigation. The animals ranged in length from 95 to 141 cm (Table 1).

The mandibles were dissected free from soft tissues and stored at −20 °C before bone characterization. After marking sites with graphite lines parallel to the lower border of the mandibular corpus

Table 1
Cortical bone specimens distributed within four *Alligator* mandibles.

Subject	Body length (cm)	Specimens from anatomical position			Sub-total
		Facial	Lingual	Basal	
J-1	95.25	3	2	0	5
J-0	107.95	5	2	1	8
J-2	130.81	7	5	0	12
J-3	140.97	10	7	0	17
Sub-total		25	16	1	42

(the mandibular plane), 42 cylindrical cortical bone samples (average 5.78 mm in diameter and 1.82 mm in thickness) were collected from the dentary, splenial, articular, and surangular bones (Fig. 2) using a low-speed dental drill. Specimens were cooled with water during preparation. The sample consisted of 25 facial, 16 lingual, and 1 ventral sample (Table 1). After preparation, all specimens were stored in a 50:50 solution of 95% ethanol and isotonic saline solution, which maintains elastic properties determined by ultrasound techniques over time [48]. Cortical bone apparent density, including the voids which are inherent in the specimens, was calculated (mg/cm^3) to the nearest 0.001 g with a Mettler-PM460 analytical balance (Mettler-Toledo International Inc, Columbus, OH, USA) dividing the weight of the dry specimen in the air by the weight of the specimen fully immersed in distilled water and multiplying this result by the density of the distilled water. Each specimen was measured three times to ensure the reliability of the density measurements [48].

Three orthogonal principal axes of stiffness within each specimen were obtained through a longitudinal ultrasonic wave pulse transmission technique [39]. The technique uses a pulse generator (Hewlett-Packard, Palo Alto, CA, USA) that produces ultrasonic waves through two longitudinally mounted piezoelectric transducers (Olympus V312, 10 MHz, immersion, 0.25 in diam., Olympus, Waltham, MA, USA) and an oscilloscope (Tektronix TDS-3032B, Tektronix, INC., Beaverton, OR, USA) that records the time delay between the transmitted signal and the output signal [48,49]. The speed of the longitudinal ultrasonic wave is measured by using the time delay between the start of the input signal to the start of the output signal in the related specimen dimension [50].

The reference graphite line served as a reference axis for 9 measurements at rotations of 22.5° in the plane of the cortical plate of the cylindrical specimens. The direction of maximum stiffness (D_3) corresponds to the direction with the highest longitudinal speed in the plane of the cortical plate (maximum error: $\pm 11.25°$). The direction of minimum stiffness (D_2), as expected in an orthotropic elastic solid, corresponded to the direction of the slowest longitudinal speed in the plane of the cortical plate, and is orthogonal to the direction of maximum stiffness. The third principal direction (D_1) is perpendicular to the plane of the cortical plate.

Elastic properties of every wet specimen were obtained using longitudinal and transverse (Olympus V156, 5 MHz, contact, 0.25 in diam., Olympus, Waltham, MA, USA) ultrasonic waves in three orthogonal directions relative to the principal stiffness axes D_1, D_2, and D_3. Elastic properties (Table 2), including the elastic modulus (E), the shear modulus (G), Poisson's ratio (v), and a ratio of anisotropy E_2/E_3 (ratio of the elastic modulus in the directions of minimum and maximum stiffness), were calculated according to elasticity and wave velocity principles [48,38,51]. The ratio E_2/E_3 measures the relative bone orthotropy in the cortical plane. As the ratio approaches 1.0, the material has similar elastic moduli along the two principal axes (D_2 and D_3) and approaches isotropy in that plane. Ratios different from 1.0 indicate differences in stiffness between planes suggesting less uniform internal organization [52].

Student's t tests adjusted for multiple comparisons were used to test for differences in density, principal elastic modulus, shear modulus, Poisson's ratio, and anisotropy between buccal and lingual sides of the mandible. One-way ANOVA with *post-hoc* multiple comparisons tests (Sidak) were used to test for significant differences in bone density and elastic properties among the four subjects [53]. The orientation of maximum stiffness was assessed by using specialized software for circular statistics (Oriana, Kovach Computing Services. Anglesey, Wales).

Results

Three orthogonal principal orientations were assigned to the elastic mechanical properties of every specimen with the following

Table 2
Averaged specimen elastic properties (mean ± SD).

Subject (ordered by size)	Mechanical properties									
	Density (g/mL)	E_1 (GPa)	E_2 (GPa)	E_3 (GPa)	G_{12} (GPa)	G_{13} (GPa)	G_{23} (GPa)	v_{12}	v_{13}	v_{23}
J-1 ($n=5$)	1.66 ± 0.159	8.10 ± 0.90	9.26 ± 1.07	19.71 ± 3.58	3.17 ± 0.21	4.45 ± 0.75	5.51 ± 0.64	0.38 ± 0.08	0.15 ± 0.15	0.08 ± 0.16
J-0 ($n=8$)	1.83 ± 0.040	9.03 ± 1.08	12.15 ± 2.08	20.44 ± 3.54	3.80 ± 0.59	5.04 ± 0.84	5.94 ± 0.82	0.31 ± 0.07	0.10 ± 0.10	0.21 ± 0.05
J-2 ($n=12$)	1.76 ± 0.055	8.66 ± 0.81	9.88 ± 0.78	20.39 ± 1.99	3.22 ± 0.42	5.00 ± 0.57	5.68 ± 0.39	0.41 ± 0.09	0.13 ± 0.06	0.13 ± 0.04
J-3 ($n=17$)	1.78 ± 0.074	9.02 ± 1.68	10.89 ± 1.99	20.82 ± 3.05	3.29 ± 0.60	5.05 ± 0.85	6.21 ± 0.82	0.44 ± 0.08	0.17 ± 0.07	0.12 ± 0.03
Mean ($n=42$)	1.77 ± 0.089	8.81 ± 1.28	10.65 ± 1.85	20.49 ± 2.86	3.35 ± 0.55	4.96 ± 0.76	5.92 ± 0.73	0.40 ± 0.09	0.14 ± 0.08	0.14 ± 0.07

SD: standard deviation.

convention: 3 and 2 are, respectively, the orientations of maximum and minimum stiffness in the plane of the cortical plate (Fig. 2), and 1 is the orientation perpendicular to the cylindrical plane of the specimen. The elastic modulus E is followed by a subscript indicating their corresponding principal direction (E_1, E_2, E_3), the shear modulus G is followed by two subscripts indicating the principal plane of shear (G_{13}, G_{12}, G_{23}), and the Poisson's ratio v is followed by a double subscript indicating the direction of the principal strain and the direction of the Poisson's strain (v_{12}, v_{13}, v_{23}), (Table 2).

Density

No significant differences were found between the average density on lingual and facial sides (Fig. 1A). On the lingual side of the mandible average cortical bone density was 1751.86 kg/m³ (SD = 91.99 kg/m³) ($n=16$), and mean density was 1781.98 kg/m³ (SD = 87.05 kg/m³) on the facial side ($n=25$). There is a significant difference in cortical bone density between subjects Jo and J1 ($F=4.958$, $p=003$), (Table 2 and Fig. 1B). The smallest individual did have the least dense bone, but the trends are not significant within the sample (Fig. 2).

Orientation of axes of orthotropy

The orientation of maximum stiffness was evaluated using Oriana software (Rockware, Inc., Golden, CO). To evaluate whether orientation data were distributed homogeneously or provided evidence of preferred direction, each of 41 specimens across the four subjects and between the two anatomical positions were tested using Rayleigh's Uniformity test, which showed that all specimens exhibited a significant orientation (Fig. 3). No significant differences were found in principal direction of maximum stiffness among the four subjects (Fig. 2).

Elastic modulus

In all specimens, no significant differences in principal elastic modulus between facial and lingual anatomical positions were found (Fig. 4C). For instance, the principal elastic modulus E_3 was 21.21 GPa (SD = 2.50 GPa) on the lingual side, and 19.89 GPa (SD = 2.98 GPa) on the facial side. There were no significant differences in principal elastic modulus among the subjects (Fig. 4B). Maximum averaged E_3 was 20.49 GPa (SD = 2.86), maximum average E_2 was 10.65 GPa (SD = 1.85), and maximum average E_1 was 8.81 GPa (SD = 1.28) (Table 2) (Fig. 4A).

Shear modulus

There were no significant differences in elastic shear modulus between the lingual and buccal sides of the mandible (Fig. 5C). In addition, *post hoc* tests showed no significant differences in shear modulus among subjects (Fig. 5B). The shear modulus is lowest in $G_{12}=3.35$ GPa (SD = 0.55 GPa), intermediate in $G_{31}=4.96$ GPa

(SD = 0.76 GPa), and highest in $G_{23}=5.92$ GPa (SD = 0.73 GPa) (Table 2 and Fig. 5A).

Poisson's ratio

Because elastic orthotropic material behavior was initially assumed for the alligator cortical bone, Poisson's ratio requires that $E_i v_{ij} = E_j v_{ji}$ and only three Poisson's ratios are reported: v_{12}, v_{13}, and v_{23} [51]. There were no significant differences between sides of the mandible (Fig. 6C). There were significant differences in Poisson's ratio v_{12} between subjects J0 and J3, and in v_{23} among
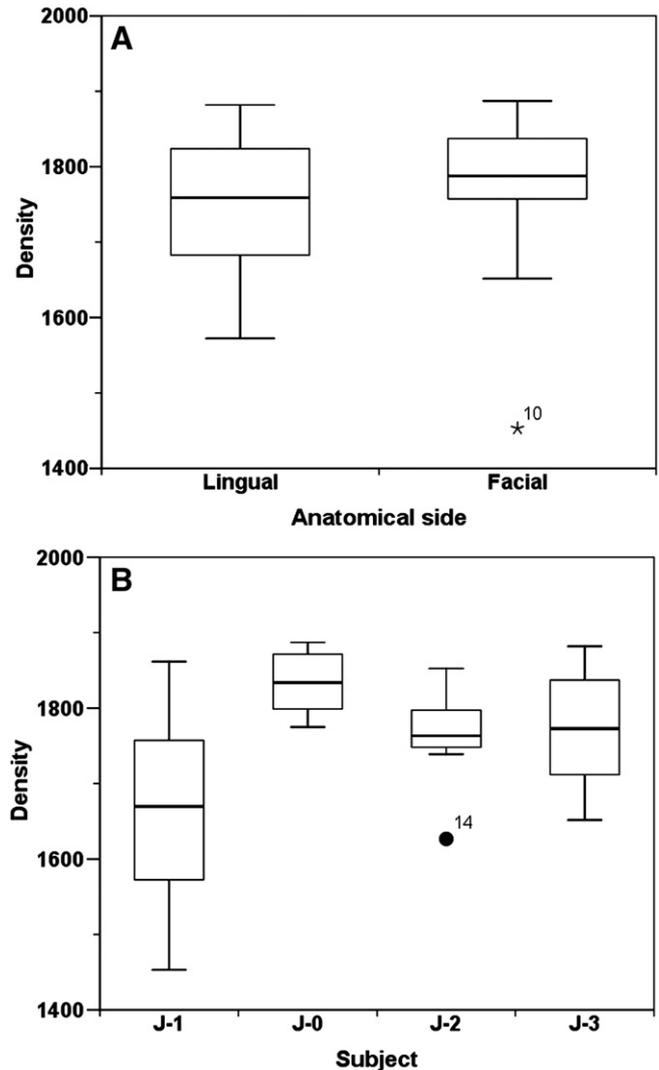

Fig. 1. Box plots of cortical bone density in kg/m³. (A) Between lingual ($n=16$) and facial ($n=25$) anatomical sides, and (B) among four subjects. Medians, quartiles, and data outliers are indicated on the graphs.
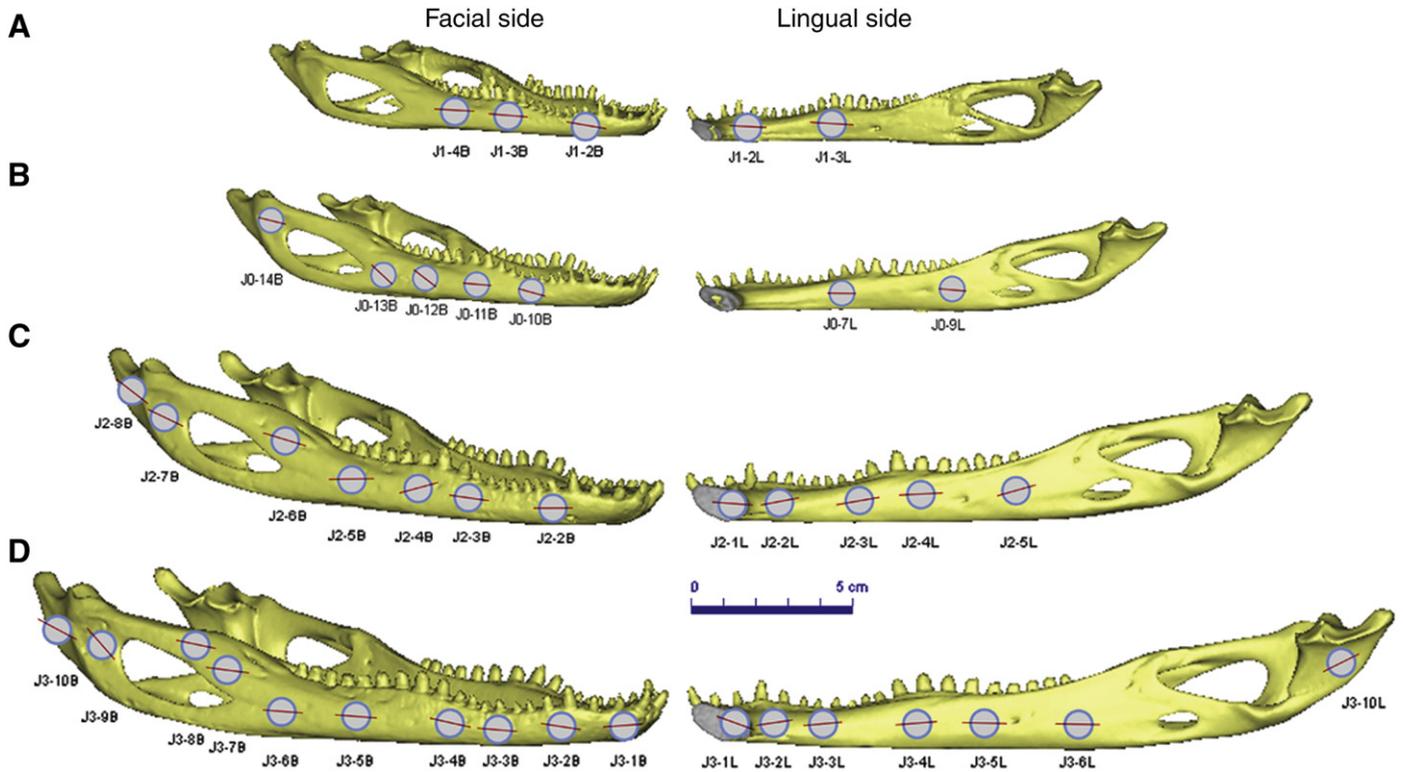
Fig. 2. Facial and lingual positions of the cylindrical specimens removed from the four mandibles. The respective orientations of the axes of maximum stiffness are shown with a red line within each subject. (A) Subject J-1; (B) Subject J-0; (C) Subject J-2; (D) Subject J-3.

subjects Jo and J1 (Fig. 6B). Averaged Poisson's ratios are the following: $v_{12} = 0.40$ (SD = 0.09), $v_{13} = 0.14$ (SD = 0.08), and $v_{23} = 0.14$ (SD = 0.07) (Fig. 6A) (Table 2).

Discussion

Density

Although both the minimum density values and the highest variability were associated with the smallest subject (J1) (Fig. 1B), there were no significant differences in cortical bone density between the lingual (splenial) and facial (dentary) faces of the mandible and among most of the subjects. It is possible to conclude a density average value of 1773 kg/m³ (SD = 89.3) from all 42 cortical bone specimens. This value is higher than previous cortical bone mineral density measurements of 1288.9 ± 9.3 mg/cm³ from the tibiae and 1385.2 ± 13.4 mg/cm³ from the femora of 7 female American alligators [54] of similar body size. However, the results of the present study report lower mineral densities than reported from humans (1850–2000 mg/cm³) [40], and macaque mandibles (2003–2056 mg/cm³) [41]. Cortical bone density in the mandibles of young alligators is less dense than that in the mandibles of mammals but denser than the lower limb bones of alligator. These differences between mandibles and long bones in alligator might suggest different approaches in adaptation to different loading regimes and regional adaptation, and remain to be further explored.

Elastic properties

The present research shows that regions of the juvenile American alligator mandible appear homogeneous but not isotropic in their elastic mechanical properties. Although the average value of E_2/E_3 is 0.53 (SD = 0.13) and E_1/E_3 is 0.44 (SD = 0.09), suggesting that the Alligator mandibular bone is close to being transversely

isotropic, there are statistical differences between E_1 and E_2 ($F = 374.2$, $p < 0.05$) suggesting elastic orthotropy. However, the differences between E_1 and E_2 are small compared to their differences with E_3. Comparison of these results with the elastic moduli of human [40] and some monkey [41] mandibles reveals that alligator mandibles are more similar in this feature to mammalian long bones since cortical bone in the corpus of human and monkey mandibles has larger differences in stiffness between the three orthotopic directions. While bone is stiffest in one direction and least stiff in another direction, the third direction is intermediate rather than being more similar to that in the least stiff direction. Data are currently lacking for comparison of mammalian mandibles with unfused symphyses.

One possible explanation for these differences in the relative amount of orthotropy is that alligator mandibles experience higher or less variable bending stresses than in mammalian mandibles, perhaps because the alligator mandible is relatively longer and less subject to force transmission across the mandibular symphysis due to a predominant pattern of unilateral food processing. The cortical bone of the alligator mandibles like mammalian postcranial long bones may also be subjected to higher bending loads than mammalian mandibles because of their greater length (Table 3). These data suggest a relationship between levels of orthotropy and the relative importance of bending stress.

Recently, Dechow et al. [55] demonstrated an important relationship between tissue elastic anisotropy and the spatial configuration of osteons, in which the long axes of the osteons represented by the Haversian canals are aligned with the axes of maximum elastic stiffness of the cortical bone in humans. In the human mandible, there is much greater variation in osteon orientation than in the human femur. The presence or absence of Haversian systems in the alligator bones studied here was not assessed. Future work should examine the relative contribution of collagen fiber orientation and osteon orientation to anisotropies in alligator bone and determine whether
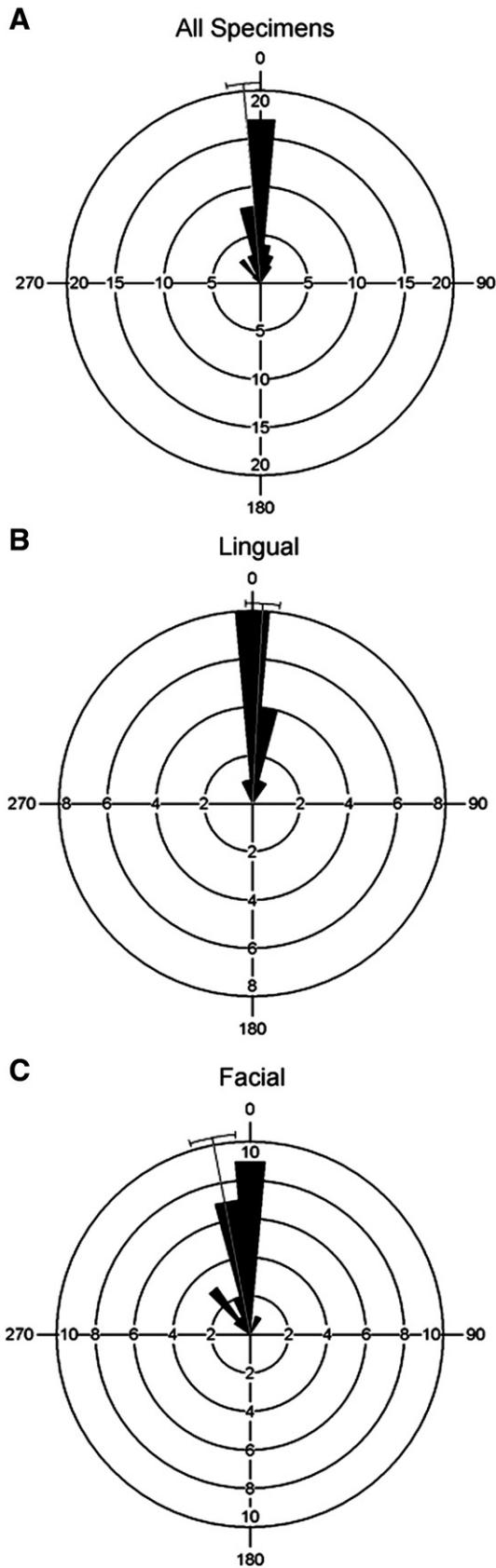
Fig. 3. Principal stiffness direction distribution is represented by Rose diagrams. (A) The principal averaged circular mean direction relative to the mandibular plane for all 41 specimens (excluding a ventral specimen) was 354.6° with a circular standard deviation of 16.1°, standard error of the mean of 2.5°, and a mean length vector (**r**) of 0.961. (B) and (C) represent principal stiffness direction between lingual and facial anatomical positions, respectively.
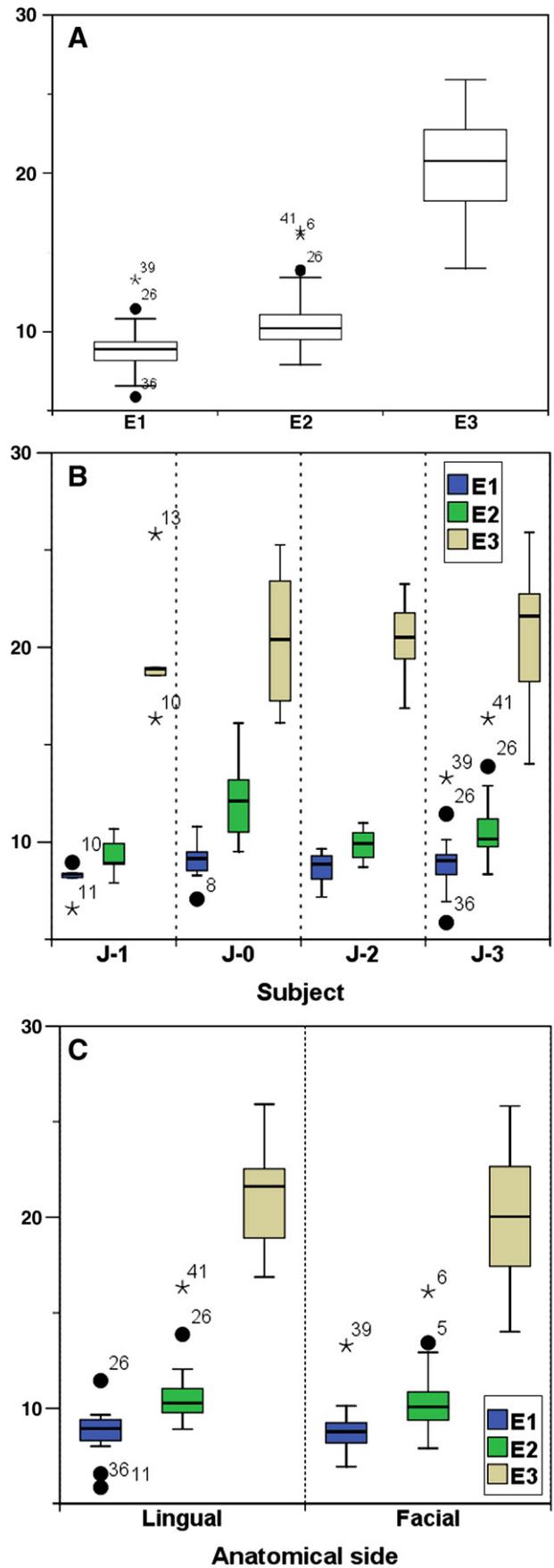

Fig. 4. Principal elastic moduli in GPa among (A) three principal orientations, (B) subjects, and (C) anatomical sites.
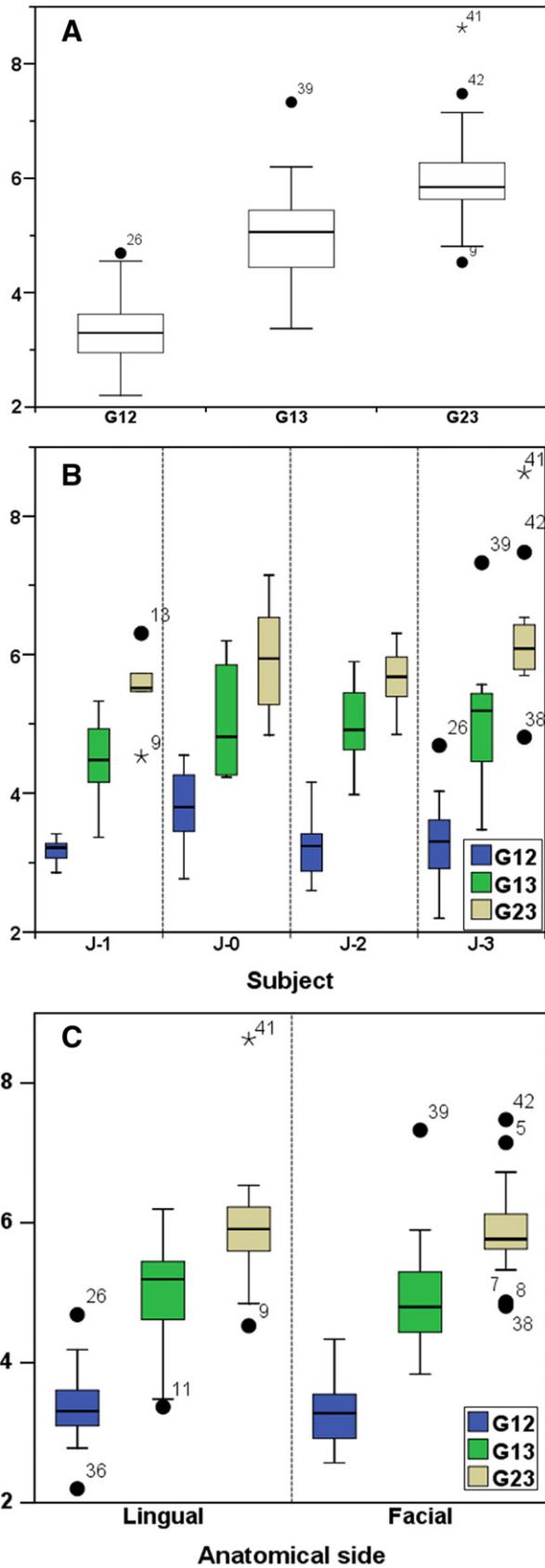
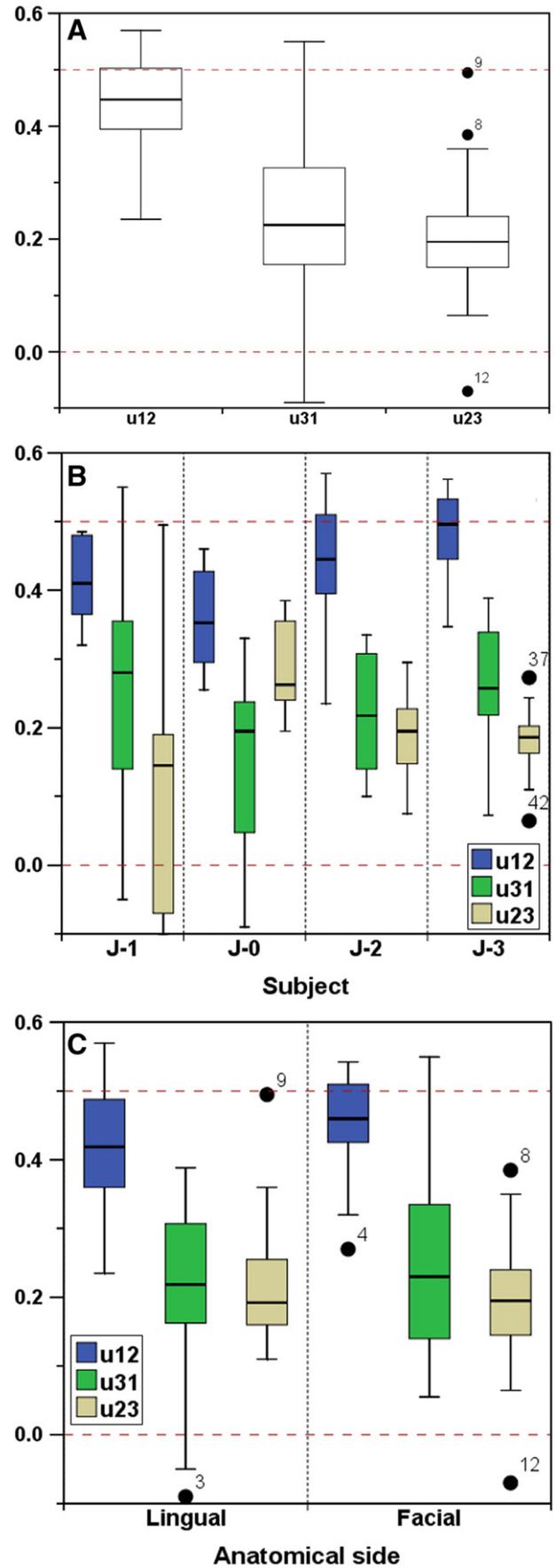Fig. 5. Principal shear modulus in GPa among (A) three principal orientations, (B) subjects, and(C) anatomical sites.

Fig. 6. (A) Principal Poisson's ratio values among (A) three principal orientations, (B) subjects, and (C) anatomical sites.

Table 3
Alligator mandibular elastic moduli in GPa compared with that found in human mandibles [54], macaque mandibles [40], baboon mandibles [46], human femurs [47], human tibiae [49], and bovine femurs [39]. 1 GPa = 10^9 N/m^2.

Elastic modulus	Alligator mandible	Human mandible	Macaque mandible	Human femur	Baboon mandible	Juvenile baboon mandibles	Human tibiae	Bovine femur
E_1	8.8	12.7	9.3	12.0	12.3	8.4	11.7	15.4
E_2	10.7	17.9	17.6	13.4	14.7	9.9	12.2	16.4
E_3	20.5	22.8	23.9	20.0	24.1	18.1	20.7	24.7

these anisotropies result from similar structural variations as those found in mammalian bone.

As noted above, high bone strain magnitudes in the alligator mandible (>4000 $\mu\varepsilon$ in tension and compression) suggest that high safety factors do not uniformly characterize the skeletal systems of *Alligator* [37]. However, one reason that high strain magnitudes can occur is if elastic moduli in a bone are very low; i.e., the bone has very low stiffness. Comparisons of the elastic moduli recorded here with those reported for primate cranial bones that experience very low strains, such as the cranial vault and supraorbital torus in macaques, humans, and baboons [46] reveal similar ranges of elastic moduli (10–20 GPa). These results suggest that the high strain magnitudes in the alligator mandibles are not attributable to a low elastic modulus.

Cortical elastic properties can be used both for biomechanical evaluations of American *Alligator* mandibles to obtain strain-stress patterns under bite loads [20,56], and to understanding the relationship between skull shape and feeding habits, especially using Finite Element Analysis (FEA) [14,57]. It has been demonstrated that agreement between surface strains recorded *in vivo* and surface strains from FEAs improves if realistic elastic properties are included in the model [44]. However, despite this, many workers continue to average the available materials properties to obtain isotropic characteristics [20,56,57]. Incorporation of these data into a FEA of the alligator mandible will provide valuable insight into the relative importance of material properties in bone mechanics and jaw function.

Acknowledgments

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