# Ontogeny, But Not Sexual Dimorphism, Drives the Intraspecific Variation of Quadrate Morphology in *Hemidactylus turcicus* (Squamata: Gekkonidae)

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Abstract: The functional components of the lizard skull are divided into the chondrocranial braincase, protective dermatocranium, lower jaw, and hyobranchial apparatus. These regions are interconnected and become operational through the quadrate, a bone critical for cranial biomechanics and support of the peripheral auditory system. The quadrate is a complex and variable structure in squamates; however, neither the intraspecific nor interspecific variation of this element has been studied in detail. We investigated the intraspecific variation of quadrate morphology within *Hemidactylus turcicus* with the use of cleared and double-stained specimens and high-resolution x-ray microcomputed tomography. Our objectives were to quantify quadrate shape and the degree of intraspecific variation within this element with the use of 2-D and 3-D geometric morphometric analyses and investigate if this variation is driven by ontogeny and/or sexual dimorphism. Our results demonstrate that ontogeny, but not sexual shape dimorphism, drives the intraspecific variation of quadrate bone morphology in *H. turcicus*. We also illustrate the benefit of using 3-D morphometric analyses on complicated morphological structures. This is the first study to quantify the intraspecific variation of a single cranial element within geckos, and it highlights the importance of using increased sample sizes to further characterize the natural variation of skeletal morphology.

Key words: Computed tomography; Cranial osteology; Geometric morphometrics; Mediterranean House Geckos

THE QUADRATE is a paired bone that is located posterolaterally in the reptile skull, flanking either side of the braincase. The overall structure of the quadrate is complex in squamates, and has been described as auricle- (Oelrich 1956), conch- (Earle 1961), shell- (Daza et al. 2008), or lamina-shaped (Evans 2008). Generally, there is a central pillar that supports a dorsal cephalic condyle and a ventral mandibular condyle. The lateral wing of the quadrate forms a posterior concavity (conch), and the midline of this structure supports the anterior edge of the tympanic membrane of the ear. The rest of the membrane circumference is supported by connective tissue (Westoll 1943). The stapes and extracolumella also possess either a direct contact or a soft-tissue connection with the quadrate. The cephalic condyle articulates with the paroccipital process of the otooccipital (chondrocranial braincase), as well as the supratemporal and squamosal (protective dermatocranium), and the mandibular condyle articulates with the articular portion of the compound bone of the lower jaw. The medial surface of the quadrate has a reduced facet for articulation with the pterygoid, dorsal to the mandibular condyle. Because of these connections, the quadrate is considered a critical functional unit for squamate cranial biomechanics and cranial kinesis (Versluys 1912; Frazzetta 1962). Anteroposterior translation of the quadrate, or streptostyly, pulls the palatal bones posteriorly, which depresses the muzzle bones at the mesokinetic joint (ventroflexion between the parietal and frontal). Multiple hypotheses exist about the function of squamate cranial kinesis (Metzger 2002), and of these, improved prey manipulation has the most support (Rieppel 1978).

Because of its functional importance in cranial biomechanics and support of the auditory system, the quadrate is particularly critical in gekkotans, which are known to exhibit pronounced cranial kinesis (Herrel et al. 1999, 2000, 2007) and hearing sensitivity (Werner et al. 2002, 2005). A recognized pattern in gecko quadrate morphology involves a modification of the quadrate suspensorium attributable to a reduction of the temporal region. A prominent cephalic condyle has strong posteromedial articulation with the paroccipital process of the otooccipital (exoccipital + opisthotic; Stephenson 1960; Daza et al. 2008), resulting in "paroccipital abutting" (Rieppel 1984). Within geckos, the squamosal is generally slender and short, and the supratemporal is often lost; therefore, the articulation between these bones and the quadrate is greatly reduced or absent (Rieppel 1984; Payne et al. 2011). Although several studies have described the skull anatomy of geckos in detail (Kluge 1962; Daza et al. 2008; Gamble et al. 2011; Daza et al. 2012; Daza and Bauer 2015), no attempt has been made to study the morphological variation of the quadrate within or between species, although individual reports have indirectly demonstrated considerable disparity between taxa.

We investigated the intraspecific variation of quadrate morphology in a large sample of *Hemidactylus turcicus* (Mediterranean House Geckos) to identify the degree of disparity present within this element at the species level. Three factors might influence the intraspecific variation of a structure: ontogenetic variation, sexual dimorphism, and random individual variation (Evans 2008). Ontogenetic variation accounts for changes that take place throughout development and growth (Bellairs and Kamal 1981), sexual dimorphism accounts for the differences between males and females (Sanger et al. 2013), and random individual variation accounts for differences in size and shape, and presence or absence of elements and/or suture points (Rieppel and Crumly 1997). We predicted that the influence of ontogeny is the most likely source of intraspecific variation because of the changes in size and percent ossification of the quadrate that occur throughout development. We did not expect to

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find differences in quadrate morphology between males and females because gekkotans are thought to exhibit low levels of sexual dimorphism compared to other squamate groups (Fitch 1981; Abouheif and Fairbairn 1997). Sexual differences in hearing thresholds and anatomy of auditory structures, such as the tympanum, have also been suggested to be low in geckos (e.g., Werner and Igíc 2002), which might further minimize male and female variation in the region of the quadrate that interacts with the auditory system. Lastly, we predicted that random individual variation in the quadrate is low because of the functional importance, and therefore potential constraint, on this element. The quadrate must articulate with the braincase, articular, and pterygoid for jaw biomechanics and cranial kinesis to be functional, and the shape is likely constrained by its articulation with cranial musculature, ligaments, and the tympanum.

## Materials and Methods

We investigated the intraspecific variation of quadrate morphology in *Hemidactylus turcicus* with the use of specimens prepared by clearing and double-staining and microcomputed tomography (CT). Thirty-eight cleared and double-stained specimens collected from nonnative populations (in Louisiana and Texas, USA) and native populations (in Turkey) were used to quantify quadrate variation with the use of 2-D geometric morphometrics. Specimens were prepared following the protocol of Bauer (1986), with Alcian Blue and Alizarin Red stains used to visualize cartilage and bone, respectively. Forty-two Florida Museum of Natural History (FLMNH) specimens collected from nonnative populations (in Alachua Co., Florida) were scanned on a GE V|tome|xm240 CT Scanner at the University of Florida Nanoscale Research Facility to quantify quadrate variation with the use of 3-D geometric morphometrics. Three-dimensional stereolithography (STL) files, CT tiff stacks, and CT settings are available to view and download from Duke University's morphological data archive (available at http://www.morphosource.org/Detail/ProjectDetail/Show/project_id/354). Both sexes and various ontogenetic stages, spanning from small juveniles to large adults, were examined (see Table S1 in the Supplemental Materials available online). The snout–vent length (SVL) of all specimens was measured using digital calipers (±0.01 mm). Head length, width, and depth of the FLMNH specimens were measured with the use of digital calipers (±0.01 mm; Table S1). Juveniles were identified by having an SVL < 44 mm (Selcer 1986), and adult males and females were identified by the presence or absence of postcloacal bones, respectively (Russell et al. 2016). The right quadrate of each cleared and double-stained specimen was dissected out (unless damaged, in which case the left was used) and photographed in posterior view under a dissecting microscope. The right quadrate of each CT specimen was digitally segmented on VGStudioMax 3.0 (Volume Graphics, Heidelberg, Germany) and exported as a PLY file for further analysis.

Two-dimensional and three-dimensional geometric morphometric analyses were utilized to quantify intraspecific variation in shape with the use of the R package geomorph v3.0.3 (Adams and Otarola-Castillo 2013). Two-dimensional landmarks and a semilandmark were digitized on each

quadrate image, and 3-D landmarks and semilandmarks were digitized on each quadrate shape file with the use of geomorph. Five fixed landmarks and one sliding semilandmark were digitized on the 2-D cleared and double-stained quadrate images, and nine fixed landmarks and four semilandmarks were digitized on the 3-D quadrate shape files (Fig. 1). The fixed landmarks correspond to homologous and repeatable points of the quadrate: the mandibular condyle, cephalic condyle, and dorsolateral edge of the lateral wing, whereas the sliding semilandmark(s) corresponds to the maximal lateral edge of the quadrate conch (in both data sets), the relative width of the medial column (3-D data set), and the anterior extent of the conch (3-D data set; Fig. 1). A generalized Procrustes analysis was performed for both data sets in geomorph, which aligns, rotates, and scales specimen landmark data to a common coordinate system and unit-centroid size to remove variation in position, orientation, and size (Rohlf and Slice 1990), resulting in a set of shape variables, or Procrustes tangent coordinates, for all specimens.

The aligned Procrustes tangent coordinates for both data sets were used to test for ontogenetic shifts in shape and sexual shape dimorphism in *Hemidactylus turcicus* quadrate morphology. A multivariate regression of quadrate shape on log centroid size (CS—the square root of summed squared distances of landmarks from the configuration centroid, Bookstein 1991; method RegScore, Drake and Klingenberg 2008) was conducted with the use of Procrustes distances, and a regression plot was generated to visualize the multivariate relationship between size and shape of quadrates. We performed a Procrustes multivariate analysis of variance (MANOVA) to test if mean quadrate shape differed between juveniles, adult males, and adult females to identify the presence or absence of ontogenetic change and sexual shape dimorphism in *H. turcicus*. We also performed a Procrustes two-way MANOVA on the 2-D data set to test if there was population-level variation (between Louisiana, Texas, and Turkey specimens) in the degree of sexual dimorphism and ontogenetic change in quadrate shape. A principal component analysis (PCA) of quadrate shape variation was performed for both the 2-D and 3-D data sets, and the Procrustes-aligned specimens were plotted in two dimensions of tangent space (PC1 and PC2), grouped by juveniles, adult males, and adult females, and scaled by SVL.

## Results

### 2-D Morphometrics

Of the 38 specimens examined with the use of 2-D morphometrics, 11 were juveniles and 27 were adults. The smallest specimen had a SVL of 22.8 mm, and the largest had a SVL of 56.1 mm. Value for SVL ranged from 48.0–56.1 mm for adult females (mean ± 1 SD = 52.05 ± 2.4 mm; $n = 14$) and 44.5–55.7 mm for adult males (mean = 50.4 ± 3.2 mm; $n = 13$). A regression of quadrate shape on log centroid size indicated significant allometry and ontogenetic change (sum of squares [SS] = 0.0159, mean square [MS] = 0.0159, df = 1, $F = 7.72$, $P < 0.001$; 10,000 iterations). A regression plot was generated to visualize the multivariate relationship between the size and shape of the quadrate bones (Fig. 2). A Procrustes MANOVA revealed that quadrate shape differed between juvenile, adult male, and adult female specimens
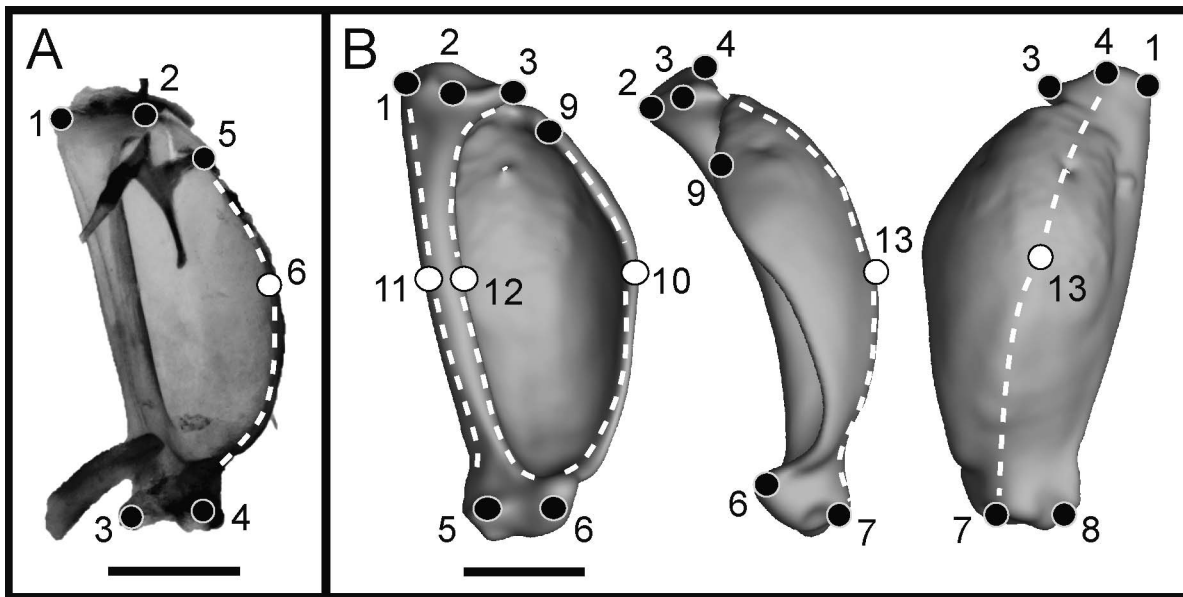
Fig. 1.—Landmarks used in geometric morphometric analyses. (A) Two-dimensional landmarks digitized on posterior view of cleared and double-stained quadrate images: Five fixed landmarks that correspond to the cephalic condyle (1,2), mandibular condyle (3, 4), and dorsolateral edge of the lateral wing (5; filled circle) and one sliding semilandmark that corresponds to the maximal lateral edge of the quadrate conch (6; open circle). (B) Three-dimensional landmarks digitized on posterior, lateral, and anterior view (left to right) of quadrate 3-D PLY shape files: Nine fixed landmarks that correspond to the cephalic condyle (1–4), mandibular condyle (5–8), and dorsolateral edge of the lateral wing (9; filled circle) and four sliding semilandmarks that correspond to the maximal lateral edge of the quadrate conch (10), relative width of the medial column (11, 12), and anterior extent of the conch (13; open circle). White dashed lines indicate the direction of the sliding semilandmarks. Scale bar = 1.00 mm.

(df = 35, SS = 0.0176, F = 4.31, Z = 3.41, P < 0.001; 10,000 iterations), and post hoc pairwise comparisons of group means indicated that juveniles possess a different quadrate shape compared to both sexes of adults, the latter of which were not statistically distinct (Table 1).

We generated a PCA plot of shape variation to demonstrate the clustering of juvenile values as being distinct from adults, but the overlap of values representing males and females, in tangent space along their principal axes (variance explained: PC1 = 29%, PC2 = 23%; Fig. 2). The PC1 axis described the shape differences driven by the relative width of the lateral wing in relation to the relative length of the medial column. Juveniles possess narrower lateral wings and shorter medial columns (negative PC1 values) and adults possess expanded lateral wings and longer medial columns (positive PC1 values). The PC2 axis described the shape differences driven by the cephalic condyle being proportionally larger than the mandibular condyle (negative PC 2 values) or by the cephalic condyle being proportionally smaller than the mandibular condyle (positive PC 2 values; see Fig. S1 in the Supplemental Materials available online). Whereas the mean quadrate shape appeared to differ among the three populations (Table 2; Fig. S2 in the Supplemental Materials available online), a two-way Procrustes MANOVA indicated that population variation in the degree of ontogenetic change and lack of sexual dimorphism in quadrate shape was not significant.

### 3-D Morphometrics

Forty-two (23 adult and 19 juvenile) *Hemidactylus turcicus* specimens were CT scanned to examine the intraspecific variation of quadrate morphology with the use of 3-D morphometrics. The smallest specimen had a SVL of 24.0 mm, and the largest had a SVL of 57.8 mm. Values for SVL ranged from 44.5 to 57.8 mm for females (mean = 52.1 ± 4.1 mm; n = 11) and from 45.4 to 56.2 mm for males (mean = 52.5 ± 3.2 mm; n = 12). A regression of quadrate shape on log centroid size indicated significant allometry and ontogenetic change (SS = 0.0346, MS = 0.0346, df = 1, F = 8.59, P < 0.001; 10,000 iterations). A regression plot was generated to visualize the multivariate relationship between size and shape of quadrates (Fig. 2B). A MANOVA revealed that quadrate shape differed between juvenile, adult male, and adult female specimens (df = 39, SS = 0.038, F = 4.70, Z = 3.83, P < 0.001; 10,000 iterations), and post hoc pairwise comparisons of group means indicated that juveniles possess a different quadrate shape compared to both sexes of adult, whereas the quadrates of adult males and females are similar (Table 3).

We generated a PCA plot of shape variation to demonstrate the clustering of juvenile values as being distinct from adults, but the overlap of values representing male and female specimens, in tangent space along their principal axes (variance explained: PC1 = 24%, PC2 = 16%; Fig. 2D). The PC1 axis described the shape differences driven by the depth of the quadrate conch and the relative width of the dorsolateral extent of the quadrate in relation to the maximum extent of the lateral wing of the quadrate. In juveniles, the quadrate conch is shallow and the dorsolateral extent of the lateral wing is the overall maximum extent of the quadrate (negative PC1 values), whereas the quadrate conch is deep in adults, and the dorsolateral extent of the lateral wing is narrower than the maximum extent, which is located near the horizontal midline of the structure (positive PC1 values). The PC2 axis described the shape differences driven by the relative width of the lateral wing in relation to
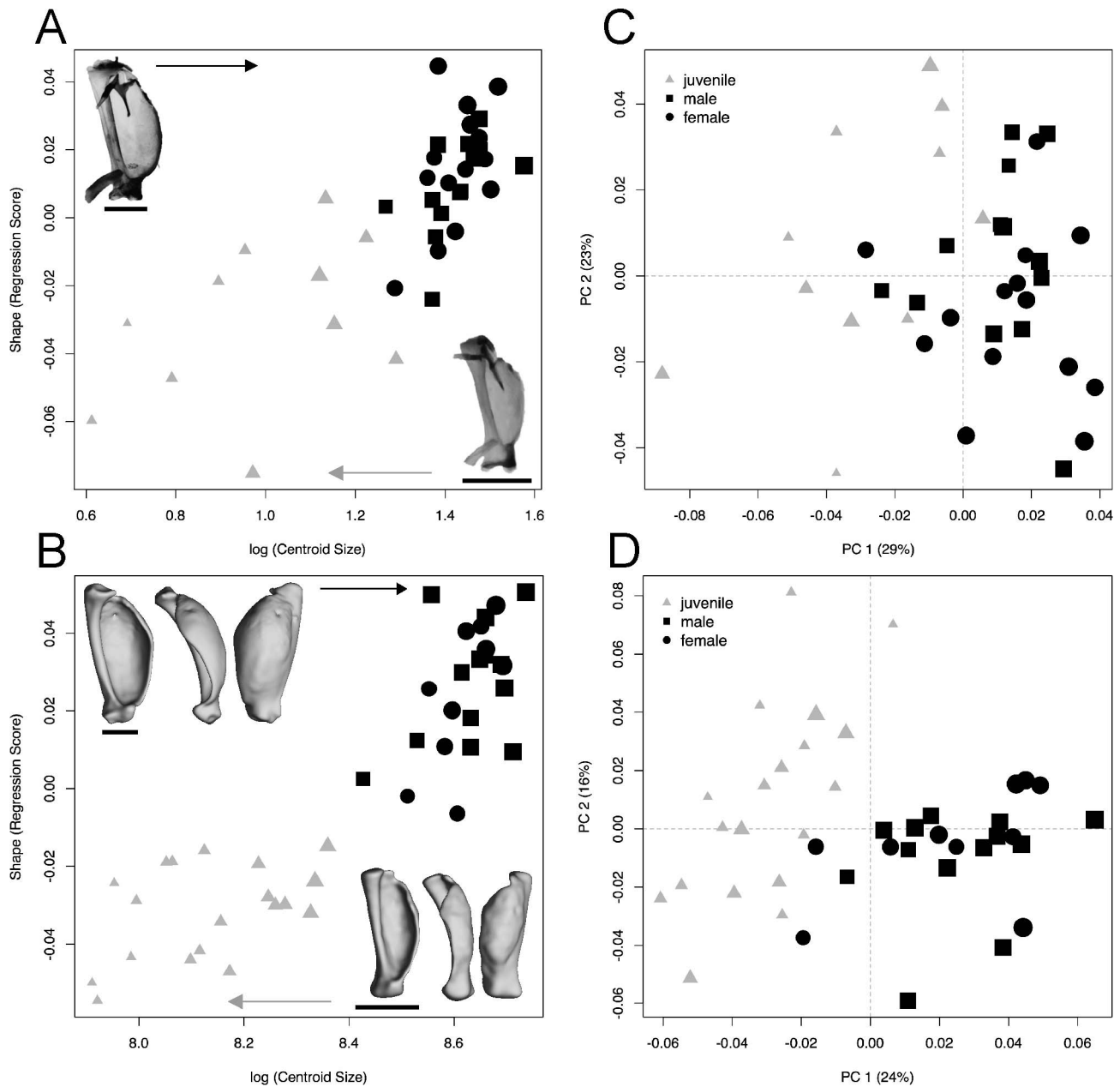
FIG. 2.—Regression plot of quadrate shape on log centroid size for (A) 2-D geometric morphometrics and (B) 3-D geometric morphometrics exhibiting significant allometry and ontogenetic change. Gray triangles = juveniles, squares = adult males, circles = adult females. Points are scaled by snout-to-vent length (SVL) of individual specimens (see Table S1 in the Supplemental Materials available online). Images of the quadrates illustrate shape differences of adults (top) and juveniles (bottom) in the 2-D and 3-D data sets (scale bars = 1.00 mm). (C) PCA plot of shape variation for 2-D geometric morphometrics and (D) 3-D geometric morphometrics illustrating the distinct clustering of juveniles (gray triangles) and adults (black symbols), but the mixture of males (squares) and females (circles) in tangent space along the PC 1 and PC 2 axes. Points are scaled by SVL of individual specimens (Table S1).

the relative length of the medial column. A subset of juveniles possess narrow quadrates (positive PC2 values) and a mixture of juveniles and adults possess wider quadrates (negative PC2 values; Fig. S3 in the Supplemental Materials available online).

### Qualitative Individual Variation

We observed little individual variation between the quadrate and its associated elements among the specimens examined. All *Hemidactylus turcicus* quadrates articulated with the paroccipital process of the otooccipital, quadrate

TABLE 1.—Pairwise comparisons of group means and *P* values associated with the 2-D data set multivariate analysis of variance examining the trends of quadrate shape differences between juvenile, adult male, and adult female *Hemidactylus turcicus*. Boldface values indicate statistical significance.

|  | Juvenile | Male | Female |
|---|---|---|---|
| Juvenile | 1 | **<0.001** | **<0.001** |
| Male | **<0.001** | 1 | 0.41 |
| Female | **<0.001** | 0.41 | 1 |

TABLE 2.—Model comparison multivariate analysis of variance indicating that mean quadrate shape of *Hemidactylus turcicus* differed between three populations (Texas, Louisiana, Turkey) and between ontogenetic stages and sexes (see values in Table 1). Population variation in the degree of ontogenetic change in quadrate shape is not significant (interaction of Population × Stage&sex). Boldface values indicate statistical significance.

|  | Statistical parameter | | | | |
| Variable | SS | MS | df | F | P |
| --- | --- | --- | --- | --- | --- |
| Population | 0.0127 | 0.0063 | 2 | 3.16 | **<0.01** |
| Stage&sex | 0.0125 | 0.0062 | 2 | 3.09 | **<0.001** |
| Population × Stage&sex | 0.0064 | 0.0016 | 4 | 0.80 | 0.58 |

TABLE 3.—Pairwise comparisons of group means and *P* values associated with the 3-D data set multivariate analysis of variance examining the trends of quadrate shape differences between juvenile, adult male, and adult female *Hemidactylus turcicus*. Boldfaced values indicate statistical significance.

|  | Juvenile | Male | Female |
| --- | --- | --- | --- |
| Juvenile | 1 | **0.001** | **0.001** |
| Male | **<0.001** | 1 | 0.83 |
| Female | **<0.001** | 0.83 | 1 |

process of the pterygoid, and articular of the lower jaw. The squamosal was positioned dorsal to the cephalic condyle in all specimens, but did not have bone-to-bone contact with the quadrate. A soft tissue connection was present between the quadrate and middle ear bones (stapes and extracolumella) via the tympanic membrane in all individuals. The cleared and double-stained specimens allowed for the visualization of percent ossification of the quadrate, determined by the relative presence of Alcian blue and Alizarin red stain, which was variable across individuals. Many specimens possessed partially cartilaginous cephalic and mandibular condyles.

## DISCUSSION

The intraspecific variation in the morphology of quadrate shape in *Hemidactylus turcicus* appears to be driven by ontogeny. Juveniles possess a narrow quadrate that has a shallow conch and a lateral wing maximum extent that is dorsal of the horizontal midline. Through ontogeny, the quadrate becomes broader, the conch becomes deeper, and the lateral maximum extent at the horizontal midline becomes much wider than the dorsolateral extent of the lateral wing, resulting in an arc-shaped conch. This shift in morphology might have potential functional implications. For example, Werner et al. (1998, 2002, 2005) and Werner and Igic (2002) demonstrated that the auditory sensitivity of many gecko species increases with body size and age. These higher hearing sensitivities are associated with middle-ear structural changes, including the increased surface area of the tympanic membrane. The deepening of the quadrate conch during ontogeny likely facilitates these modifications, as the posterior surface acts as the attachment point for the anterior edge of the tympanic membrane and the concavity itself acts as an acoustic chamber (part of the external auditory meatus). The ontogenetic shift in auditory sensitivity might be further coupled with vocal behavior, as juvenile *H. turcicus* have different vocalizations compared to adults (Frankenberg 1982). The cranial biomechanic capabilities of juveniles and adults might also be influenced by the ontogenetic change in quadrate shape, as suggested by the pattern of juvenile *H. turcicus* consuming smaller and softer prey items than adults (Saenz 1996). As the quadrate laterally expands during ontogeny, the area for attachment of the jaw adductors increases, which likely results in higher bite forces as overall head growth increases maximum gape.

Previous research has documented a male-dominated sexual size dimorphism in body length (Granatosky and Krysko 2014) and head size in *Hemidactylus turcicus* (Saenz and Conner 1996; Granatosky and Krysko 2014). Johnson et al. (2005) further demonstrated that the sexual dimorphism in head size is the result of differential growth patterns following sexual maturity in males and females, and not the result of diet partitioning. Our results demonstrated that the quadrate of adult male and female geckos did not differ in shape, and this lack of sexual shape dimorphism might indicate that the head size dimorphism between male and female *H. turcicus* is too subtle to produce divergence in quadrate morphology. Our data for means and ranges of head length, width, and depth in male and female *H. turcicus* largely overlap with one another (see Table S2 in Supplemental Materials available online), potentially supporting this hypothesis. Alternatively, other regions of the skull that are structurally and functionally independent of the quadrate, such as the snout, might account for head size differences.

The results of the 2-D and 3-D geometric morphometric analyses were largely similar in that both data sets indicate an influence of ontogeny, and a lack of sexual shape dimorphism, in quadrate morphology. The 3-D regression plots and PCA (Fig. 2B,D) illustrate a more distinct separation between juveniles and adults in tangent shape space than the 2-D regression plots and PCA (Fig. 2A,C). The quadrate is considered a strongly three-dimensional element (Evans 2008), and the 2-D landmarks only measured variation visible in posterior view of the structure, while the 3-D landmarks measured more comprehensive variation, such as the quadrate conch depth that differed between juveniles and adults. The 2-D data set likely also contains more error, as the delicate cleared and doubled-stained quadrates were sometimes damaged during dissection and were likely not in the exact same orientation and angle when photographed; issues that were not present when working with the 3-D shape files. Both the 2-D and 3-D analyses indicated the presence of intraspecific shape variation that was not explained by ontogenetic stage or sex (Fig. 2), including the relative sizes of the cephalic and mandibular condyles (Figs. S1, S3). This might be a product of random individual variation or shape deviations driven by influences not measured in this study, such as variation in the size of the adductor mandibulae cranial musculature that inserts onto the quadrate (Daza et al. 2011). Qualitatively, we observed little random individual variation in the articulation points between the quadrate and other cranial elements. No specimens possessed a bone-to-bone contact between the quadrate and squamosal, although these two elements were connected through soft tissue in all of the cleared and double-stained specimens.

Although mean quadrate shape in the 2-D data set differed among the three localities sampled, we did not detect any population-level variation in the degree of

ontogenetic change and lack of sexual shape dimorphism in quadrate morphology between the two nonnative populations and native population (Table 2; Fig. S2). The mean quadrate shape differences between these populations are likely attributable to biases in the number and size range of juveniles and adults sampled, as the 15 Turkey specimens included 6 juveniles (range 22.8–42.8 mm) and 9 adults (47.2–52.4 mm), the 5 Texas specimens included 3 juveniles (26.7–39.3 mm) and 2 adults (47.4–52.8 mm), and the 19 Louisiana specimens included 3 juveniles (31.3–40.6 mm) and 16 adults (44.5–56.1 mm). Granatosky and Krysko (2014) demonstrated limited morphological variation (SVL, head dimensions) in *Hemidactylus turcicus* across nonnative populations in the United States. To our knowledge, however, morphological variation between native and nonnative populations of this species had not been investigated previously.

There is a need for increased sample sizes in squamate morphological research (Bell et al. 2003; Olori and Bell 2012), particularly in computed tomography studies (e.g., Bell and Mead 2014), to further characterize the intraspecific variation of the lizard skull and to identify patterns of variation and phylogenetically informative characters of disarticulated skeletal elements. This is the first study to quantify the intraspecific variation of a single cranial element within geckos and highlights the importance of using increased sample sizes to further characterize the natural variation of skeletal morphology. Furthermore, we utilized both 2-D and 3-D geometric morphometric analyses and illustrated the benefit of using 3-D data on complex morphological structures. Future research directions include quantifying the interspecific variation of the quadrate bone within Gekkota, and investigating the interactions of phylogeny, function, and allometry influencing the morphological diversity of this, and other, structures.

SUPPLEMENTAL MATERIAL

Supplemental Material associated with this article can be found online.

TABLE S1.—*Hemidactylus turcicus* specimens examined in this study. Available online at https://doi.org/10.1655/ Herpetologica-D-17-00011.ST1

TABLE S2.—Summary table of snout–vent length and head dimension measurements for Florida Museum of Natural History (FLMNH) *Hemidactylus turcicus* examined in the 3-D data set. Available online at https://doi.org/10.1655/ Herpetologica-D-17-00011.ST2

FIG. S1.—PCA plot of shape variation for 2-D geometric morphometrics and thin plate splines of PC 1 and 2 minima and maxima (geomorph function plotRefToTarget, meth-od="TPS") illustrating the variation explained. Available online at https://doi.org/10.1655/Herpetologica-D-17-00011. SF1

FIG. S2.—PCA plot of shape variation for 2-D geometric morphometrics grouped by population. Available online at https://doi.org/10.1655/Herpetologica-D-17-00011.SF2

FIG. S3.—PCA plot of shape variation for 3-D geometric morphometrics and warped shape meshes of PC 1 and 2 minima and maxima (geomorph function plotRefToTarget, method="surface") illustrating the variation explained. Available online at https://doi.org/10.1655/Herpetologica-D-17-00011.SF3

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