

## Spatiotemporal variation in the Eastern Box Turtle (*Terrapene carolina*)

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Variation is a key component of the evolutionary process. However, variation often is poorly understood within a given species. Alternatively, where variation is understood, it often is characterized by features found in soft tissues that rarely fossilize and therefore are unsuitable for exploring questions of variation through time. The Eastern Box Turtle, the *Terrapene carolina* complex, presents an excellent opportunity to explore spatiotemporal patterns of variation because extant species have high levels of variation in soft-tissue characters as well as morphological variation in skeletal characters. Importantly, it also has a published fossil record that includes shells that are suitably complete enough and abundant enough to be used in statistical analyses of shape. Variation within this species complex, both in the modern and fossil record, often is explained by subspecific variation, or variation due to the presence of lineages within a species that have begun to separate but are not fully separated from one another, or are reemerging after a temporary separation.

To explore patterns of spatiotemporal variation, I used geometric morphometrics to quantify the shape of 200 Recent and 44 fossilized shells of *T. carolina*. First, I analyzed differences in the shapes of nominative subspecies in the modern record, both qualitatively and quantitatively. Then, I compared the results from the modern biota to that of the fossilized specimens.

Visual inspection of the average shape of each of the four nominative subspecies of *T. carolina* found in the United States showed that although differences existed, they were so subtle that they could not be objectively applied to other studies. Statistical analyses of shape provided mixed results. Results of pairwise comparisons indicated significant differences between subspecies, while the results of assignments tests and canonical variates analyses indicated insignificant or unreliable differences. In sum, results indicate that differences between putative subspecies are more statistically significant than they are biologically significant, and may not be the best explanation for the patterns of variation seen in the modern record. More importantly, the inability of statistical analyses to reliably identify individuals of a subspecies based on skeletal features means that subspecies cannot be identified in the fossil record.

Differences between the shapes of fossilized and modern shells were greater than the differences between various nominative modern subspecies, further indicating that applying subspecific identifications to fossil specimens is inappropriate. Fossilized specimens are, on average, larger than recent specimens, and may have distinctive characters not generally found in recent specimens. Furthermore, fossils from some localities have patterns of size and shape variation that are unique in comparison both to other fossils and to recent specimens of *T. carolina*. Now that these patterns of variation are not masked by hypothesized evolution from one modern subspecies to another, better explanations for patterns of variation in the modern and fossil record can be explored.

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