ARTICLES

Herpetological Review, 2023, 54(2), 181–185.

Supramarginal Scute Count of Alligator Snapping Turtles (*Macrochelys temminckii*) in Texas, USA

The genus *Macrochelys* (Alligator Snapping Turtles) is the only extant turtle clade whose members possess supramarginal scutes (Joyce 2016). The extinct genera *Proganochelys* (Ascarrunz and Sánchez-Villagra 2022), *Platychelys* (Sullivan and Joyce 2017), and *Boremys* (Joyce and Lyson 2015) also all possessed supramaginal scutes. However, supramarginals in these four genera do not likely represent homologous structures. *Platychelys* is a stem-pleurodire (Sullivan and Joyce 2017) unlike the cryptodires *Macrochelys* and *Boremys*, whereas *Proganochelys* is an early testudinatan that may represent a common ancestor to both cryptodires and pleurodires (Gaffney et al. 1987). Pritchard (2006) argued that supramarginals in *Macrochelys* are an apomorphic trait, which is supported by the absence of the scutes in all its extant relatives.

These unique scutes of *Macrochelys* are located on each side of the carapace between the costal and marginal scutes. Specifically, they are inferior to the first through third costal scutes and superior to the fourth through seventh marginal scutes (Fig. 1). With the exception of ontogenetic irregularities and apomorphies in several families (e.g., Kinosternidae, Trionychidae), the number of costal scutes (4 per side), marginal scutes (12 per side), and vertebral scutes (5) on modern turtles is highly conserved (Zimm et al. 2017). However, in *Macrochelys*, the number of supramarginals varies from 1–5 per side (Pritchard 2006). Three per side has been reported as the most frequently observed condition (Pritchard 2006), or erroneously, as the maximum number (Joyce 2016). The number of supramarginals present on individuals could be a plastic trait susceptible to environmental conditions during development (Zimm et al. 2017) and may also be an inherited trait that varies predictably among populations across the range of the genus.

The hypothesis that supramarginal number may vary across the range of *Macrochelys* was first proposed by Pritchard (2006), who presented evidence that individuals from the Apalachicola drainage in Georgia tended to have fewer supramarginals than individuals from the Mississippi drainage of Louisiana. However, to our knowledge, there have been no efforts to report region- or watershed-specific supramarginal count data that would contribute evidence to support or falsify this hypothesis. Taxonomic evaluation of the genus has confirmed that other aspects of its carapacial morphology vary among allopatric lineages (Thomas et al. 2014; Folt and Guyer 2015). Populations in the Suwannee River watershed at the eastern range edge of the

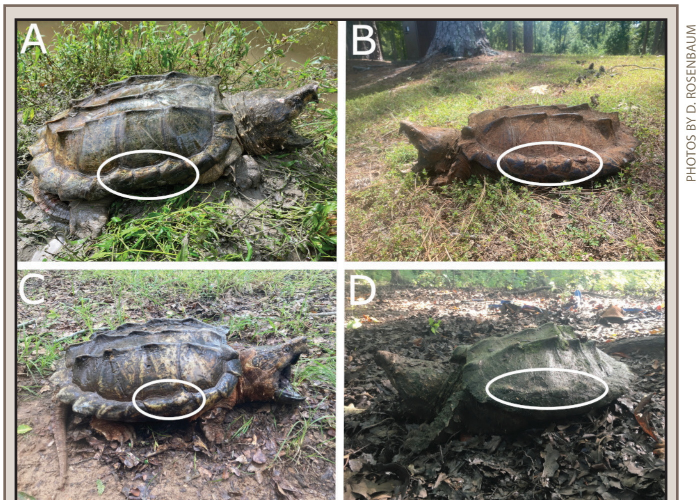

Fig. 1. *Macrochelys temminckii* (Alligator Snapping Turtles) sampled during survey efforts from April through October 2020 and April through September 2021 in watersheds of eastern Texas, United States, with encircled supramarginal scutes: A) an individual sampled from the Trinity watershed, exhibiting the typical morphology of three supramarginal scutes; B) an individual sampled from the Neches watershed, exhibiting four left supramarginal scutes (four supramarginals were also present on the right side); C) an individual also sampled from the Neches watershed, exhibiting two right supramarginal scutes (three supramarginals were present on the left side); D) an individual sampled from the Sabine watershed with a kyphotic carapace and four left supramarginal scutes.

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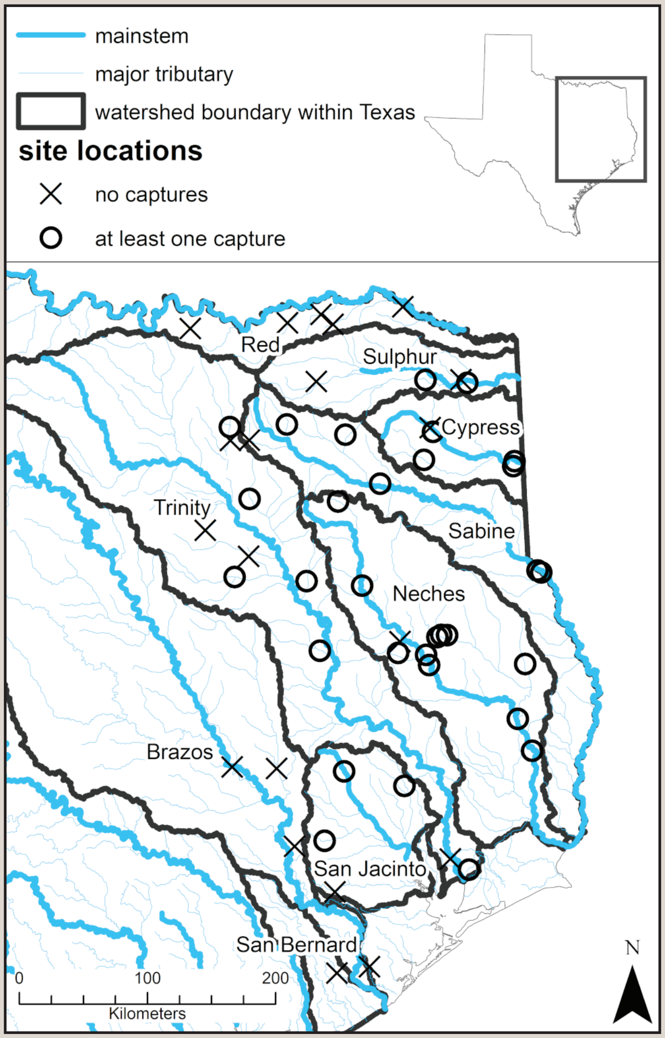

Fig. 2. Survey locations for *Macrochelys temminckii* (Alligator Snapping Turtle) in eastern Texas, United States, that were sampled from April through October 2020 and April through September 2021. Sites are indicated as circles or crosses, representing locations where at least one individual of the species or none was detected, respectively. The Mississippi watershed is represented in Texas by the watersheds of the Red, Sulphur, and Cypress Rivers in the northeastern portion of the study area. The Sabine, Neches, Trinity, and San Jacinto watersheds drain directly into the Gulf of Mexico. We did not detect turtles from the Brazos and San Bernard River watersheds, which are west of known extant populations in Texas.

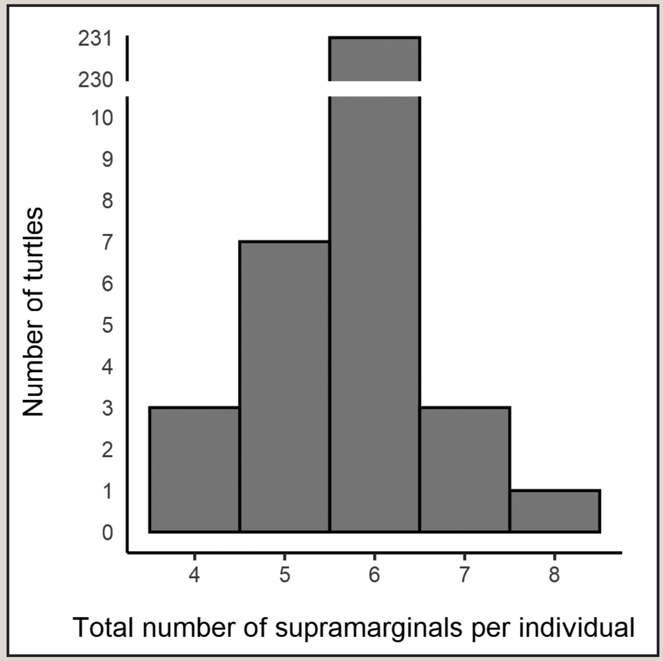

Fig. 3. Frequency histogram depicting the range in number of supramarginal scutes documented from *Macrochelys temminckii* (Alligator Snapping Turtles) in Texas, United States, from April through October 2020 and April through September 2021. The majority of Texas *M. temminckii* exhibited 3 marginals per side (93.9% of sample), although aberrant counts were documented from turtles occupying the Trinity, Neches, and Sabine watersheds. Note the break in range on the y-axis.

genus (*M. suwanniensis*; Suwannee Alligator Snapping Turtle) exhibit more lunate, deeper, and wider caudal notches relative to populations of *M. temminckii* (Alligator Snapping Turtle) to the west (Thomas et al. 2014).

Due to the limited overland dispersal ability of *Macrochelys*, gene flow between watersheds it occupies is restricted (Roman et al. 1999; Echelle et al. 2010). Variation in supramarginal phenotype between watersheds, if present, could correspond to population structure and inter-drainage genetic variation in the genus similar to other aspects of its morphology (Thomas et al. 2014). If this is the case, the number of supramarginals could provide preliminary visual evidence for region of origin of illegally collected specimens, and if the number is a conserved trait within particular watersheds, any deviation could serve as indirect preliminary evidence of translocation (Pearson et al. 2020a). In a recent study on the distribution of *M. temminckii* (Alligator Snapping Turtle) in Texas (Rosenbaum et al. 2023), we investigated the number and location of supramarginal scutes on each captured individual. Our objectives were to elucidate the mean number of supramarginals exhibited by individuals at the southwestern extent of the species' range, and to assess if there are differences in supramarginal number among Texas watersheds and across the range of the species.

Methods

We conducted hoop trap surveys at 51 water bodies (i.e., sites) throughout the purported range of *M. temminckii* in Texas from April through October 2020 and April through September 2021 (Fig. 2). Watersheds represented in this sampling effort were the Mississippi (in tributaries and impoundments within the Red, Sulphur, and Cypress watersheds), the Sabine, Neches (including the Angelina River), Trinity, San Jacinto, Brazos, and San Bernard watersheds (Fig. 2). Each hoop trap had a single, finger-throated funnel and consisted of four 1.2-m diameter hoops and 2.54-cm mesh. PVC canisters baited with fish were installed at the farthest hoop from the entrance of each trap. We deployed traps adjacent to submerged structure (e.g., fallen trees), undercuts, or low energy pools, when available, and secured them to trees or other structures above the water's surface (additional details regarding site selection and trapping methods are outlined by Rosenbaum et al. 2023). At most sites, we deployed 15 hoop traps for three consecutive nights, for 45 trap-nights (i.e., the product of the number of traps and the number of nights they were deployed) of effort per site. However, logistical constraints during eight site

Table 1. Numbers of *Macrochelys temminckii* (Alligator Snapping Turtle) sampled in Texas, United States, from April through October 2020 and April through September 2021. Observed combinations of right and left supramarginal scute numbers and the number of turtles exhibiting each combination are specified, along with observed per-watershed frequencies of turtles exhibiting different supramarginal scute counts.

Watershed	# of turtles sampled	Right/left/total supramarginal scute count	# of turtles exhibiting supramarginal arrangement	% of turtles with this arrangement
Mississippi	20	3/3/6	20	100.0
Sabine	39	2/4/6	1	2.6
		3/3/6	36	92.3
		3/4/7	1	2.6
		4/3/7	1	2.6
Neches	119	2/2/4	1	0.8
		2/3/5	2	1.7
		3/2/5	1	0.8
		3/3/6	113	95.0
		3/4/7	1	0.8
		4/4/8	1	0.8
Trinity	53	2/2/4	2	3.8
		3/2/5	4	7.5
		3/3/6	47	88.7
San Jacinto	14	3/3/6	14	100.0
All watersheds	245	2/2/4	3	1.2
		2/3/5	2	0.8
		3/2/5	5	2.0
		2/4/6	1	0.4
		3/3/6	230	93.9
		4/3/7	1	0.4
		3/4/7	2	0.8
		4/4/8	1	0.4

sampling efforts required fewer nights of trapping and the use of fewer hoop traps. We checked traps approximately every 24 h. When *M. temminckii* were captured, we counted the number of supramarginals on the anatomical right and left side of each captured individual and noted any unique or abnormal carapacial features. All *M. temminckii* were released adjacent to their capture locations.

Results

We captured 245 *M. temminckii* from 31 sites, and the majority of individuals (231 turtles, 94.3%) possessed six supramarginal scutes in total (Table 1). The mean (± SD) number of supramarginals per individual was 5.97 (± 0.32), and the means for both right and left sides were similar (2.98 ± 0.18 and 2.98 ± 0.22, respectively). Despite the uniformity in count, supramarginals ranged from 2–4 per side (Figs. 1 and 3) and we documented eight combinations of right and left supramarginal counts (Table 1). Eleven individuals (4.5% of captures) had an uneven number of supramarginals per side. There was no apparent pattern in scute count attributable to location, as turtles captured in the Trinity (N = 6 individuals), Neches (N = 6), and Sabine (N = 3) watersheds deviated from the typical three scutes per side (Table 1).

We observed two individuals with prominent carapace abnormalities. One individual with a count of two and four supramarginals on the right and left sides, respectively (Table 1), had other extreme abnormalities that were presumably congenital in origin. The spine and carapace were kyphoscoliotic, and the most anterior supramarginal scutes on each side were situated forward from and not in contact with posterior ones (Fig. 1D). The second individual possessed an extra pair of marginal scutes, for a total of 26. Although this turtle had the usual three supramarginal scutes per side, the right anterior and left posterior supramarginals were highly reduced.

Discussion

Our study found that the majority of *M. temminckii* throughout eastern Texas possessed three supramarginal scutes per side. These observations corroborate scute counts to the east of our sampling area in the Mississippi watershed of Louisiana, where 10 of 11 sampled individuals possessed three supramarginals per side (Pritchard 2006). In another sample of Louisiana turtles from an unspecified locale, however, 25 of 92 individuals (27%) possessed four supramarginals per side (Pritchard 2006). Despite the higher frequency of greater scute number in this sample, 64 individuals (70%) possessed three per side. Another dataset of 29 *M. temminckii* from the Mississippi watershed of Louisiana shows congruency with this sample, confirming 17 individuals (59%) to have three supramarginals per side and six individuals (21%) to have four per side. These observations indicate that *M. temminckii* to the east of Texas populations in the Mississippi watershed may exhibit higher frequencies of four supramarginals per side (Glorioso and Waddle 2021a, b). In contrast to both Texas and Louisiana *Macrochelys*, 24 of 54 individuals (44%) from the Apalachicola watershed in Georgia exhibited only two supramarginals per side (Pritchard 2006).

Carapace scute number is conserved among turtle clades (Zimm et al. 2017). This finding is consistent with the limited variation in scute number we observed in Texas, as is the relatively limited among-drainage genetic diversity in western *M. temminckii* that has been documented from mitochondrial and microsatellite DNA (Roman et al. 1999; Echelle et al. 2010). *Macrochelys temminckii* sampled from the Neches, Trinity, and Mississippi watersheds exhibited the same mitochondrial haplotype and low population structuring, despite the large distances between watersheds (Roman et al. 1999; Echelle et al. 2010; it should be noted that Trinity watershed populations were represented by a sample of only three individuals in these studies). The apparent differences and greater variation in scute number exhibited by Apalachicola watershed *Macrochelys* is also consistent with these turtles representing a more distantly related lineage and having greater mitochondrial DNA haplotype diversity, respectively (Roman et al. 1999). However, without greater understanding of variation (or lack thereof) in scute number across the range of *Macrochelys*, it is still uncertain whether this morphological feature is indicative of phylogenetic relationships among populations.

Aberrant carapace morphology and pholidosis are affected by environmental factors (e.g., pressure, temperature, and moisture extremes) during embryonic development (Zimm et al. 2017). The low frequency of individuals with a total supramarginal count deviating from six and the absence of apparent site- or watershed-specific variability in our study could suggest that these individuals represent developmental anomalies. In addition to the two *M. temminckii* we documented with other carapace aberrations along with variant supramarginals, Pearson et al. (2020b) documented one *M. temminckii* with two supramarginals per side along with extra vertebral scutes. These associations of supramarginal scute aberrations with other carapace abnormalities further support the hypothesis that supramarginal number depends on the developmental environment.

There would be additional support that environmental stressors influence supramaginal number if *Macrochelys* at the extreme peripheries of their range (e.g., Illinois, Kansas) show high variation in supramarginal number or a modal count differing from three per side, because these areas are presumably at the threshold of tolerable climate during incubation (Thompson et al. 2017). A fossilized specimen of *M. temminckii* from the Brazos watershed in Texas (to the west of the species' extant distribution) possessed four supramarginals per side (Hay 1911). However, as the only specimen from this region, it presents negligible support for the hypothesis.

Currently, publicly available data on supramarginal number across the range of *Macrochelys* are limited relative to other morphological data (e.g., carapace length and mass). Therefore, applicability of our results to the conservation of the species is similarly limited, yet some inference can be made. Although we documented that number of scutes cannot be used to morphologically distinguish watershed of origin of *M. temminckii* in Texas, it may be inferred that an individual with a number differing from three per side is relatively unlikely to have originated from Texas. For example, an individual confiscated from the black market with two supramarginal scutes per side is more likely to have originated from a region such as the Apalachicola River, where two scutes per side is more frequent than in Texas. We encourage researchers to report average supramarginal counts throughout the range of *Macrochelys* so that a clearer understanding of geographic morphological variation in the genus may be attained. This information not only has the potential for application to conservation; it may provide insight to how scute number aligns with intrageneric phylogenetic relationships, and how the developmental environment may influence turtle carapace development.

Acknowledgments.—This research was funded by a U.S. Fish and Wildlife State Wildlife Grant through Texas Parks and Wildlife (TPWD) and a McIntire Stennis capacity grant. Survey efforts were conducted under TWPD Scientific Permit for Research SPR-0519-087 and SFASU IACUC project approval number 2019-11. We thank John Michael Arnett, Aubrey Pelletier, Laura St. Andrews, and Jake Swanson, who helped conduct survey efforts. Additional help with sampling was provided by Reuber Antoniazzi, Veda Allen, Alexandra Alterman, John Barnett, Matt Buckingham, Valerie Castillo, Claire Haffner, Zachary Hutchens, Kasey Jobe, Regan Lehmann, Carmen G. Montaña, Sarah Rosenbaum, Carson Salter, Tatiana Suárez-Joaqui, Ashley Wahlberg, Scott Wahlberg, Jessica R. Yates, and Liam Wolff. Permission to conduct research on public lands was granted by the U.S. Fish and Wildlife Service, the U.S. Forest Service, and the Texas Parks and Wildlife Department. We are grateful to the private landowners who permitted us to access their properties to survey. This paper was written and prepared in part by U.S. Government employees on official time and therefore is in the public domain and not subject to copyright. This research was supported in part by the USDA Forest Service. The findings and conclusions in this publication are those of the author(s) and should not be construed to represent an official USDA, Forest Service, or U.S. Government determination or policy.

Literature Cited

Ascarrunz, E., and M. R. Sánchez-Villagra. 2022. The macroevolutionary and developmental evolution of the turtle carapacial scutes. Vertebr. Zool. 72:29–46.

Echelle, A. A., J. C. Hackler, J. B. Lack, S. R. Ballard, J. Roman, S. F. Fox, D. M. Leslie, and R. A. Van Den Bussche. 2010. Conservation genetics of the alligator snapping turtle: cytonuclear evidence of range-wide bottleneck effects and unusually pronounced geographic structure. Conserv. Genet. 11:1375–1387.

Folt, B. and C. Guyer. 2015. Evaluating recent taxomonic changes for alligator snapping turtles (Testudines: Chelydridae). Zootaxa 3947:447–450.

Gaffney, E. S., J. H. Hutchison, F. A. Jenkins, and L. J. Meeker. 1987. Modern turtle origins: the oldest known cryptodire. Science 237:289–291.

Glorioso, B. M. and J. H. Waddle. 2021a. Data from a turtle trapping effort targeting alligator snapping turtles (*Macrochelys temminckii*) in the Atchafalaya Basin beginning in 2019: U.S. Geological Survey data release. Available at: http://doi.org/10.5066/P9N40V06. Accessed 6 April 2023.

——— and ———. 2021b. Data from 2019 occupancy survey of alligator snapping turtles, *Macrochelys temminckii*, in south-central Louisiana. U.S. Geological Survey data release. Available at: https://doi.org/10.5066/P90JT34K. Accessed 6 April 2023.

Hay, O. P. 1911. A fossil specimen of the alligator snapper (*Macrochelys temminckii*) from Texas. Proc. Am. Philos. Soc. 50:452–455.

Joyce, W. G. 2016. A review of the fossil record of turtles of the clade Pan-Chelydridae. Bull. Peabody Mus. Nat. His. 57:21–56.

———, and T. R. Lyson. 2015. A review of the fossil record of turtles of the clade Baenidae. Bull. Peabody Mus. Nat. His. 56:147–183.

Pearson, L., G. Berry, L. Haralson, G. Brown, B. Kreiser, and C. Qualls. 2020a. Conservation genetics of the alligator snapping turtle (*Macrochelys temminckii*) in Mississippi. Presented at: 18th Annual Symposium on the Conservation and Biology of Tortoises and

Freshwater Turtles; Virtual conference.

———, L. Haralson, G. Brown, and C. Pellecchia. 2020b. *Macrochelys temminckii* (alligator snapping turtle). Geographic Distribution Note. Herpetol. Rev. 51:74–75.

Pritchard, P. C. H. 2006. The Alligator Snapping Turtle: Biology and Conservation. 2nd Edition. Krieger, Malabar, Florida. 140 pp.

Roman, J., S. D. Santhuff, P. E. Moler, and B. W. Bowen. 1999. Population structure and cryptic evolutionary units in the alligator snapping turtle. Conserv. Biol. 13:135–142.

Rosenbaum, D., D. C. Rudolph, D. Saenz, L. A. Fitzgerald, R. E. Nelson, C. S. Collins, T. J. Hibbitts, R. W. Maxey, P. Crump, and C. M. Schalk. 2023. Distribution and demography of the alligator snapping turtle (*Macrochelys temminckii*) in Texas: a 20-year perspective. Southeast. Nat. 22:197–220.

Sullivan, P. M., and W. G. Joyce. 2017. The shell and pelvic anatomy of the late Jurassic turtle *Platychelys oberndorferi* based on material from Solothurn, Switzerland. Swiss J. Palaeontol. 136:323–343.

Thomas, T. M., M. C. Granatosky, J. R. Bourque, K. L. Krysko, P. E. Moler, T. Gamble, E. Suarez, E. Leone, K. M. Enge, and J. Roman. 2014. Taxonomic assessment of alligator snapping turtles (Chelydridae: *Macrochelys*), with the description of two new species from the southeastern United States. Zootaxa 3786:141–165.

Thompson, D. M., D. B. Ligon, J. C. Patton, and M. Papes. 2017. Effects of life-history requirements on the distribution of a threatened reptile. Conserv. Biol. 31:427–436.

Zimm, R., B. P. Bentley, J. Wyneken, and J. E. Moustakas-Verho. 2017. Environmental causation of turtle scute anomalies *in ovo* and *in silico*. Integr. Comp. Biol. 57:1303–1311.