Exploring Eastern Musk Turtle (*Sternotherus odoratus*) Population Dynamics and Phenotypic Plasticity in Comal Springs, Texas

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Abstract

Freshwater turtles are vital to aquatic ecosystems but are increasingly affected by anthropogenic change. The eastern musk turtle (*Sternotherus odoratus*) is a small, omnivorous species inhabiting spring systems in Central Texas, where invasive gastropods have become abundant. This study investigates whether dietary shifts toward these gastropods are associated with variations in head and body morphology. Seventy-one individuals were captured in June and July 2024. Morphometric data and fecal samples were collected to assess diet composition and morphological variations. Dietary analyses identified *Tarebia granifera* as the dominant prey item. Males exhibited stronger allometric relationships between head width and body size. Head width did not significantly differ between sexes. A comparison with museum specimens revealed significant increases in carapace length and head width. These findings suggest that invasive prey may be driving morphological changes through phenotypic plasticity and highlight the capacity for freshwater turtles to adapt to novel ecological pressures.

Keywords: *Sternotherus odoratus*, freshwater turtles, invasive species, phenotypic plasticity, morphology, aquatic ecosystems, Texas

Dedication

What is the meaning of life? We are blessed with the curse of never truly knowing the answer to that question, yet we can speculate and come up with our own personized meanings that bring us peace and sanity. To me, the meaning of life is whatever you wake up and fear losing the most. To my mom and my dad, you are my meaning of life.

I would like to dedicate this thesis to my parents, *Robin Owen* and *Denise Owen*, who have always fostered and supported my interests in reptiles and wildlife. You have nurtured my love for the outdoors and showed me the value of curiosity, patience, and respect for the natural world. You have been extraordinary parents who have nourished me, loved me, and, most importantly, always believed in me. I will never be able to repay you for the countless sacrifices you have made in order for me to be successful. I love you more than life itself. Thank you for everything.

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1.0 Introduction

1.1 Global and Regional Turtle Conservation Challenges

Turtles are among the most imperiled vertebrate groups, with over 60% of all species classified as threatened or recently extinct (IUCN, 2025; Lovich et al., 2018). Turtles are increasingly threatened by anthropogenic pressures such as habitat degradation, poaching, invasive species, and climate change (Dupuis-Désormeaux et al., 2019; Polich, 2017; Selman et al., 2013; Stokeld et al., 2014). These threats contribute to population declines, reduced genetic diversity, and disrupted ecosystem functions (Iverson, 1982; Lovich & Ennen, 2013; Rodríguez-Caro et al., 2023; Stanford et al., 2020). As both vulnerable and ecologically valuable organisms, the conservation of freshwater turtles is essential for maintaining freshwater biodiversity and ecosystem health across the globe (Ahmed et al., 2022; Buhlmann et al., 2009; Dudgeon et al., 2006).

Freshwater turtles are integral to freshwater ecosystems, contributing to ecological balance through their roles as both consumers and prey (Ahmed et al., 2022; Dudgeon et al., 2006). Their diverse feeding habits significantly influence energy flow, nutrient cycling, and overall biodiversity within these systems (Lovich et al., 2018). Turtles are vulnerable to predation throughout their life cycle, particularly during nesting and as hatchlings (Moldowan, 2023). Their nesting activity also plays a key ecological role by transferring aquatic-derived energy and nutrients into terrestrial food webs, as eggs laid on land become valuable resources for a variety of scavengers and predators (Boarman, 2003; Dupuis-Desormeaux et al., 2021; Moldowan, 2023; Stokes et al., 2024). Turtles also act as bioindicators, reflecting changes in water quality, temperature, oxygen levels, and pollution (De Solla et al., 2007; Dos Santos et al., 2021; Otten et al., 2023).

1.2 The Kinosternidae Family and Ecological Traits

In North America, there are 57 species of freshwater turtles, including the family Kinosternidae which include mud (genus *Kinosternon*) and musk (genus *Sternotherus*) turtles (Brown, 2020; Buhlmann et al., 2009; Platt et al., 2016; Wilhelm & Plummer, 2012). These small cryptic turtles have large heads, domed shells, and musk glands that produce a foul-smelling effluence when threatened. Kinosternid turtles are well adapted to a range of aquatic environments ranging from shallow, turbid waters where they forage by sifting through substrate to clear, spring-fed systems (Laverty et al., 2016; Munscher et al., 2020; Picard et al., 2011; Platt et al., 2016). They are opportunistic feeders that consume a broad range of prey items including aquatic invertebrates (e.g., gastropods, insects, and crustaceans), small vertebrates (e.g., fish), and plant material (e.g., seeds and macrophytes) (Folkerts, 1968; Marion et al., 1991; Morrison et al., 2019; Wilhelm & Plummer, 2012). Like many freshwater turtles in North America, they are highly vulnerable to habitat degradation, road mortality, poaching and disease (Dodd, 1988; Iverson, 1982; Lovich et al., 2018; Lovich & Ennen, 2013). Given their increasing exposure to anthropogenic threats, advancing our understanding of kinosternid turtles is essential for developing targeted conservation strategies for this often-overlooked freshwater turtle family.

The Eastern musk turtle (*Sternotherus odoratus*) is a small freshwater turtle that belongs to the family Kinosternidae (Figure 1). It has a dark brown to black carapace, a yellowish to brown plastron, and two light stripes on the sides of its head. It also has a pair of Rathke’s glands, commonly referred to as musk glands, that produce a foul-smelling liquid when threatened, giving it the common name of “stinkpot” (Brown, 2020; Ehrenfeld & Ehrenfeld, 1973; Moll & Dazet, 2014). *Sternotherus odoratus* is widely distributed throughout the Eastern United States including into Southern Canada (Mitchell, 1985; Patterson & Lindeman, 2009;

Picard et al., 2011). *Sternotherus odoratus* are active throughout the year in southern and spring-fed habitats but hibernate in colder regions (Bulté et al., 2024; Munscher et al., 2020). *Sternotherus odoratus* reach sexual maturity relatively early, between 4 and 8 years of age, and may live over two decades in the wild (Canadian Herpetological Society, 2025). *Sternotherus odoratus* are considered generalist feeders, consuming a diverse range of prey (Brown, 2020; Wilhelm & Plummer, 2012). Their diet includes aquatic invertebrates such as gastropods, mollusks, insects, and crustaceans; small vertebrates like fish; and various type of aquatic vegetation, including seeds and other types of plant matter (Brown, 2020; Morrison et al., 2019; Patterson & Lindeman, 2009; Wilhelm & Plummer, 2012).

In Texas*,* *S. odoratus* occur in the eastern and central regions. The Comal Springs population, located in central Texas, represents one of the westernmost range limits for the species. This specific population is notable for individuals exhibiting unusually large heads and pronounced 'saddling' of the anterior carapace (Bramble et al., 1984; Iverson, 2020; Morrison et al., 2019; E. Munscher, 2019). This population also shows considerable variability in the degree of megacephaly, with head morphology expressed along a continuum rather than as a binary trait (Eric C. Munscher & Andrew D. Walde, pers. comm. Figure 3). Comal Springs supports a diverse assemblage of native and invasive gastropods, which form an important dietary component for *S. odoratus* (Morrison et al., 2019). Likely introduced through the release of unwanted aquarium specimens, invasive species such as quilted melania (*Tarebia granifera*)*,* red-rimmed melania (*Melanoides tuberculata*), and giant ramshorn snail (*Marisa cornuarietis*) now occur alongside native taxa including acute bladder snail (*Physella acuta*) and Balcones elimia (*Elimia comalensis*) (Horne et al., 1992; Karatayev et al., 2009, Figure 4.). These invasive gastropods are potentially influencing the cranial morphology and foraging ecology of *S.*

odoratus in this population, as Morrison et al. (2019) documented that individuals consume many of these taxa. The riverbed in parts of Comal Springs is now blanketed with their shells (Figure 5), suggesting that megacephaly expression may be linked to the presence and abundance of these novel prey items.

Figure 1. (a) Two adult *Sternotherus odoratus* showcasing head morphology differences between a megacephalic male (bottom individual) and a non-megacephalic male (top individual). (b) Shows plastron (ventral) views of a male (left) and female (right) for comparison. Photographs taken in July 2024 at Comal Springs, Texas, USA.

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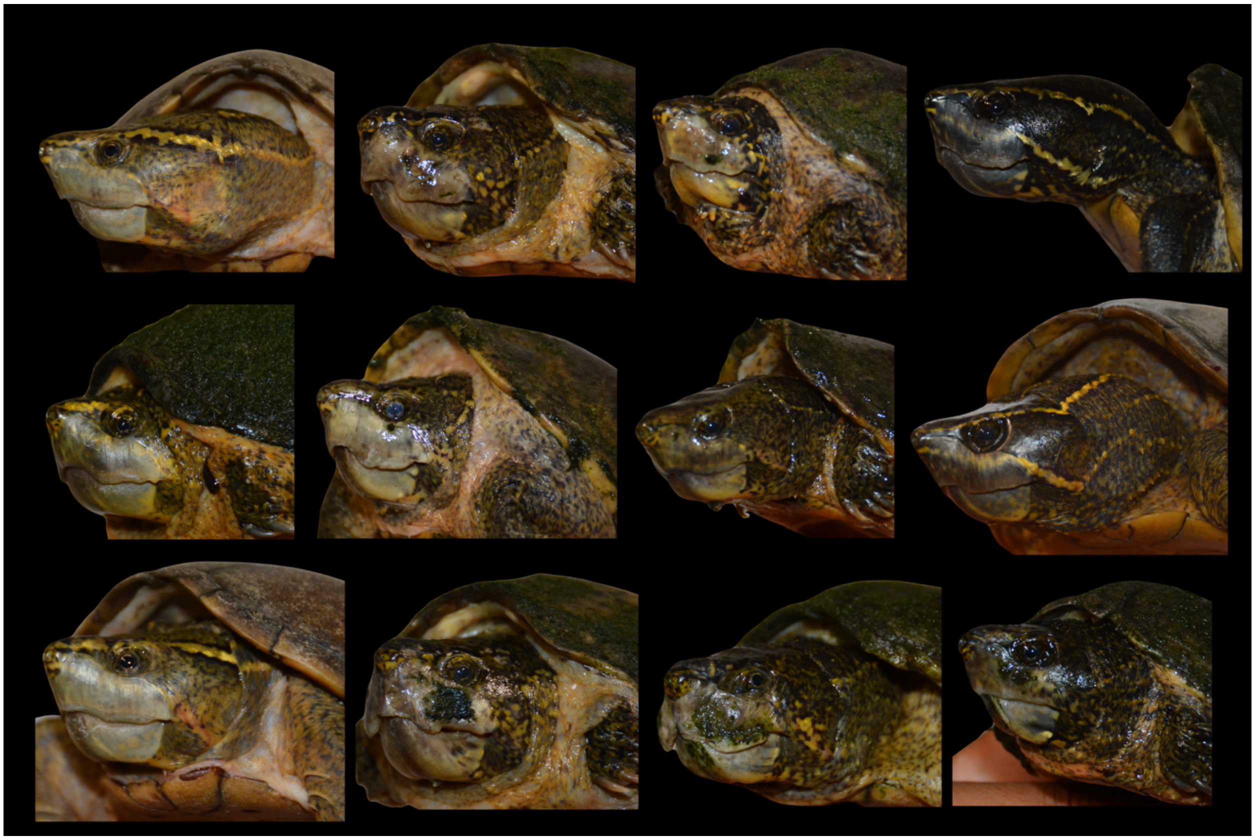

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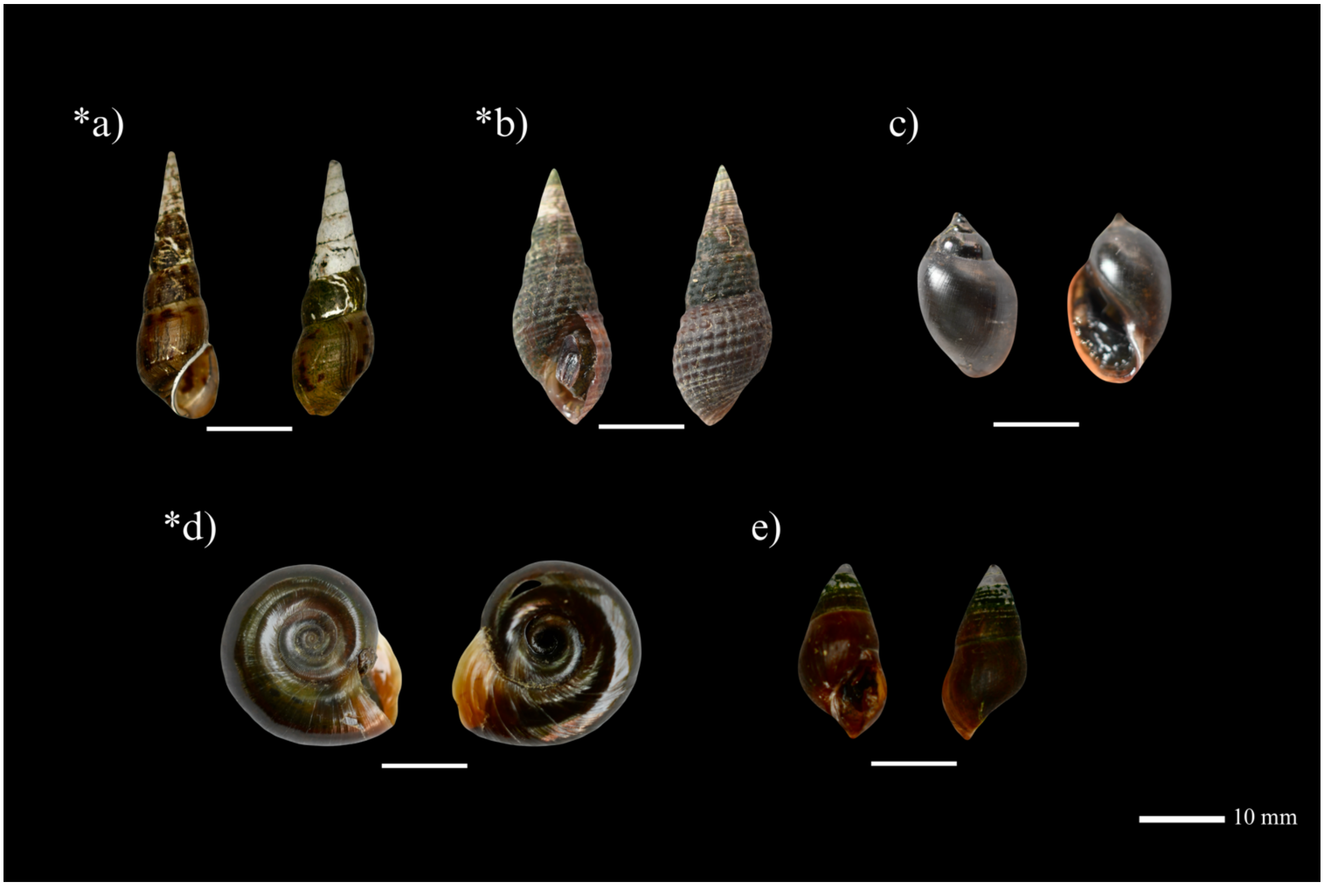

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Figure 5. Section of riverbed at Comal Springs, Texas, USA. This area is blanketed by a mixture of live and dead shells of invasive gastropods, primarily *Tarebia granifera*, *Melanoides tuberculata* and *Marisa cornuarietis*.

1.3 Texas Turtle Diversity and Conservation Barriers

Due to the region's high degree of endemism, the Southeastern United States is a global hotspot for tortoise and freshwater turtle diversity, ranking second worldwide after the Indo-Burma hotspot (Buhlmann et al., 2009; Lovich et al., 2018). Texas contains nearly half of the United States' tortoise and freshwater turtle diversity and ranks among the most ecologically diverse states, with 36 native species representing 9 families and 15 genera (Dixon, 2000; Ernst et al., 2009; Ricardez & Franklin, 2025). Several species are endemic to the state, such as the Cagle's map turtle (*Graptemys caglei*), the Texas tortoise (*Gopherus berlandieri*), and the Texas map turtle (*Graptemys versa*), (Dixon, 2000; Ernst et al., 2009; Texas Parks and Wildlife, 2020). Other species, such as the Western alligator snapping turtle (*Macrochelys temminckii*) and the Texas diamondback terrapin (*Malaclemys terrapin*) are currently listed as threatened or endangered at the state or federal level (Haskett & Guillen, 2008; Munscher et al., 2023; Texas Parks and Wildlife , 2020). Turtle species across Texas provide important ecological functions, while also holding economic and cultural significance throughout the region (Ceballos & Fitzgerald, 2004).

Despite this level of species diversity and endemicity, turtle research in Texas remains relatively limited, particularly when compared to states like Florida, which share similar species richness but a higher volume of published work (Johnston et al., 2025; Munscher et al., 2020; Riedle et al., 2016). One major barrier is the high proportion of private land ownership in the state (Brown, 1998). According to the Texas Center for Policy Studies (2000) and the Texas General Land Office (2013), over 90 percent of the land area in Texas is owned by private entities. Gaining access for long-term ecological research can be challenging, and negative perceptions of threatened species and environmental regulation among some landowners may further hinder collaboration and trust. Studying long-lived vertebrate taxa such as tortoises and freshwater turtles is particularly dependent on access to these long-term study sites, yet in Texas, securing and maintaining such access can be especially difficult. These social dynamics can restrict survey efforts and lead to significant knowledge gaps in species distribution, abundance, and population trends. Habitat loss in Texas is another pressing issue. Ongoing urbanization, industrial development, and agricultural developments have degraded many of the aquatic and terrestrial habitats critical to aquatic turtle survival and reproduction (Williams, 2003; Zhang et al., 2022; Zhao et al., 2016). Native habitats are being fragmented and drained, reducing nesting opportunities and increasing turtles' exposure to pollution, invasive species, poaching, and road mortality (Ahmed et al., 2022; Brown et al., 2011; Buhlmann et al., 2009; Ceballos & Fitzgerald, 2004). These negative effects can lead to localized extirpations or even population-level extinctions (Lovich & Ennen, 2013; Stanford et al., 2020).

These constraints such as restricted land access, limited research, and widespread habitat degradation pose major challenges to tortoises and freshwater turtle conservation in Texas. Given the ecological importance of accessible sites and systems in Texas and the limited baseline data for many turtle populations, research efforts like this study in Comal Springs are vital for informing evidence-based conservation and management strategies.

1.4 Morphology, Diet, and the Concept of Megacephaly in Turtles

Across multiple taxonomic groups within the animal kingdom, the structure of an organism’s feeding apparatus is directly linked to its dietary capabilities. In all species of turtles, skull morphology including shape, size, and jaw musculature, play a key role in determining dietary specialization (Danaisawadi et al., 2016; Smith & Temple, 1982; Starck et al., 2007). This can range from plant and algal material to soft-bodied invertebrates, omnivorous diets, or hard-shelled prey (Lindeman, 2006; Morrison et al., 2019; Natchev et al., 2011; Platt et al., 2016.; Wilhelm & Plummer, 2012). This relationship has been extensively studied in durophagous (hard-prey-eating) freshwater turtle species. Among them the genus *Graptemys* (map and sawback turtles) are notable for pronounced sexual dimorphism in both body size and head morphology, which is closely linked to sex-specific niche partitioning and dietary specialization within this genus. (Bulté & Blouin-Demers, 2008; Lindeman, 2006; Lindeman et al., 2020; Richards-Dimitrie et al., 2013).

One trait commonly associated with a durophagous diet is known as megacephaly, a term derived from Latin roots meaning "*mega*" (large) and "*cephaly*" (head) (Iverson, 2020; Patterson & Lindeman, 2009). This morphological trait has been documented in at least 19 genera across 9 turtle families (Iverson, 2020; McKnight et al., 2023). Most commonly associated with mollusk or aquatic gastropod consumption, megacephaly represents an ecological and evolutionary response to durophagy; in theory it allows individuals to exploit hard-shelled prey more efficiently (Iverson, 2020; Morrison et al., 2019; Natchev et al., 2011; Pfaller et al., 2010).

Phenotypic plasticity is the capacity for a single genotype to produce different phenotypes in response to environmental conditions (Pigliucci, 2001). Whether megacephaly arises from genetic adaptation or phenotypic plasticity still remains uncertain as it often varies geographically and reflects differences in the local environment and prey availability (Iverson, 2020; Iverson et al., 1989). In most aquatic turtle populations where megacephalic individuals have been observed, it is considered a plastic response to diet rather than a genetically fixed trait (Iverson, 2020). However not all turtle species follow this pattern. In the Cooper Creek Turtle (*Emydura macquarii emmotti*), megacephaly appears to be a genetically driven trait shaped by sexual selection, as it is predominantly expressed in females (McKnight et al., 2023). A similar pattern is observed in the genus *Graptemys*, where females are typically larger than males. In some species, such as the Barbour's map turtle (*Graptemys barbouri*) and the Pearl River map turtle (*Graptemys pearlensis*), this sexual dimorphism reaches an extreme, with females exhibiting pronounced megacephaly associated with strong sexual size dimorphism and ecological niche partitioning(Godwin et al., 2014; Lindeman, 2000; Lindeman et al., 2020). Understanding where freshwater turtles fall along this plasticity-genetic continuum is critical for interpreting the mechanisms underlying its adaptive morphological variation.

Megacephaly is a rare and potentially vulnerable trait, as it often correlates with a significant dietary shift toward hard-shelled prey, promoting trophic specialization (Lindeman, 2000). The shift from generalist to specialist feeding strategies can increase a population's reliance on a narrow range of prey, heightening sensitivity to environmental change. Turtles that express the megacephalic trait may struggle to forage effectively if key prey items decline due external factors like habitat loss, invasive species, or other disturbances. Observations from other studies have described megacephalic *Emydura victoriae* individuals struggling to feed on aquatic vegetation, prompting remarks such as "what a tremendous disadvantage the megacephalic state becomes" (Cann & Sadlier, 2017; McKnight et al., 2023). This degree of ecological specialization, combined with narrower dietary and habitat requirements, may increase their vulnerability to anthropogenic stressors and elevate the risk of local extinction (Rodríguez-Caro et al., 2023).

1.5 Current Knowledge and Knowledge Gaps in Comal Springs Turtle Research

Despite the ecological significance of Comal Springs, Texas, research on its native turtle populations remains limited. A study conducted by Munscher et al. (2020) documented the diverse turtle assemblage within the spring ecosystem. Four native species were identified: the Eastern musk turtle (*Sternotherus odoratus*), Texas river cooter (*Pseudemys texana*), red-eared slider (*Trachemys scripta elegans*), and common snapping turtle (*Chelydra serpentina*). These species occupy distinct ecological niches, exhibit varied morphological and behavioral adaptations and face different levels of conservation concern. Munscher et al. (2019) identified *S. odoratus* as the most abundant turtle species in Comal Springs, estimating a remarkably high population density of approximately 1,690 individuals per hectare, among the highest ever recorded for this species. This population density far exceeds previous reports for *S. odoratus*, such as the 9.5 individuals/ha recorded at Ichetucknee Springs (Chapin and Meylan, 2011) and even surpasses the high densities of the congeneric *S. minor* reported in a similar spring ecosystem (461 individuals/ha, Munscher et al., 2019). In addition to its exceptionally high abundance, *S. odoratus* was the only species in the community to exhibit a male biased sex ratio. This skewed sex ratio could influence mating dynamics and long-term population viability, particularly if female recruitment is limited. The findings indicate that the turtle assemblage in Comal Springs is comparable in species richness to other well-studied freshwater spring habitats, such as Rainbow River in Marion County, Florida. This further emphasizes the ecological value and location of this unique spring system in the state of Texas.

1.6 Study Objectives and Predictions

Freshwater springs are ecologically unique and highly vulnerable systems, increasingly impacted by urban development and hydrological modification. The introduction of invasive species further disrupts these habitats by altering trophic dynamics and native species interactions. This research focuses on identifying associations between dietary composition and head morphology within the Comal Springs population of *Sternotherus odoratus* and aims to evaluate whether trophic shifts toward invasive snails correspond to altered growth patterns, phenotypic plasticity, or sexual dimorphism. To explore these relationships, the following predictions were tested:

1. Megacephalic individuals consume more invasive snails than non-megacephalic individuals.
2. Individuals consuming more invasive snails will exhibit larger heads and wider alveolar crushing surfaces.
3. Sex-based differences are expected in both dietary composition and the scaling of morphological traits.
4. Individuals from the extant population are expected to show morphological divergence in morphological traits compared to historical museum specimens.

2.0 Materials and Methods

2.1 Study Site: Comal Springs, Texas

Comal Springs is located in New Braunfels, Texas and is the largest spring system west of the Mississippi River (Crowe & Sharp Jr., 1997). Comal Springs lies within the Edwards Plateau Savanna Ecoregion and supports numerous federally protected species, including the fountain darter (*Etheostoma fonticola*), Comal Springs riffle beetle (*Heterelmis comalensis*), Comal Springs dryopid beetle (*Stygoparnus comalensis*) and Peck's cave amphipod (*Stygobromus pecki*) (Cooke et al., 2015; Crowe & Sharp Jr., 1997; Gibson et al., 2008; Huston et al., 2015; Olsen et al., 2016). It forms the headwaters of the Comal River and is comprised of multiple discharge points distributed along a 1,300-meter reach that creates Landa Lake (Gibson et al., 2008). Comal springs has undergone extensive impoundment and channelization, producing a habitat characterized by lentic conditions (Tolley-Jordan & Owen, 2008). Historical discharge measurements indicate an average flow of approximately 8,200 L/s between 1927 and 2005 (USGS), with earlier records from 1882 to 1926 suggesting even higher flows of up to 9,900 L/s (Brune, 1975, 1981). Studies conducted by the Edwards Aquifer Authority (EAA) in 2002 have shown that groundwater entering Comal Springs may travel from recharge areas as far as 225 km west. The age of discharged water can vary significantly, ranging from a few hours to multiple decades. With the exception of a six-month dry period in 1956, following a prolonged seven-year drought, the springs have maintained continuous flow (Brune, 1975, 1981).

2.2 Sampling Methods

Two sampling methods were used to effectively capture *S. odoratus.* Sampling was conducted from June 29th, 2024, to August 1st, 2024 in Texas, and focused on peak activity periods, while avoiding extreme temperatures and rain events. The first method used to collect *S.*

odoratus was active sampling, which involved snorkel surveys and conducting visual and tactile searches to locate and capture individuals by hand or with a dip net. Snorkel surveys were conducted in clear, calm water and with appropriate safety equipment and precautions. Sampling took place at regular intervals and durations, depending on weather conditions and turtle activity levels.

The second method used to capture *S. odoratus* was passive trapping. This method involved the use of low-cost, baited crayfish traps placed in accessible areas of waterbodies selected for sampling (Figure 7). Traps were baited with buffalo chicken and deployed in shallow water (1–3 meters deep), secured between two vertical poles driven into the substrate (Munscher et al., 2017). For most traps (including all those left overnight), a 150 mm section of foam pool noodle was placed inside to ensure that 15–30 cm of the trap remained above the water surface, allowing for any trapped turtles access to air, to prevent drowning. Bait was changed daily during trap checks. Each trap was labeled with the researcher's contact information and the Texas Parks and Wildlife Scientific Research Permit Number (SPR-0212-019) to minimize public interference or removal.

Some traps were fully submerged and allowed to rest on the river bottom. These traps were checked at two-hour intervals to ensure that no turtle remained without access to air for a duration that could result in mortality. Upon inspection, captured individuals were promptly removed and placed in a 102 L plastic tote with 5–8 cm of river water and were transported back to the lab. All capture and handling protocols were approved by the Texas Parks and Wildlife Department (Scientific Permit Number SPR-0212-019) and the York University Animal Care Committee (Certificate Number 2024-10).

2.3 Data Collection: Body Morphometrics

A total of 71 *S. odoratus* (40 males, 31 females) were captured during the June 29th, 2024, to August 1st, 2024 sampling period of this study. Capture status (new or recapture) was recorded for each individual. Recaptures were identified by the presence of marginal scute notches and/or detection of a pre-existing PIT (Passive Integrated Transponder) tag using a Yanzeo AR180, EMID Fox-B compatible handheld PIT tag reader. Each turtle was measured for standard body morphometrics, including sex (M/F), maximum carapace length (CL max), straight-line carapace length, carapace width (CW), shell height (SH), maximum plastron length (PL max), straight-line plastron length (SPL) and mass (g) (Table 1, Figure 8). Carapace and plastron dimensions were recorded using Haglöf Mantax Tree Calipers. Body mass was measured with a CGOLDENWALL High Precision Digital Lab Scale. Cranial morphometrics were measured for head width (HW), alveolar width (AW) and alveolar height (AH) (Table 1, Figure 9). Head width and alveolar measurements were obtained using a FineSource Electronic Digital Caliper (0–150 mm). Head trait phenotype was recorded as either MEGA for megacephalic individuals or NON for non-megacephalic individuals. All individuals were also checked for overall health and body condition, noting any areas of damage, leech load, and other abnormalities (Figure 10).

In addition to data collected during the field sampling period, two additional datasets were incorporated to provide temporal context and broaden the scope of the analyses. The first dataset consisted of long-term monitoring data provided by the Turtle Survival Alliance – North American Freshwater Turtle Research Group (TSA–NAFTRG), which surveys Comal Springs as part of its volunteer-based long-term science program. The TSA–NAFTRG long-term dataset

(2012–2020) includes standard body morphometric (SCL, CW, SPL, SH, mass and sex) and head width (HW) measurements for 1,659 individuals (n = 1,157 males, 502 females).

The second dataset is comprised of museum specimen records (1940–1989). A total of 31 *S. odoratus* individuals were collected and preserved from Comal and adjacent counties in central Texas. This data was obtained through requests to multiple natural history collections including Mayborn Museum Complex, Texas Cooperative Wildlife Collection, and Texas Natural History Collections. The datsete includes specimen metadata such as object name, collection date, locality, collector, descriptive notes and two morphometric measurements, head width (HW) and straight-line carapace length (SCL). These historical records were used to provide a baseline for comparison of morphological traits over time.

2.4 Data Collection: Fecal Samples

Dietary data were obtained through the collection of 71 live *S. odoratus* via fecal samples. All fecal samples were collected from *S. odoratus* individuals that were captured earlier in the day. Captured individuals were housed for up to 24 hours in individual plastic containers with a capacity of approximately 0.9 liters. The container was filled with 3–4 cm of distilled water, or enough to reach approximately halfway up the turtle's shell height. A single individual *S. odoratus* was placed inside the plastic container which was then stored at ambient room temperature and out of direct sunlight. Containers were labeled with turtle ID, date, time, and location of capture. Containers were sealed with two rubber bands to prevent *S. odoratus* from pushing open the lid of the plastic container and escaping (Figure 11). Water with feces were filtered using a disposable coffee filter and changed every 12 hours, either until a 12-hour period passed without fecal output or until the 24-hour holding window ended (Figure 12). After a fecal sample was obtained, all *S. odoratus* individuals were released at their exact site of capture.

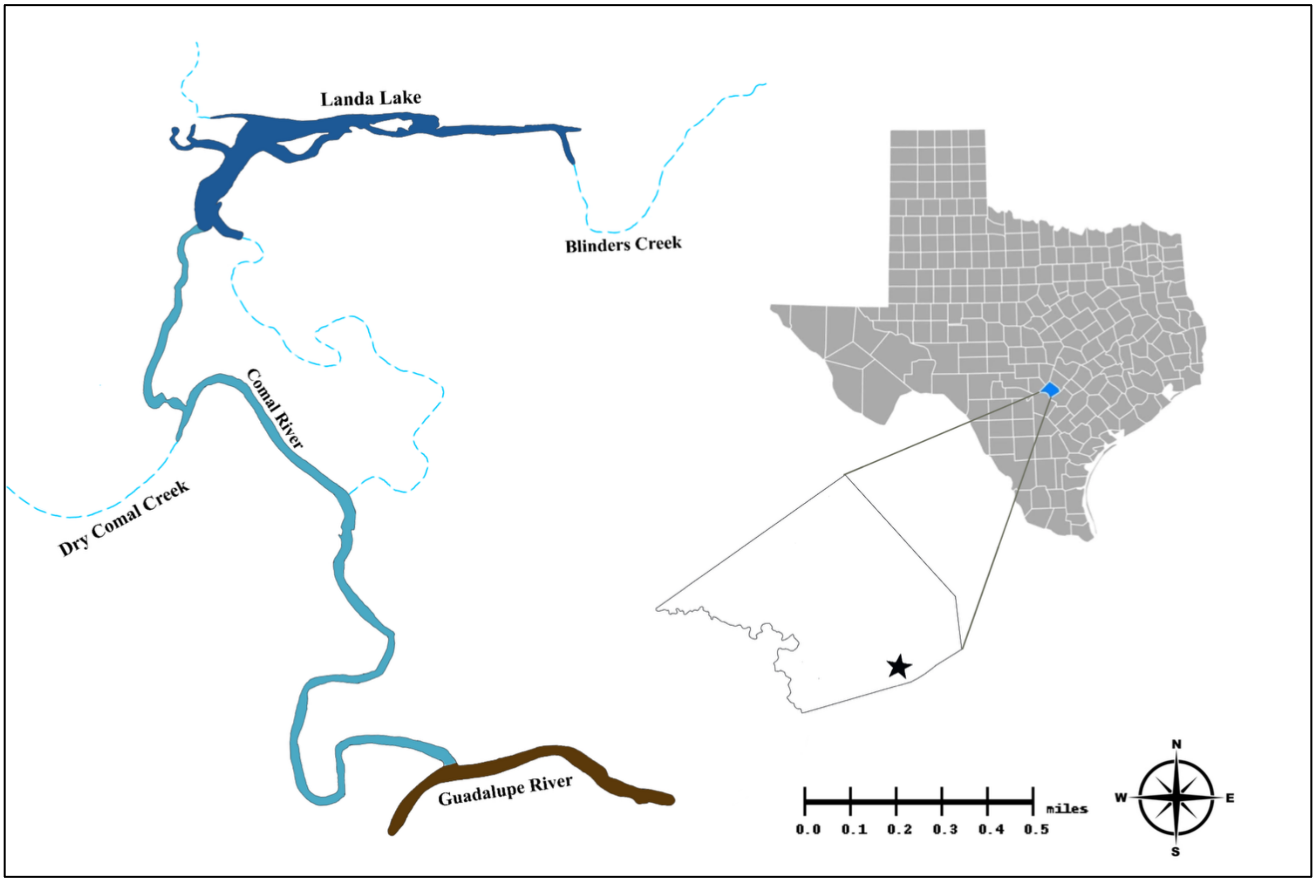

Figure 6. Map of the Comal Springs River system in Comal County, Texas, USA. Map shows Landa Lake and its associated tributaries, including Blinders Creek and Dry Comal Creek. The Comal River flows southeast into the Guadalupe River. The inset map shows the location of Comal County (blue dot) within Texas. The enlarged black star indicates the location of Comal Springs in the county map. Stream segments are colored by type: Landa Lake (dark blue), Comal River (light blue), tributaries (dashed light blue), and the Guadalupe River (brown).

Figure 7. Baited crayfish trap setup used for passive capture of *Sternotherus odoratus* in Comal Springs, Texas, USA. Traps were deployed in accessible areas of selected waterbodies and secured with rope to two poles to prevent drifting away, facilitating stable placement and retrieval.

Trait	Code	Definition	Unit
Body morphometric trait			
Sex	–	Biological sex of the individual, determined by external secondary sexual characteristics (M = male, F = female, J = juvenile)	–
Maximum carapace length	CL max	The longest dimension of the carapace, measured with the top end of the calipers aligned parallel to the anterior marginal scutes and the bottom end aligned parallel to the posterior marginal scutes to capture the furthest overall length of the shell.	mm
Straight-line carapace length	SCL	Straight-line distance from the anterior nuchal notch to the posterior margin of the carapace.	mm
Carapace width	CW	Maximum lateral width of the carapace measured at its broadest point.	mm
Shell height	SH	Maximum vertical height of the shell measured from the plastron to the highest point of the carapace.	mm
Maximum plastron length	PL max	The longest dimension of the plastron, measured with the top end of the calipers aligned parallel to the anterior edge of the gular scutes and the bottom end aligned parallel to the posterior edge of the anal scutes to capture the furthest overall length of the plastron.	mm
Straight-line plastron length	SPL	The straight-line distance between the anterior and posterior margins of the plastron, measured from the midline between the gular scutes at the anterior to the midline between the anal scutes at the posterior.	mm
Mass	–	The body mass of each turtle measured in grams	g
Head morphometric trait			
Head width	HW	Maximum width of the head at the widest point behind the eyes	mm
Alveolar width	AW	Maximum width across the upper alveolar (jaw) surfaces	mm
Alveolar height	AH	Vertical distance from the lower to upper alveolar margins at the midline	mm

Table 1. Body and head morphometric traits measured in mature male, female, and juvenile eastern musk turtles (*Sternotherus odoratus*) from Comal Springs. Also see Figures 8 and 9 for visual representation of measured traits.

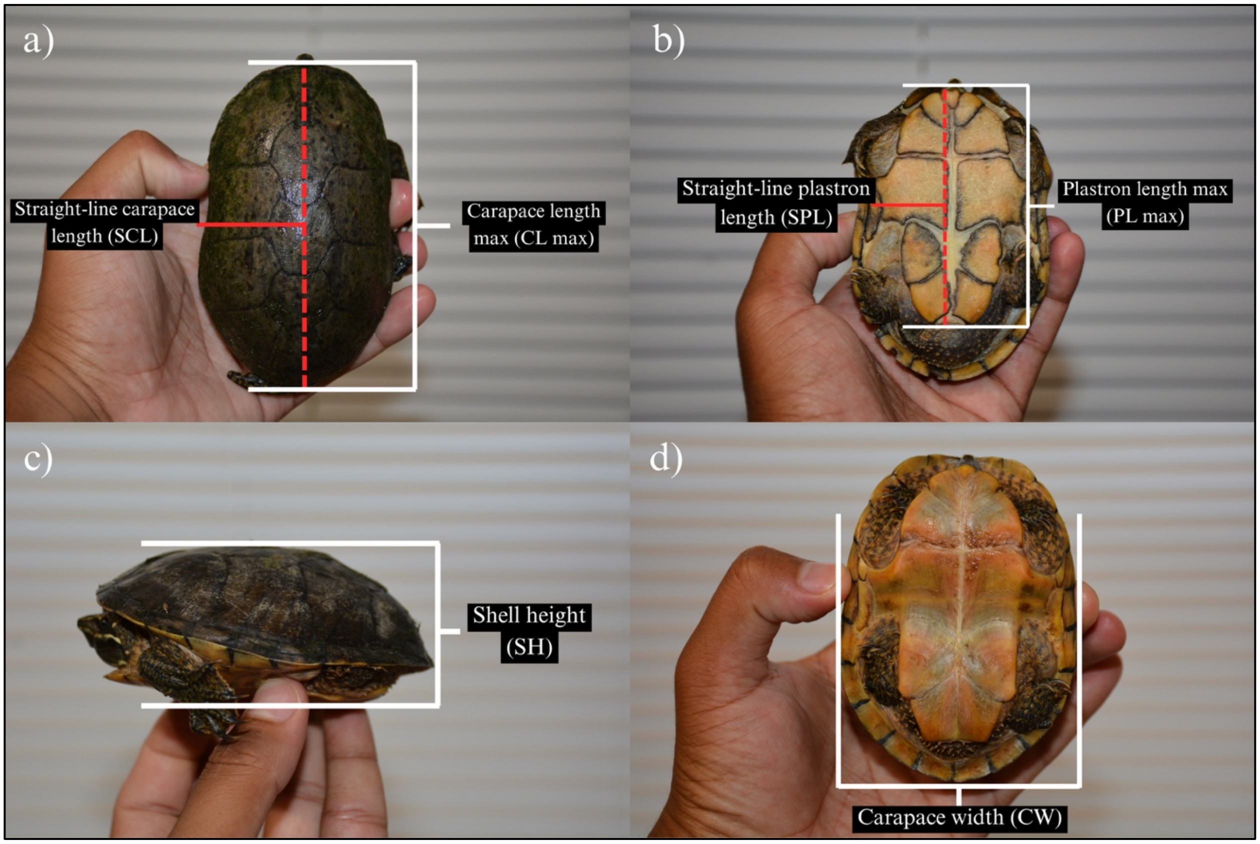

Figure 8. Visual representation of standard body morphometric traits measured in *Sternotherus odoratus*. (a) Carapace length max (CL max) and straight-line carapace length (SCL) measured along the midline of the carapace; (b) Plastron length max (PL max) and straight-line plastrong length (SPL) measured along the plastron midline; (c) Shell height (SH) measured from the highest point of the carapace to the plastron; and (d) Carapace width (CW) measured at the widest point of the shell.

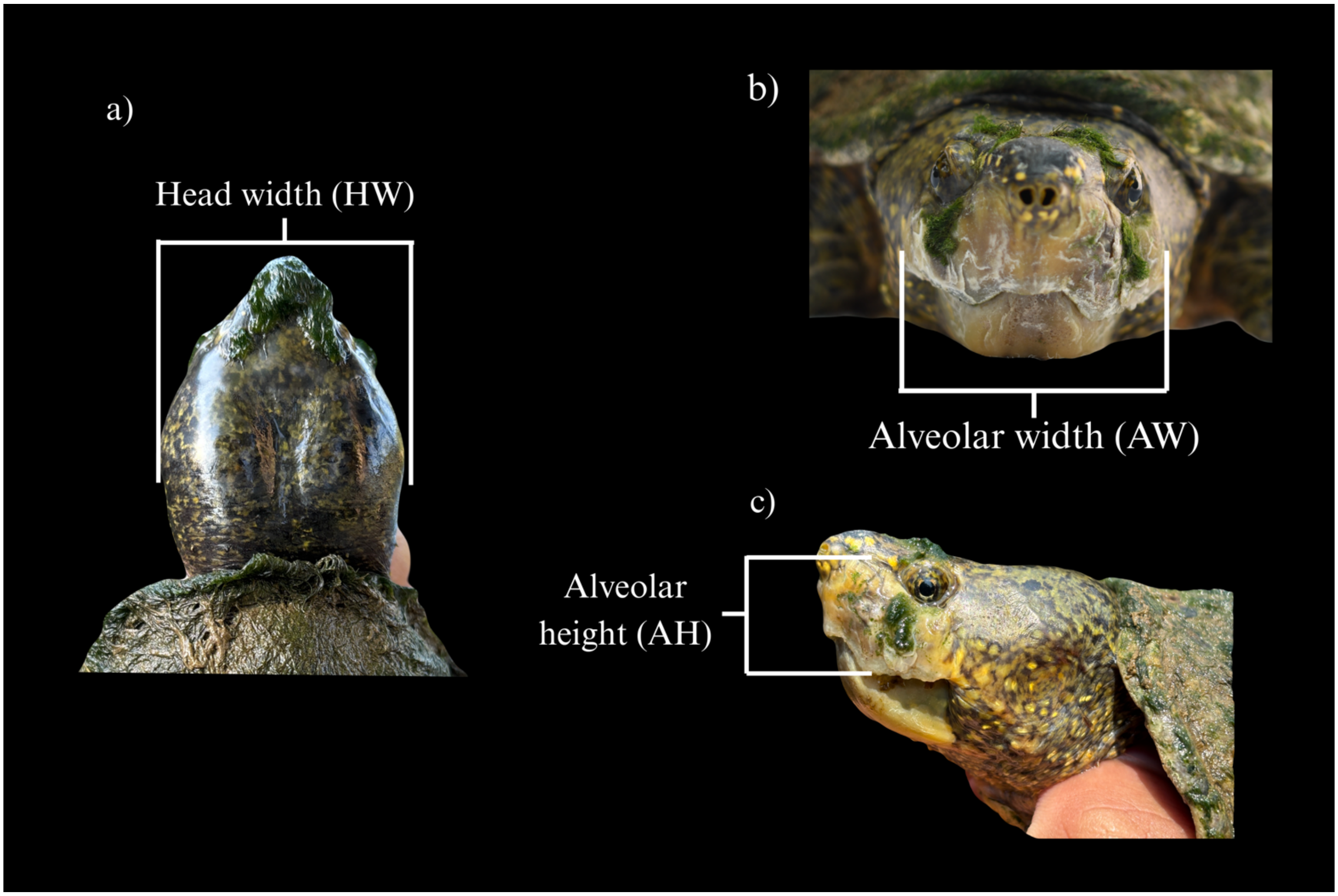

Figure 9. Head morphometric measurements taken from *Sternotherus odoratus*. (a) Head width (HW) measured at the widest point posterior to the eyes; (b) Alveolar width (AW) measured across the crushing surfaces of the maxilla; and (c) Alveolar height (AH) measured vertically from the alveolar surface to the ventral margin of the jaw. All measurements were obtained using a FineSource Electronic Digital Caliper (0–150 mm). White lines indicate the placement of digital calipers during measurement.

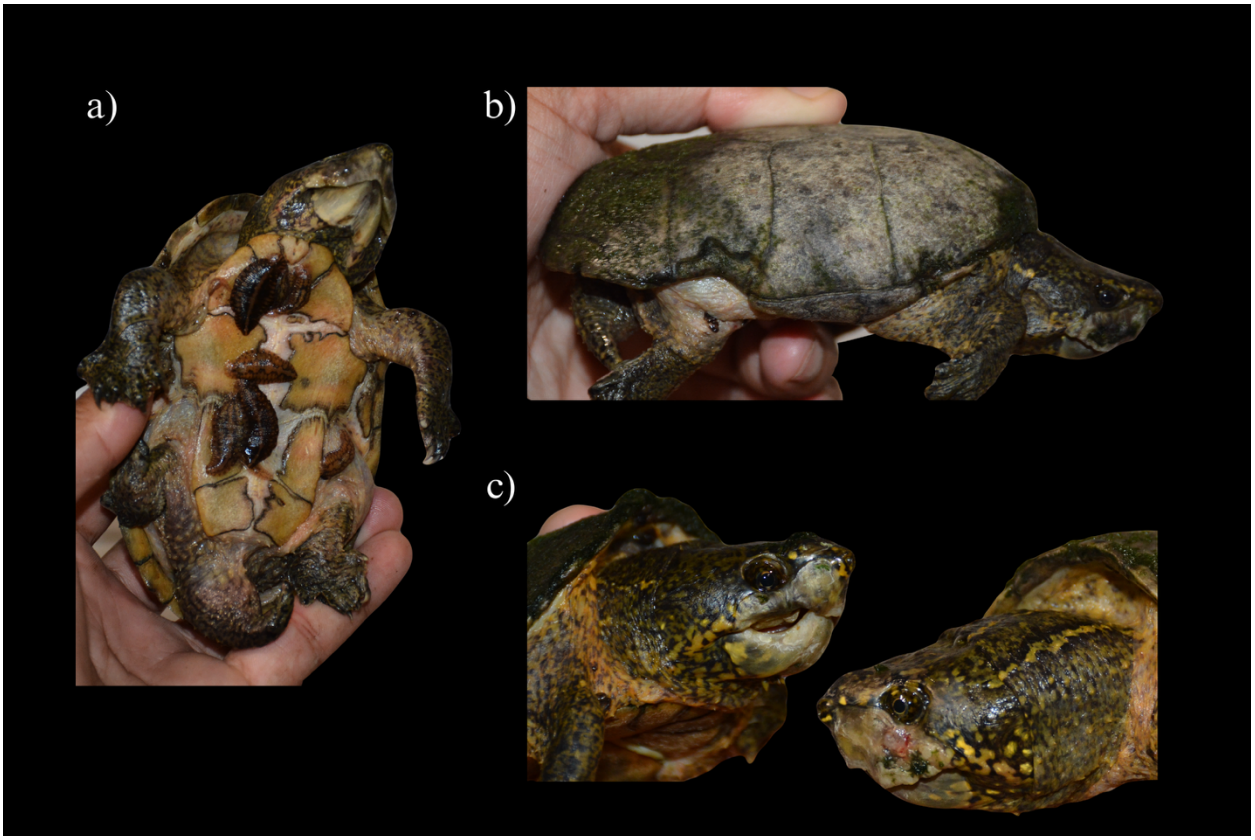

Figure 10. Examples of observed external conditions in *Sternotherus odoratus* from Comal Springs, Texas. (a) Ventral view of an adult male exhibiting a heavy leech load on the plastron. (b) Healed carapace damage extending into marginal and costal scutes on the right lateral margin. (c) Examples of keratin damage to the beak, including worn, irregular edges and scabbing/bleeding.

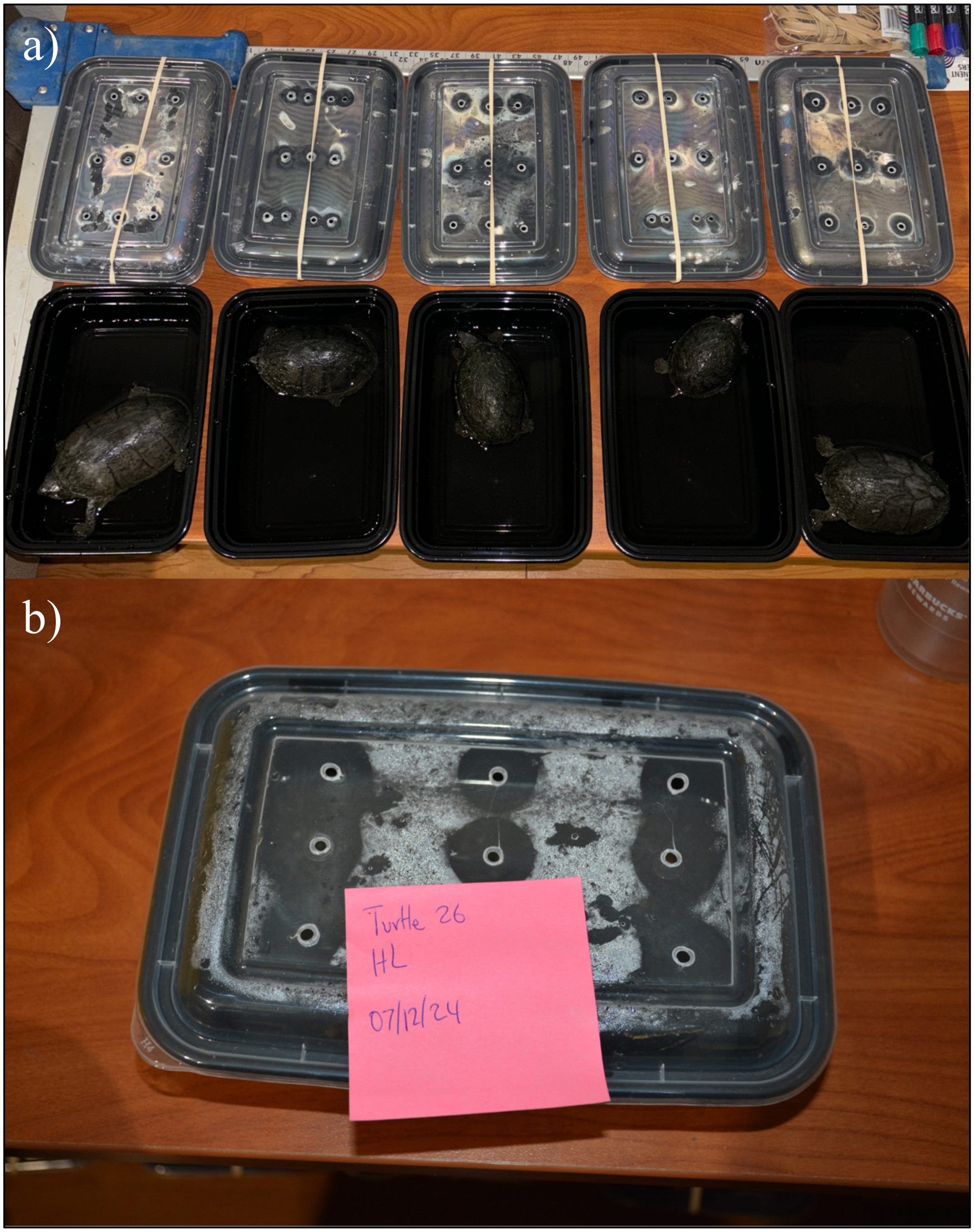

Figure 11. (a) Example of 24 hr individual turtle housing used during fecal collection. Each turtle was placed in a labeled plastic container (~0.9 L capacity) with 4 cm of distilled water at ambient room temperature. (b) Containers were labeled with turtle ID, date, and location of capture and sealed with rubber bands to prevent escape.

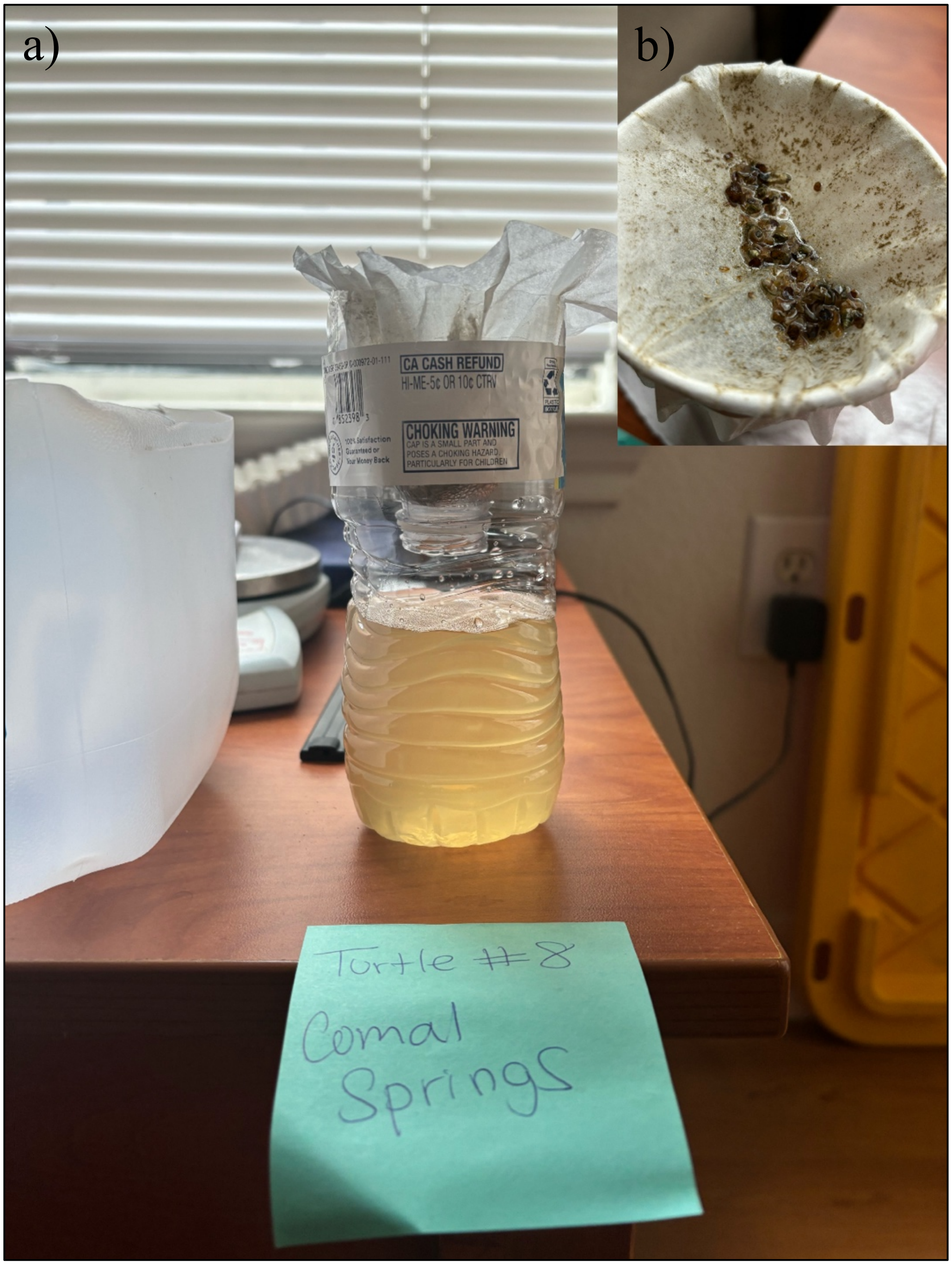

Figure 12. (a) Fecal sample filtration setup using a disposable coffee filter containing material collected from an individual *Sternotherus odoratus*. Filters were used to strain fecal matter from 4 cm of distilled water in each container. (b) Fecal particulates left behind after passing through the filter. These particulates are then left to sit and dry for 24 hours before being transferred into a 5 ml vial.

2.5 Fecal Sample Preservation and Analysis

Fecal material from each turtle was preserved in 70% ethanol and stored in 5 mL vials labeled with the date, time, capture location, and turtle identification number (Figure 13). Vials were kept in a cool, dark place until transfer and processing in the laboratory. Dietary items in the fecal samples were sorted and identified to the lowest Operational Taxonomic Units (OTUs) using a Walter Products WP-1F® zoom stereo microscope at up to 45× magnification. Processing began by gently emptying the preserved sample into a Cole-Parmer Aluminum Smooth-Walled Weighing Dish and examining it under the dissection microscope. Using fine-tipped tweezers the larger and more intact gastropod shells were removed first. Each shell was placed into its own labeled weighing dish according to species for later weighing. The analysis then proceeded sequentially from the largest visible fragments to progressively smaller material, ensuring that all identifiable shells were separated before moving to finer shell fragments. When only minute, dust-like shell fragments remained, these were pooled into a separate dish and recorded as unidentified gastropods (Figure 14). Other dietary items, such as arthropod remains, plant material, and miscellaneous organic matter, were separated from the gastropod material and grouped into their respective categories. Macroscopic sorting included washing, sieving, and hand-sorting the feces to identify items based on shape, structure, and appearance (Figure 15). The contents of each vial were then dried and weighed to the nearest 0.001 g using an OHAUS Adventurer® Balance Scale, and the weight of each taxon was measured following OTU identification.

Figure 13. Preserved fecal samples stored in 5 ml vials containing 70% ethanol. Each vial was labeled with the individuals identification number, date, and capture location for dietary analysis.

Figure 14. Example of unsorted fecal material from *Sternotherus odoratus* showing larger shell fragments primarily composed of *Pyrgulopsis* sp. and *Tarebia granifera*, algal material, and fine "shell dust" consisting of minute, unidentifiable gastropod fragments recorded as "unidentified snails."

Figure 15. Fecal samples, depicting varying levels of fecal amount and composition, were spread on dishes for microscopic analysis. Samples were dried and hand-sorted to identify dietary items based on morphology, color, texture, size, and weight.

3.0 Results

3.1 Diet Composition and Sex-Based Differences

Head width distributions were analyzed to evaluate whether morphometric variation supported discrete megacephalic and non-megacephalic groupings (n = 71, MEGA = 38, NON = 33). A Hartigan's Dip Test was used to test for departures from unimodality in order to objectively assess the shape of the head width distributions. The test returned no evidence of bimodality (D = 0.031, *p* = 0.92). A Gaussian mixture modelling (GMM) was applied to further evaluate potential clustering. The GMM fits probabilistic normal components and identifies the most parsimonious model based on the Bayesian Information Criterion (BIC). The GMM supported a single normal component (log-likelihood = –207.92, BIC = –424.36), indicating that head widths varied along a continuous gradient rather than forming two statistically distinct modes (Figure 16). The predictive strength of head width as a classifier of phenotype was then assessed using a receiver operating characteristic (ROC) analysis, which quantifies the discriminatory performance of a continuous variable. The ROC curve yielded an area under the curve (AUC) of 0.98, indicating near-perfect separation between megacephalic and non-megacephalic individuals. The optimal Youden threshold (24.35 mm) corresponded closely with the visually determined 24.5 mm cutoff and achieved high classification performance (accuracy = 0.94, sensitivity = 0.89, specificity = 1.00).

Broad dietary trends reveal clear differences in prey composition between megacephalic and non-megacephalic *S. odoratus* (Figure 17). We conducted a dietary analysis of *Sternotherus odoratus* using fecal samples and identified prey items across five major taxonomic categories: gastropods, bivalves, arthropods, vegetation, and other material. A total of 17 prey taxa were recorded. Gastropods represented the largest overall category for both sexes, followed by vegetation, arthropods, bivalves, and other items. While gastropods dominated the diet of both phenotypes, megacephalic individuals consumed them at a notably higher proportion (77.8%) compared to non-megacephalic individuals (68.7%). In contrast non-megacephalic individuals showed a more balanced diet, with higher relative intake of bivalves (6.6%), arthropods (6.5%), and vegetation (17.6%), suggesting a more generalized foraging strategy.

Refining the analysis to a finer taxonomic scale reveals clearer dietary differences between the two phenotypes (Figure 18). Quilted melania (*Tarebia granifera*) made up 58.3% of the megacephalic individuals' diet, compared to only 38.2% in non-megacephalic individuals. Invasive gastropods (*Tarebia granifera*, *Melanoides tuberculata* and *Marisa cornuarietis*) accounted for a greater proportion of the diet in megacephalic turtles (67.4%) than in non-megacephalic turtles (51.6%), while native gastropods (*Pyrgulopsis* spp., *Physella acuta* and *Elimia comalensis*) contributed comparatively less (32.6% and 48.4%, respectively). Other items such as *Pyrgulopsis* sp. and *Procambarus clarkii* were also more prominent in megacephalic individuals. Non-megacephalic individuals consumed a greater diversity of items, including plant seeds (*Ludwigia repens*), bivalves (*Corbicula fluminea*), and other minor prey taxa (unidentified plant material and unidentified insects).

A non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis dissimilarities was used to visualize fine scale dietary composition across head forms (Figure 19). Prey count data were log-transformed prior to analysis, and the dataset comprised individual turtle diet profiles, including counts of all identified prey taxa (gastropods, arthropods, bivalves, plant material and other) standardized by total prey items per individual turtle. Ellipses represent 95% confidence intervals for each head form group. A permutational multivariate analysis of variance (PERMANOVA; *adonis2* function, *vegan* package v2.6-4; Oksanen et al., 2015) with

999 permutations detected no significant difference in overall diet composition between head forms ($F_{1,69} = 1.381$, $R^2 = 0.0196$, $p = 0.228$).

A non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis dissimilarities was used to visualize variation in broad diet composition between head forms (Figure 20). Diet composition was summarized into five prey categories (gastropods, bivalves, arthropods, vegetation, and other prey) and expressed as relative proportions per individual turtle. The two-dimensional NMDS ordination provided a good representation of dietary dissimilarity (stress = 0.071). Points represent individual turtles, with polygons enclosing head-form groups. The ordination revealed substantial overlap between megacephalic and non-megacephalic individuals, indicating limited differentiation in diet composition. Consistent with this visual pattern, an analysis of similarity (ANOSIM; vegan package v2.6-4; Oksanen et al., 2015) based on 999 permutations detected no significant difference in overall diet composition between head forms ($R = -0.017$, $p = 0.882$, $n = 71$).

The Index of Relative Importance (IRI) was calculated to evaluate the contribution of each prey taxon to the diet. The Index of Relative Importance integrates three metrics: percent by number *(%N*), percent by weight (*%W*), and percent frequency of occurrence (*%F*):

$$IRI = \%N + \%W + \%F$$

Percent IRI was then calculated to standardize values across all prey taxa:

$$\%IRI = \frac{IRI}{\sum IRI} \times 100$$

We calculated *%N* from prey counts, *%W* using biomass measurements, and *%F* from the proportion of samples containing each prey item. Values were computed separately for males and females to assess sex-specific dietary patterns (Table 2). In males the highest IRI values were recorded for gastropods (143.47), vegetation (109.96), arthropods (101.72), and *Tarebia granifera* (84.22). Other notable items included *Pyrgulopsis* sp. (66.72), *Procambarus clarki* (52.16), *Marisa cornuarietis* (50.47), and algae (57.94). In females, vegetation (155.36), arthropods (110.30), *Pyrgulopsis* sp. (91.97), and gastropods (142.79) ranked highest. Additional important items included *Tarebia granifera* (73.13), *Procambarus clarki* (58.74), *Marisa cornuarietis* (57.57), and algae (62.23). *Elimia comalensis* occurred in both sexes (M: 26.20; F: 41.36), while *Melanoides tuberculata* showed lower values (M: 22.75; F: 25.91). The only bivalve recorded was *Corbicula fluminea* (M: 8.23; F: 22.51). Items in the "other" category were more prominent in males (90.48) than in females (53.88), with rocks being the main contributor.

All gastropod prey items were categorized as either invasive or native species, and a Beta regression was performed using the proportion of invasive gastropods in each individual's diet as the response variable. Megacephalic turtles exhibited a slightly higher mean proportion of invasive snails (0.47 ± 0.44, $n = 38$) compared to non-megacephalic turtles (0.39 ± 0.41, $n = 33$), but the difference was not statistically significant ($\beta = 0.07 \pm 0.08$, $z = 0.95$, $p = 0.34$; Pseudo $R^2 = 0.017$). A Wilcoxon rank-sum test supported this result ($W = 724$, $p = 0.26$). Although the trend was in the predicted direction, high within-group variability indicates that head form alone does not strongly predict the proportion of invasive prey consumed.

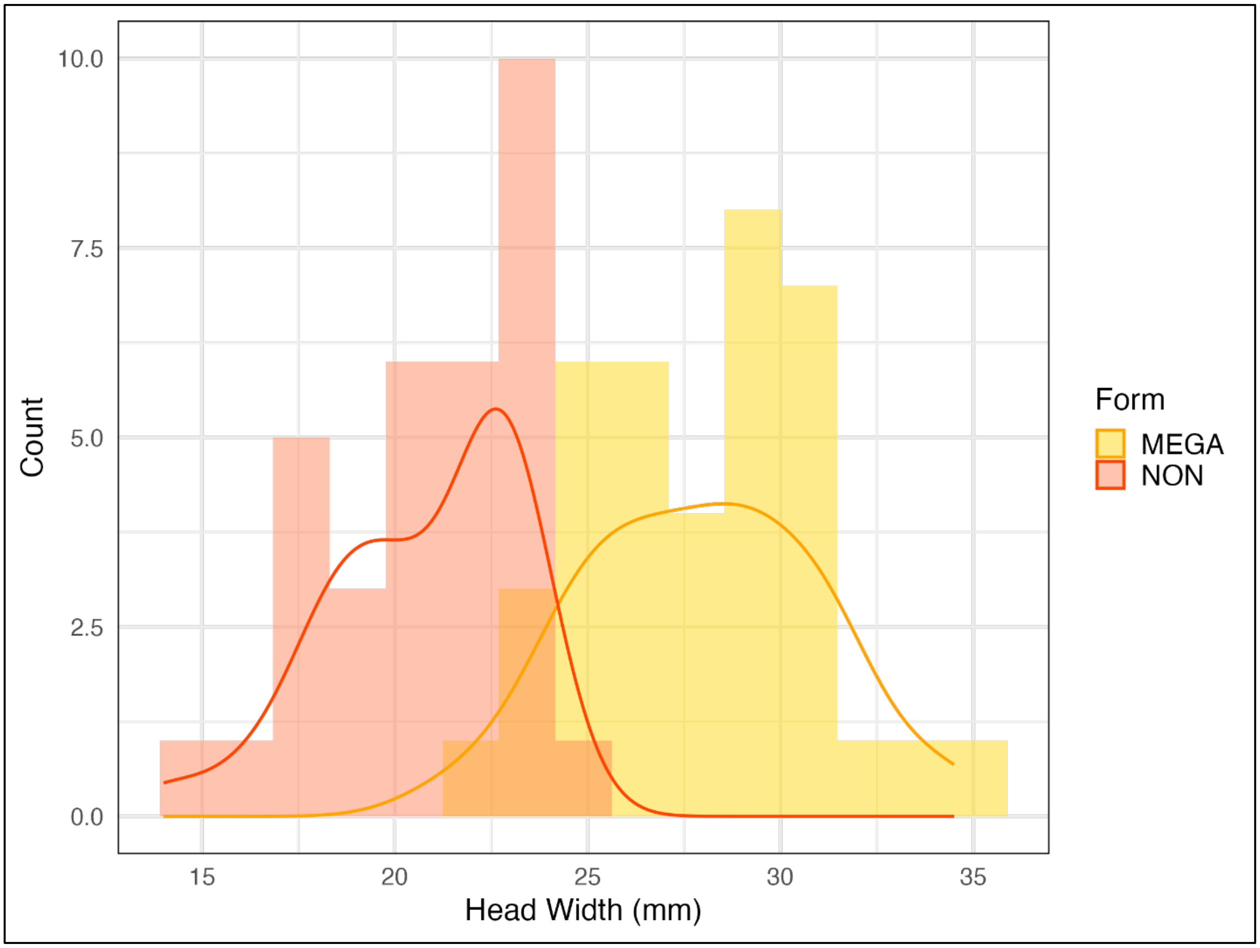

Figure 16. Distribution of head width (HW, mm) in *Sternotherus odoratus* classified as megacephalic (MEGA, yellow) and non-megacephalic (NON, red). Histogram bars represent individual counts; overlaid density curves illustrate the distribution shape for each group. n = 71 individuals sampled from Comal Springs, Texas, USA (June–August 2024).

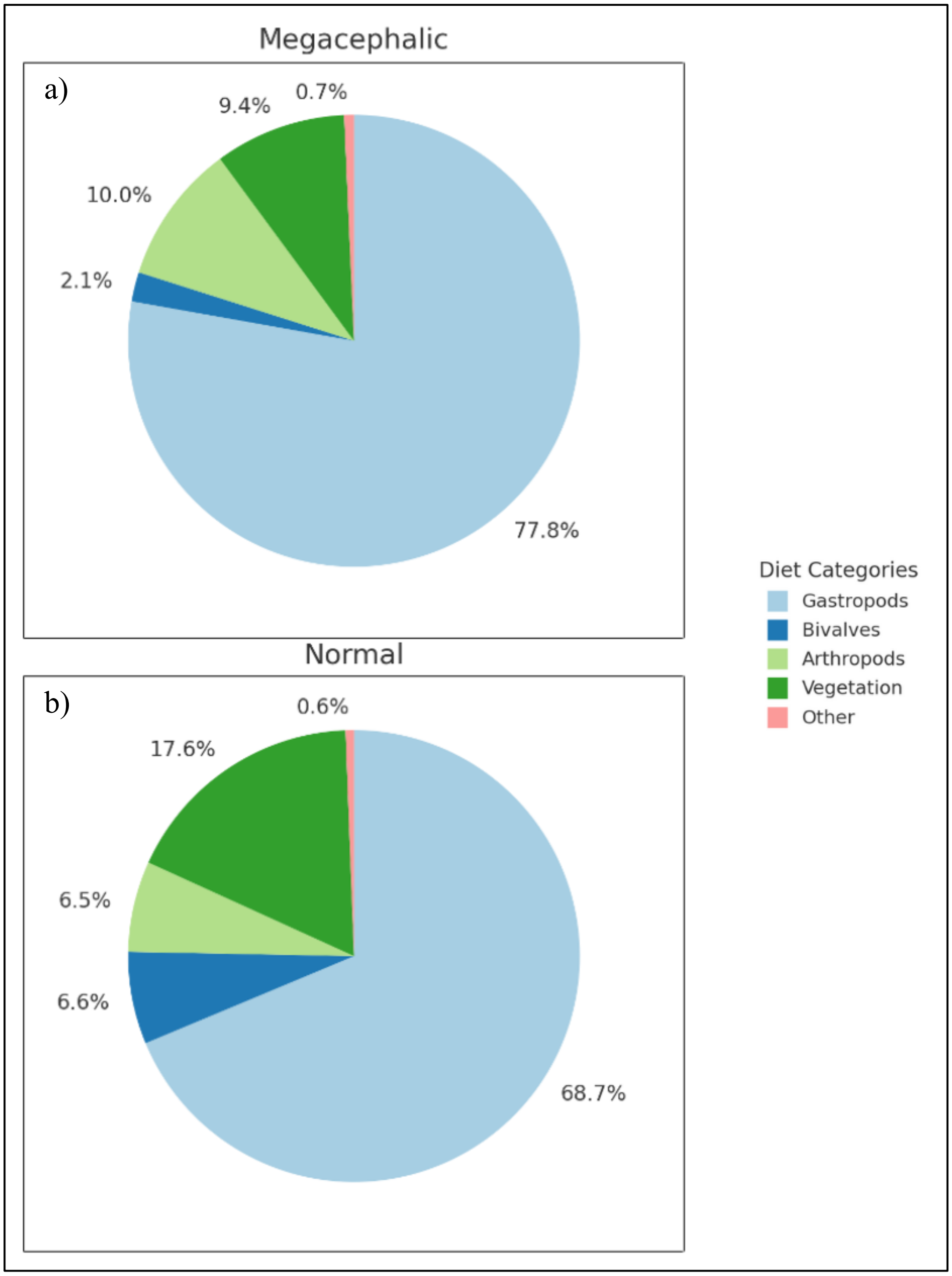

Figure 17. Proportional representation of major diet categories in *Sternotherus odoratus* classified as (a) megacephalic and (b) non-megacephalic (normal). Pie charts show dietary composition based on fecal analysis, categorized into 5 major taxonomic groups: gastropods, bivalves, arthropods, vegetation, and other items.

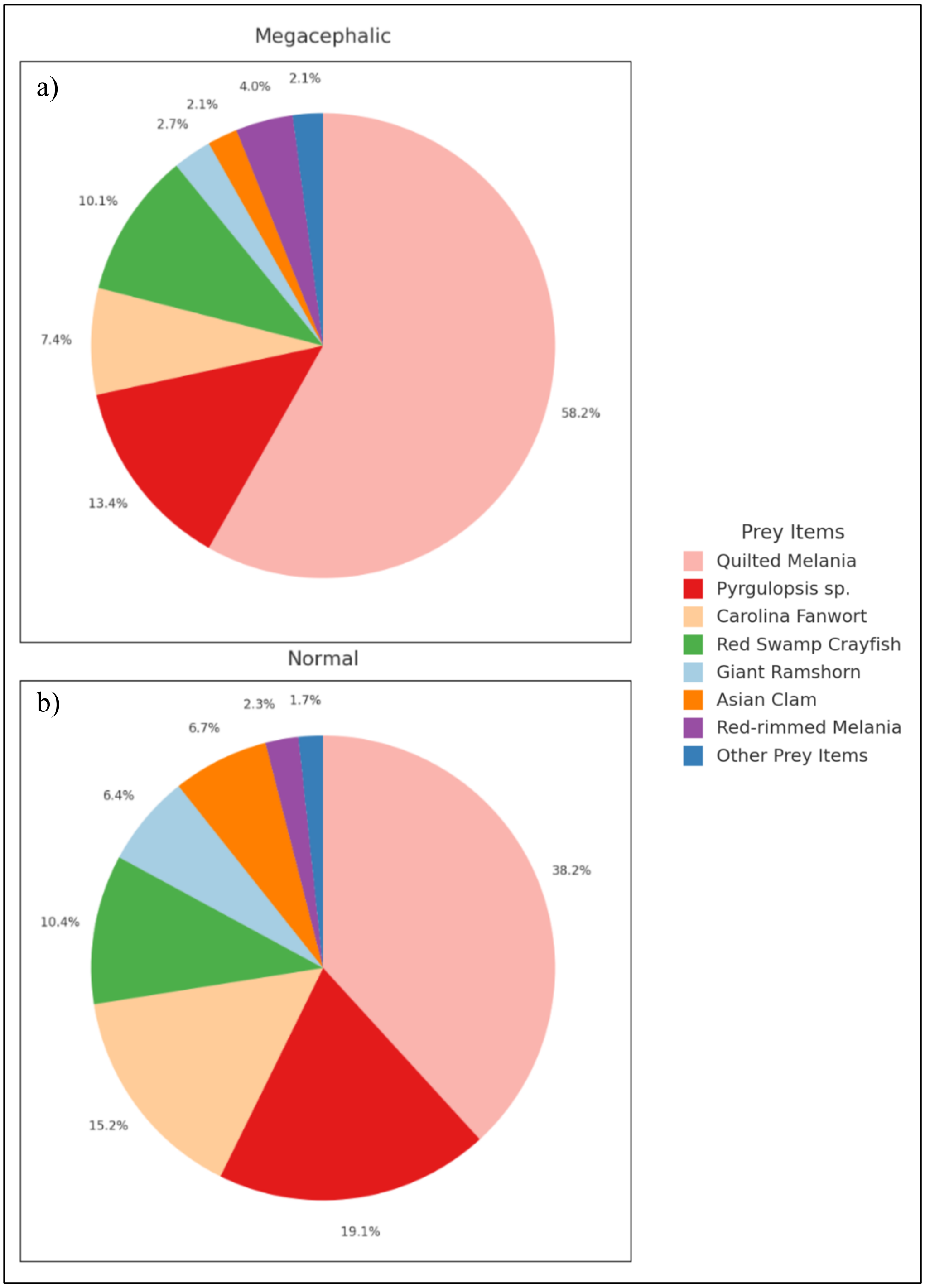

Figure 18. Proportional representation of fine-scale dietary items consumed by *Sternotherus odoratus* classified as (a) megacephalic and (b) non-megacephalic (normal). Percentages reflect relative abundance of prey items within fecal samples. Prey items included one species of bivalve *Corbicula fluminea*, invasive gastropods *Tarebia granifera, Melanoides tuberculata*, and *Marisa cornuarietis*. Native gastropods include *Pyrgulopsis sp.* Aquatic vegetation includes *Cabomba caroliniana* seeds. Invertebrates include *Procambarus clarki*.

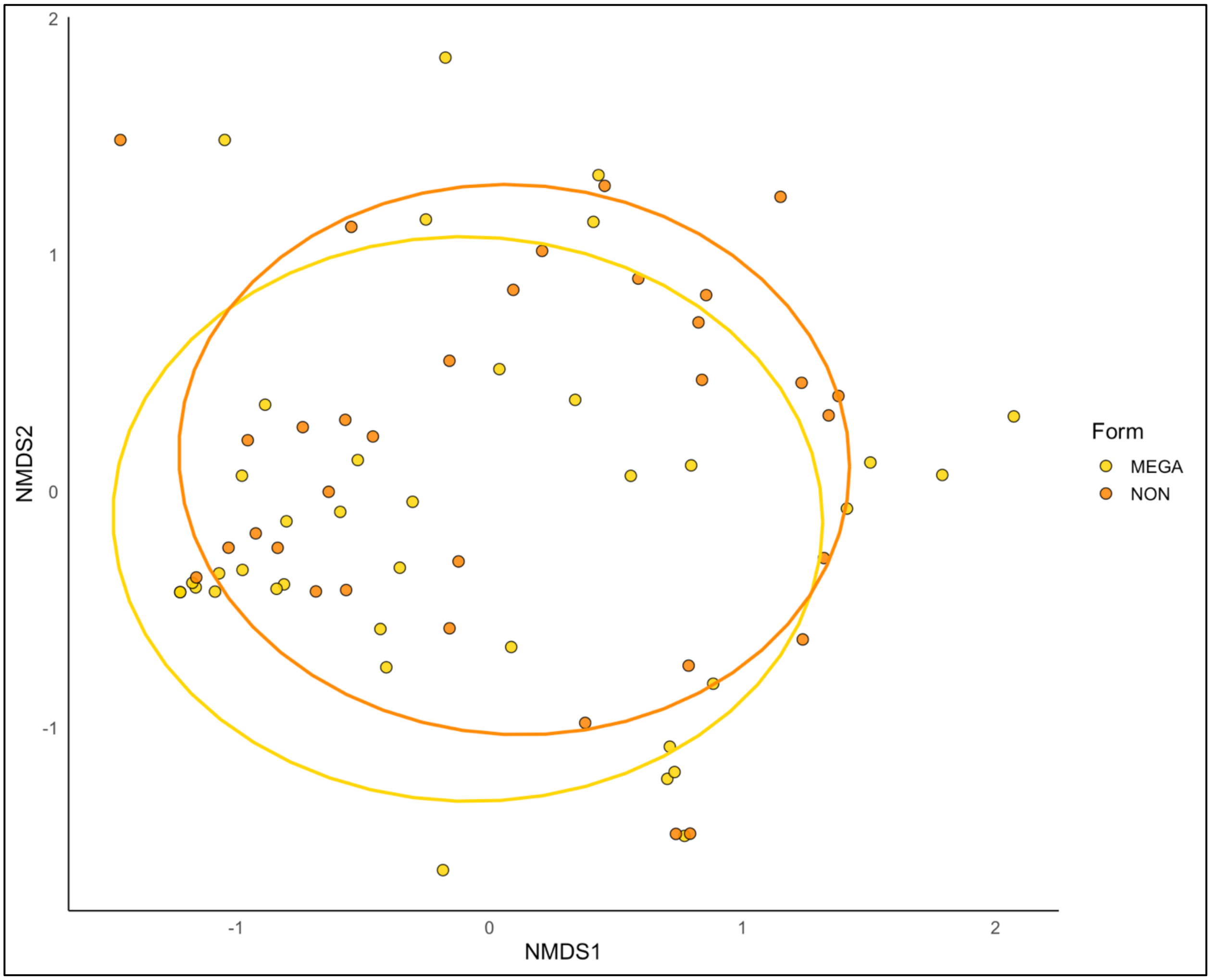

Figure 19. Non-metric multidimensional scaling (NMDS) ordination of fine scale dietary composition in *Sternotherus odoratus* based on Bray–Curtis dissimilarities of log-transformed prey count data. Points represent individual turtles, with colors indicating head form: MEGA (megacephalic, yellow) and NON (non-megacephalic, orange). Ellipses indicate 95% confidence intervals for each form group.

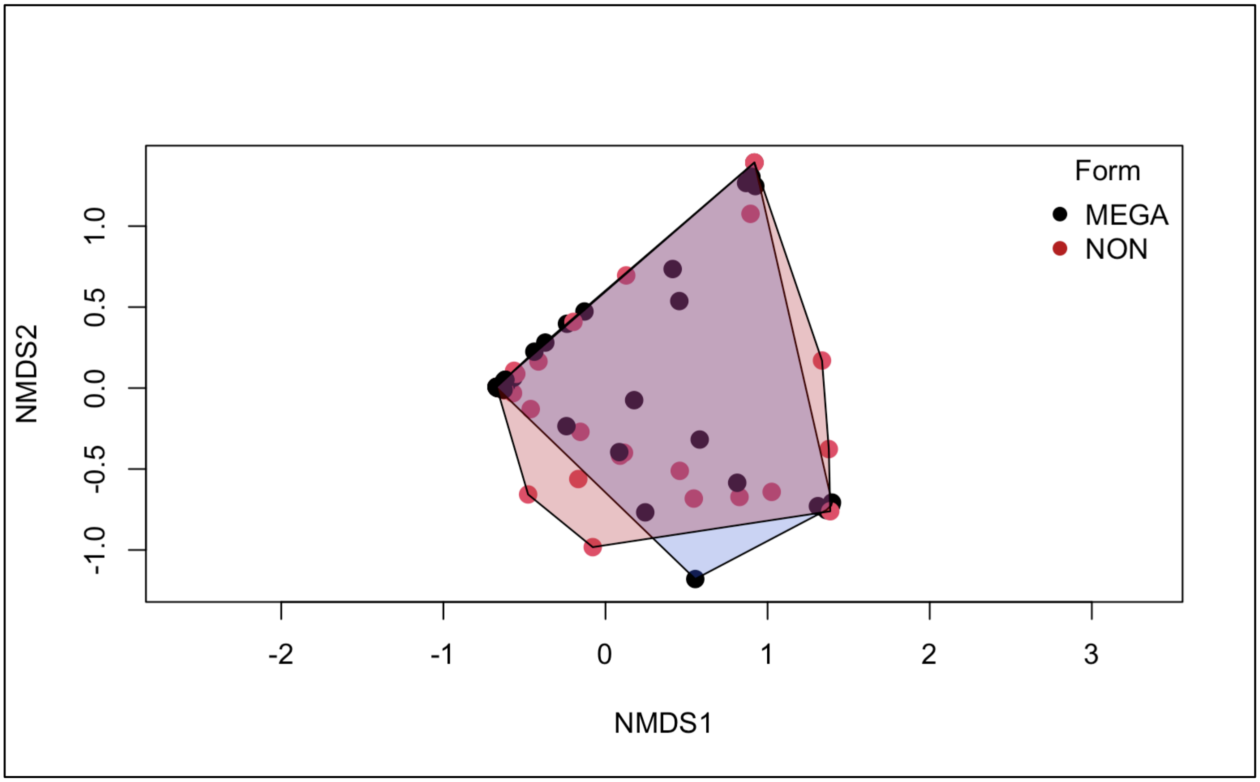

Figure 20. Non-metric multidimensional scaling (NMDS) ordination of broad dietary composition in *Sternotherus odoratus* based on Bray–Curtis dissimilarities of proportional prey data (gastropods, bivalves, arthropods, vegetation, and other prey). Points represent individual *Sternotherus odoratus*, with colors indicating head form: MEGA (megacephalic, black) and NON (non-megacephalic, red). Polygons outline the dietary space of each form group.

Taxon	Total Weight (M / F)	Frequency (M / F)	Percent Weight (M / F)	Percent Freq (M / F)	Index of Relative Importance (M / F)
Gastropods	18037.60 / 15888.20	35 / 29	55.97 / 49.24	87.50 / 93.55	143.47 / 142.79
Tarebia granifera	13093.00 / 7553.00	21 / 17	31.72 / 18.30	52.50 / 54.84	84.22 / 73.13
Melanoides tuberculata	1134.00 / 44.00	8 / 8	2.75 / 0.11	20.00 / 25.81	22.75 / 25.91
Marisa cornuarietis	1226.00 / 1126.00	19 / 17	2.97 / 2.73	47.50 / 54.84	50.47 / 57.57
Pyrgulopsis sp.	1743.20 / 4675.00	25 / 25	4.22 / 11.32	62.50 / 80.65	66.72 / 91.97
Elimia comalensis	526.30 / 1173.00	10 / 12	1.20 / 2.65	25.00 / 38.71	26.20 / 41.36
Physella acuta	15.10 / 13.20	6 / 6	0.04 / 0.03	15.00 / 19.35	15.04 / 19.39
Bivalves	300.00 / 1304.00	3 / 6	18.70 / 81.30	7.50 / 19.35	26.20 / 100.65
Corbicula fluminea	300.00 / 1304.00	3 / 6	0.73 / 3.16	7.50 / 19.35	8.23 / 22.51
Arthropods	1929.10 / 1629.10	19 / 20	54.22 / 45.78	47.50 / 64.52	101.72 / 110.30
Procambarus clarki	1923.00 / 1611.10	19 / 17	4.66 / 3.90	47.50 / 54.84	52.16 / 58.74
Stygoparnus comalensis	5.00 / 7.00	2 / 4	0.01 / 0.02	5.00 / 12.90	5.01 / 12.92
Unidentifed insect	1.10 / 11.00	2 / 1	0.00 / 0.03	5.00 / 3.23	5.00 / 3.25
Vegetation	1824.10 / 3393.20	30 / 28	34.96 / 65.04	75.00 / 90.32	109.96 / 155.36
Algae	183.10 / 389.10	23 / 19	0.44 / 0.94	57.50 / 61.29	57.94 / 62.23
Hydrilla verticillata	85.00 / 15.10	6 / 6	0.21 / 0.04	15.00 / 19.35	15.21 / 19.39
Ludwigia repens seed	0.00 / 1.00	0 / 1	0.00 / 0.00	0.00 / 3.23	0.00 / 3.23
Cabomba caroliniana seed	1326.00 / 2959.00	8 / 10	3.21 / 7.17	20.00 / 32.26	23.21 / 39.43
Unidentifed plant	230.00 / 29.00	2 / 2	0.56 / 0.07	5.00 / 6.45	5.56 / 6.52
Other	184.02 / 97.03	10 / 6	65.48 / 34.52	25.00 / 19.35	90.48 / 53.88
Fabrict lint	2.02 / 1.02	3 / 3	0.00 / 0.00	7.50 / 9.68	7.50 / 9.68
Plastic	0.00 / 0.01	0 / 1	0.00 / 0.00	0.00 / 3.23	0.00 / 3.23
Rock	182.00 / 96.00	7 / 4	0.44 / 0.23	17.50 / 12.90	17.94 / 13.14

Table 2. Index of Relative Importance (IRI) for dietary items found in the fecal samples of male (M) and female (F) *Sternotherus odoratus*. IRI was calculated for each taxon based on its proportional contribution by weight (g), frequency of occurrence, and relative abundance. Values are sorted by sex to highlight dietary composition and rank order of importance.

3.2 Allometric Scaling of Head and Body Traits by Sex

To assess whether the allometric relationship between body size and head width differed between male and female individuals, we performed a linear regression using log-transformed values of carapace length (CL) and head width (HW), including an interaction term for sex (log_CL ~ log_HW * Sex) on the long-term dataset for the Comal Springs *S. odoratus* population provided by the TSA-NAFTRG (Figure 21). This approach allowed us to evaluate differences in both the intercepts and slopes of the log–log relationship, a common method for testing sexual dimorphism in morphological scaling. The model explained a substantial proportion of the variation in head width (Adjusted $R^2 = 0.856$), and all terms were highly significant ($p < 0.001$). Females (baseline group) had an intercept of –1.0366 and a slope of 1.2346, while males exhibited a higher intercept (+0.2533) and a shallower slope (1.2346 – 0.1416 = 1.09). These parameters indicate that the scaling of head width with carapace length differs significantly between sexes (interaction: $t = –4.624$, $p < 0.001$), with the model capturing 85.6 % of the total variance in head width.

We used a log-log linear model with an interaction term (log_Weight ~ log_HW * Sex) on the current long-term population dataset for the Comal Springs *S. odoratus*, provided by the TSA-NAFRTG, in order to examine whether the relationship between head width and weight differs between males and females (n = 1659, M = 1157, F = 502, Figure 22). This model also explained a large proportion of variation (Adjusted $R^2 = 0.859$), and all predictors were highly significant ($p < 0.001$). Females had an intercept of 0.524 and a slope of 0.423, whereas males showed a slightly higher intercept (+0.079) and a shallower slope (0.423 – 0.059 = 0.364). The interaction term was significant (log(Weight):Sex $t = –5.73$, $p < 0.001$), indicating that head–body allometric scaling differs between sexes. Overall, both models revealed strong, significant relationships between head width and body size (carapace length and weight) with clear sex-based differences in scaling parameters.

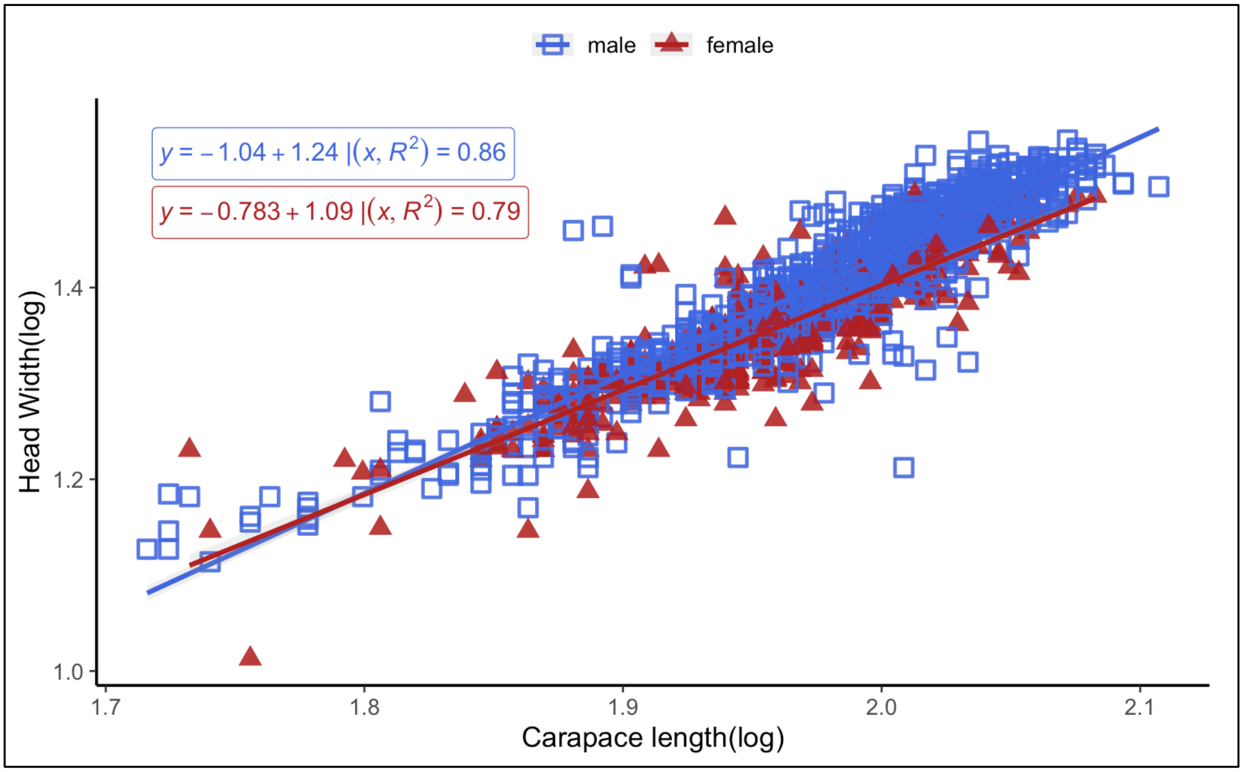

Figure 21. Linear model results showing the relationship between log-transformed head width (HW) and log-transformed straight-line carapace length (SCL) in *Sternotherus odoratus* (*n* = 1659; males = 1157, females = 502), with sex included as an interaction term. Males are represented by blue open squares and females by red triangles. Lines represent least-squares regressions with 95% confidence intervals.

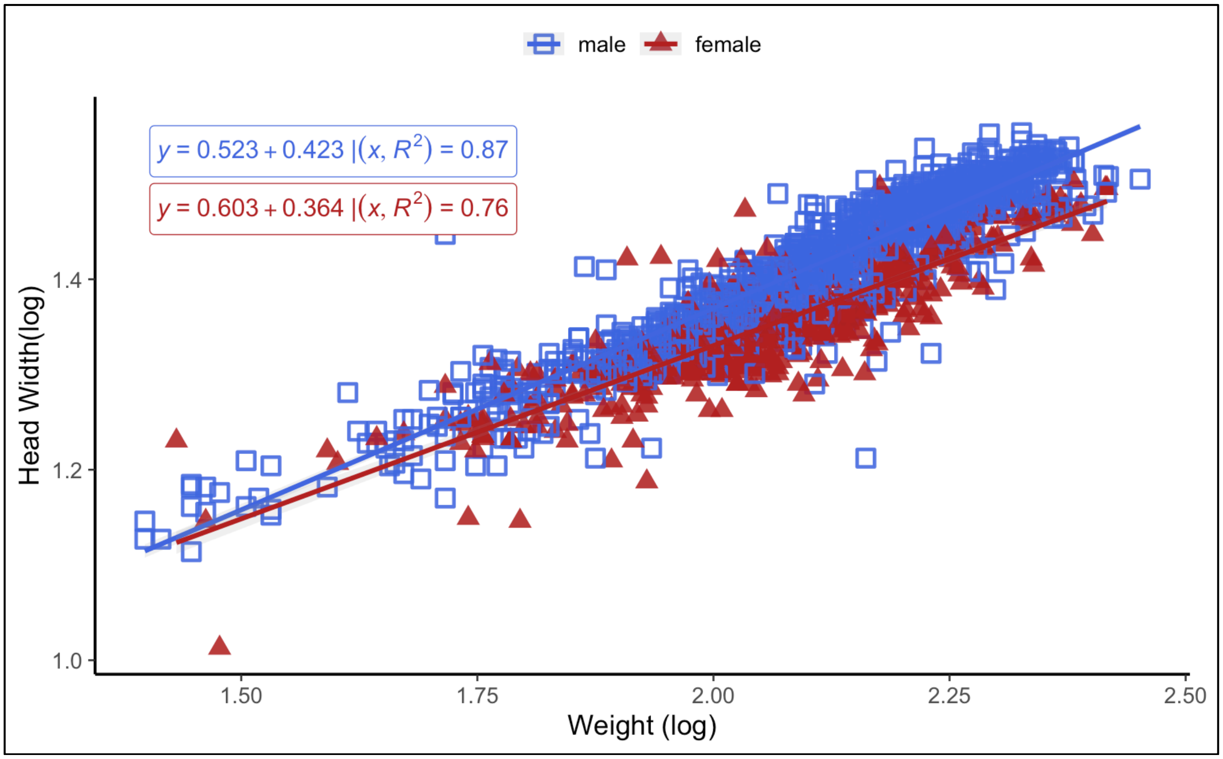

Figure 22. Linear regression results showing the relationship between log-transformed head width (HW) and log-transformed body weight (g) in *Sternotherus odoratus* (*n* = 1659; males = 1157, females = 502), with sex included as an interaction term. Males are represented by blue open squares and females by red triangles. Lines represent least-squares regressions with 95% confidence intervals.

3.3 Allometric Relationships Across Morphological Traits

To examine whether the allometric scaling relationships between body size and other morphological traits differ between male and female *S. odoratus*, we performed a series of log-log linear regressions using head width (log_HW) as the predictor and included interaction terms with sex (e.g., log_AW ~ log_HW * sex). These regressions were performed on data from the most recent sampling effort that was conducted between June and August 2024 ($n = 71$; $M = 40$, $F = 31$, Figure 23). This dataset was selected because it included additional cranial measurements, specifically alveolar width and height, that were not recorded in the TSA-NAFTRG dataset.

This model allowed us to evaluate potential sexual dimorphism in intercepts and slopes. For alveolar width (AW), the model explained a large proportion of variance (Adjusted $R^2 = 0.801$), and log_HW was highly significant ($p < 0.001$). However, neither the sex effect nor the interaction was significant, suggesting that while AW increases with HW, this scaling relationship does not significantly differ between males and females. A similar pattern was observed for alveolar height (AH), with significant allometric scaling (log_HW: $\beta = 0.836$, $p < 0.001$, Adjusted $R^2 = 0.615$), but no significant sex-based differences. Carapace length (CL_min) also showed strong positive scaling with head width ($\beta = 0.599$, $p < 0.001$, Adjusted $R^2 = 0.724$), and again, no evidence of sexual dimorphism in scaling. Carapace width (CW) followed the same trend ($\beta = 0.456$, $p < 0.001$, Adjusted $R^2 = 0.532$), with sex and interaction terms not statistically significant. Lastly, body mass scaled significantly with head width ($\beta = 1.846$, $p < 0.001$, Adjusted $R^2 = 0.797$), and this relationship did not differ between males and females (interaction $p = 0.975$).

Two-way ANOVAs tested the effects of sex, head form (phenotype: megacephalic [MEGA] vs. non-megacephalic [NON]), and their interaction on six morphological traits in *S. odoratus* (Table 4). Head form had a significant effect on all six traits, with megacephalic individuals exhibiting greater values than non-megacephalic individuals for mass ($F_{1,67} = 42.053$, $p < 0.001$, $\eta^2 = 0.386$), carapace length ($F_{1,67} = 43.786$, $p < 0.001$, $\eta^2 = 0.395$), carapace width ($F_{1,67} = 19.663$, $p < 0.001$, $\eta^2 = 0.227$), head width ($F_{1,67} = 70.416$, $p < 0.001$, $\eta^2 = 0.512$), alveolar width ($F_{1,67} = 48.830$, $p < 0.001$, $\eta^2 = 0.422$), and alveolar height ($F_{1,67} = 22.634$, $p < 0.001$, $\eta^2 = 0.253$) (Table 4). These effect sizes indicate moderate to large morphological differences associated with head form phenotype. Sex effects were detected only for carapace width ($F_{1,67} = 9.147$, $p = 0.0035$, $\eta^2 = 0.120$), with males having slightly wider carapaces than females; no other traits showed significant sex differences ($p > 0.05$). No significant Sex*Form interactions were found for any trait ($p > 0.05$). Boxplots illustrate the consistent morphological differences between head forms, with megacephalic (MEGA) individuals showing higher values across all measured traits, particularly head width and alveolar width, which display the largest separation between forms (Figure 24). Variability within each form overlaps substantially between sexes, reflecting the lack of significant Sex*Form interactions in the ANOVA.

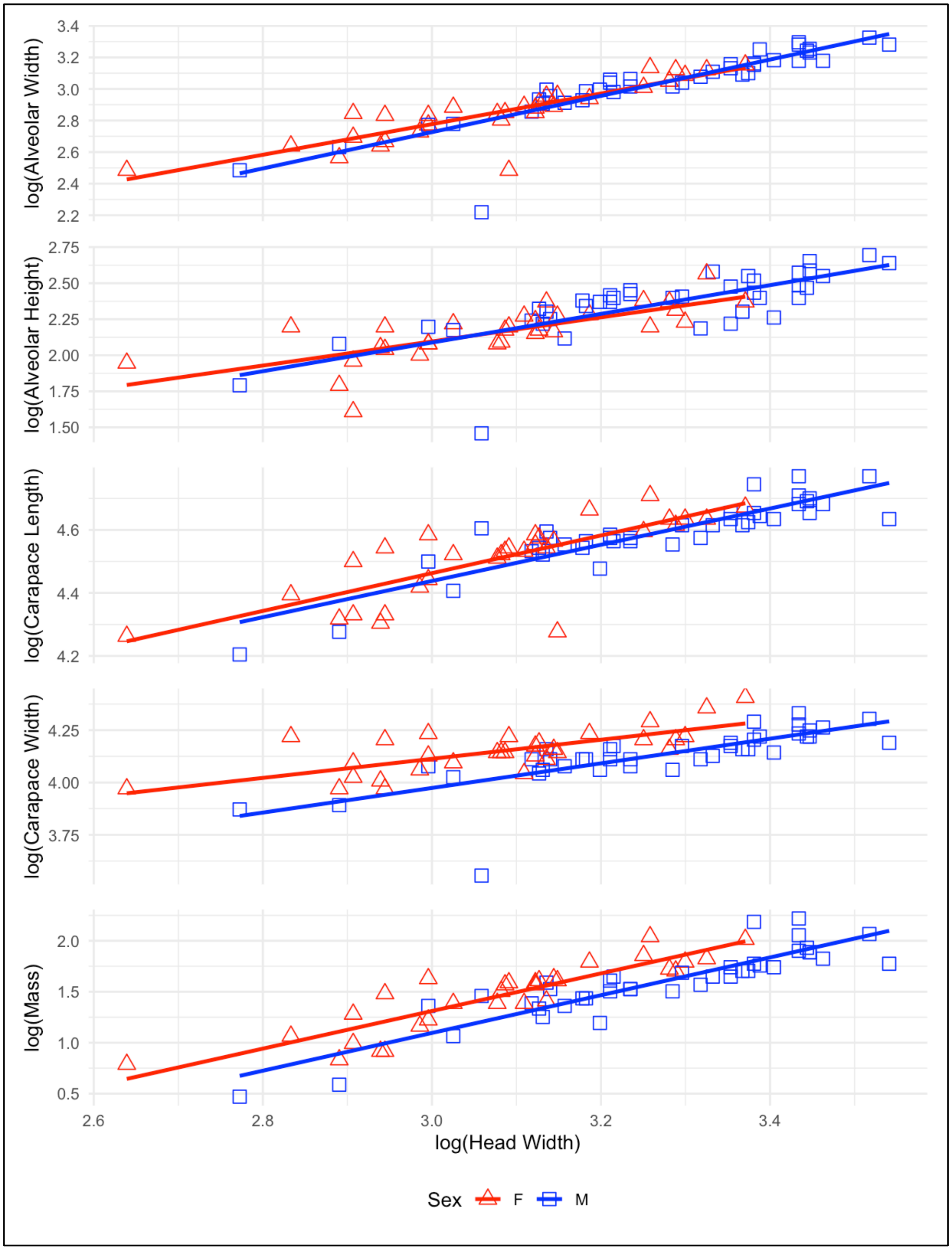

Figure 23. Allometric scaling relationships between head width (log_HW) and five morphological traits (alveolar width (AW), alveolar height (AH), straight-line carapace length (CL), carapace width (CW), and mass (g) in male (n = 40) and female (n = 31) *S. odoratus*. Log-log linear regressions were used to assess sexual dimorphism in intercepts and slopes.

Trait	**Effect**	***df*1**	***df*2**	***F***	***p***	**partial η²**
Mass	Sex	1	67	3.131	0.0814	0.045
	Form	1	67	42.053	**p<0.001**	0.386
	Sex*Form	1	67	0.127	0.7223	0.002
Carapace Length	Sex	1	67	0.357	0.5521	0.005
	Form	1	67	43.786	**p<0.001**	0.395
	Sex*Form	1	67	0.002	0.9615	0
Carapace Width	Sex	1	67	9.147	**0.0035**	0.12
	Form	1	67	19.663	**p<0.001**	0.227
	Sex*Form	1	67	0.653	0.422	0.01
Head Width	Sex	1	67	0.96	0.3307	0.014
	Form	1	67	70.416	**p<0.001**	0.512
	Sex*Form	1	67	0.125	0.725	0.002
Alveolar Width	Sex	1	67	0.231	0.6325	0.003
	Form	1	67	48.83	**p<0.001**	0.422
	Sex*Form	1	67	0.016	0.8991	0
Alveolar Height	Sex	1	67	2.047	0.1572	0.03
	Form	1	67	22.634	**p<0.001**	0.253
	Sex*Form	1	67	0.021	0.8849	0

Table 3. Results of two-way analysis of variance (ANOVA) testing the effects of sex, head form with megacephalic (MEGA) and non-megacephalic (NON) phenotypes and their interaction on six morphological traits in *Sternotherus odoratus*. Reported statistics include numerator and denominator degrees of freedom (df_1, df_2), F-values, p-values, and partial η² effect sizes. All significant p-values ($p < 0.05$) are indicated in bold.

Trait	**Male (NON)**	**Female (NON)**	**Male (MEGA)**	**Female (MEGA)**
Alveolar height (mm)	10.51 ± 1.31	8.35 ± 1.27	11.26 ± 2.01	8.97 ± 1.36
Alveolar width (mm)	22.16 ± 1.12	16.35 ± 2.18	22.44 ± 3.55	16.84 ± 2.62
Carapace length (mm)	105.86 ± 4.18	90.21 ± 9.26	104.44 ± 7.31	88.67 ± 11.42
Carapace width (mm)	71.29 ± 6.63	61.58 ± 5.12	64.19 ± 7.35	57.44 ± 5.55
Head width (mm)	27.03 ± 1.13	20.61 ± 2.46	28.13 ± 3.32	21.13 ± 2.71
Mass (g)	6.41 ± 0.87	4.00 ± 1.07	5.56 ± 1.42	3.49 ± 1.17

Table 4. Mean (± SD) morphological measurements for male and female *Sternotherus odoratus* with megacephalic (MEGA) and non-megacephalic (NON) phenotypes. Measurements include alveolar height, alveolar width, straight line-carapace length, carapace width, head width, and body mass

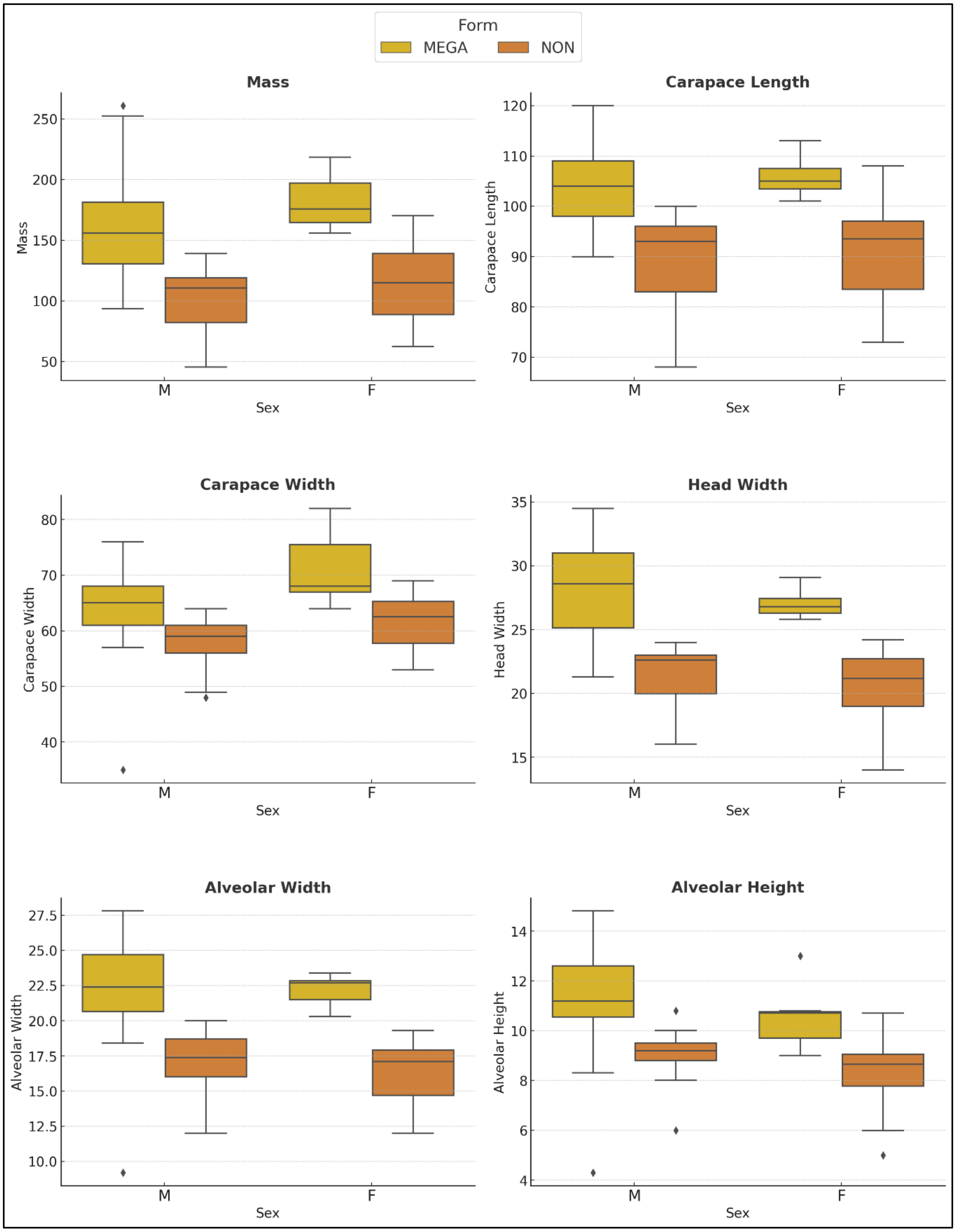

Figure 24. Boxplots comparing morphological traits in *Sternotherus odoratus* by sex and head form with megacephalic (MEGA) and non-megacephalic (NON) phenotypes. Each panel displays the distribution of a specific trait: mass, straight-line carapace length, carapace width, head width, alveolar width, and alveolar height. Legend indicates head form phenotype.

3.4 Temporal Morphological Shifts: Museum vs Current

To evaluate potential morphological shifts over time, we compared head width and carapace length measurements between historical (museum; 1940–1989, n =31) and recently sampled (current; 2013–2024) *S. odoratus* specimens. Boxplot comparisons reveal significant differences in the distribution of both traits between the museum specimens and the current specimens (Figure 25). Statistical analyses using Welch's two-sample t-tests revealed that carapace length was significantly greater in current specimens (mean = 95.4 mm, median = 97 mm, n = 1690) compared to museum specimens (mean = 62.4 mm, median = 68.8 mm, n = 31), with a t-value of 9.19, df = 30.51, and $p < 0.001$. Head width was significantly larger in current specimens (mean = 25.3 mm, median = 25.4 mm) than in museum specimens (mean = 16.3 mm, median = 17.1 mm), with a t-value of 11.35, df = 31.30, and $p < 0.001$.

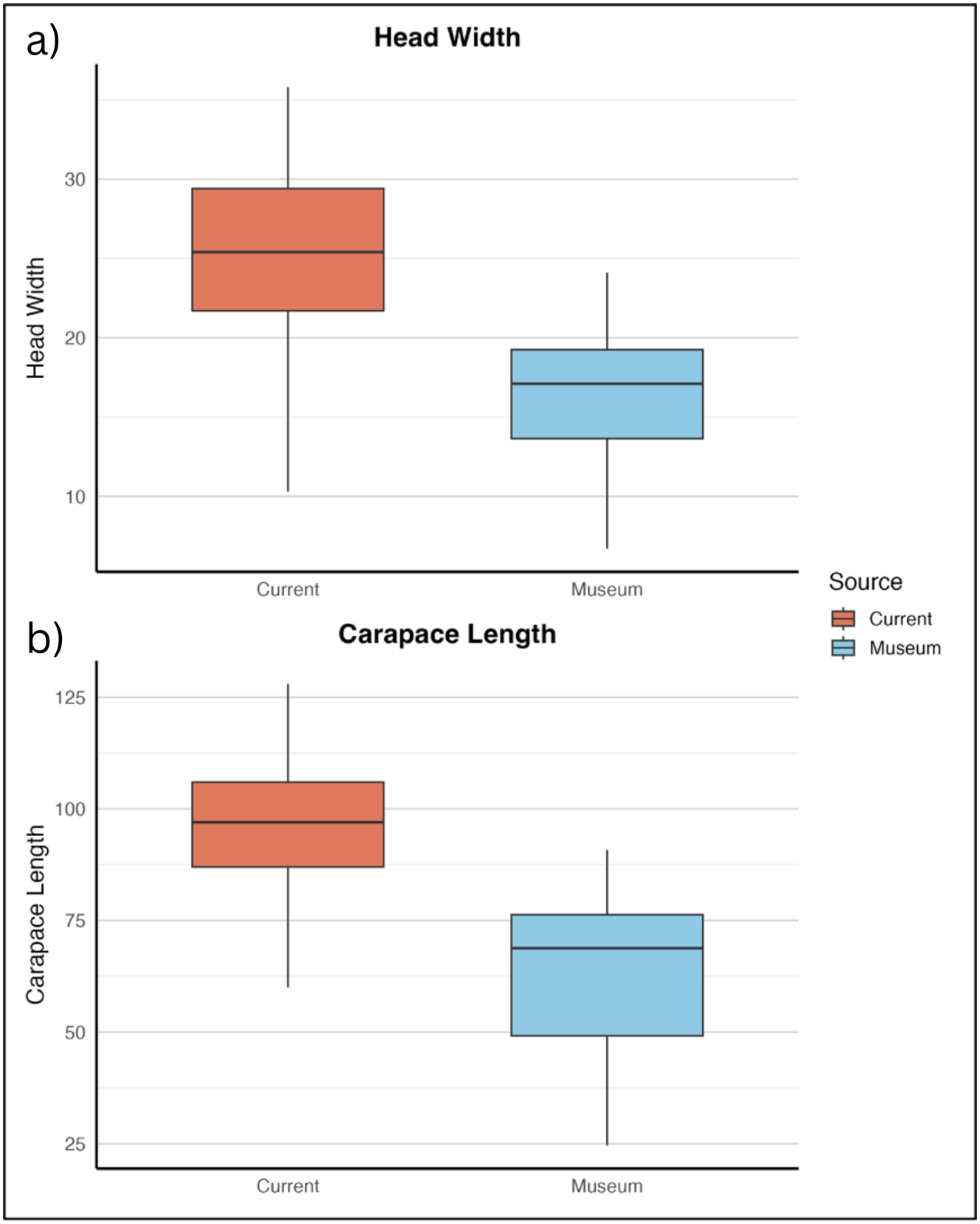

Figure 25. Boxplots comparing a) head width and b) straight-line carapace length between museum (1940–1989) and current (2013–2024) *Sternotherus odoratus* specimens. Data were filtered to remove outliers, and the legend indicates the source of the samples.

4.0 Discussion

4.1 Study Overview and Hypotheses

Understanding how native wildlife adapts to rapidly changing ecosystems is a central challenge in modern ecology, especially as invasive species reshape food webs and habitats across the globe (Calizza et al., 2021). Studying the adaptive responses of *S. odoratus* in Comal Springs adds to our scientific understanding of freshwater turtle ecology, morphology, and behavior. In this study we investigated how invasive prey consumption influences the head morphology and dietary patterns of *S. odoratus* in a unique spring system heavily invaded by invasive aquatic gastropods. Given the ecological importance of freshwater springs and the potential for invasive species to alter trophic dynamics, we hypothesized that dietary shifts driven by invasive aquatic gastropods would shape *S. odoratus* morphology and population-level traits. Specifically, we tested the following predictions: (1) megacephalic individuals consume more invasive snails than non-megacephalic individuals; (2) individuals that consume more invasive snails will exhibit differences in head morphology; (3) males and females will differ in both diet composition and morphological trait scaling; and (4) extant *S. odoratus* individuals will show altered body morphology patterns compared to historical museum specimens.

4.2 Diet Composition and Sex-Based Variation

To investigate dietary variation in *Sternotherus odoratus*, we used two complementary approaches: form-based comparisons of prey composition and an Index of Relative Importance (IRI) to assess sex-based dietary patterns. Individuals were first categorized by head phenotype (megacephalic vs. non-megacepahlic) and compared for both broad and fine-scale diet composition using fecal analysis. Our analysis provides insights into the diet of this unusually dense and isolated population. T*arebia granifera*, a non-native gastropod, dominated the diets of both males and females and showed the highest Index of Relative Importance (IRI) values. Males consumed a broader diversity of prey including other invasive snails and vegetation while females exhibited a narrower dietary range, suggesting a more specialized or selective foraging strategy within this system. Non-metric multidimensional scaling (NMDS) ordinations indicated considerable overlap in prey composition between head forms, and a permutational multivariate analysis of variance (PERMANOVA) found no significant difference in prey type composition between megacephalic and non-megacephalic individuals. These patterns, based on fecal analysis, suggest broadly similar prey assemblages for both phenotypes. While fecal analysis is less invasive and more practical than stomach flushing, its accuracy can be limited by the degradation and partial digestion of food items during passage through the digestive system in *S. odoratus*.

The results indicate a subtle dietary shift toward invasive species, particularly *Tarebia granifera*, and reveal some sex-based and head-form based differences in resource use. While megacephalic turtles consumed a greater proportion of invasive snails on average, the difference between head forms was not statistically significant. This pattern is consistent with the expectation that head morphology may influence the extent of durophagous feeding behavior. Males also exhibited a broader dietary range than females which may reflect differences in behavior, ecological roles, or energetic demands. These patterns suggest that both head morphology and sex influence diet composition in this population, with megacephalic individuals showing a tendency toward a more durophagous feeding strategy, while non-megacephalic individuals appear to maintain a broader or more generalized diet. The observed 9% difference in prey abundance indicates that this pattern should be interpreted as a trend rather than a strict specialization.

4.3 Contextualizing with Previous Studies

To our knowledge, only one other study has examined the effects of invasive snail consumption by *S. odoratus* population in Comal Springs. Morrison et al. (2019) analyzed fecal samples from the same spring system and observed dietary compositions dominated by invasive gastropods and hard-shelled prey items. Gastropods were present in 90% of all samples, with three non-native snail species dominating the diet composition: *Melanoides tuberculata* (78% of samples), *Tarebia granifera* (50%), and *Marisa cornuarietis* (16%). This elevated mollusk consumption was notably higher than most historical dietary records for the species and appears to result from the long-established presence and abundance of these invasive snails over the past three decades (Berry, 1975; Ernst, 1986; Wilhelm & Plummer, 2012). These findings reinforce the capacity for *S. odoratus* to act as trophic generalist that are capable of opportunistic specialization in response to altered prey landscapes.

A similar pattern in dietary shift in response to invasive mollusks was documented by Wilhelm and Plummer (2012), who investigated the foraging ecology of *S. odoratus* in a creek system in Arkansas. *Sternotherus odoratus* were radiotracked in a small urban creek heavily invaded by the Asiatic clam (*Corbicula fluminea*). Mollusks were the dominant dietary component by both volume (89.2%) and mass (97.8%), with *C. fluminea* alone accounting for 72% of mollusk consumption. This study represents a striking shift from historical accounts in which bivalves rarely dominated the species' diet. The study found evidence supporting sexual dimorphism in diet and body size. Females consumed significantly greater volumes and mass of *C. fluminea* than males, while males consumed more snails. These findings suggest that the foraging patterns of *S. odoratus* reflect localized prey availability rather than intrinsic prey preference and underscore the potential for invasive species to restructure not only the diets but also the sexual niche dynamics of native turtle populations. These findings from Arkansas and Texas reveal a broader ecological trend, that *S. odoratus* are capable of exhibiting remarkable dietary plasticity and may become increasingly reliant on invasive mollusks in ecosystems where they become dominant.

Other studies conducted across *S. odoratus* populations in North America support these findings. A study conducted by Patterson and Lindeman (2009) in Pennsylvania documented that the invasion of zebra (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*) was linked to a morphological shift and diet dominated by these invasive bivalves. Diet composition correlated strongly with head and alveolar width. Larger *S. odoratus* consumed proportionally more mussels suggesting morphological responses to tougher hard-shell prey. In Southwestern Missouri, Ford and Moll (2004) documented significant seasonal and sexual variation in diet of *S. odoratus*. They noted that while both sexes ate similar taxonomic prey groups, females consumed larger volumes, especially crayfish, during the peak nesting season, reflecting reproductive energy needs. Monthly dietary shifts also corresponded with differences in activity linked to nesting and mating. Compared to our study, we did not detect any seasonal dietary variation, likely due to limited sampling period and the unique characteristics of the Comal Spring system, where water temperatures remain relatively constant year-round (23.1°C to 23.9°C) and seasonal fluctuations are minimal (Brune, 1981). We acknowledge that Ford and Moll’s findings highlight the potential for pronounced temporal foraging shifts in this species when reproductive cycles and longer-term patterns are accounted for.

These studies demonstrate that *S. odoratus* exhibits considerable trophic flexibility. Populations feed heavily on invasive organisms when abundant, and adjust prey use according to biological or ecological conditions. The patterns observed at Comal Springs, including the dominance of invasive gastropods and subtle sex-based dietary, differences align with the broader ecological knowledge of the species. Future studies should aim to sample *S. odoratus* populations from non-invaded sites to directly assess system-level dietary divergence and evaluate whether invasive gastropods are driving similar patterns of resource specialization elsewhere in Comal County, Texas, USA.

4.4 Support for Megacephaly and Morphological Change

In support of the second prediction, allometric models on the long-term dataset revealed significant sexual dimorphism in *S. odoratus* head morphology. Males exhibited a steeper scaling slope between carapace length and head width, whereas females had a higher intercept, suggesting that males develop proportionally larger heads as they grow. The dominance of invasive, hard-shelled snails in the Comal Springs diet, particularly *Tarebia granifera* and *Melanoides tuberculata*, likely exerts strong selective or plastic pressures on cranial morphology. Comparable dietary–morphological relationships have been reported in other *S. odoratus* populations (Moll & Moll, 2004; Morrison et al., 2019) and in unrelated taxa such as cichlid fishes (*Neochromis greenwoodi*), where jaw morphology shifts in response to prey hardness (Bouton et al., 2002) . The pattern observed in Comal Springs, is more consistent with phenotypic plasticity than with fixed genetic divergence because head-form variation is continuous rather than bimodal, and because the rapid proliferation of invasive snails in Comal Springs likely occurred over too short a timescale for strong genetic differentiation to evolve. Head width was confirmed to be an exceptionally strong morphological predictor of head phenotype, with a cutoff of approximately 24.5 mm providing an empirically justified and field-practical criterion for classifying megacephalic and non-megacephalic individuals. These differences in head morphotype are likely allowing individuals to optimize feeding performance in response to local prey availability.

4.5 Sex-Based Morphological Scaling and Ecological Roles

We found only partial support for our third prediction. While dietary analysis revealed subtle differences, such as males consuming a slightly broader range of prey types, morphometric data did not support significant sexual dimorphism in body mass or trait scaling. Across allometric models based on the June - August 2024 dataset, head width was a strong predictor of morphological traits, including alveolar width, alveolar height, carapace length, and body mass. Our results indicate that although head width is a strong predictor of variation in multiple morphological traits, there is no evidence of sex-specific differences in allometric scaling across these traits, suggesting that these physical characteristics grow proportionally with head width in a similar manner in both male and female *S. odoratus*. However, neither the intercepts nor slopes of these relationships differed significantly between sexes, indicating that there are consistent growth patterns and proportional scaling of traits regardless of sex. While males tend to have larger median values for most traits (e.g., carapace width) the degree of overlap in the distributions supports the conclusion that sexual dimorphism in these traits is limited. These findings suggest that while head morphology and diet composition vary slightly between males and females, the underlying morphological scaling is largely conserved and does not reflect strong sex-specific adaptation as observed in other durophagous turtle species (e.g., *Graptemys* spp.). *Sternotherus odoratus* in Comal Springs may exhibit a more generalized response to ecological conditions, rather than one tightly structured by sexual niche partitioning.

4.6 Evidence for Long-Term Morphological Shifts

The fourth prediction was supported, which was that morphological traits in *S. odoratus* have shifted over time likely in response to changing environmental conditions such as prey availability. The significant morphological differences observed in carapace length and head width between museum (1940–1989) and current (2013–2024) *S. odoratus* specimens suggest an ecological response to the introduction of several invasive aquatic gastropod species to the Comal Springs ecosystem. Similar long-term morphological shifts have been detected by comparing historic museum specimens with modern populations in other species of turtles (e.g., western pond turtles; (Nicholson et al., 2020). These morphological shifts appear to coincide with the introduction of *Tarebia granifera* in the 1930s, *Melanoides tuberculata* in the 1960s and *Marisa cornuarietis* in the 1980s (Horne et al., 1992; Karatayev et al., 2009; Murray, 1964). Invasive aquatic gastropods have become key prey items for *S. odoratus*, and their presence in the ecosystem is likely driving the observed shift in head and body size of this population.

Morphological comparisons show that museum specimens exhibited greater variation but slightly smaller median head widths, whereas the current *S. odoratus* display higher median carapace lengths and head widths within narrower ranges. This pattern is consistent with size-selective pressures favoring individuals better equipped to handle mechanically challenging prey. While direct bite-force data are lacking, studies demonstrate that shell-crushing resistance varies with shell composition and local resource availability (Chaves-Campos et al., 2012). Laboratory studies in South Africa, where *Melanoides tuberculata* is native and *Tarebia granifera* is invasive, have shown that *T. granifera* shells are mechanically stronger than those of *M. tuberculata*, supporting the idea that thicker, more robust shells may require greater crushing force and influence head morphology (Miranda et al., 2016). The overwhelming abundance of invasive gastropods in Comal Springs likely increases their encounter rate during foraging, making them a consistent component of the diet. This combination of constant exposure and harder shell structure could jointly drive the observed shifts in head morphology. Although direct bite force measurements were not available in this study, the observed shifts align with broader theories of phenotypic plasticity, where species alter physical traits in response to novel ecological pressures (Stearns, 1989). Understanding these changes are crucial for assessing the long-term effects of invasive species on native fauna and for informing conservation strategies aimed at maintaining species' ecological and evolutionary resilience in the face of environmental disturbances.

4.7 Adaptive Morphological Responses and the Role of Phenotypic Plasticity

The morphological changes observed in *Sternotherus odoratus* may reflect a broader ecological phenomenon in which native species undergo trait shifts in response to novel ecological pressures. Documented cases of similar changes across turtle taxa provide further context for interpreting these findings. In the Texas map turtle (*Graptemys versa)*, Lindeman (2006) reported increases in head size in populations consuming the invasive Asiatic clam (*Corbicula fluminea*), noting that larger-headed females were more effective at processing hard-shelled prey. This aligns with findings in *Sternotherus odoratus*, where head morphology is associated with a diet dominated by invasive gastropods.

Beyond aquatic turtles, invasive species have induced morphological and phenotypic variation in a variety of vertebrate taxa. Research in Trinidad on guppies (*Poecilia reticulata*), exposed to invasive predators has revealed that these fish have the capability to develop streamlined bodies and larger caudal peduncles aiding in improved escape performance (O'Steen et al., 2002). In Galápagos finches (*Geospiza fortis*), rapid shifts in beak size and shape have occurred in response to competition with the invasive large ground finch (*Geospiza magnirostris*) (Grant & Grant, 2006). In the Eastern United States native red-backed salamanders (*Plethodon cinereus*) have shown reduced head width and body size in areas invaded by the larger and more aggressive Northern slimy salamander (*Plethodon glutinosus)*, likely reflecting competitive displacement (Adams, 2004). A recent study on behavioural interactions between a threatened native killifish (*Valencia letourneuxi*) and the invasive eastern mosquitofish (*Gambusia holbrooki*) found that the presence of *G. holbrooki* altered foraging and activity patterns of *V. letourneuxi*, indicating that invasive species and the subsequent environmental pressures they exert can drive not only morphological change but also rapid phenotypic and behavioural adjustments (Kapakos et al., 2024). These examples demonstrate that such responses, whether structural or behavioural, are not limited to a single lineage but represent a common mechanism by which native species adapt to novel ecological pressures.

In many cases the observed trait shifts have occurred within relatively short time frames, often within just a few decades. This supports the hypothesis that phenotypic plasticity or rapid selection can drive morphological change. Phenotypic plasticity is a well-documented mechanism in sessile organisms (e.g., plants) where mobility constraints demand adaptability through plastic traits (Bradshaw, 1965; Sultan, 2000). Plasticity in animals is often presumed to be less pronounced due to their ability to escape adverse conditions by moving to more favorable environments (Borges, 2008). As in the Comal Springs population of *S. odoratus*, these changes often reflect altered resource availability or shifts in predator-prey dynamics, reinforcing the importance of understanding phenotypic plasticity as a response to invasive species.

In spatially constrained systems such as spring-fed aquatic habitats, plasticity may become even more ecologically relevant. In the case of Comal Springs, *S. odoratus* are effectively limited in their spatial distribution by spring outflows and habitat fragmentation, including hardened shorelines and spillways. This environmental confinement may promote morphological variation as an adaptive strategy in lieu of dispersal. Evidence from other reptiles also supports this. Italian wall lizards (*Podarcis sicula*) translocated to a new island showed rapid morphological and digestive tract changes within several decades, consistent with dietary shifts and plastic responses (Herrel et al., 2008). Understanding the extent to which plasticity underlies the observed morphological variation in *S. odoratus* has implications not only for the species' adaptive capacity but also for broader evolutionary theory. If megacephaly represents a plastic, reversible trait, it may enhance resilience to shifts in prey communities. If this trait becomes fixed through natural selection, it may drive increased ecological specialization and heighten susceptibility to future environmental changes.

The apparent morphological shift in *S. odoratus* appears to be occurring within a relatively short timescale, potentially within a single generation. This rapid response suggests that even long-lived vertebrate taxa like freshwater turtles may possess underappreciated capacity for short-term phenotypic adjustment. This makes our findings particularly exciting, as they highlight a rare instance where morphological plasticity in a reptile may emerge swiftly in response to environmental change, rather than across evolutionary time. Such cases are rare and provide powerful insight into the resilience, mechanisms, and limits of adaptability in long-lived vertebrates.

4.8 Future Research Directions

Although this study supports megacephaly in *S. odoratus* from Comal Springs as a phenotypically plastic trait driven by diet, the ecological and developmental mechanisms behind its variable and sometimes extreme expression within this population still remain unclear.

Understanding these mechanisms is not only important for advancing evolutionary theory, but equally important for informing conservation strategies in a highly altered spring system that is increasingly affected by invasive species, habitat alteration, and climate change.

Future research should investigate whether megacephaly is underpinned by heritable genetic or epigenetic mechanisms. Genomic analyses comparing individuals across the full morphological gradient, could identify candidate genes or regulatory pathways associated with the expression of megacephalic individuals. Epigenetic profiling may reveal environmentally responsive gene expression linked to diet, offering insight into how plastic traits are maintained across generations, regardless of their heritability. Controlled feeding experiments with hatchlings raised to adults on different prey types (e.g., low, medium & high prey-item hardness) would provide causal evidence for diet-induced morphological shifts. Parallel studies quantifying bite force and internal cranial morphology, using CT imaging or novel 3D scanning approaches (The Biodiversity Group, 2025), alongside assessments of potential trade-offs such as swimming efficiency, would provide deeper insight into the functional significance of megacephaly. Developing a standardized megacephaly index, combining external morphometrics and performance data, would enable reproducible comparisons across individuals, populations, and even other freshwater turtle species that exhibit megacephaly.

Spatial ecology research within this population is equally important. Spatial mapping of capture locations of megacephalic and non-megacephalic *S. odoratus* in relation to prey distribution and habitat features could determine whether megacephalic individuals are clustered in foraging-rich microhabitats or if their occurrence is system-wide. Food plot surveys within Comal Springs would quantify prey availability and help better understand dietary preference in relation to prey-type abundance. Comparative studies between invaded and non-invaded systems in Central Texas would reveal whether dietary shifts and associated morphologies are unique to Comal Springs or reflect broader regional patterns. Validating fecal analysis against stomach flushing would improve the accuracy of dietary assessments, particularly for soft-bodied or other highly digested prey items. These approaches offer an integrative framework for investigating the drivers, functions, and conservation implications of phenotypic plasticity in the Comal Springs population of *S. odoratus* and may provide valuable insights into the adaptive capacity of freshwater turtles responding to ecological change.

4.9 Environmental Pressures and Conservation Challenges

The broader ecological importance of Comal Springs, particularly considering climate change, should also be considered. As a spring-fed system dependent on the Edwards Aquifer, Comal Springs is susceptible to stochastic weather events, especially prolonged droughts, which are becoming more frequent and are largely driven by greenhouse gas emissions, land-use alterations, and unsustainable water management (AghaKouchak et al., 2021; Angélil et al., 2014; He & Ding, 2023). These changes in landscape hydrology could drastically reduce spring discharge, alter water temperature, and shift aquatic species community composition (Sharp, 2019). Such conditions may impact the abundance and distribution of both native and invasive prey, potentially disrupting the trophic structure that currently supports such a high population density of *S. odoratus* found in Comal Springs. Continued long-term monitoring is critical to detect and respond to changes in spring hydrology and prey availability before they cause unforeseen impacts on native turtle populations and broader ecosystem stability.

As the human population grows urbanization and habitat encroachment increasingly threaten the ecological integrity of this sensitive spring ecosystem (Diego, 2012). Comal Springs is increasingly encroached upon by urban development, including high-end residential neighborhoods and a golf course immediately adjacent to the lake (E. Munscher, 2019). These land-use changes have already resulted in the reinforcement of shorelines with concrete walls, altering natural riparian zones and likely reducing the availability of suitable nesting habitat for turtle species in Comal Springs (Eric Munscher & Andrew Walde, pers. comm.). The reinforced shorelines and presence of two spillways have effectively "boxed in" *S. odoratus* within Landa Lake, fragmenting habitat and restricting movement. Evaluating nesting success, juvenile recruitment, and movement ecology in this highly altered landscape would be crucial for informing habitat restoration or management strategies.

Considering these pressures, conservation efforts should prioritize maintaining hydrological integrity, preserving natural shorelines, and limiting further habitat destruction. Engaging with local stakeholders especially private landowners, city planners, and recreational users, could help mitigate further degradation of this spring and promote coexistence between human development and all kinds of native wildlife. The Comal Springs population of *S. odoratus* offers access to a rare, long-term dataset within a unique natural laboratory and may serve as a sentinel system for predicting how other spring-dwelling organisms respond to invasive species, habitat disturbances, and climate change. These insights highlight the need for integrative conservation research that unites morphology, behavior, physiology, and habitat modeling to better understand the long-term resilience of aquatic turtle species amid rapidly evolving environmental pressures.

5.0 Conclusion

This study demonstrates that the Comal Springs population of *Sternotherus odoratus* exhibits significant morphological and dietary shifts associated with the long-term presence of invasive aquatic gastropods. Megacephalic individuals consumed a higher proportion of invasive gastropods and displayed significantly larger heads and crushing surface dimensions, supporting the role of diet-driven phenotypic plasticity. While males tend to have slightly larger values for certain traits, extensive overlap between sexes suggests limited sexual dimorphism in trait scaling. Comparisons with historical museum specimens reveal increases in head width and carapace length, consistent with a rapid morphological response to changes in prey availability. These findings highlight the potential for long-lived vertebrates to exhibit short-term adaptive changes in response to novel ecological pressures, particularly in spatially constrained habitats. Understanding the drivers and limits of such plasticity is essential for predicting species' resilience in ecosystems undergoing invasion, habitat alteration, and climate change, and for informing targeted conservation strategies in sensitive spring systems like Comal Springs.

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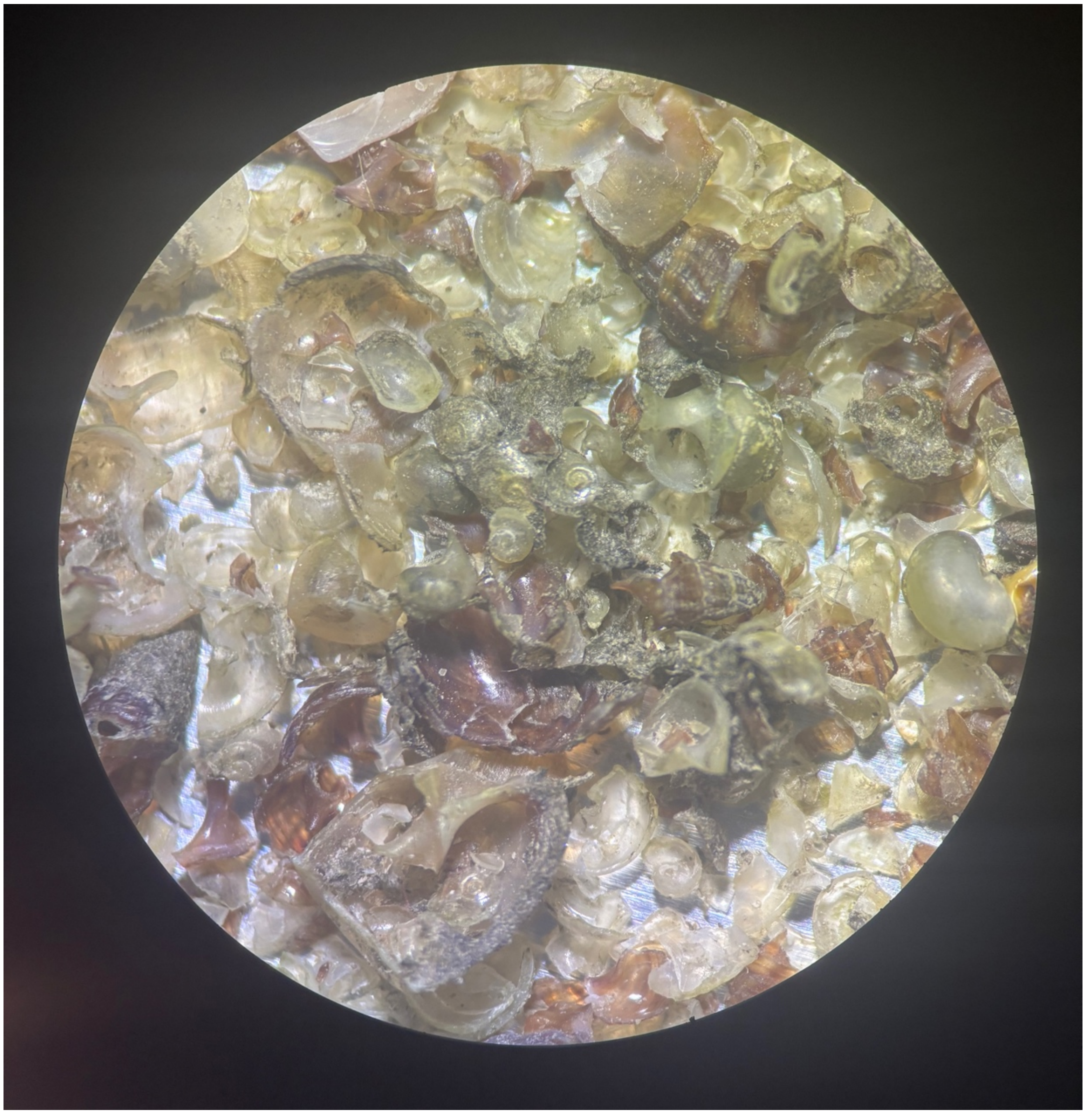
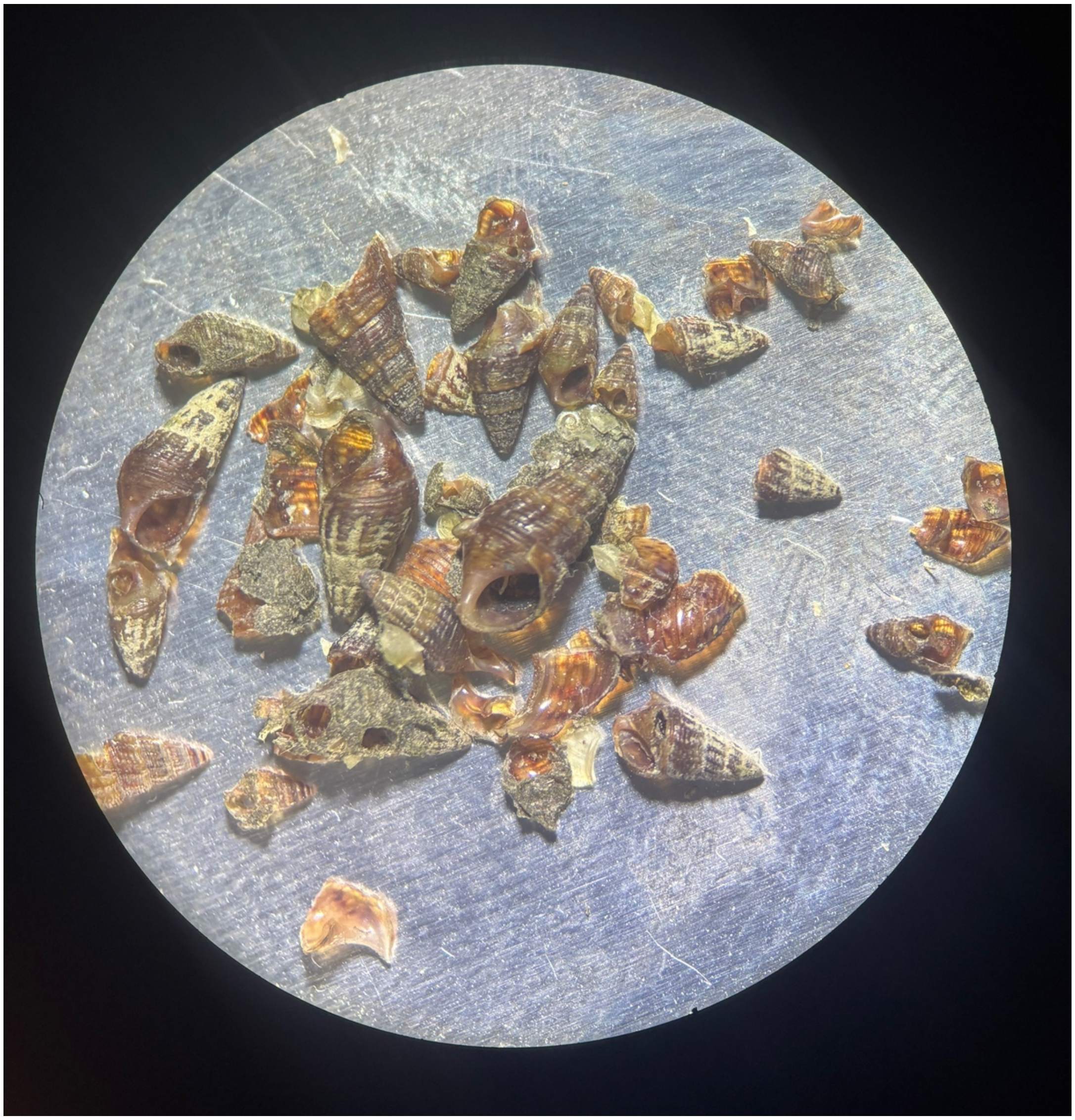
Appendix A.

Photographs of selected prey items from fecal samples of *Sternotherus odoratus* from Comal Springs, Comal County, Texas.

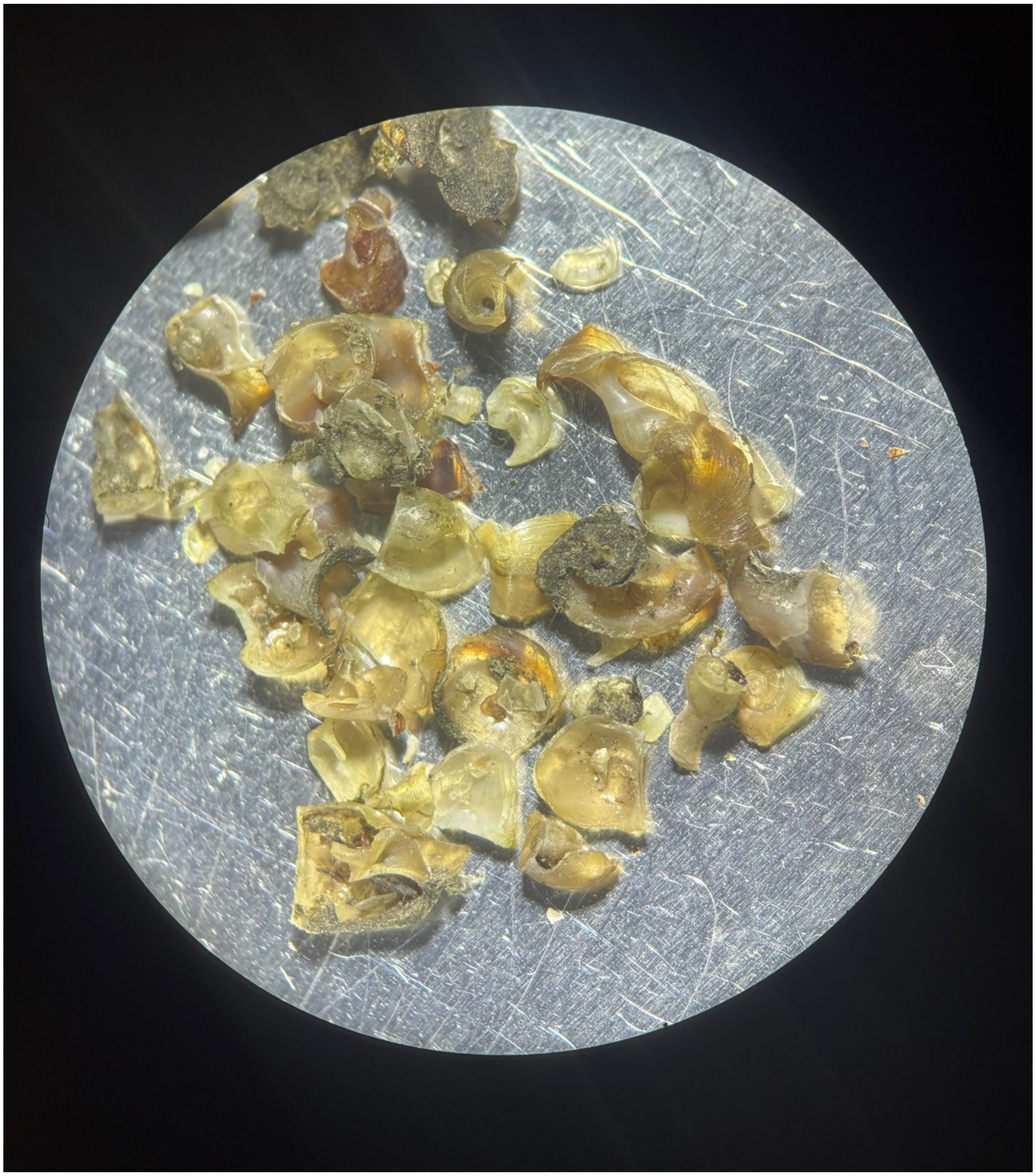


Typical sample of aquatic gastropod shell material including operculum from *Tarebia granifera*, *Melanoides tuberculata*, *Marisa cornuarietis* and *Pyrgulopsis sp.*

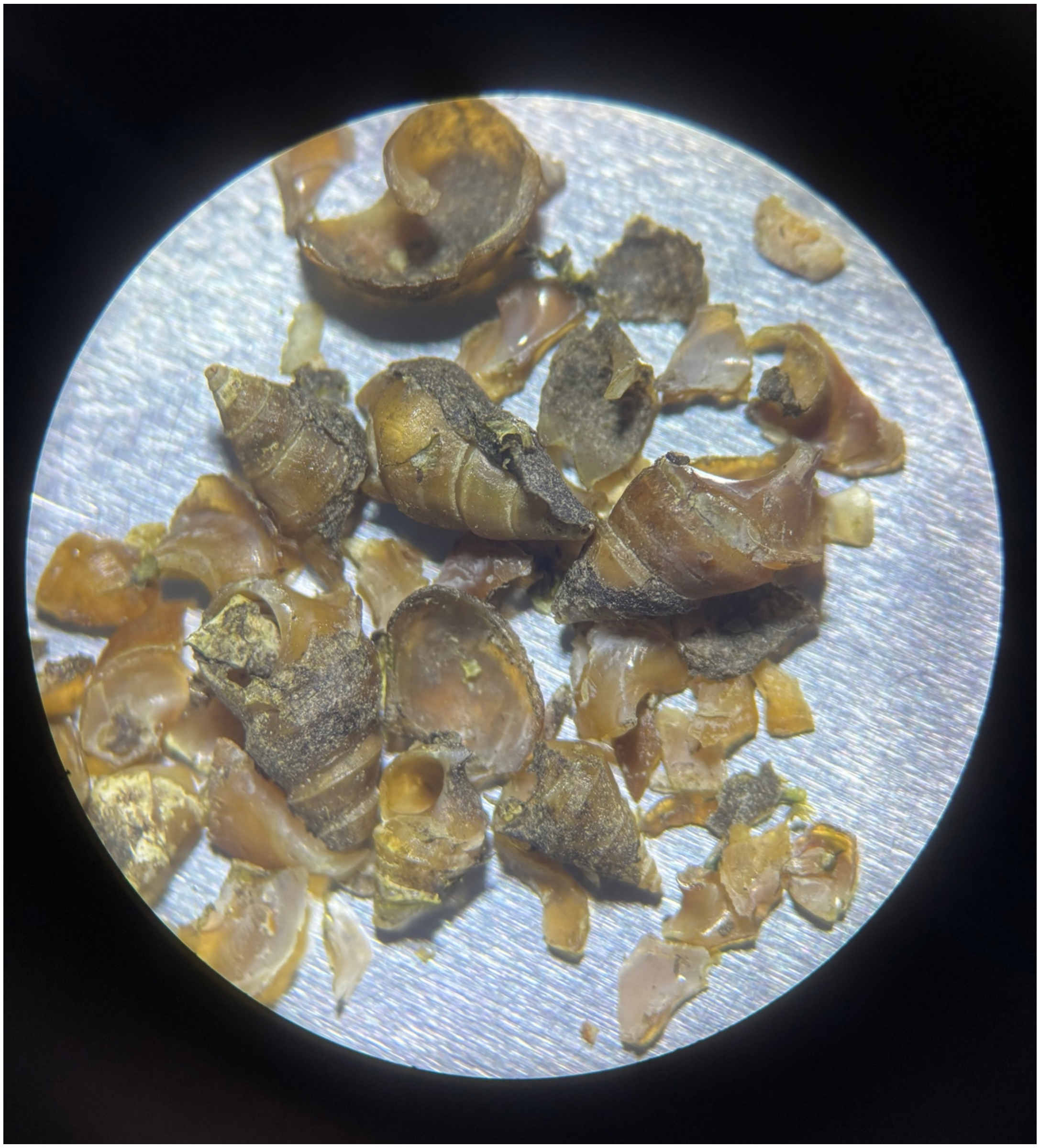


Tarebia granifera.

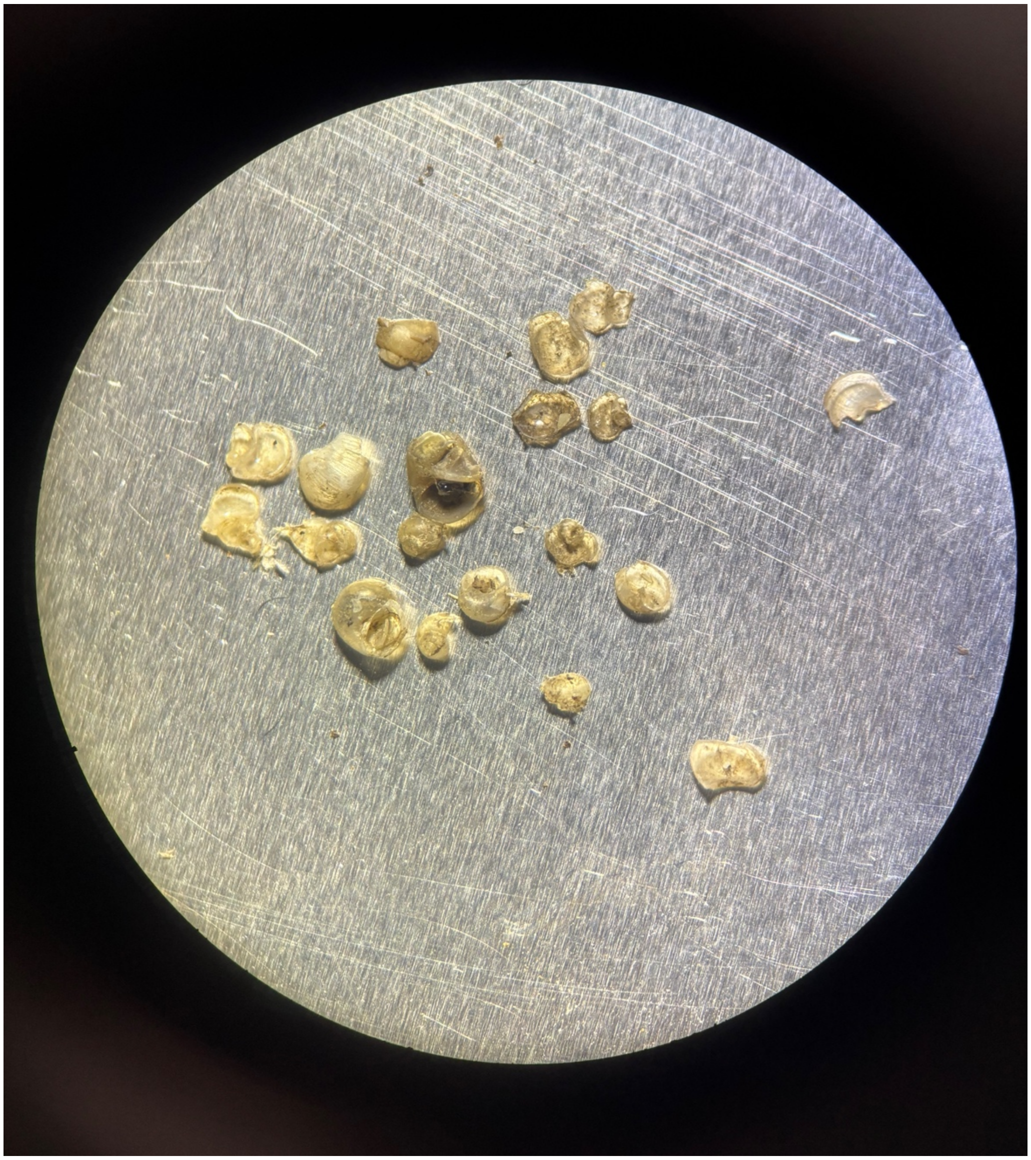
Melanoides tuberculata.



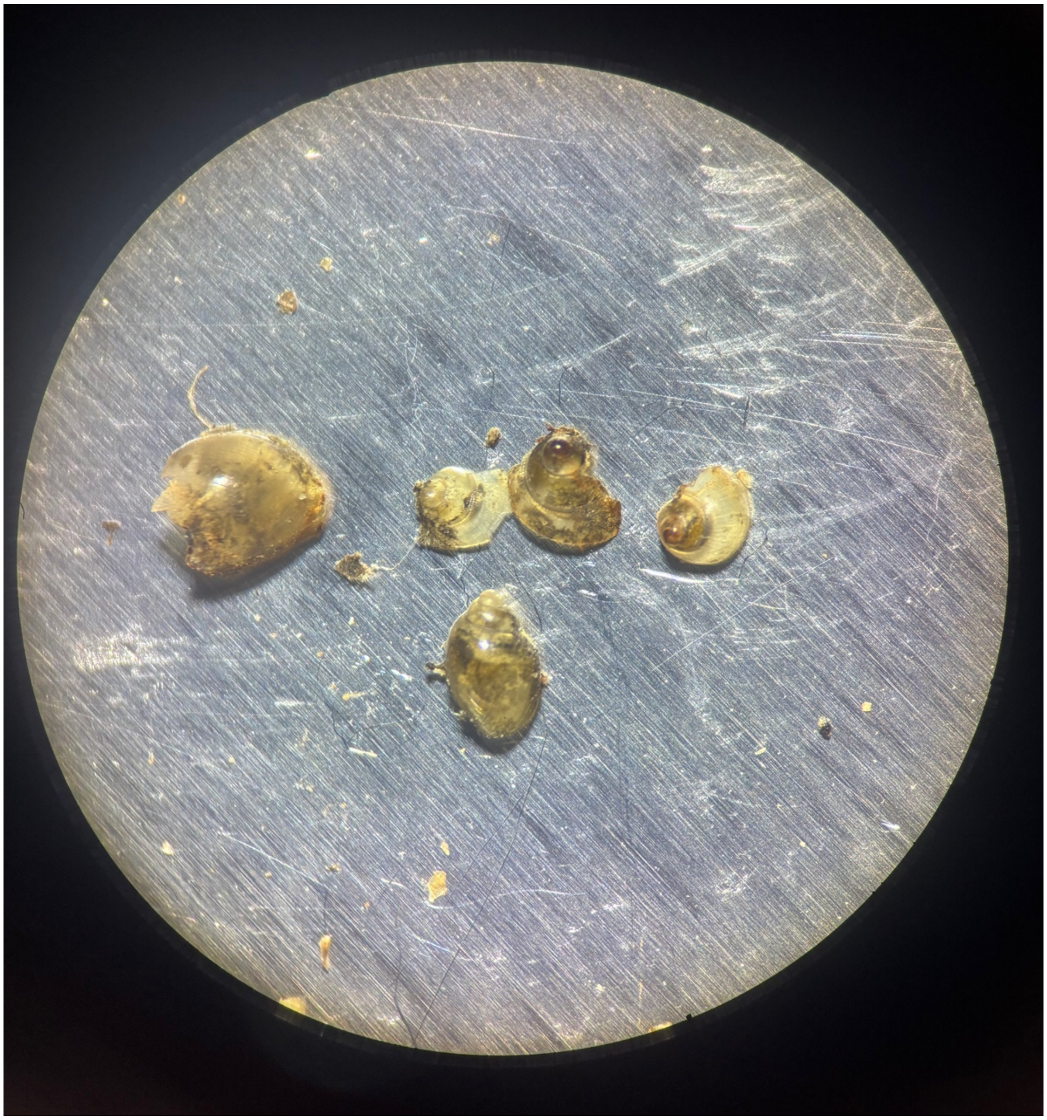
Marisa cornuarietis.



Elimia comalensis

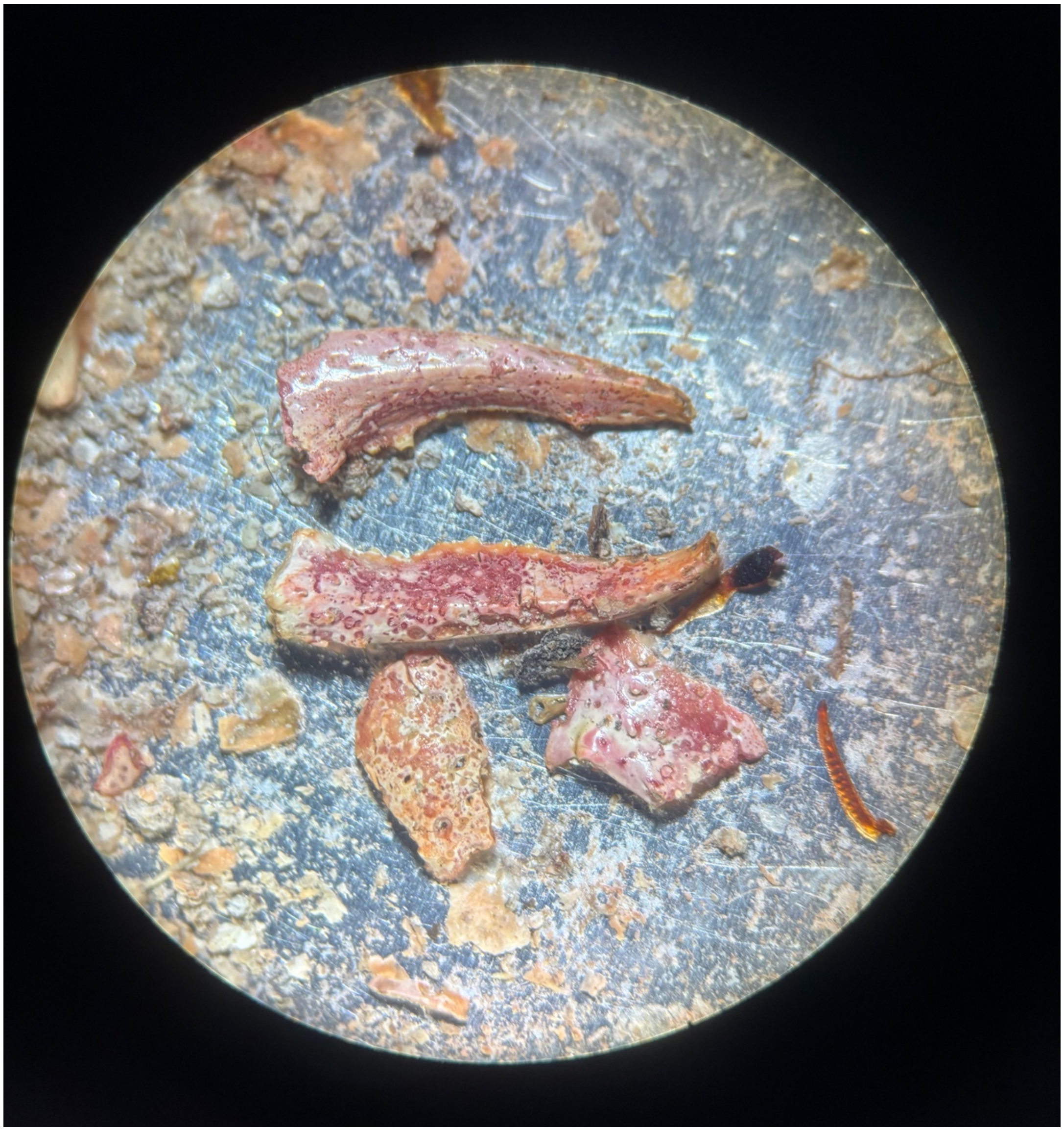


Pyrgulopsis sp.



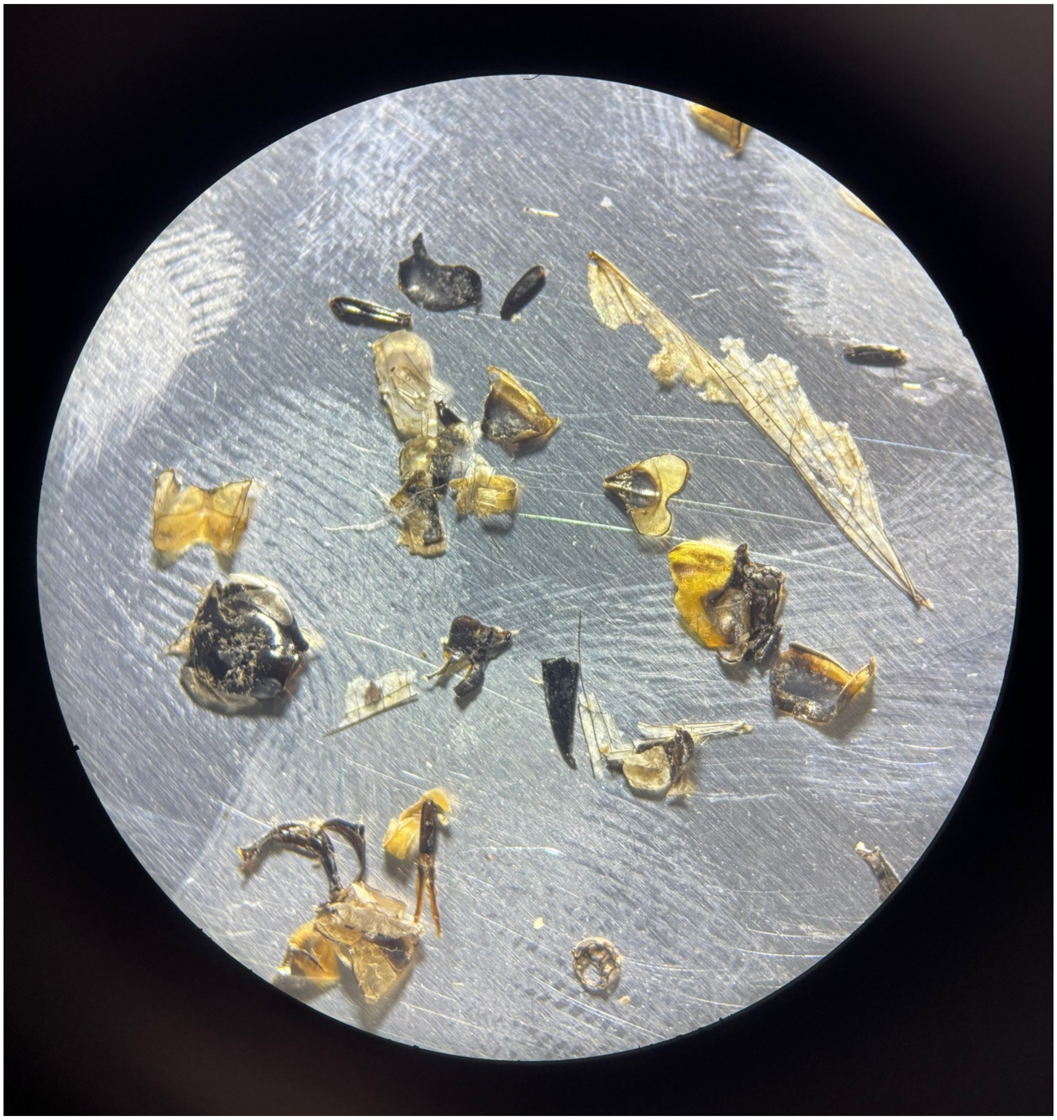
Physella acuta.

Corbicula fluminea.

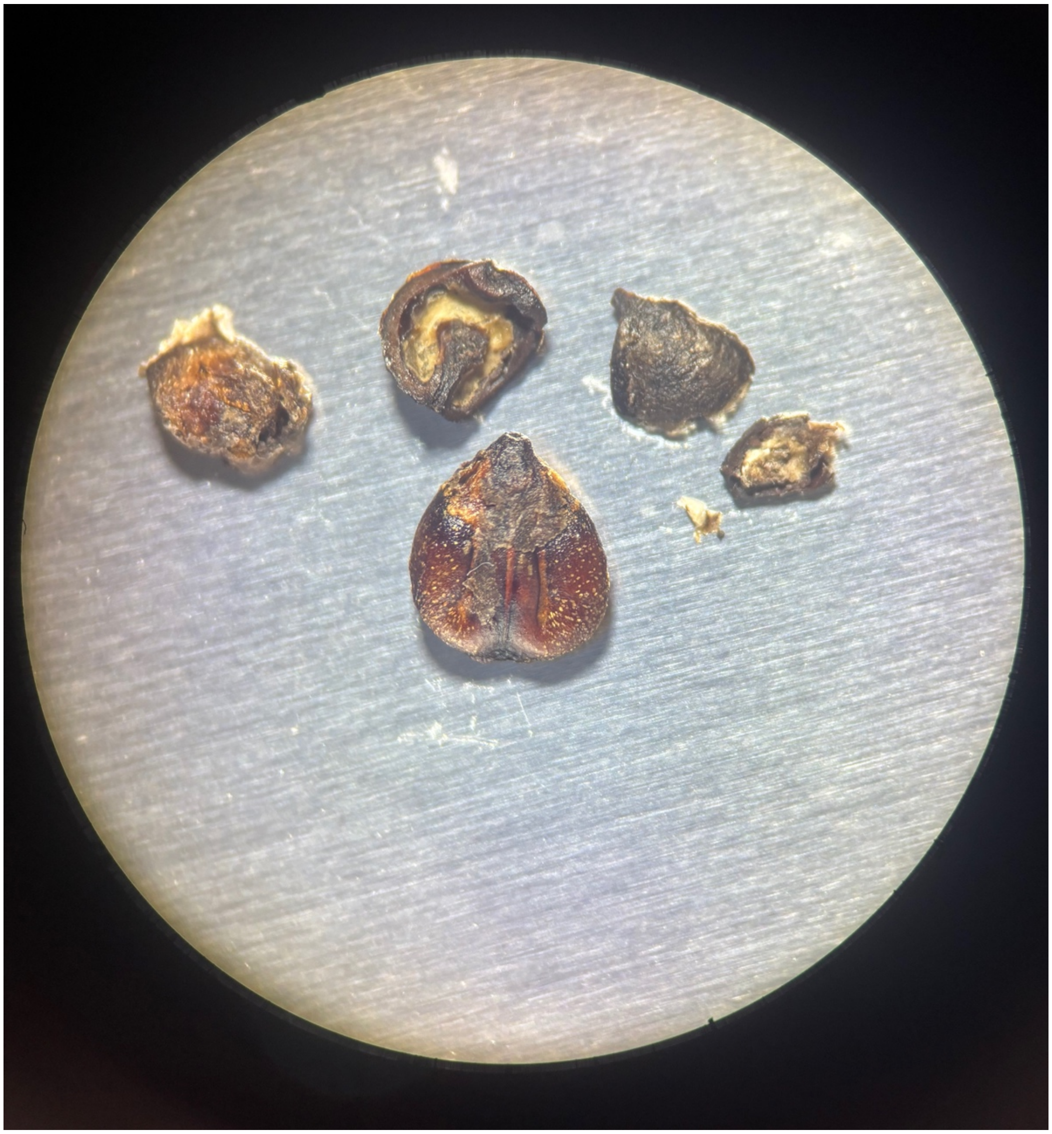


Procambarus clarki exoskeleton fragments.

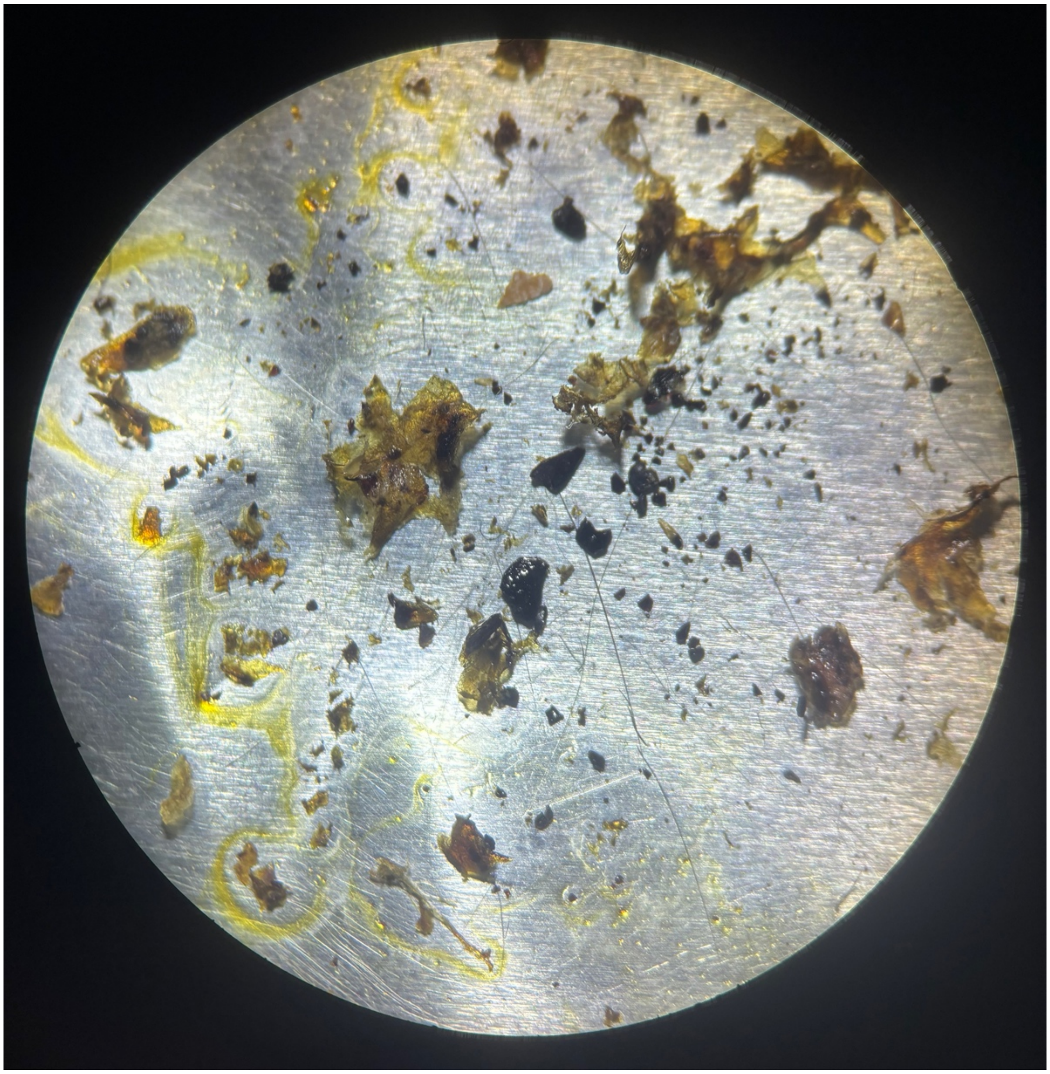
Stygoparnus comalensis.



Unidentified arthropod.



Cabomba caroliniana seeds.



Unidentified plant matter.