PLOS ONE

RESEARCH ARTICLE

# Body-size evolution in gastropods across the Plio-Pleistocene extinction in the western Atlantic

**Brendan M. Anderson**[1]*, **Elizabeth Petsios**[2], **Jessica Behn**[3¤], **Amy Betz**[4], **Warren D. Allmon**[1], **Bruce S. Lieberman**[4], **Jonathan R. Hendricks**[1,5]

**1** Paleontological Research Institution, Ithaca, NY, United States of America, **2** Department of Geosciences, Baylor University, Waco, TX, United States of America, **3** Biological Sciences Program, Cornell University, Ithaca, NY, United States of America, **4** Biodiversity Institute and Department of Ecology & Evolutionary Biology, Dyche Hall, University of Kansas, Lawrence, KS, United States of America, **5** Milwaukee Public Museum, Milwaukee, WI, United States of America

¤ Current address: Department of Forensic Science, Henry C. Lee Institute of Forensic Science, West Haven, CT, United States of America
* BMA53@Cornell.edu

**Citation:** Anderson BM, Petsios E, Behn J, Betz A, Allmon WD, Lieberman BS, et al. (2024) Body-size evolution in gastropods across the Plio-Pleistocene extinction in the western Atlantic. PLoS ONE 19(12): e0313060. https://doi.org/10.1371/journal.pone.0313060

**Editor:** Murtada D. Naser, University of Basrah, IRAQ

**Received:** June 27, 2024

**Accepted:** October 18, 2024

**Published:** December 13, 2024

**Data Availability Statement:** All relevant data are within the manuscript and its Supporting Information files.

**Funding:** This material is based upon work supported by the National Science Foundation under Award No. 2225014 to JRH and WDA and 2225011 to BSL, and a Panorama grant from the University of Kansas Biodiversity Institute to AB. There was no additional external funding received for this study. Funders did not play a role in the

## Abstract

The Plio-Pleistocene turnover event in the western Atlantic following the closure of the Central American Seaway involved high rates of extinction for both gastropod and bivalve molluscs. This extinction was associated with declining nutrient conditions and has been presumed to be associated with a decrease in molluscan body size. Previous work which has been concordant with this expectation, however, has either focused on bivalves or not considered the effects of the recovery post extinction. In three phylogenetically diverse clades, we found that body-size evolution in gastropods across the turnover event is likely tied to ecology. One clade increased in size, one decreased, and another exhibited no substantial change. Individual species lineages exhibit a mixture of microevolutionary changes from the Pliocene to today. This study indicates that gastropod body-size evolution may be more complex than in bivalves, with ecology and other functional traits playing a significant role. Macroevolutionary processes, especially whether a clade re-radiated post extinction, were found to be important. Indeed, a low portion of extant diversity consists of survivors from clades that increased in size or have similar size distributions among their species relative to the Pliocene.

## Introduction

### The western Atlantic Plio-Pleistocene extinctions

Major environmental change and high faunal turnover have made the Neogene–recent western Atlantic a model system for studying the macroevolutionary dynamics that led to the region's modern coastal ecosystems [1,2]. This system is characterized not only by high extinction, peaking around 2 Ma, but also with significant origination leading to similar modern

study design, data collection and analysis, decision to publish, or manuscript preparation.

**Competing interests:** The authors have declared that no competing interests exist.

levels of diversity relative to the Plio-Pleistocene, albeit with different taxonomic composition and differences in species' abundance [2–6]. The extinction was regional but severe and basin wide, with around 70% of gastropod species [3,7], and 47–65% of bivalves [3,8] going extinct. This system is well documented, with a rich fossil record, and the extinction occurred in relatively recent geologic history, making it ideal for studying not only how extinction impacts ecologically relevant traits but also how recovery can interact with apparently selective extinction pulses. Most work studying this event has focused on the southwest Caribbean, especially Panama [2,6,9,10], though the event is known to have impacted Florida as well [3,7,11,12].

The turnover event was not simply a transient perturbation but rather represented a permanent shift in ecosystems associated with changing environmental conditions. Nutrients declined in the western Atlantic following the closure of the Central American Seaway. The formation of the Central American Isthmus was completed ~2.8 Ma [13,14], cutting off connections to eastern Pacific waters. Resulting oceanographic changes impacted local upwelling [2,12,15–17]. Subsequent global cooling during the Pleistocene modified the hydrologic cycle and may have impacted delivery of nutrients via runoff [18,19]. Hardground habitats and seagrasses also expanded, altering the habitats occupied by marine mollusks [2,5,6,20]. Some studies indicate that predation intensity may also have declined in the region but evidence for changes to predation intensity is limited [21–23]. A possible increase in parasitism in some taxa [24] may be related to declines in predation intensity [25,26], but it is difficult to determine how much of this signal may be taphonomic without further study. In contrast, Sime & Kelley [27] showed stability in predation intensity across the turnover event and highlighted the potential importance for regional variation in response.

Habitat association [2,6], feeding mode [2,6,14,28], and larval ecology [2,17,29,30] have each been observed to be associated with survivorship in this event and success across the boundary, as has metabolic rate, a trait related to body size [1].

## Body-size evolution

The impact of evolutionary processes and mass extinction on macroinvertebrate body size has long been of paleontological interest (e.g., 31–35). From a theoretical perspective, selection pressures can act in the same or opposite directions on species within a clade and the constituent populations of each species [36–41]. This results in complex relationships between body-size variation across species-rich clades and among organisms within individual species. Body-size evolution is also an interesting feature to examine in the context of the Plio-Pleistocene of the western Atlantic (PPWA) because the relationship between available nutrients and the distribution of average or maximum species body sizes in a community may not be tied to the microevolutionary responses observed in the constituent species under high and low nutrient conditions. For example, the distribution of sizes in a population may be centered around a smaller mean under low-nutrient conditions. Under high-nutrient conditions, however, it is possible the community supports more species overall, including both small and large species.

Marine mollusks represent a major component of the Mesozoic to Pleistocene fossil record. Compared with other marine poikilotherms, mollusks exhibit distinctive body-size trends and responses to environmental changes [42] including the effect of body size on species duration and extinction risk (e.g., work by Payne & Heim [34], Monarrez et al. [35], Pietsch et al. [41], Jablonski [43], and Crampton et al. [44]). Some studies have recovered conflicting trends across different clades [44,45] whereas others have revealed no trend [43]. There can even be conflicting trends in body-size responses to different extinction events [46]. This suggests that understanding body-size evolution in different clades of mollusks is a complex problem affected by several factors. In some cases, the most pronounced factors are how body size influences group-level characters like species' geographic range (see Jablonski & Hunt [47] for discussion of geographic range size as a group-level character), especially via the relationship between geographic range size and extinction risk. In other cases, body size is correlated with other organismal traits such as fecundity or other aspects of an organism's life history or ecology (see reference 41 for further discussion of traits that have been linked to body size in a variety of taxa), and these other factors may be what is primarily determining extinction risk. Lastly, there are factors related to chance and contingency [48].

Recently, Monarrez et al. [49], in an important paper, demonstrated that geographic range is likely to be a more significant influence on survivorship than body size. However, selectivity for body size was distinguishable from selectivity on geographic range in their analyses. Further, extinction models that included body size were preferred over geographic range-only models for gastropods but not bivalves [49], indicating patterns may vary across mollusks. Smaller-bodied gastropod genera were found to have higher extinction risk during both background and mass extinction events, whereas bivalves exhibited almost no selectivity on body size during mass extinctions [49].

While global-scale patterns of selectivity during mass and background extinctions observed at the generic level may yield consistent long-term patterns, the regional event in the PPWA may not conform to this pattern. Indeed, Monarrez et al. [49] noted that local extinction dynamics may deviate from the broader-scale patterns they observed and additively contribute to extinction dynamics during background intervals. The extinction event in the PPWA has been characterized previously as resulting in a smaller body sized post-extinction fauna [5].

In the PPWA, chionine bivalves (placed in *Chione*, *Chionopsis*, and *Lirophora*) decreased in size in the western Atlantic across the boundary [50]. Corbulid bivalves also exhibited a body-size decline for the PPWA, yet over the same interval in the eastern Pacific body size increased [51,52]. *Strombina*-group gastropods did not exhibit a significant long-term trend in body-size change in the Neogene western Atlantic, although they did show a significant increase in size in the eastern Pacific [29]. However, it is notable that the three extant species in the western Atlantic are larger compared to Plio-Pleistocene forms [29].

The differences between patterns in the PPWA and other regions and times may be attributable to the very specific environmental changes experienced in the PPWA, such as changes in nutrient availability. The association between the PPWA extinction event and a shift to lower-nutrient conditions could be expected to influence the relationship between body size and extinction. For instance, body size in mollusks is generally correlated with nutrient availability [53], which declined in the post-Pliocene of the western Atlantic. Therefore, all other factors being equal, one may expect the pre-extinction fauna to consist of larger body-sized mollusks than the post-extinction fauna [54–58]. In this study, we tested the hypothesis that modern members of gastropod clades in the region differ in body size from the representatives of those same clades in PPWA. We compared all constituent species belonging to three gastropod clades from before and after the extinction, as well as examined body-size evolution in surviving species lineages across the extinction event.

## Geologic setting of the extinction

Fossiliferous units of the PPWA include primarily unlithified sands, silts, and clays, while the fossil record in Florida includes both sands and siliciclastic bearing carbonates ("shell beds") [59–62]. The stratigraphic correlations among units of the United States Atlantic Coastal Plain and Florida are complex, with the chronostratigraphy of various units continuing to improve even in recent years [27,59,60,63–65]. Herein, we follow the stratigraphic framework used in Friend et al. [66] (S1 Fig), which was based on the work of Lyons [62], Saupe et al. [63], Campbell [67], Ward & Gilinsky [68], Allmon et al. [3], Hendricks [69], Kittle et al. [70], Dowsett et al. [65], and references therein.

S1 **Fig** Stratigraphic correlation of important Pliocene-Pleistocene fossiliferous units of Florida and the Atlantic Coastal Plain. Modified from Friend et al. [66], text Fig 1.

The Piacenzian is represented in Virginia and North Carolina by the Yorktown Fm., in the Carolinas and Georgia by the Duplin and Raysor formations, and in Florida by portions of the Jackson Bluff, Nashua, and Tamiami formations (represented by Pinecrest beds 5–9 of the Tamiami Fm.). The Gelasian is represented by the Chowan River Fm. in Virginia and North Carolina and the Bear Bluff Fm. in North and South Carolina. In Florida, the upper portion of the Nashua and Tamiami formations (Pinecrest beds 2–4), and the Caloosahatchee Formation are considered Gelasian (earliest Pleistocene). The James City and Waccamaw formations overly the Chowan River and Bear Bluff formations in North and South Carolina, straddling the boundary between the Gelasian and subsequent Calabrian. The Canepatch Fm. in South Carolina and the Bermont and Ft. Thompson units in southern Florida appear to substantially post-date the extinction event. The Caloosahatchee, Bermont, and Ft. Thompson "formations" have been combined into the Okeechobee Fm. by Scott [71], but this name is not in wide use. Based on faunal differences these have been treated as separate units in the recent paleontological literature [22,66,72,73].

## Taxon selection

Three phylogenetically diverse families spanning the Plio-Pleistocene and recent were chosen for analysis and represent clades with distinct ecologies: Conidae (Caenogastropoda: Neogastropoda), Tegulidae (Vetigastropoda: Trochoidea), and non-*Vermicularia* Turritellidae (Caenogastropoda: Cerithioidea). These taxa were selected because each clade experienced notable turnover at the extinction, and each has at least one species lineage which survived from the Plio-Pleistocene to the modern (Fig 1; species list in S1 Table).

## Conidae

Cone snails are an extremely diverse family of venomous, predatory gastropods with high species diversity in both modern communities and fossil assemblages in Florida [69,74]. Multiple species frequently co-occur, most likely due to high degree of specialization on different prey species [75]. Conidae are also of evolutionary interest because of their extremely rapid rates of speciation [74,76]. Fossil Conidae of the western Atlantic Coastal Plain have also been subject to relatively recent systematic revision [69], which included the collection of measurements from several hundred fossil specimens. Twenty-four species of Conidae (19 of *Conus* and five of *Conasprella*) were present in the PPWA prior to the extinction interval. Twenty-four species also live in the region today (17 of *Conus* and seven of *Conasprella*), and eight of these species have a fossil record (three of *Conasprella* and five of *Conus*). *Conus patricius* was present in the PPWA, but is now restricted to the eastern Pacific. *Conus amphiurgus* has been reported from the Bermont Fm. [77], which we consider post-extinction, but we note that this has not been verified based on museum specimens [69].

## Tegulidae

Tegulids are grazers on micro- and macroalgae as well as sea grasses [78,79]. Recent species inhabit shallow water habitats with some species living within the splash zone and intertidal waters and others restricted to subtidal zones [80]. Florida fossil Tegulidae have been relatively understudied compared with the other families considered herein. Modern tegulids are represented in the region by two species of the genus *Agathistoma*, three of *Tegula*, and *Cittarium*

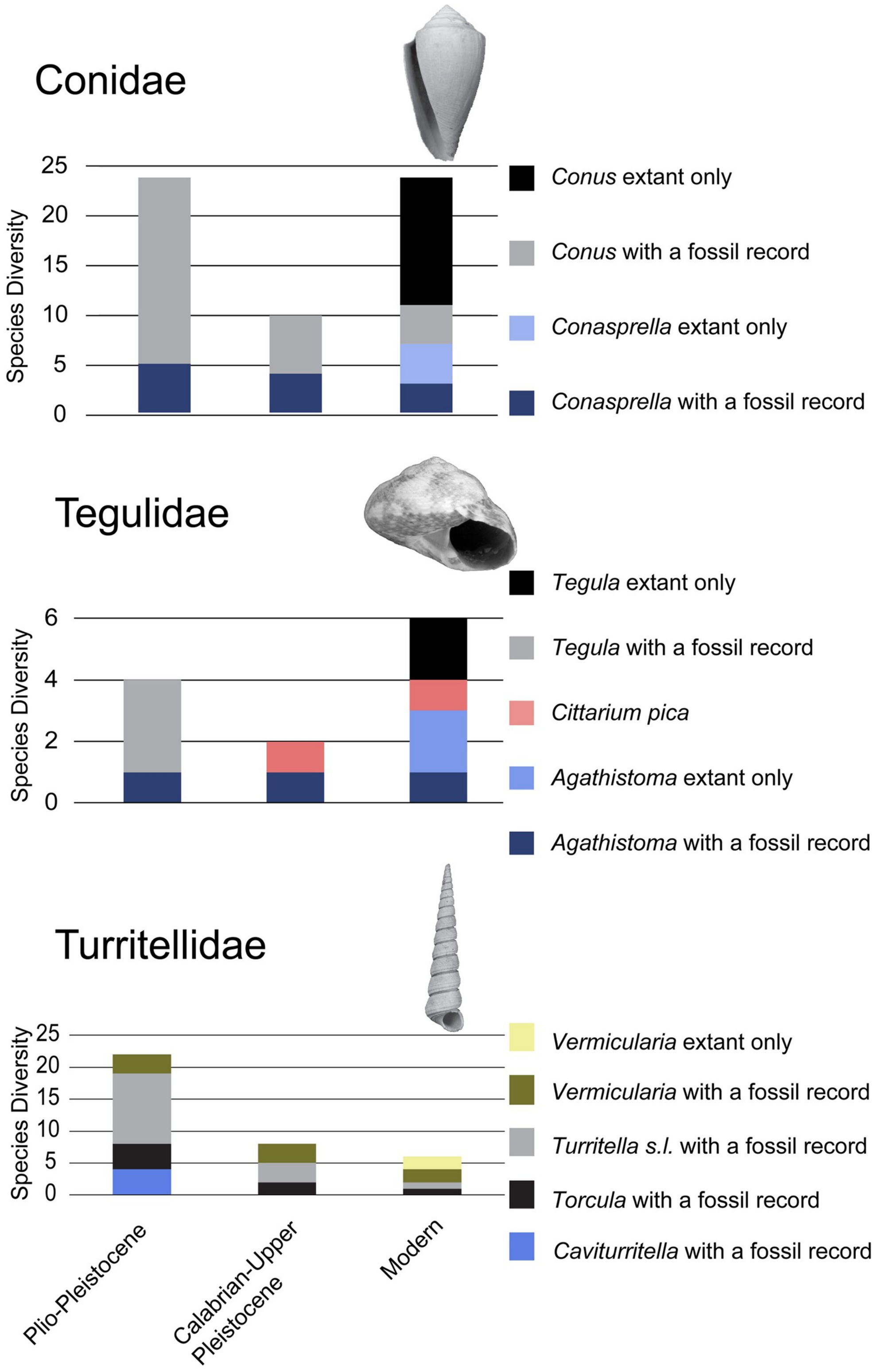

**Fig 1. Diversity of each focal taxon in Florida and the Atlantic Coastal Plain throughout the study interval.** Species are divided according to whether they have a fossil record or represent post-turnover origination. Plio-Pleistocene is Piacenzian–Gelasian, the next time bin is Calabrian–upper Pleistocene, and modern is present day diversity in the region. This time division was chosen rather than the end of the Pliocene because in Florida the Nashua Fm. and Pinecrest Beds within the Tamiami Fm. cross the Piacenzian-Gelasian boundary, and substantial faunal

turnover occurred not at the Pliocene-Pleistocene boundary but was completed shortly thereafter. The interval designated Calabrian-Upper Pleistocene corresponds to the James City, Waccamaw, Bermont, Canepatch, and Ft. Thompson Formations (see S1 Fig). Our subsequent analyses do not depend on the selection of this post-extinction, but pre-modern time category, it is presented here to demonstrate the proportion of modern species that have fossil records dating to this time. *Torcula exoleta* (Linnaeus, 1758) is believed to be a direct descendant by anagenesis of *Torcula perattenuata* (Heilprin, 1886) [66] and is therefore represented as a lineage with a fossil record. Representative images of species are as follows: Conidae, *Conus adversarius* Conrad, 1840, University of Florida 66443, modified from Hendricks [69], plate 7, figure 13; Tegulidae, *Tegula exoluta* (Conrad, 1843) Paleontological Research Institution 70266, modified from the Neogene Atlas of Ancient life, used under Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License; Turritellidae, *Caviturritella magnasulcus* (Petuch, 1991) Carnegie Museum 35625, modified from Friend et al. [66], figure 16.

https://doi.org/10.1371/journal.pone.0313060.g001

*pica* (Linnaeus, 1758). There is some dispute as to whether *Cittarium pica*, which is significantly larger in body size than the other tegulid genera, is properly nested within Tegulidae or is a close relative [81], but we include it here and perform analyses both including and excluding this species. *Cittarium pica* appears in the late Pleistocene Miami Limestone (~130 ka based on uranium series dating [82,83]), which is post-extinction. One species of *Agathistoma* and three of *Tegula* were present in the PPWA. We treated *Tegula* (*Monodonta*) *kiawahensis* Tuomey and Holmes, 1856 as a likely synonym of *Tegula exoleta* (Conrad, 1843) following Dall [84] and Campbell [67]. *Agathistoma fasciatum* (Born, 1778) ranges across the extinction boundary.

### Turritellidae

Turritellidae are primarily semi-infaunal suspension feeders, also known to deposit-feed [85–87]. They have a diverse and abundant fossil record [87–89] and were disproportionately impacted by the PPWA extinction [2,3,5,6]. We excluded the turritellid genus *Vermicularia*, which has a different ecology (generally more reef-associated) and morphology (*Vermicularia* are uncoiled, making axial length comparisons non-analogous) when compared with other turritelld genera [90]. A recent phylogenetic treatment of Pliocene-to-recent species in Florida and the Atlantic Coastal Plain [66] indicated that at least three evolutionary lineages of non-*Vermicularia* turritelline gastropods were present, with two of these recognized as the genera *Caviturritella* and *Torcula*. Twenty fossil species were present in the Plio-Pleistocene of Florida and the Atlantic Coastal Plain, but only two remain in the region: *Torcula exoleta* (likely the direct descendant of *T. perattenuata* [66]) and *Turritella* (*sensu lato*) *perexilis* (= *Turritella acropora* [66]).

## Methods

Body size was represented by specimen length, recorded parallel to the coiling axis, and maximum body size for each species and mean sizes of fossil and recent specimens were investigated. Data were collected at the species level as differences in how species are assigned to genera may obscure real changes in community composition [91]. Cone snail species were evaluated using both maximum size and the typical size metric of Kohn [74]. Species synonymies and taxonomic assignments generally follow Hendricks [69], Friend et al. [66], and WoRMS [92]. An exception is that Hendricks [69] previously considered *Conasprella stearnsii* and *Conasprella jaspidea* synonymous, but Kohn [74] demonstrated that they are distinct; new measurement data were collected for these two species for this study with updated species determinations. The tegulid synonymy used herein is outlined in S2 Table. Newly collected specimen data were taken from specimens from the US Atlantic Coastal Plain or the Florida-Bahama Platform, however previously published data (e.g., data from Hendricks [69] and Kohn [74]), may have included specimens from outside of the present study region for wideranging species. Additional information on the methods used to determine each species' body-size measurements are available in the supplemental text (S1 Text). Species measurement data used in our analyses are available in S3 Table along with species authority information.

When comparing the average size of species within each clade in the region before and after the extinction, we used the mean size of all species present in the region at the time to make the comparisons (whether each constituent species' size was represented by the typical, average, or maximum size known for that specific species). We do not believe that "average size" is a real, emergent property that is held intrinsically by a higher taxon (clade), especially as the taxonomic assignment of a natural group of species to a certain rank is ultimately a human construct [91]. We are using these metrics as descriptors for how similarly conceptualized clades differ in aggregate properties in particular local instantiations at different time periods. A shift in the average body size for a given clade could be accomplished in a number of ways (e.g., preferential extinction, or speciation, of members which are smaller, or larger, than the original mean of the group, or greater changes during speciation towards smaller, or larger, body sizes). This descriptive property of a clade can however indicate whether macroevolutionary processes are favoring larger or smaller forms following the extinction event. We chose mean size rather than median as a size descriptor for our clades as they tended to be normally distributed and means were more likely to be impacted by the presence or absence of large or small outlier species, which could facilitate detection of changes that impacted which extremes were supported before or after the extinction.

Data were visualized and t-tests were performed in PAST v. 2.17c [93]. Additional statistical analyses (described below) were performed in R v. 4.3.2 [94] implemented in RStudio [95]. In Florida the extinctions may have occurred in two pulses [96], with the primary pulse at the Tamiami-Caloosahatchee boundary and a second pulse at the end of Caloosahatchee time. For our analyses we compared recent species with a pre-extinction fauna which included both Pliocene and earliest Pleistocene strata (Pinecrest beds of the Tamiami Fm., Caloosahatchee Fm., Nashua, Bear Bluff, and Chowan River Formations; see S1 Fig).

Using R [94], each family was evaluated using body-size data for all constituent species occurring in the region to determine whether the mean sizes of the recent species in the clade are aberrant relative to the size distribution of fossil species' means for each family. Log-transformed data were used to evaluate body-size differences in each clade across the extinction, following the treatment of other multi-taxon datasets [97,98]. A size distribution for each family was generated by random resampling with replacement 1,000 times of $N_m$ species' log-transformed body sizes from among the pre-extinction interval fossil species, where $N_m$ is the number of surviving species. This was used as the test distribution representing what we might expect if speciation or extinction were not biased towards or against large or small body sizes but were of equal magnitude to the total change in diversity, i.e. a "non-selective turnover." This process was then repeated drawing $N_f$, the number of fossil species from the pre-extinction log body-size distribution, and $N_m$ from the modern log body-size distribution. We then compared the modern resampled distributions to the fossil and test distributions to determine whether extant species are larger or smaller than chance. If the mean of the modern resampled distribution fell within the 50% confidence window for test distribution, we concluded the turnover event did not alter the size distribution more than expected by chance. If the modern size distribution of a clade fell outside of this window, we concluded that the turnover event may have altered the average body size in the clade. This analysis was first performed using mean (Tegulidae and Turritellidae) or typical size (Conidae) for each species and then repeated using maximum size to represent each species' size. For ancestor-descendant comparisons, data were visualized for each species in box plots, and 2-sample t-tests were conducted comparing ancestor-descendant populations.

# Results

## Clade-level analyses

For Conidae, the average species size was 40.9 mm (typical sizes) or 59.0 mm (maximum sizes) in the Plio-Pleistocene and 35.4 mm (typical sizes) or 62.0 mm (maximum sizes) in the modern, and these differences were not statistically significant ($t>0.75$, $p = 0.44$; $t>0.19$, $p = 0.84$ for typical and maximum sizes, respectively). Extinct species also did not differ significantly in size from surviving species (i.e., without considering species which originated post-extinction) by either metric. The mean of the resampled modern body-size distributions fell within the 50% confidence window of the non-selective turnover scenario, indicating no meaningful change (Fig 2). These results were replicated when maximum sizes were used to represent species' sizes (S2 Fig).

**S2 Fig** Clade body sizes using log transformed maximum recorded size to represent each species' size. Data are presented for each family, from left to right, as the actual distribution of species body size prior to the extinction, a distribution of means when the data are resampled up to the number of pre-extinction species 1000 times with replacement, a non-selective turnover scenario represented by the distribution of mean sizes when the pre-extinction species' sizes are resampled 1000 times using the number of extant species, a distribution of means when the modern species' sizes are resampled 1000 times with replacement using the modern number of species for each sample, and the actual size distribution of the modern taxa.

For Tegulidae, the average species size was 8.6 mm (mean sizes) or 11.5 mm (maximum sizes) in the Plio-Pleistocene and 19.0 mm (mean sizes) or 35.0 mm (maximum sizes) in the modern, but these differences were not statistically significant (for mean sizes, $t = 1.1$, $p = 0.30$, unequal variance $t = 1.4$, $p = 0.23$; for maximum sizes $t = 1.01$, $p = 0.34$, unequal variance $t = 1.27$, $p = 0.26$). The mean size of modern tegulids is heavily influenced by *Cittarium pica*, a very large species that originated in the late Pleistocene and which actually may not properly belong to Tegulidae (though it is closely related if not a member of the family). Excluding *Cittarium pica*, modern tegulids are 11.7 mm (the mean of each species average size) or 16.6 mm (the mean of each species maximum size), which preserves the direction of the signal (modern species are larger on average than Plio-Pleistocene species), but this difference is not statistically significant even when *C. pica* is included. Only one species survived the extinction, but it does not differ substantially in size from the species which became extinct (8.6 mm for surviving species versus 8.5 mm average size of extinct species). Resampled post-extinction means are substantially higher than for the non-selective turnover scenario, suggesting the modern tegulid species are larger than expected by chance (Fig 2). This result is replicated when maximum sizes are used to represent species' body size (S2 Fig).

For Turritellidae, the average species size was 65 mm (mean sizes) or 96 mm (max sizes) for Plio-Pleistocene species and 38 mm (mean sizes) or 56 mm (max sizes) for the modern. These changes were not significant under a permutation t-test ($t = 1.72$, $p = 0.10$; $t = 1.56$, $p = 0.14$ for mean and maximum sizes, respectively), however only two turritellid species live in the region in the modern. Extinct species did not differ significantly in size from survivors (66 mm vs 62 mm—note that there was evolution, discussed below, in the *Torcula perattenuata-exoleta* lineage, and this comparison was made using the Plio-Pleistocene body-size distribution for this lineage). The resampled size distribution for the modern turritellids fell below the 50% confidence window of the non-selective turnover scenario, indicating that turritellids are smaller than expected by chance (Fig 2). When maximum sizes are used, this change is much less dramatic (S2 Fig). In this case, the actual mean falls within the central quartiles of the non-selective turnover scenario, although the resampled mean fell outside this window.

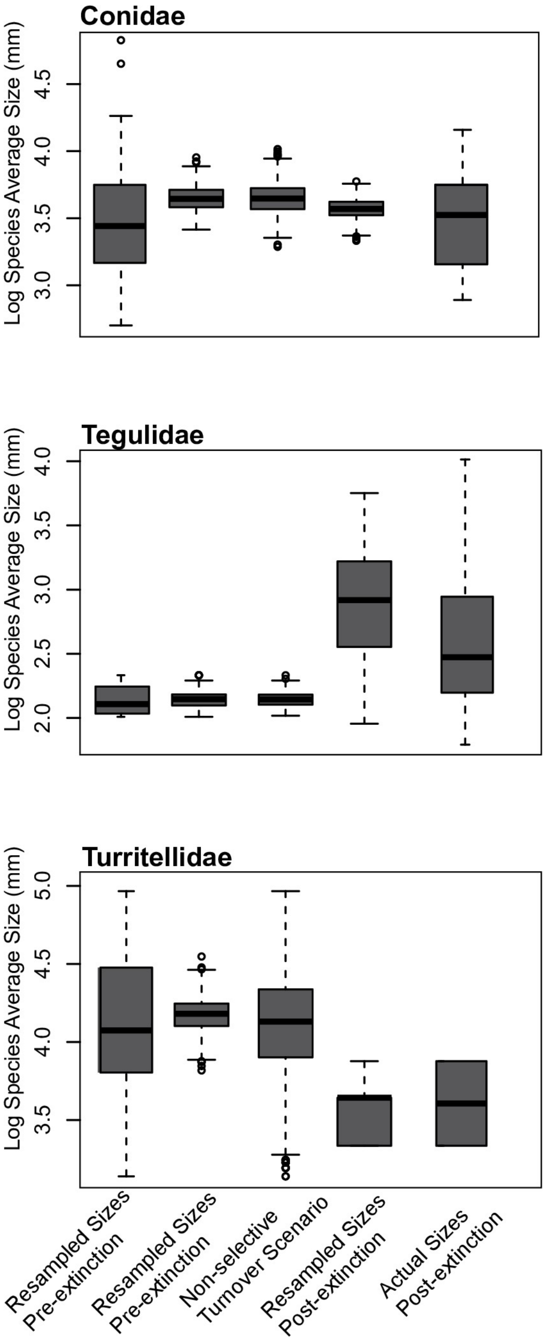

**Fig 2. Clade body sizes using log transformed mean adult size to represent each turritellid and tegulid species' size, and typical size to represent the size of each species belonging to Conidae (see Kohn [74] and supplemental text (S1 Text) for additional information on this methodology).** Data are presented for each family from left to right, as the actual distribution of species body size prior to the extinction, a distribution of means when the data are resampled up to the number of pre-extinction species 1000 times with replacement, a non-selective turnover scenario represented by the distribution of mean sizes when the pre-extinction species' sizes are resampled 1000 times using the number of extant species, a distribution of means when the modern species' sizes are resampled 1000 times with replacement using the modern number of species for each sample, and the actual size distribution of the modern taxa.

https://doi.org/10.1371/journal.pone.0313060.g002

## Conidae species-lineage analyses

Fossil and modern populations of *Conasprella jaspidea* (Gmelin, 1791), *Conasprella stearnsii* (Conrad, 1869), *Conus anabathrum* Crosse, 1865, *Conus daucus* Hwass, 1792, and *Conus spurius* Gmelin, 1791 were evaluated (Fig 3). One *Conasprella* species showed a statistically significant changes in body size between fossil and extant populations—modern *C. stearnsii* are smaller than their fossil counterparts (17.9 mm vs. 20.5 mm; t-test $p < 0.01$), although this result was not significant when a Bonferroni [99] corrected α of 0.007 is applied). In contrast, one *Conus* species also showed a statistically significant difference, but of opposite sign: modern *Conus daucus* are larger than their fossil population (24.9 mm vs 34.5 mm; t-test $p < 0.001$), a result which remains significant when using a Bonferroni corrected α of 0.007. *Conasprella jaspidea* did not change in size (20.8 mm for modern examples and 20.8 mm for fossil specimens; t-test $p = 0.99$). Excluding the measurements taken from figured specimens rather than measurements made directly from collections materials (7 specimens of *C. jaspidea* as detailed in S3 Table), the modern examples are smaller (18.3 mm) on average, but this

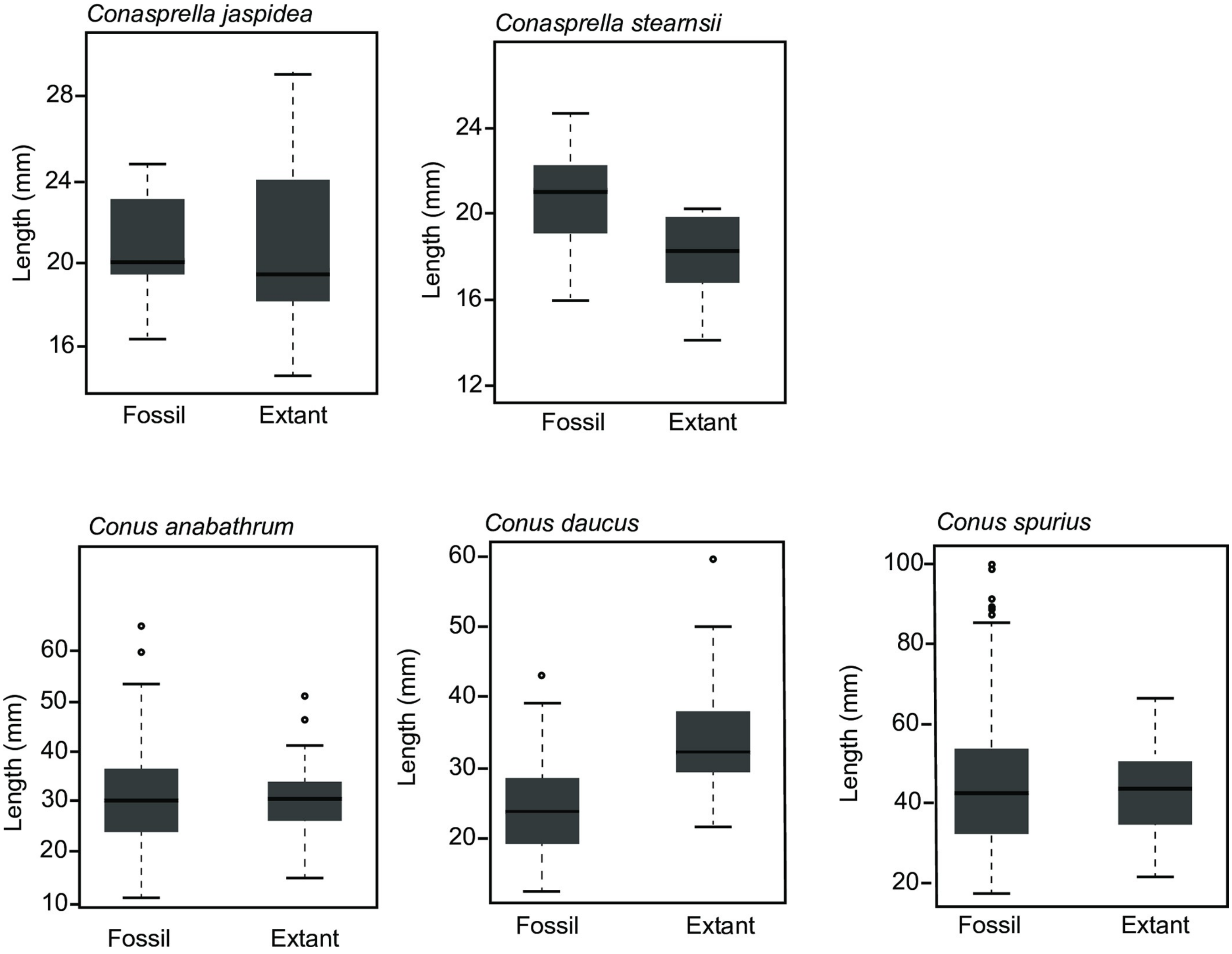

**Fig 3. Shell-length distribution of species belonging to the family Conidae that survived the extinction event comparing Plio-Pleistocene to modern shells.** Only *Conasprella stearnsii* and *Conus daucus* had statistically significant changes in body size.

https://doi.org/10.1371/journal.pone.0313060.g003

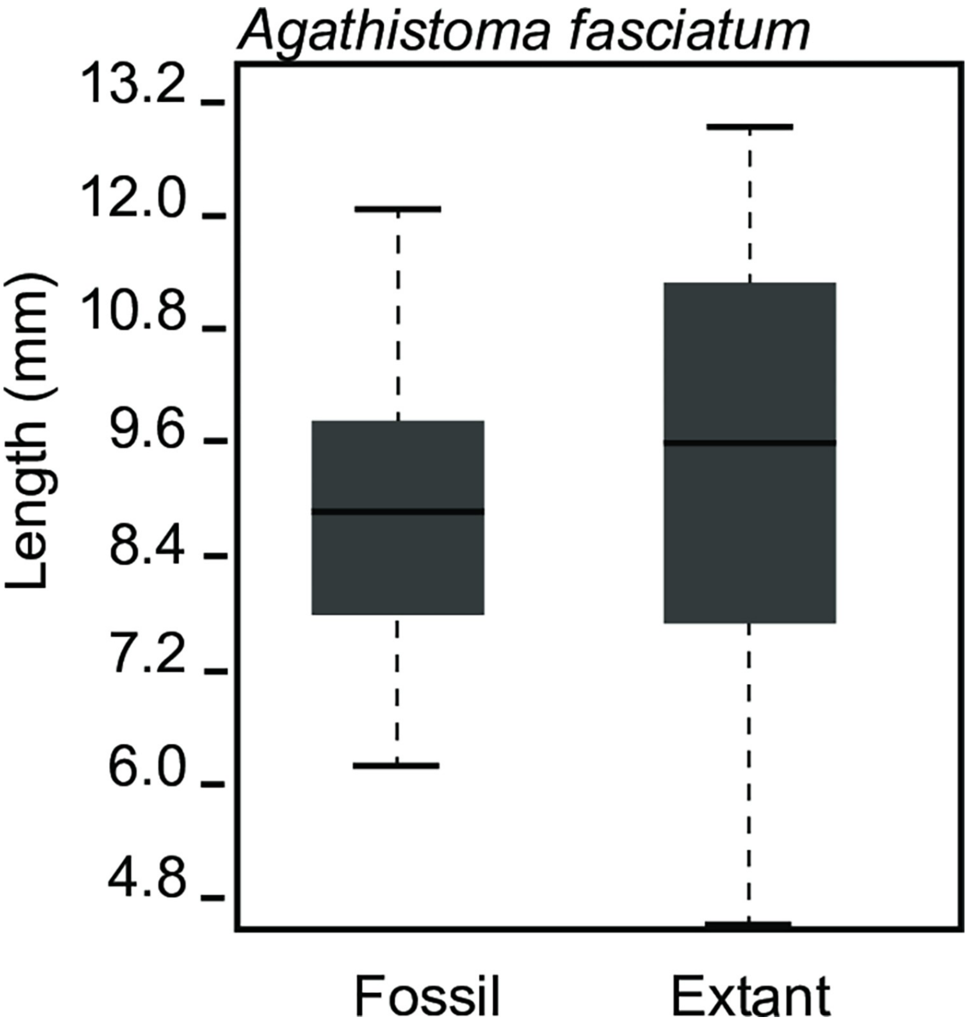

**Fig 4. Shell length distribution for fossil and modern *Agathistoma fasciatum* comparing Plio-Pleistocene to extant shells.** Modern *A. fasciatum* are not statistically distinct from fossil forms.

https://doi.org/10.1371/journal.pone.0313060.g004

difference is not statistically significant. Neither of the remaining *Conus* species showed statistically significant differences in specimen length in fossil versus modern populations. Extant *C. anabathrum* averaged 30.6 mm, while fossil *C. anabathrum* averaged 31.5 mm. Extant *C. spurius* averaged 42.1 mm in length, while fossil *C. spurius* averaged 45.4 mm (S3 Table).

## Tegulidae species-lineage analysis

The single lineage which survived from the Pliocene, *Agathistoma fasciatum*, had an average fossil length of 8.6 mm and an average modern length of 9.4 mm, but this difference was not statistically significant (Fig 4).

## Turritellidae species-lineage analysis

One turritellid species-lineage, *Turritella perexilis* (= *T. acropora*) maintained a highly similar shell length across the turnover event (27.4 mm vs 28.1 mm for fossil and extant, respectively, a difference which was not statistically significant) (Fig 5). *Torcula exoleta* is, however, much smaller than its likely anagenetic ancestor *Torcula perattenuatta* [66], and this difference is

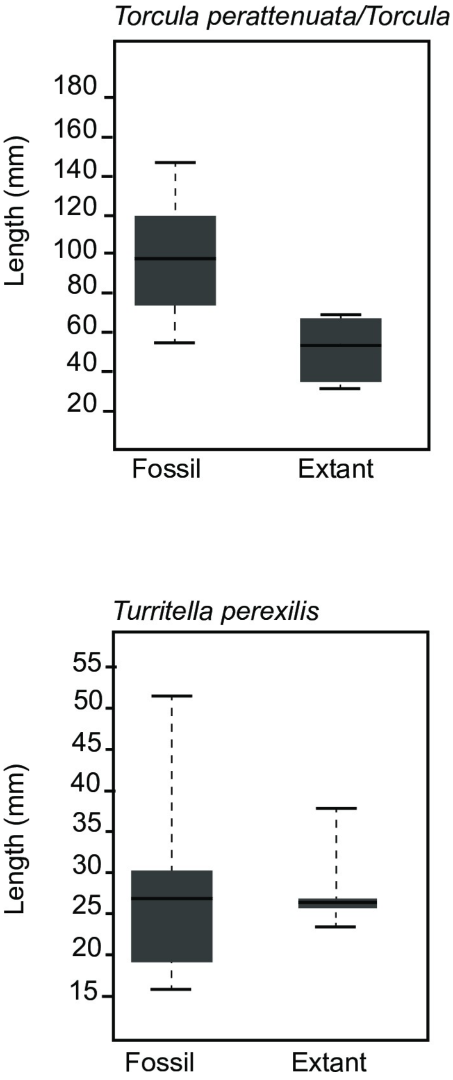

**Fig 5. Shell length distribution of species belonging to the family Turritellidae which survived the extinction event comparing Plio-Pleistocene to extant shells.** *Torcula perattenuata* is compared with *Torcula exoleta*, which is believed to be its anagenetic descendant following the phylogeny of Friend et al. [66] *Turritella perexilis* is the senior synonym of *Turritella acropora*, the name typically applied to extant forms [66].

https://doi.org/10.1371/journal.pone.0313060.g005

statistically significant even after applying a Bonferroni correction (mean 48.3 mm vs 97.0 mm; t-test p <0.001; Fig 5).

## Discussion

### Body-size evolution and the meaning of trait changes in clades

Changes in body size among the species of molluscs in a region through time could be the result of: 1, natural selection on organismic properties; 2, ecological and environmental changes affecting phenotype (in the case of gastropods, temperature, availability of nutrients, and carbonate saturation may each have ecophenotypic effects); 3, macroevolutionary processes causing differential speciation and extinction rates between species with large body size versus small body size either directly or indirectly (if, for example, body size is linked to a species-level trait like geographic range size; or to another organismic trait such as larval type, that in turn is related to a species-level trait like geographic range [44,100–102], leading to substantial diversity differences [38]; 4, phylogenetic biases, if for some reason species with large-bodied organisms were more likely to give rise to species with large-bodied organisms, whereas species with small-bodied organisms were equally likely to give rise to small or large-bodied organisms [37]; 5, chance; and 6, a combination of some or all of these factors (see also Pietsch et al. [41]). In addition, once extinction eliminates a clade in a region, recovery in that group might be precluded, unless there were opportunities for biogeographic invasion, but these seem to have been limited in this case.

We may draw macroevolutionary rather than macroecological conclusions as the taxa considered herein, as well as the modern molluscan fauna in the region generally, are most likely the result of *in situ* speciation. The modern faunas of the US Atlantic Coastal Plain and Florida (the Caloosahatchian biogeographic province of Petuch [103]) are most similar to species that inhabited the region in the Pliocene (as the modern Caribbean molluscan fauna is most similar to the Pliocene Gatunian biogeographic province of Petuch [103]) indicating that the shift in taxonomic composition is most likely due to differences in *in situ* speciation rather than long-range dispersal [104,105]. Additionally, the life history traits of the taxa under study make it most likely that any Pleistocene-recent originations occurred locally. Extant tegulids have non-planktotrophic larvae [106–109] and most Conidae [74] and Turritellidae [17] in the modern western Atlantic have larvae expected to require little to no planktotrophy to metamorphose [74,110–112].

## How each clade behaved across the turnover event

The return to past levels of diversity of Conidae in Florida and the US Atlantic Coastal Plain included a return to a similar size distribution relative to the pre-extinction community; the very largest species were lost and new species have not yet achieved these large sizes. The impression that taxa are smaller may be the result of the "no-Gullivers" phenomenon [113], rather than a decline in species average body size following the extinction (either within lineages, the lilliput effect *sensu* Urbanek [114], or within a clade; see Abbott et al. [115] for further discussion of various uses of the term "lilliput effect" in the literature). In this case, we—as paleontological observers—are taking exceptional notice of the absence of one or two very large species, although the clade has a similar size distribution in the modern as it did prior to the extinction (see Harzhauser et al. [116] for a contrasting example where loss of large species was associated with overall decline in clade body size).

The evolution of larger species in Tegulidae may reflect a response to availability of the specific resources used by these species (seagrasses and algae growing on hard substrates [2,6,117]), despite overall decline in nutrient levels. Low connectivity [107] related to short duration in the plankton and high microhabitat partitioning [118] may both have contributed to high speciation and extinction (volatility) in this clade (although the relationship between larval mode and speciation rate in gastropods is not straightforward [102]).

Florida Tegulidae and Conidae originations appear to primarily occur post-extinction, with many recent species having no fossil record (Fig 1). Some extant species of Conidae may have Gelasian or Calabrian origins, but the rate of origination does not appear elevated (using the stratigraphic range data of Hendricks [69]). These clades that rediversified appear to have reoccupied much of the ecological space that may have been associated with their prior body-size distribution, especially in Florida where temperatures are similar to pre-extinction conditions. These new taxa may represent diversification within Florida and the US Atlantic Coastal Plain from the surviving species, immigration from neighboring regions, or in-situ radiation(s) following immigration events. Additional molecular genetic and phylogenetic work incorporating both fossil species and biogeographic information will be needed to determine precisely which species are of local origin. This post-extinction diversification appears to have different timing than originations in the southwest Caribbean where increased origination preceded extinctions [6,9].

Non-*Vermicularia* Turritellidae likely declined in size as a clade because the extinction was not followed by any cladogenesis in the surviving regularly-coiled taxa (*Caviturritella*, *Torcula* or *Turritella* s.l.), and because the genus *Caviturritella*, which was generally large bodied [119], was extirpated [66]. The extant regularly coiled western Atlantic Turritellidae may therefore be "dead clades walking" [17,120–122]. The decline of filter-feeding taxa associated with soft substrates is a pervasive characteristic of the turnover event [14], noted not only in turritellids but across bivalve taxa with similar ecology, including declines in the abundance of suspension-feeding bivalves compared to other feeding modes [6]. In contrast, cladogenesis continued to occur in *Vermicularia*, which differ from other turritellids in that many species are adapted to live on hardground environments, including reefs [90].

Gastropod taxa had higher speciation and extinction rates than bivalves across the turnover event [6] and, based on the patterns observed in our data, post-extinction speciation during recovery was an important part of body-size evolution and how this differed among gastropod families. The relatively rapid origination of many taxa which re-occupied a similar suite of body sizes to the extinct taxa also suggests that body size may be a particularly labile trait in gastropods. Bivalves have been documented to have decreased growth rates yet obtained similar sizes under the new environmental conditions by gaining longer lifespans [28,123] (see Palmer et al. [124] for an example from this study system). It is unknown whether gastropods exhibit similar patterns, but there is some evidence to the contrary in Turritellidae, which do not seem to have a higher frequency of long-lifespan species at high latitudes [58].

## Comparison to basal metabolic rates in PPWA molluscs

Recently Strotz et al. [1] found that bivalves and gastropod species containing organisms that had higher basal metabolic rates (BMRs)–which are associated with larger body sizes–had higher rates of extinction within the same study region and interval. The pattern was most pronounced in species with narrow geographic distributions and was more significant in bivalve species than gastropods. Because Strotz et al. [1] considered taxa from a broader range of taxonomic groups, used somewhat different taxonomic concepts and body-size data, and did not consider body size directly, but rather BMR, it is not possible to directly compare their results with ours. However, the difference in pattern may be attributable to several factors, including differences in number of species, differences in number of higher taxa, or relative proportions of taxa with narrow versus broad geographic range. Evaluating a broader suite of taxa and including additional data on functional traits, including larval mode, metabolic rate, lifespan, relationship to substrate, as well as information on species' geographic range may help determine what selectivity occurred during the extinction, and better characterize how post-recovery communities differ from the Pliocene community.

# Conclusions

Gastropods are diverse in both species richness and ecological disparity. This ecological diversity complicates the identification of general rules for how taxa will respond to environmental change. The patterns of clade body-size evolution considered here did not directly correspond to microevolutionary changes within constituent lineages, except for the Turritellidae, the most severely impacted clade evaluated. More consistent patterns have also been recovered in analyses of bivalves than gastropods [1]. The turritellids are ecologically similar to most bivalves as semi-infaunal suspension and deposit feeders [87,88], suggesting that ecological factors were more significant for determining extinction impact than class membership. A weaker signal observed for selectivity in BMR in Gastropoda compared to Bivalvia [1] may therefore reflect the aggregation of a variety of gastropod groups which each responded in a manner consistent with their specific ecologies.

While there is a strong desire to find general rules which can be used to predict the ecological responses of taxa to environmental change, evaluations of maximally inclusive groups (e.g. benthic poikilotherms, mollusks, gastropods) must be balanced with studies of the natural history, ecology, and evolutionary responses of at least some of their constituent taxa or we may elide discovery of significant ecological-evolutionary relationships. Body-size evolution is an important potential evolutionary response to changing environmental conditions beyond extinction/migration, and our data suggest that the evolutionary response in this trait to the PPWA mass extinction was not generalizable across Gastropoda. Extrapolating from previously published data on mollusks generally across the PPWA event (including the bivalve case studies which have previously been important for characterizing the event's impact) we might predict that decreased nutrient supply would have resulted in smaller body sizes for gastropods as well. However, in evaluating an ecologically diverse set of families of gastropods we found no class-level rule for gastropods, with each family behaving differently across the event (one increasing in size, one decreasing in size, and one remaining nearly identical in size distribution). Ecological differences, the impact of contingency in the form of extirpation or subclade extinction, and differences in recovery all appear to have contributed to the different responses we observed among gastropod families. Natural history data on a wider variety of taxa [125] and analyses evaluating the relationship between extinction, speciation, and ecological traits including body size [126,127] are urgently needed to assess what information is needed to best predict evolutionary responses to climate and other environmental changes.

## Supporting information

**S1 Text. Additional details of methods used to obtain size information and summary of supplemental files.**
(DOCX)

**S1 Fig. Regional stratigraphic correlation.**
(TIF)

**S2 Fig. Statistical analyses of clade body size across the event using maximum size to define each species' body size.**
(TIF)

**S1 Table. Species assigned toe each time bin for text Fig 1.**
(XLSX)

**S2 Table. Tegulid synonymy used herein.**
(DOCX)

**S3 Table. All measurement data obtained for this study.**
(XLSX)

## Acknowledgments

The authors thank G. Dietl, D. Friend, L. Skibinski, V. Wang (PRI), and Roger Portell (UF) for assistance with accessing and studying relevant collections. We thank T. A. Neubauer, G. J.

Vermeij, and an anonymous reviewer for their helpful reviews that improved this manuscript. No permits were required for the described study, which complied with all relevant regulations.

## Author Contributions

**Conceptualization:** Brendan M. Anderson.

**Data curation:** Brendan M. Anderson, Jessica Behn, Jonathan R. Hendricks.

**Formal analysis:** Brendan M. Anderson, Elizabeth Petsios.

**Funding acquisition:** Bruce S. Lieberman, Jonathan R. Hendricks.

**Investigation:** Brendan M. Anderson, Elizabeth Petsios, Jessica Behn, Amy Betz, Jonathan R. Hendricks.

**Methodology:** Brendan M. Anderson, Jonathan R. Hendricks.

**Project administration:** Warren D. Allmon, Bruce S. Lieberman, Jonathan R. Hendricks.

**Resources:** Bruce S. Lieberman, Jonathan R. Hendricks.

**Supervision:** Warren D. Allmon, Bruce S. Lieberman, Jonathan R. Hendricks.

**Validation:** Brendan M. Anderson, Jonathan R. Hendricks.

**Visualization:** Brendan M. Anderson.

**Writing – original draft:** Brendan M. Anderson.

**Writing – review & editing:** Brendan M. Anderson, Elizabeth Petsios, Warren D. Allmon, Bruce S. Lieberman, Jonathan R. Hendricks.

## References

1. Strotz LC, Saupe EE, Kimmig J, Lieberman BS. Metabolic rates, climate and macroevolution: a case study using Neogene molluscs. Proc R Soc Lond B Biol Sci. 2018; 285(1885): 20181292. https://doi.org/10.1098/rspb.2018.1292 PMID: 30135165
2. Jackson JBO'Dea A. Evolution and environment of Caribbean coastal ecosystems. Proc Natl Acad Sci U S A. 2023; 120(42): e2307520120. https://doi.org/10.1073/pnas.2307520120 PMID: 37816056
3. Allmon WD, Rosenberg G, Portell RW, Schindler KS. Diversity of Pliocene-Recent mollusks in the western Atlantic: Extinction, origination, and environmental change. In Jackson JBC, Budd AF, Coates AG, editors. Evolution and Environment in tropical America. Chicago: University of Chicago Press; 1996. pp. 271–302.
4. Jackson JB, Johnson KG. Life in the last few million years. Paleobiology. 2000; 26(S4): 221–235. https://doi.org/10.1017/S0094837300026944
5. Allmon WD. Nutrients, temperature, disturbance, and evolution: a model for the late Cenozoic marine record of the western Atlantic. Palaeogeogr Palaeoclimatol Palaeoecol. 2001; 166(1–2): 9–26.
6. Todd JA, Jackson JB, Johnson KG, Fortunato HM, Heitz A, Alvarez M, Jung P. The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. Proc R Soc Lond B Biol Sci. 2002; 269(1491): 571–577. https://doi.org/10.1098/rspb.2001.1923 PMID: 11916472
7. Stanley SM, Campbell LD. Neogene mass extinction of Western Atlantic molluscs. Nature. 1981; 293 (5832): 457–459.
8. Stanley SM. Anatomy of a regional mass extinction: Plio-Pleistocene decimation of the western Atlantic bivalve fauna. Palaios. 1986; 1(1):17–36. https://doi.org/10.2307/3514456
9. Budd AF, Foster CT Jr., Dawson JP, Johnson KG. The Neogene Marine Biota of Tropical America (NMITA) database: accounting for biodiversity in paleontology. J Paleontol. 2001; 75: 743–751.
10. Smith JT, Jackson JBC. Ecology of extreme faunal turnover of tropical American scallops. Paleobiology. 2009; 35(1): 77–93. https://doi.org/10.1666/07054.1

11. Allmon WD, Rosenberg G, Portell RW, Schindler KS. Diversity of Atlantic Coastal Plain mollusks since the Pliocene. Science. 1993; 260(5114): 1626–1629. https://doi.org/10.1126/science.260.5114.1626 PMID: 17810204
12. Allmon WD, Emslie SD, Jones DS, Morgan GS. Late Neogene oceanographic change along Florida's west coast: evidence and mechanisms. J Geol. 1996; 104(2): 143–162. https://doi.org/10.1086/629811
13. O'Dea A, Lessios HA, Coates AG, Eytan RI, Restrepo-Moreno SA, Cione AL, et al. Formation of the Isthmus of Panama. Sci Adv. 2016; 2(8): e1600883. https://doi.org/10.1126/sciadv.1600883 PMID: 27540590
14. Yasuhara M, Huang HH, Reuter M, Tian SY, Cybulski JD, O'Dea A, et al. Hotspots of Cenozoic tropical marine biodiversity. In: Hawkins SJ, Lemasson AJ, Allcock AL, Bates AEByrne M, Evans AJ, et al., editors. Oceanography and Marine Biology: An Annual Review. Bova Raton: CRC Press; 2022: 243–300. https://doi.org/10.1201/9781003288602-5
15. Jones DS, Allmon WD. Records of upwelling, seasonality and growth in stable-isotope profiles of Pliocene mollusk shells from Florida. Lethaia. 1995; 28(1): 61–74.
16. Anderson BM, Hendy A, Johnson EH, Allmon WD. Paleoecology and paleoenvironmental implications of turritelline gastropod-dominated assemblages from the Gatun Formation (Upper Miocene) of Panama. Palaeogeogr Palaeoclimatol Palaeoecol. 2017; 470: 132–146. https://doi.org/10.1016/j.palaeo.2017.01.026
17. Sang S, Friend DS, Allmon WD, Anderson BM. Protoconch enlargement in Western Atlantic turritelline gastropod species following the closure of the Central American Seaway. Ecol Evol. 2019; 9(9): 5309–5323. https://doi.org/10.1002/ece3.5120 PMID: 31110681
18. Grossman EL, Robbins JA, Rachello-Dolmen PG, Tao K, Saxena D, O'Dea A. Freshwater input, upwelling, and the evolution of Caribbean coastal ecosystems during formation of the Isthmus of Panama. Geology. 2019; 47(9): 857–861. https://doi.org/10.1130/G46357.1
19. Scholz SR, Petersen SV, Escobar J, Jaramillo C, Hendy AJ, Allmon WD, et al. Isotope sclerochronology indicates enhanced seasonal precipitation in northern South America (Colombia) during the Mid-Miocene Climatic Optimum. Geology. 2020; 48(7): 668–672. https://doi.org/10.1130/G47235.1
20. Allmon WD. Role of temperature and nutrients in extinction of turritelline gastropods: Cenozoic of the northwestern Atlantic and northeastern Pacific. Palaeogeogr Palaeoclimatol Palaeoecol. 1992; 92(1–2): 41–54.
21. Dietl GP. Coevolution of a marine gastropod predator and its dangerous bivalve prey. Biol J Linn Soc Lond. 2003; 80(3): 409–436. https://doi.org/10.1046/j.1095-8312.2003.00255.x
22. Dietl GP, Herbert GS, Vermeij GJ. Reduced competition and altered feeding behavior among marine snails after a mass extinction. Science. 2004; 306(5705): 2229–2231. https://doi.org/10.1126/science.1106182 PMID: 15618513
23. Paul S, Herbert GS. Plio–Pleistocene drilling predation in Florida bivalves: Predator identity, competition, and biotic change. Palaeogeogr Palaeoclimatol Palaeoecol. 2014; 404: 67–77. https://doi.org/10.1016/j.palaeo.2014.03.040
24. Petsios E, Farrar L, Tennakoon S, Jamal F, Portell RW, Kowalewski M, et al. The Ecology of Biotic Interactions in Echinoids: Modern Insights into Ancient Interactions. Elements of Paleontology. 2023. https://doi.org/10.1017/9781108893510
25. Temple SA. Do predators always capture substandard individuals disproportionately from prey populations?. Ecology. 1987; 68(3): 669–674. https://doi.org/10.2307/1938472
26. Walsman JC, Cressler CE. Predation shifts coevolution toward higher host contact rate and parasite virulence. Proc R Soc Lond B Biol Sci. 2022; 289(1978): 20212800. https://doi.org/10.1098/rspb.2021.2800 PMID: 35858064
27. Sime JA, Kelley PH. Common mollusk genera indicate interactions with their predators were ecologically stable across the Plio-Pleistocene extinction. Palaeogeogr Palaeoclimatol Palaeoecol. 2016; 463: 216–229. https://doi.org/10.1016/j.palaeo.2016.10.012
28. Kirby MX, Jackson JB. Extinction of a fast-growing oyster and changing ocean circulation in Pliocene tropical America. Geology. 2004; 32(12): 1025–1028. https://doi.org/10.1130/G21039.1
29. Jackson JBC, Jung P, Fortunato H. Paciphilia Revisited: Transisthmian evolution of the *Strombina group* (Gastropoda: Columbellidae). In: Jackson JBC, Budd AF, Coates AG, editors. Evolution and Environment in tropical America. Chicago: University of Chicago Press; 1996. pp. 234–270.
30. Fortunato H. Reproduction and larval development of the *Strombina*-group (Buccinoidea: Columbellidae) and related gastropods: testing the use of the larval shell for inference of development in fossil species. Bollettino Malacologico. 2002; 38(Suppl. 4):111–126.

**31.** Cope ED. On the evolution of the Vertebrata, progressive and retrogressive. Am Nat. 1885; 19(2): 140–148. https://doi.org/10.1086/273923

**32.** Stanley SM. An explanation for Cope's rule. Evolution. 1973; 27(1): 1–26. https://doi.org/10.1111/j.1558-5646.1973.tb05912.x PMID: 28563664

**33.** Payne JL, Boyer AG, Brown JH, Finnegan S, Kowalewski M, Krause RA Jr, et al. Two-phase increase in the maximum size of life over 3.5 billion years reflects biological innovation and environmental opportunity. Proc Natl Acad Sci U S A. 2009; 106(1): 24–27. https://doi.org/10.1073/pnas.0806314106 PMID: 19106296

**34.** Payne JL, Heim NA. Body size, sampling completeness, and extinction risk in the marine fossil record. Paleobiology. 2020; 46(1): 23–40. https://doi.org/10.1017/pab.2019.43

**35.** Monarrez PM, Heim NA, Payne JL. Mass extinctions alter extinction and origination dynamics with respect to body size. Proc R Soc Lond B Biol Sci. 2021; 288(1960): 20211681. https://doi.org/10.1098/rspb.2021.1681 PMID: 34610766

**36.** Vrba ES, Gould SJ. The hierarchical expansion of sorting and selection: sorting and selection cannot be equated. Paleobiology. 1986; 12(2): 217–228. https://doi.org/10.1017/S0094837300013671

**37.** Lieberman BS. Phylogenetic trends and speciation: analyzing macroevolutionary processes and levels of selection. In: Erwin D, Anstey R, editors. New approaches to speciation in the fossil record. New York: Columbia University Press; 1995. pp. 316–339.

**38.** Lieberman BS, Vrba ES. Hierarchy theory, selection, and sorting. BioScience. 1995; 45(6): 394–399. https://doi.org/10.2307/1312719

**39.** Jablonski D. Micro-and macroevolution: scale and hierarchy in evolutionary biology and paleobiology. Paleobiology. 2000; 26(S4): 15–52. https://doi.org/10.1017/S0094837300026877

**40.** Congreve CR, Falk AR, Lamsdell JC. Biological hierarchies and the nature of extinction. Biol Rev Camb Philos Soc. 2018; 93(2):811–26. https://doi.org/10.1111/brv.12368 PMID: 28944555

**41.** Pietsch C, Gigliotti M, Anderson BM, Allmon WD. Patterns and processes in the history of body size in turritelline gastropods, Jurassic to Recent. Paleobiology. 2023; 49(4): 621–641. https://doi.org/10.1017/pab.2023.7

**42.** Chattopadhyay D, Chattopadhyay D. Absence of general rules governing molluscan body-size response to climatic fluctuation during the Cenozoic. Hist Biol. 2020; 32(8): 1071–1080. https://doi.org/10.1080/08912963.2018.1563894

**43.** Jablonski D. Body size and macroevolution. In: Jablonski D, Erwin DH, Lipps JH. Evolutionary paleobiology. Chicago: Chicago University Press; 1996. pp. 256–289.

**44.** Crampton JS, Cooper RA, Beu AG, Foote M, Marshall BA. Biotic influences on species duration: interactions between traits in marine molluscs. Paleobiology. 2010; 36(2):204–223. https://doi.org/10.1666/09010.1

**45.** Harnik PG. Direct and indirect effects of biological factors on extinction risk in fossil bivalves. Proc Natl Acad Sci U S A. 2011; 108(33): 13594–13599. https://doi.org/10.1073/pnas.1100572108 PMID: 21808004

**46.** Lockwood R. Body size, extinction events, and the early Cenozoic record of veneroid bivalves: a new role for recoveries?. Paleobiology. 2005; 31(4): 578–590.

**47.** Jablonski D, Hunt G. Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: organismic versus species-level explanations. Am Nat. 2006; 168(4): 556–564. https://doi.org/10.1086/507994 PMID: 17004227

**48.** Gould SJ. Tempo and mode in the macroevolutionary reconstruction of Darwinism. Proc Natl Acad Sci U S A. 1994; 91(15): 6764–6771. https://doi.org/10.1073/pnas.91.15.6764 PMID: 8041695

**49.** Monarrez PM, Heim NA, Payne JL. Reduced strength and increased variability of extinction selectivity during mass extinctions. R Soc Open Sci. 2023; 10(9): 230795. https://doi.org/10.1098/rsos.230795 PMID: 37771968

**50.** Roopnarine PD. Systematics, biogeography and extinction of chionine bivalves (Early Oligocene-Recent) in the Late Neogene of tropical America. Malacologia. 1996; 38(1–2): 103–42.

**51.** Anderson LC. Temporal and geographic size trends in Neogene Corbulidae (Bivalvia) of tropical America: using environmental sensitivity to decipher causes of morphologic trends. Palaeogeogr Palaeoclimatol Palaeoecol. 2001; 166(1–2): 101–120.

**52.** Anderson LC, Roopnarine PD. Evolution and phylogenetic relationships of Neogene Corbulidae (Bivalvia; Myoidea) of tropical America. J Paleontol. 2003 Nov; 77(6): 1086–1102.

**53.** Vermeij GJ. Biogeography and adaptation: patterns of marine life. Cambridge: Harvard University Press; 1978.

**54.** Palmer AR. Relative cost of producing skeletal organic matrix versus calcification: evidence from marine gastropods. Mar Biol. 1983; 75:287–292.

**55.** Teusch KP, Jones DS, Allmon WD. Morphological variation in turritellid gastropods from the Pleistocene to recent of Chile: association with upwelling intensity. Palaios. 2002; 17(4): 366–377.

**56.** Teusch KP, Guralnick R. Environmentally driven variation in ancient populations of turritellids: evaluating the causal link. Paleobiology. 2003; 29(2): 163–180.

**57.** Ramajo L, Pérez-León E, Hendriks IE, Marbà N, Krause-Jensen D, Sejr MK, et al. Food supply confers calcifiers resistance to ocean acidification. Sci Rep. 2016; 6(1): 19374. https://doi.org/10.1038/srep19374 PMID: 26778520

**58.** Anderson BM, and Allmon WD. High calcification rates and inferred metabolic trade-offs in the largest turritellid gastropod, Turritella abrupta (Neogene). Palaeogeogr Palaeoclimatol Palaeoecol. 2020; 544: 109623. https://doi.org/10.1016/j.palaeo.2020.109623

**59.** Ward LW, Bailey RH, Carter JG, Horton JW, Zullo VA. Pliocene and early Pleistocene stratigraphy, depositional history, and molluscan paleobiogeography of the Coastal Plain. The Geology of the Carolinas: University of Tennessee Press, Knoxville, Tennessee. 1991: 274–289.

**60.** Ward LW. Molluscan biostratigraphy of the Miocene, middle Atlantic Coastal Plain of North America. Virginia Museum of Natural History; 1992.

**61.** Jones DS, Randazzo AF. The marine invertebrate fossil record of Florida. In: Randazzo AF, Jones DS, editors. The Geology of Florida. Gainesville: University Press of Florida; 1997. pp. 89–117.

**62.** Lyons WG. Post-Miocene species of *Latirus* Montfort, 1810 (Mollusca: Fasciolariidae) of southern Florida, with a review of regional marine biostratigraphy. Bull Fla Mus Nat Hist. 1991; 35: 131–208.

**63.** Saupe EE, Hendricks JR, Portell RW, Dowsett HJ, Haywood A, Hunter SJ, et al. Macroevolutionary consequences of profound climate change on niche evolution in marine molluscs over the past three million years. Proc R Soc Lond B Biol Sci. 2014; 281(1795): 20141995. https://doi.org/10.1098/rspb.2014.1995 PMID: 25297868

**64.** Johnson AL, Valentine AM, Leng MJ, Schöne BR, Sloane HJ. Life history, environment and extinction of the scallop *Carolinapecten eboreus* (Conrad) in the Plio-Pleistocene of the US eastern seaboard. Palaios. 2019; 34(2): 49–70. https://doi.org/10.2110/palo.2018.056

**65.** Dowsett HJ, Robinson MM, Foley KM, Herbert TD. The Yorktown Formation: Improved stratigraphy, chronology, and paleoclimate interpretations from the US mid-Atlantic Coastal Plain. Geosciences. 2021; 11(12): 486. https://doi.org/10.3390/geosciences11120486

**66.** Friend D.S., Anderson B.M., Altier E., Sang S., Petsios E., Portell R.W. et al. Systematics and phylogeny of Plio-Pleistocene species of Turritellidae (Gastropoda) from Florida and the Atlantic Coastal Plain. Bull Am Paleontol. 2023;(402): 1–74. https://doi.org/10.32857/bap.2023.402.01

**67.** Campbell LD. Pliocene molluscs from the Yorktown and Chowan river formations in Virginia. Commonwealth of Virginia, Department of Mines, Minerals, and Energy, Division of Mineral Resources; 1993.

**68.** Ward LW, and Gilinsky NL. Molluscan assemblages of the Chowan River Formation. Part A. Biostratigraphic analysis of the Chowan River Formation (upper Pliocene) and adjoining units, the Moore House Member of the Yorktown Formation (upper Pliocene) and the James City Formation (lower Pliocene). Virginia Museum of Natural History Memoir 3. 1993. pp. 1–32.

**69.** Hendricks J.R. The genus *Conus* (Mollusca: Neogastropoda) in the Plio-Pleistocene of the southeastern United States. Bull Am Paleontol. 2009 [2008];(375): 1–178.

**70.** Kittle BA, Portell RW, Lee HG, Roberts SW. Mollusca—Nashua Formation (Late Pliocene to Early Pleistocene). Florida Fossil Invertebrates. 2013; 15: 1–40.

**71.** Scott TM. Coastal Plains stratigraphy: the dichotomy of biostratigraphy and lithostratigraphy-a philosophical approach to an old problem. In: Scott TM, Allmon WD, editors. The Plio-Pleistocene stratigraphy and paleontology of southern Florida: Florida Geological Survey Special Publication 36; 1992. pp. 21–26.

**72.** Scott TM. Geology of the Florida Platform: Pre-Mesozoic to Recent. In: Buster NA and Holmes CW. Gulf of Mexico Origin, Waters, and Biota: Volume 3, Geology. 2009: 17–31.

**73.** Stringer GL, Hulbert RC Jr, Nolf D, Roth P, Portell RW. A rare occurrence of matched otoliths and associated skeletal remains of *Apogon townsendi* (Osteichthyes) from the Caloosahatchee Formation (early Pleistocene) of Florida. Bull Fla Mus Nat Hist. 2017; 55(40): 89–103.

**74.** Kohn AJ. *Conus* of the Southeastern United States and Caribbean. Princeton: Princeton University Press; 2014.

**75.** Puillandre N, Bouchet P, Duda TF Jr, Kauferstein S, Kohn AJ, Olivera BM, et al. Molecular phylogeny and evolution of the cone snails (Gastropoda, Conoidea). Mol Phylogenet Evol. 2014; 78: 290–303. https://doi.org/10.1016/j.ympev.2014.05.023 PMID: 24878223

76. Stanley SM. Predation defeats competition on the seafloor. Paleobiology. 2008; 34(1): 1–21. https://doi.org/10.1666/07026.1

77. Petuch EJ. Atlas of Florida Fossil Shells (Pliocene and Pleistocene Marine Gastropods). Evanston: Chicago Spectrum Press; 1994.

78. Yee EH, Murray SN. Effects of temperature on activity, food consumption rates, and gut passage times of seaweed-eating *Tegula* species (Trochidae) from California. Mar Biol. 2004; 145: 895–903. https://doi.org/10.1007/s00227-004-1379-6

79. Boyd AD, Walker NS, Valdez SR, Zhang YS, Altieri AH, Gulis V, et al. Invertebrate grazing on live turtlegrass (*Thalassia testudinum*): A common interaction that may facilitate fungal growth. Front Mar Sci. 2022; 8: 789380. https://doi.org/10.3389/fmars.2021.789380

80. Somero GN. Linking biogeography to physiology: evolutionary and acclimatory adjustments of thermal limits. Front Zool. 2005; 2(1): 1–9. https://doi.org/10.1186/1742-9994-2-1 PMID: 15679952

81. Dornellas AP, Couto DR, Simone LR. Morphological phylogeny of the Tegulinae (Mollusca: Vetigastropoda) reinforces a Turbinidae position. Cladistics. 2019; 36: 129–163. https://doi.org/10.1111/cla.12400 PMID: 34618952

82. Osmond JK, Carpenter JR, Windom HL. Th230/U234 age of the Pleistocene corals and oolites of Florida. J Geophys Res. 1965; 70(8): 1843–1847.

83. Broecker WS, Thurber DL. Uranium-series dating of corals and oolites from Bahaman and Florida Key limestones. Science. 1965; 149(3679): 58–60. https://doi.org/10.1126/science.149.3679.58 PMID: 17737788

84. Dall WH. Tertiary fauna of Florida with especial reference to the Miocene Silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River. Part II. Transactions of the Wagner Free Institute of Science of Philadelphia 3. 1892: 201–473.

85. Graham A. On a ciliary process of food-collecting in the gastropod *Turritella communis* Risso. Proc Zool Soc Lond. 1938; 108(3): 453–463.

86. Carrick N. Aspects of the Biology of Molluscs on the Continental Shelf Off Sydney, NSW, with Particular Reference to the Population Biology of *Gazameda gunni* (Reeve, 1849) [Doctoral dissertation]. Sydney: University of Sydney;1980.

87. Allmon WD. Natural history of turritelline gastropods (Cerithiodea: Turritellidae): a status report. Malacologia. 2011; 54(1–2): 159–202. https://doi.org/10.4002/040.054.0107

88. Allmon WD. Ecology of Recent turritelline gastropods (Prosobranchia, Turritellidae): current knowledge and paleontological implications. Palaios. 1988: 259–84. https://doi.org/10.2307/3514657

89. Plotnick R. The most common fossil. Medium.com. 2018; https://plotnick.medium.com/the-most-common-fossil-2f893db74f2b, accessed 24 November 2023.

90. Anderson BM, and Allmon WD. Phylogeny and systematics of fossil and recent Vermicularia (Caenogastropoda: Turritellidae). Malacologia. 2023; 66(1): 1–59. https://doi.org/10.4002/040.066.0101

91. Hendricks JR, Saupe EE, Myers CE, Hermsen EJ, Allmon WD. The generification of the fossil record. Paleobiology. 2014; 40(4):511–28. https://doi.org/10.1666/13076

92. Ahyong S.; Boyko C.B.; Bailly N.; Bernot J.; Bieler R.; Brandão S.N. et al. World Register of Marine Species. 2023; Available from https://www.marinespecies.org.

93. Hammer Ø, Harper DA. Past: paleontological statistics software package for education and data analysis. Palaeontologia Electronica. 2001; 4(1): 1.

94. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2021. https://www.R-project.org/.

95. Team RStudio (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA; URL http://www.rstudio.com/.

96. Petuch EJ. Molluscan diversity in the Late Neogene of Florida: evidence for a two-staged mass extinction. Science. 1995; 270(5234): 275–277. https://doi.org/10.1126/science.270.5234.275

97. Payne J. L. Evolutionary dynamics of gastropod size across the end-Permian extinction and through the Triassic recovery interval. Paleobiology. 2005; 31: 269–290.

98. Benson R. B. J., Godoy P., Bronzati M., Butler R. J., and Gearty W. Reconstructed evolutionary patterns for crocodile-line archosaurs demonstrate impact of failure to log-transform body size data. Commun Biol. 2022; 5: 171. https://doi.org/10.1038/s42003-022-03071-y PMID: 35217775

99. Hochberg Y. A sharper Bonferroni procedure for multiple tests of significance. Biometrika. 1988; 75: 800–802.

100. Jablonski D, Lutz RA. Larval ecology of marine benthic invertebrates: paleobiological implications. Biol Rev Camb Philos Soc. 1983; 58(1): 21–89.

101. Bhaud M. Relationship between larval type and geographic range in marine species-complementary observations on gastropods. Oceanologica Acta. 1993; 16: 191–198.
102. Friend DS, Anderson BM, Allmon WD. Geographic contingency, not species sorting, dominates macroevolutionary dynamics in an extinct clade of neogastropods (Volutospina; Volutidae). Paleobiology. 2021; 47(2): 236–250. https://doi.org/10.1017/pab.2020.60
103. Petuch EJ. Geographical heterochrony: Comtemporaneous coexistence of Neogene and recent molluscan faunas in the Americas. Palaeogeogr Palaeoclimatol Palaeoecol. 1982; 37(2–4): 277–312.
104. Vermeij GJ. From Europe to America: Pliocene to recent trans-Atlantic expansion of cold-water North Atlantic molluscs. Proc R Soc Lond B Biol Sci. 2005; 272(1580): 2545–2550. https://doi.org/10.1098/rspb.2005.3177 PMID: 16271981
105. Petuch EJ. Biogeography and biodiversity of western Atlantic mollusks. Boca Raton: CRC Press; 2013.
106. Moran AL. Spawning and larval development of the black turban snail *Tegula funebralis* (Prosobranchia: Trochidae). Mar Biol. 1997; 128: 107–114. https://doi.org/10.1007/s002270050074
107. Hellberg ME. Sympatric sea shells along the sea's shore: the geography of speciation in the marine gastropod *Tegula*. Evolution. 1998; 52(5): 1311–1324.
108. Kulikova VA, Omel'yanenko VA. Reproduction and larval development of the gastropod mollusk *Tegula rustica* in Peter the Great Bay, Sea of Japan. Russ J Mar Biol. 2000; 26: 128–30.
109. Dornellas AP, Graboski R, Hellberg ME, Lotufo TM. Phylogeography of *Agathistoma* (Turbinidae, Tegulinae) snails in tropical and southwestern Atlantic. Zool Scr. 2022; 51(1): 76–90. https://doi.org/10.1111/zsc.12517
110. Thorson G. Reproductive and larval ecology of marine bottom invertebrates. Biol Rev Camb Philos Soc. 1950; 25(1): 1–45. https://doi.org/10.1111/j.1469-185x.1950.tb00585.x PMID: 24537188
111. Shuto T. Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. Lethaia. 1974; 7(3): 239–56.
112. Duda TF Jr, Kohn AJ. Species-level phylogeography and evolutionary history of the hyperdiverse marine gastropod genus *Conus*. Mol Phylogenet Evol. 2005; 34(2): 257–272. https://doi.org/10.1016/j.ympev.2004.09.012 PMID: 15619440
113. Brayard A, Nützel A, Stephen DA, Bylund KG, Jenks J, Bucher H. Gastropod evidence against the Early Triassic Lilliput effect. Geology. 2010; 38(2): 147–150. https://doi.org/10.1130/G30553.1
114. Urbanek A. Biotic crises in the history of Upper Silurian graptoloids: a palaeobiological model. Hist Biol. 1993; 7(1): 29–50.
115. Abbott CP, Webster M, Angielczyk KD. Ontogenetic mechanisms of size change: implications for the Lilliput effect and beyond. Paleobiology. 2023; 50(1): 130–149. https://doi.org/10.1017/pab.2023.26
116. Harzhauser M, Guzhov A, Landau BM, Kern AK, Neubauer TA. Oligocene to Pleistocene mudwhelks (Gastropoda: Potamididae, Batillariidae) of the Eurasian Paratethys Sea–Diversity, origins and mangroves. Palaeogeogr Palaeoclimatol Palaeoecol. 2023; 630: 111811. https://doi.org/10.1016/j.palaeo.2023.111811
117. Domning DP. Sirenians, seagrasses, and Cenozoic ecological change in the Caribbean. Palaeogeogr Palaeoclimatol Palaeoecol. 2001; 166(1–2): 27–50.
118. Riedman ML, Hines AH, Pearse JS. Spatial segregation of four species of turban snails (Gastropoda: Tegula) in central California. The Veliger. 1981; 24(2): 97–102.
119. Friend DS, Anderson BM, Allmon WD. The hollow newel state in gastropods: when snail shells are open-axis. J Molluscan Stud. 2024; 90(1): eyae001. https://doi.org/10.1093/mollus/eyae001
120. Jablonski D. Survival without recovery after mass extinctions. Proc Natl Acad Sci U S A. 2002; 99(12): 8139–8144. https://doi.org/10.1073/pnas.102163299 PMID: 12060760
121. Barnes BD, Sclafani JA, Zaffos A. Dead clades walking are a pervasive macroevolutionary pattern. Proc Natl Acad Sci U S A. 2021; 118(15): e2019208118. https://doi.org/10.1073/pnas.2019208118 PMID: 33827921
122. Jablonski D. Evolvability and macroevolution: overview and synthesis. Evol Biol. 2022; 49(3): 265–291. https://doi.org/10.1007/s11692-022-09570-4
123. Moss DK, Ivany LC, Judd EJ, Cummings PW, Bearden CE, Kim WJ, et al. Lifespan, growth rate, and body size across latitude in marine Bivalvia, with implications for Phanerozoic evolution. Proc R Soc Lond B Biol Sci. 2016; 283(1836): 20161364. https://doi.org/10.1098/rspb.2016.1364 PMID: 27488653
124. Palmer KL, Moss DK, Surge D, Turek S. Life history patterns of modern and fossil *Mercenaria* spp. from warm vs. cold climates. Palaeogeogr Palaeoclimatol Palaeoecol. 2021; 566: 110227. https://doi.org/10.1016/j.palaeo.2021.110227

**125.** Greene HW. Organisms in nature as a central focus for biology. Trends Ecol Evol. 2005; 20(1): 23–27. https://doi.org/10.1016/j.tree.2004.11.005 PMID: 16701336

**126.** Blanckenhorn WU. The evolution of body size: what keeps organisms small?. Q Rev Biol. 2000; 75(4): 385–407. https://doi.org/10.1086/393620 PMID: 11125698

**127.** Harnik PG, Lotze HK, Anderson SC, Finkel ZV, Finnegan S, Lindberg DR, et al. Extinctions in ancient and modern seas. Trends Ecol Evol. 2012; 27(11): 608–617. https://doi.org/10.1016/j.tree.2012.07.010 PMID: 22889500