

# High calcification rates and inferred metabolic trade-offs in the largest turritellid gastropod, *Turritella abrupta* (Neogene)

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## ABSTRACT

*Turritella abrupta* (Miocene-Pliocene) is the largest species known from the diverse Jurassic-Recent gastropod family Turritellidae. In addition to having achieved long length and substantial width, the species produces shells of exceptional thickness, even before secondary shell deposition. We investigated the paleoecology of this species through analysis of drilling and peeling frequencies with comparisons to co-occurring turritellid species. We used oxygen isotopic sclerochronology to infer the growth rate and lifespan of *T. abrupta* and to make comparisons with other modern and fossil tropical species, including the living species *Turritella terebra*, with the first sclerochronologies for both of these species presented herein. We find that *T. abrupta* was fast-growing, long-lived, and comparatively effective at resisting predation. *T. abrupta* was notably widespread geographically and temporally, but was a relatively rare component of faunas when compared with co-occurring turritellids. High rates of shell carbonate construction (in excess of 35 g in the first year of life) likely depended on habitats conducive to calcification. Late Miocene cooling and eastern Pacific carbonate limitation are implicated in the range contraction and eventual extinction of this species.

“A snail's shell is its castle”

Kohn, 1999:169

## 1. Introduction

The evolution of giantism (often termed “gigantism”; Gould and MacFadden, 2004), as well as trends towards large body size in clades have long been of significant interest to both paleobiologists and neontologists. As size is a character of all organisms, studies of this trait are relevant to macroevolutionary and biogeographic theory, with potentially broad applications (Bergmann, 1847; Peters and Wassenberg, 1983; Kingsolver and Pfennig, 2004; Angilletta Jr et al., 2004; Payne et al., 2009; Lamsdell and Braddy, 2010; Watson et al., 2012; Berke et al., 2013; Smith et al., 2016; Payne et al., 2016; Deline et al., 2018). In order to understand how large size is attained in ontogeny, we must ask what selective advantages influence a particular population (or taxon) when large size is attained, what selective trade-offs may be involved at the organismal (or species) level, and whether broad patterns arise from similar or a variety of distinctive causes. Large size may provide protection from predation (Paine, 1976; Palmer, 1979; Tull and Bohning-Gaese, 1993; Cote et al., 2001; Kingsolver and Pfennig, 2004;

Griffiths and Gosselin, 2008; Pruden et al., 2018), and rapid early growth minimizes the time an organism spends at its most vulnerable sizes.

Turritellid gastropods are an excellent taxon for considering this kind of broad pattern in the history of life for several reasons: they are perhaps the most commonly occurring macroscopic body fossils in the fossil record (Plotnick, 2018), they are globally distributed, and they have an excellent Jurassic-Recent fossil record (Allmon, 2011; Das et al., 2018). There are approximately 140 valid living species and ca. 800 valid known fossil species, with a mean size ~6 cm in length (Pietsch, personal communication, October 30, 2018). The Miocene-Pliocene species *Turritella abrupta* Spieker, 1922, attains the largest size, with maximum shell lengths exceeding 20 cm (Fig. 1). Here we explore a variety of aspects of *T. abrupta*'s paleobiology, including growth and calcification rates, frequency of drilling and peeling predatory attacks and repairs, geographic distribution, and community composition. In comparison with other co-occurring or modern tropical turritellids, this large species exhibits high rates of growth and calcification and high frequency of attack survival, but very low relative abundance in assemblages in which it occurs (which is unusual among turritellids; Allmon, 2007). The thickness of the shell is particularly notable when compared with other turritellids, including those which attain large

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Fig. 1. Large specimens of *Turritella abrupta* Spieker, 1922. Scale bar is 1 cm. A. NMB 18529 B. PRI 8264.

shell lengths.

Both primary and secondary shell deposition in *Turritella abrupta* is composed principally of crossed-lamellar aragonite (Anderson and Allmon, 2018). Thickening crossed-lamellar shells directly improves predation resistance (e.g., Andrews, 1974; Currey, 1976; Wainwright et al., 1976; Vermeij, 1977; Palmer, 1979; Vermeij, 1993; West and Cohen, 1996; Cote et al., 2001; Sälgeback, 2006; Avery and Etter, 2006; Ragagnin et al., 2016). Thick shells of this microstructure are, however, energetically expensive to produce (Currey, 1977; Palmer, 1979; Palmer, 1983; Weiner et al., 1984; Lowenstam and Weiner, 1989; Avery and Etter, 2006; de Paula and Silveira, 2009; Lischka and Riebesell, 2017; Peck et al., 2018; Vendrasco et al., 2018). Calcification is metabolically demanding for molluscs when compared to somatic tissue growth (Palmer, 1983; Palmer, 1992; Watson et al., 2017), and individual molluscs with high rates of calcification may require greater food supply than those with lower rates (Ramajo et al., 2016).

## 2. Materials and methods

### 2.1. Specimens examined

We directly examined specimens of *Turritella abrupta* in the collections of the LACM, NMB, PRI, STRI, UF, and the USNM (institutional

Table 1

Institutional abbreviations used in this paper.

Institution	
AMNH	American Museum of Natural History, New York, NY, USA
CASG	California Academy of Sciences Geology collection, San Francisco, CA, USA
LACM	Natural History Museum of Los Angeles County, Los Angeles, CA, USA
LSJU	Leland Stanford Junior University, Palo Alto, CA, USA
NMB	Naturhistorisches Museum Basel, Basel, Switzerland
PRI	Paleontological Research Institution, Ithaca, NY, USA
STRI	Smithsonian Tropical Research Institution, Panama City, Panama
UCSB	University of California, Santa Barbara, CA, USA
UF	Florida Museum of Natural History, Gainesville, FL, USA
USNM	National Museum of Natural History, Smithsonian Institution, Washington DC, USA

abbreviations used are identified in Table 1) to assess morphological variation (example specimens depicted in Fig. 2). We also searched these collections to find specimens of various sizes that possessed apertural calluses (indicating size at mortality, and therefore that secondary thickening had not taken place; Fig. 3), and those that did not contain compacted sediment, facilitating shell mass assessment. Complete specimens of this species are unknown, and we selected two large specimens which possessed ontogenetically early whorls (distinguished both by size and a more rounded whorl profile) for stable isotope sclerochronology; LACM 42097 from Isla Cubagua, Venezuela and PRI 68731 from Rio Tupisa, Panama. We compared growth and calcification rates in *Turritella abrupta* with *T. altilira* (Fig. 4B), which co-occurs with it in the Miocene Gatún Formation (Panama), as data are available for a large number of specimens of *T. altilira* previously examined using oxygen isotopic sclerochronology, facilitating size-at-age estimation (Anderson et al., 2017). We also examined a specimen of the recent large tropical turritellid *T. terebra* using isotopic sclerochronology. Comparison to living species also included examination of specimens of *Turritella bacillum* (Fig. 4C) and *Turritella duplicata* (Fig. 4D), in the collections of PRI. These species were chosen because they are relatively large and from tropical environments, and isotopic data are available for assessing ontogenetic age (Waite and Allmon, 2013, 2016; Kwan et al., 2018).

Measurements were taken of shell thicknesses using a digital caliper at the midpoint of the whorl measured or were obtained from previously published measurements obtained in the same manner, except as described below. Pleural angle (the angle created by lines drawn tangent to the last whorls on opposite sides of the shell; Fig. 2) was measured following the procedure of Allmon (1996). The theoretical apex system (Johnson et al., 2017) was employed to estimate total shell length from specimens which did not have apices.

### 2.2. Stable isotope sclerochronology

Stable isotope sclerochronology is a technique that infers paleoseasonality based on the isotopic composition of shell material as precipitated along the growing shell aperture. Molluscs precipitate shell carbonate in isotopic equilibrium with sea water with the proportion of  $^{18}\text{O}$  and  $^{13}\text{C}$  incorporated dependent on seawater chemistry and, in the case of  $^{18}\text{O}$ , ambient temperature; these data can be used to infer paleoclimate information (Grossman and Ku, 1986; Jones and Allmon, 1995; Andreasson and Schmitz, 1996; Andreasson and Schmitz, 2000; Latal et al., 2006; Ivany, 2012; Ivany et al., 2014). In the tropics, strong seasonal variation in  $\delta^{18}\text{O}$  is primarily due to either freshwater input from terrestrial runoff (bringing isotopically light oxygen and carbon) or cool upwelling waters, which cause the incorporation of heavier oxygen with cooler temperatures while simultaneously incorporating isotopically lighter  $\delta^{13}\text{C}$  (Jones and Allmon, 1995; Tao et al., 2013; Waite and Allmon, 2016; Graniero et al., 2017; Anderson et al., 2017). These data on paleoseasonality can then be used to determine life

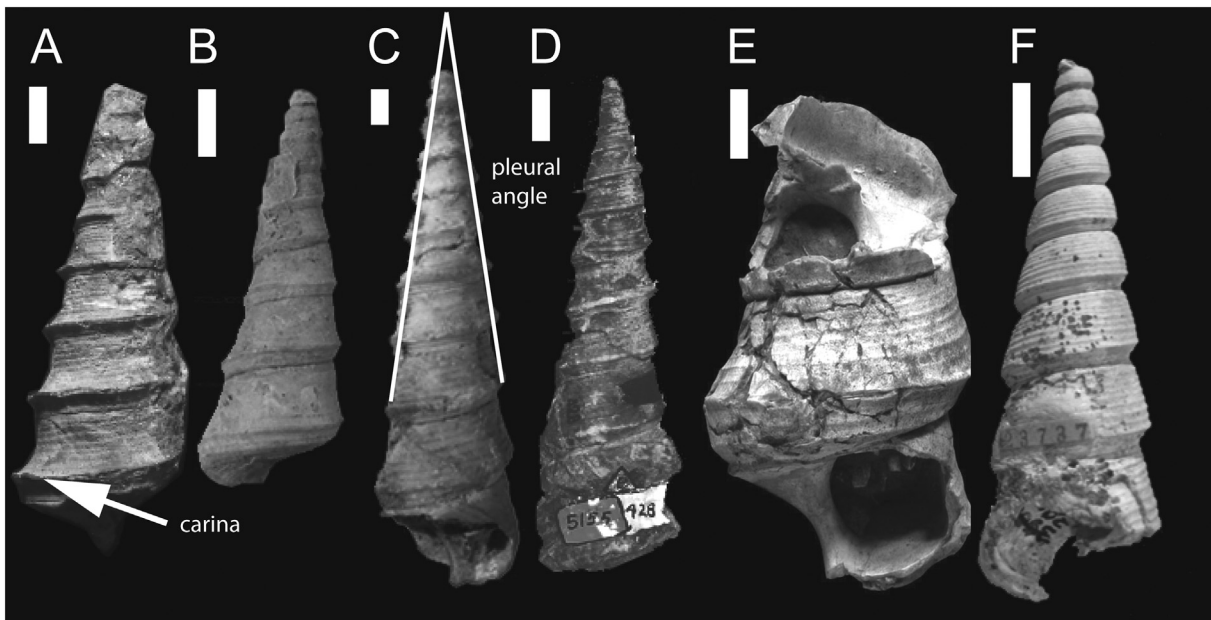


Fig. 2. Synonyms, and geographically or stratigraphically important examples of *Turritella abrupta* Spieker, 1922. A. *Turritella abrupta* Spieker, 1922, Holotype USNM 562351, Zorritos Formation, Peru. B. *T. abrupta*, Spieker, 1922, UCSB 6382, Rincon Formation, Santa Rosa Island, CA. C. *T. bösei* Hertlein and Jordan, 1927, Syntype CASG 71372.00 (formerly LSJU 5157), San Ignacio Formation, Mexico D. Hypotype CASG 71535.00 (formerly LSJU 5155) *T. bösei* Hertlein and Jordan, 1927 of Hertlein and Wiedey (1928) Temblor Formation, southern Los Angeles Basin, CA, USA. E. *Turritella robusta* Grzybowski, 1899 *fredeai* Hodson 1926 Paratype PRI 21418, Falcón, Venezuela. F. *T. abrupta* Spieker, 1922, USNM 287255 Agueguexquite Fm., Veracruz, Mexico, showing the more even sculpture and more rounded whorl profile visible in the adapical portion of the shell.

Photos of A, B, C, and D courtesy of J.T. Smith. Carina and pleural angle indicated on specimens A and C, respectively. Scale bars are 1 cm.

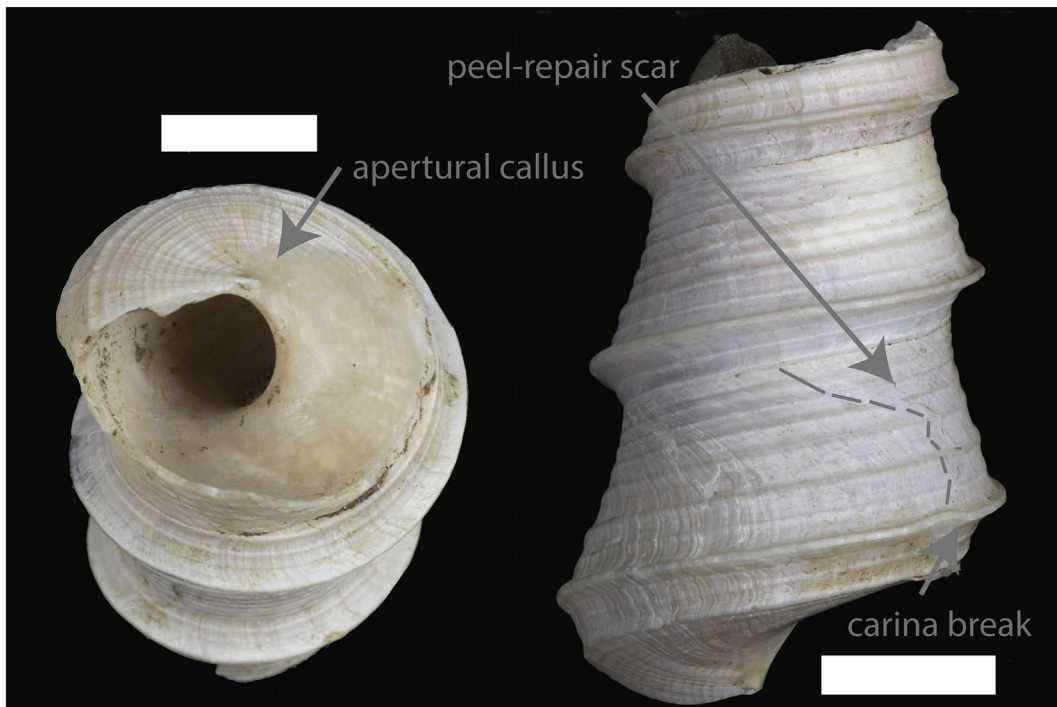


Fig. 3. Images of a *Turritella abrupta* specimen, PRI 82022, showing both an apertural callus and a peel-repair scar. The peel-repair scar is shallow relative to the size of the shell and the form is indicated in the grey dotted line, placed slightly aperture-ward of the break. It is most easily identified in the image by following the break upward from the distortion in the carina caused by the damage to the shell. Scale bars are 1 cm.

history information such as lifespan and growth rates (Jones, 1988; Allmon et al., 1992; Jones and Quitmyer, 1996; Jones and Gould, 1999; Buick and Ivany, 2004; Allmon, 2011; Waite and Allmon, 2016).

For specimens selected for isotopic analyses, scanning electron microscopy was employed to evaluate the presence of original crossed-

lamellar microstructure by using a JEOL JCM-5000 Neoscope (Fig. S1A). SEM images were obtained without any conductive coating or etching. Material removed from the surface of the basal portion of the shell was powdered and analyzed using x-ray diffraction with a Scintag Theta-Theta Diffractometer; we used quartz as an internal standard to

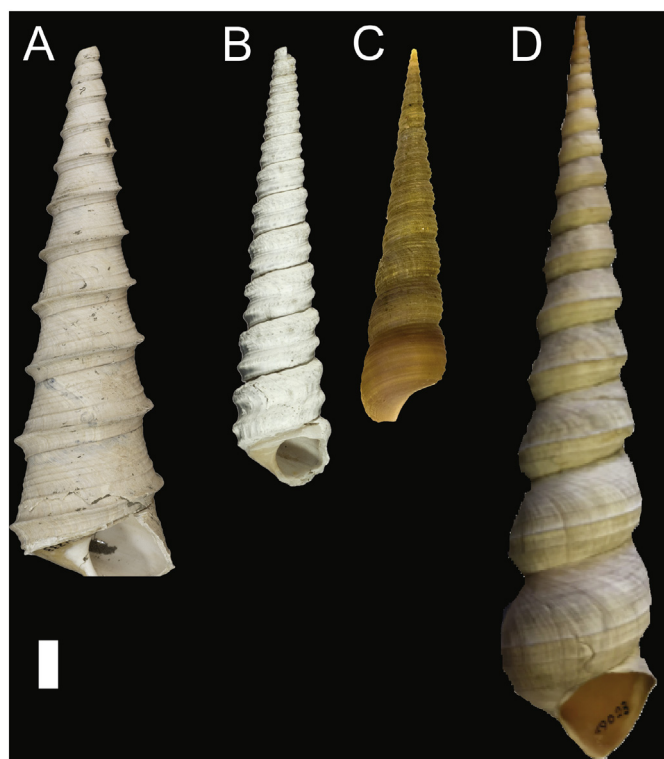


Fig. 4. Tropical turritelid species used in growth and calcification rate comparisons. A. *Turritella abrupta* Spieker, 1922, Miocene of Panama (STRI 17721) B. *Turritella (Torcula) altilira* Conrad 1857, Miocene of Panama (STRI 17721) C. *Turritella bacillum* Kiener, 1843, Recent, Hong Kong (WDA, personal collection) D. *Turritella duplicata* Linnaeus, 1758, Recent, Sri Lanka (AMNH 49023). Scale bar is 1 cm.

confirm aragonite composition (Fig. S1B). Specimens were washed and cleaned ultrasonically; any area with residual materials or discoloration was not sampled. Samples were taken with a dental drill, roughly parallel to growth lines. The smaller specimen (PRI 68731) was sampled at higher resolution (approximately 1 cm of spiral distance between samples - precise measurements available in supplementary data file on isotopic data). Evaluating the isotopic curve derived from this specimen guided the lower resolution sampling (approximately 3 cm of spiral distance between samples) of early whorls of the larger specimen (LACM 42097). Whorls in LACM 42097 that were larger than the size observed in PRI 68731 were sampled at higher resolution than early whorls (approximately 1 cm spiral distance between samples). Isotopic analysis of PRI 68731 was conducted at the University of Florida using a Finnigan-MAT 252 with Kiel III carbonate preparation device. Isotopic analysis of LACM 42097 was conducted at the University of Kansas using a Finnigan MAT 253 with a Kiel III carbonate preparation device. NBS-19 was used as a standard at the University of Florida, with mean  $\delta^{13}\text{C}$  of 2.07 and  $\delta^{18}\text{O}$  of  $-2.05$  prior to laboratory correction. The University of Kansas used multiple standards; NBS-18, with mean  $\delta^{13}\text{C}$  of  $-5.15$  and mean  $\delta^{18}\text{O}$  of  $-23.32$ ; NBS-19, with mean  $\delta^{13}\text{C}$  of 1.85 and mean  $\delta^{18}\text{O}$  of  $-2.26$ ; and dolomite 88b with mean  $\delta^{13}\text{C}$  of 2.05 and  $\delta^{18}\text{O}$  of  $-6.04$ . Analytical error was less than  $\pm 0.10\text{‰}$  for both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  at both facilities.

The method of Tao et al. (2013) was employed to determine whether seasonality observed in the sclerochronologies was likely due to freshwater input or seasonal upwelling. A positive correlation (R) between O and C isotopic values through the axis corresponding with the ontogeny of the organism indicates freshwater contribution with isotopically light carbon delivered by runoff associated with isotopically light rainwater (Jones and Allmon, 1995; Tao et al., 2013; Anderson et al., 2017). In contrast a negative correlation is indicative of

upwelling, with cold water (recorded as a heavier oxygen isotopic excursion) associated with isotopically light carbon (Jones and Allmon, 1995; Tao et al., 2013; Anderson et al., 2017). It should be noted that the correlation of O–C values is faithful to the relative influence of seasonal upwelling or freshening in tropical environments, even when R values are not statistically significant (Tao et al., 2013). Due to the rapid growth implied by the shape of the oxygen isotope curve, it would not be appropriate to include all of the mild fluctuations from early growth when evaluating whether there are seasonal correlations between oxygen and carbon isotopic values, following the procedure of Tao et al. (2013), as this would overrepresent the season of early growth when there is little variability. Excluding the earliest samples from PRI 68731 places an equal number in each inferred season (total N included = 30).

### 2.3. Estimation and comparison of calcification rates

First-year shell deposition (mass) was directly measured in live-collected *Turritella bacillum* from Hong Kong (with size at one year determined by isotopic sclerochronology (Kwan et al., 2018)); size was estimated for the extinct species *Turritella abrupta* and *Turritella (Torcula) altilira*, with size at one year determined from isotopic sclerochronology. Shell thickness measurements were obtained from specimens bearing an apertural callus at the axial midpoint of the apertural whorl. The measured thicknesses (Table S1) were found to be consistently  $\sim 3.2$  mm at the midpoint of the height of the apertural whorl, and ranged between 2.8 and 6 mm thick on the carina (the sharply projecting spiral cord near the base of the whorl in *T. abrupta* that becomes more pronounced throughout ontogeny). An average thickness of 3.3 mm was used to represent mean thickness at any given point on the shell after 31 mm in length from the theoretical apex (see Johnson et al., 2017) was achieved. *Turritella altilira* was observed to have a thickness of 1.5 mm, while *T. terebra* had a thickness of 1.25 mm for most of its length. As no specimens of *T. abrupta* bearing an apertural callus at early whorls were located, additional data were obtained from micro-computed tomography ( $\mu\text{CT}$ ) measurement of PRI 68731 using a GE CT-120 at the Cornell Biotechnology Resource Center. Measurements were taken using RadiAnt DICOM viewer software on whorls that were not substantially secondarily filled with shell material (Fig. S2). While these measurements may incorporate some degree of secondary shell deposition, stable isotope sclerochronology (below) and insertion of multiple septa prohibiting redeposition in the earliest whorls suggest that this deposition would also have been during the first year of life, although not contemporaneous with the growing edge of the shell (see Anderson and Allmon, 2018 for further discussion).

Shell mass was measured directly in two specimens of *Turritella abrupta* that were collected with lateral breaks, so that any impacted sediment could be removed. An idealized hollow conic approximation (tangent to the shell at the midpoint of the whorl, not the carina) was used to estimate the total mass deposited during the first year of life. The surface area of the tangent cone was calculated, and then tangent shell volume was estimated using with a thickness of 1.5 mm for the first 31 mm of shell length, and 3.3 mm afterward, and a density for aragonite of  $2.93 \text{ g/cm}^3$  (Dyar et al., 2008). This is necessarily an underestimate of shell mass, as the tangent cone does not include the adapical and adapertural shell wall of each whorl, only the externally visible shell. *Turritella altilira* mass was estimated using a conic approximation based on the mean length of growth at 1 year obtained from 10 specimens (Anderson et al., 2017) and a mean shell thickness of 1.5 mm. Specimens of *T. bacillum* collected at one year of age were available in PRI collections and were cleaned and weighed directly.

### 2.4. Assessment of predation frequency and prey effectiveness

Turritellids have frequently been examined for evidence of drilling and peeling predation, with frequency of attack (Drilling Frequency-DF

and Peel-Repair frequency) known to vary substantially among species and localities (Allmon et al., 1990; Pierrehumbert and Allmon, 2018). Comparisons of DF and Peel-Repair frequency are best made among those species which co-occur, but it is notable that failed drilling of turrnellids is relatively uncommon across all datasets (i.e., < 10% of drilled individuals, often much less (Allmon et al., 1990, Tull and Bohningaese, 1993, Mallick et al., 2013, Mallick et al., 2014, Anderson et al., 2017)).

PRI (Systematic and Hodson Collections) and STRI (col # 17721) collections from Panama and Venezuela including *Turritella abrupta* were examined to determine frequency of drilling and peeling predation in this species and to facilitate comparisons with co-occurring turrnellid species of moderate size. Drilling by naticid and muricid gastropod predators is a frequent component of paleoecological studies, with both successful and unsuccessful predation events being well preserved in the fossil record (Dudley and Vermeij, 1978; Vermeij et al., 1980; Allmon et al., 1990; Hagadorn and Boyajian, 1997; Alexander and Dietl, 2003; Mallick et al., 2014). Prey effectiveness was determined as the ratio of incomplete drillholes to the sum of incomplete and complete drillholes (Vermeij, 1987; Kelley and Hansen, 2003; Mallick et al., 2013).

Unsuccessful attempts at peeling predation by crabs can also be recorded on gastropod shells as peel-repair scars (Vermeij, 1982; Vermeij, 1987; Allmon et al., 1990; Huntley and Kowalewski, 2007; Stafford et al., 2015; Pierrehumbert and Allmon, 2018). The relationship between successful and unsuccessful predation attempts is less clear, as successful predation often results in the destruction of the shell and its removal from the fossil record (Vermeij, 1980; Vermeij et al., 1989; Dietl and Kosloski, 2013; Smith et al., 2018). In this study, we consider survival of repeated predation attempts as evidence of higher prey effectiveness, while peel-repair frequency is a combination of predation pressure (inclusive of predator density and prey-preferences), prey availability, and prey effectiveness.

### 2.5. Distribution data

Stratigraphic and geographic information was derived from both museum collections and the Paleobiology Database (PBDB; downloaded 9-12-18). Records of these species include occurrences in the Ferrotepec (middle Miocene), Isidro (early Miocene), San Ignacio (early Miocene), and Trinidad (late Miocene) Formations (Mexico), the Angostura (late Miocene) and Progreso (middle Miocene) Formations (Ecuador), the Cardalitos (middle Miocene) and Zorritos (early Miocene) Formations (Peru), the Caujarao (middle Miocene), La Rosa (early Miocene), Urumaco (late Miocene), and Araya (late Pliocene) Formations (Venezuela), the Gatún (late Miocene) and Tuirá (late Miocene) Formations, (Panama), the Monterey (middle Miocene), Rincon (early Miocene), Temblor (early Miocene), and Vaqueros (early Miocene) Formations, (United States), and the Castilletes (middle Miocene), Jimol (early Miocene), and Tubara (late Miocene) Formations (Colombia). Age estimates used in this paper for these formations were based on PBDB records, except as noted.

### 2.6. Assessment of community composition

Only bulk-collected samples were used to evaluate the relative abundance of *Turritella abrupta* compared with other turrnellid species. They were sourced from the Gatún Formation, Panama, and the Castilletes and Jimol Formations, La Guajira Peninsula, Colombia, and were the only *T. abrupta*-bearing bulk collections available. As turrnellids are prone to breakage, a minimum number of individuals (MNI) was established for all turrnellid species in each sample, following the procedure of Johnson et al. (2017).

## 3. Systematic paleontology

Gastropoda

Cerithioidea Fleming 1822

Turritellidae Lovén 1847

*Turritella* Lamarck 1799

*Remarks:* We follow the convention of considering neotropical turrnellid species part of *Turritella sensulato*, in the absence of evidence placing them in another genus. *Turritella abrupta* is unlikely to be closely related to *Turritella sensu stricto* (e.g., *Turritella sensu Marwick, 1957*); living turrnellids from the neotropical Americas belong to two deeply divergent clades, *Torcula* and an as-yet unnamed clade, which are distinguished mainly on the order of appearance of apical spiral sculpture (Sang et al., 2019). Unfortunately, no protoconch-bearing whorls of *Turritella abrupta* have been found. Pending revision of Recent and fossil turrnellid genera, we do not seek to place *T. abrupta* in an extant or extinct genus or as a stem or crown member of either living western Atlantic/tropical eastern Pacific clade (Sang et al., 2019). *Turritella s.l.* is a commonly used generic assignment for turrnellids in the absence of compelling morphological or biogeographic reasons to make a definitive assignment (e.g., Allmon, 1996; DeVries, 2007; Allmon, 2011), and should not be taken to imply that *T. abrupta* is not a member of either of these clades or other biogeographically plausible genera.

*Turritella abrupta* Spieker, 1922

*Synonymy:* 1899 *Turritella (Haustator) robusta* sp. nov.; Grzybowski, 1899: 646, pl. 20: 3 (Non *T. robusta* Gabb, 1864)

1922 *Turritella robusta* Grzybowski, 1899; Woods in Bosworth 1922: 84, pl. 4: 6.

1922 *Turritella charona* sp. nov.; Spieker, 1922: 67–72, pl. IV: 7.

1922 *Turritella robusta* Grzybowski, 1899; Spieker, 1922: 67–72, pl. IV: 5.

1922 *Turritella robusta* Grzybowski, 1899 var. *abrupta* var. nov.; Spieker, 1922: 67–72, 85 pl. IV: 6.

1925 *Turritella supraconcava* sp. nov.; Hanna and Israelsky, 1925: 59.

1925 *Turritella trinitaria* sp. nov.; Maury 1925: 382, pl. 53: 10.

1926 *Turritella robusta* Grzybowski, 1899 *fredeai* ssp. nov.; Hodson, 1926:13, pl. 5: 1–3, pl. 6: 2,5, pl. 7: 1,6,7, pl. 9: 7, pl. 29: 6 (Non *T. robusta* Gabb, 1864).

1927 *Turritella bösei* sp. nov.; Hertlein and Jordan, 1927: 634, pl. 19: 2.

1927 *Turritella abrupta* Spieker, 1922; Anderson, 1927: 89, pl. 4: 6.

1928 *Turritella bösei* Hertlein and Jordan, 1927; Wiedey, 1928: 117–119, pl. 10: 7, pl. 11: 1, 3, 5.

1929 *Turritella fredeai* Hodson, 1926; Anderson, 1929: 119, pl. 17: 1.

1929 *Turritella supraconcava* Hanna and Israelsky, 1925; Weisbord, 1929: 263, pl. 44: 3–4.

1932 *Turritella abrupta* Spieker, 1922; Olsson, 1932: 200.

1938 *Turritella trinitaria* Maury, 1925; Vokes, 1938: 26, pl. 29.

1941 *Turritella abrupta* Spieker, 1922; Merriam, 1941: 48, pl. 29: 4; pl. 30: 6; pl. 31: 2–4.

1951 *Turritella abrupta* Spieker, 1922; Marks, 1951: 99.

1956 *Turritella abrupta* Spieker, 1922; Petters and Sarmiento, 1956: 20.

1957 *Turritella abrupta* Spieker, 1922; Woodring, 1957: 106–107, pl. 23: 6, 15, 16.

1964 *Turritella abrupta* Spieker, 1922; Olsson, 1964: 190–191, pl 35: 1a-1d.

1965 *Turritella supraconcava* Hanna and Israelsky, 1925; Rollins, 1965: 57.

1985 *Turritella abrupta* Spieker, 1925; Jones and Hassan, 1985: 328.

1989 *Turritella abrupta* Spieker, 1922 *fredeai* Hodson, 1926; Smith,

1989: 28, pl. 2: 3–4.

1991 *Turritella abrupta* Spieker, 1922 *fredeai* Hodson, 1926; Smith, 1991: 648, pl. 3: a, c.

2013 *Turritella abrupta* Spieker, 1922; Hendy, 2013: 214.

2018 *Turritella abrupta* Spieker, 1922; Anderson and Allmon, 2018: 449, pl. 1: C.

2018 *Turritella abrupta* Spieker, 1922; Alberti and Reich, 2018: pl. 6: 45.

**Material:** Holotype USNM 562351 as *T. robusta*, var. *abrupta*, Zorritos, Peru; additional figured specimens USNM 643905, USNM 643903, LACM 42097, PRI 68731.

**Description:** Large and heavy-shelled turritellid. Early whorls rounded and evenly ornamented, with later whorls carinate in profile and developing a strongly keeled spiral ornament near, but not at the base of the whorl. Keel may bend adapically, but commonly is even. Other ornamentation is distinct but with no strong differentiation among spiral cords. Apical end of specimen typically completely filled secondarily; specimens are frequently broken far from apex. Lateral growth line trace strongly prosocline, with the inflection located in bottom third of the whorl. Lateral sinus depth is moderate, but the large whorl height and adapertural location of the apex of the growth line trace results in a shallow semi-circular curve after a long prosocline trace. Aperture rectangular. Apex unknown.

**Remarks:** *Turritella abrupta* was originally described as *Turritella robusta* var. *abrupta* from the Miocene Zorritos (Cardalitos) Formation, Peru (Spieker, 1922). *Turritella (Haustator) robusta* Grzybowski 1899, however, is a preoccupied homonym of the Californian Cretaceous *Turritella robusta* Gabb, 1864 (Woodring, 1957: p. 107). Other synonyms include *Turritella bösei* Hertlein and Jordon, 1927 and *Turritella robusta fredeai* Hodson, 1926. *Turritella ocoyana* Conrad 1857 has sometimes been considered a synonym of *Turritella abrupta* (e.g., discussion in Woodring, 1957; Addicott, 1970b), but is distinguishable from *T. abrupta* by its less rounded whorl profile in early whorls, a broader slope beneath the carina, and a less acute carina (Spieker, 1922), which may show multiple lineations on close inspection of large, well-preserved whorls.

**Stratigraphic range:** Specimens are also known from the Jimol (17.8–17.5 Ma) and Castilletes (~17.5–14.2 Ma) Formations of the Guajira Peninsula, Colombia, representing some of the earliest records of the species from a formation with excellent chronostratigraphic control derived from Sr isotope values (Hendy et al., 2015). Less chronostratigraphic control is available for the Zorritos Formation (Peru) and the Isidro Formation (Mexico), each of which is also early Miocene (23–16 Ma). The last Atlantic occurrence (and also last global appearance datum) of the species is the Pliocene Araya Formation, Cubagua, Venezuela (Landau et al., 2008; Landau and da Silva, 2010), dated to 3.2–2.4 Ma, based on planktonic foraminifera (Castro and Mederos, 1997). The last Pacific occurrence of *T. abrupta* is in the Trinidad Formation, "member A of McCloy (1984), of late Miocene age based on nanofossils, from southern Baja California (T. Schwennicke, 2019, personal communication).

**Geographic range:** *T. abrupta* is known from the eastern Pacific, from southern California to Peru, including Baja and Southern Mexico, and also from the western Atlantic, from Panama and northern South America as far east as Venezuela. *Turritella abrupta* is not known from the Caloosahatchian Province of Petuch (1982) (which includes eastern Mexico, the US Gulf Coast, and the Greater Antilles).

## 4. Results

### 4.1. Stable isotope sclerochronology

The specimen sampled at higher resolution (PRI 68731) clearly shows a two-year lifespan with a deceleration in spiral growth after the first year (Fig. 5), typical of other turritellids (Allmon, 2011). Seasonal differences in growth rate imply that growth was faster during

particular seasons, possibly associated with higher nutrient input from terrestrial freshwater runoff, during both years. LACM 42097 (Fig. 6) is estimated to have lived 4.5–5 years, also with a deceleration of growth after the first year. A deep (~3 cm) peel-repair scar between 420 and 444 mm likely removed the shell deposited during the inferred wet-season (low  $\delta^{18}\text{O}$ ) of the third year of the organism's life. First-year spiral growth may have been substantially less for LACM 42097 than for PRI 68731, but as both specimens are missing substantial portions of their apices, this variability cannot be confirmed.

The sclerochronology of the sampled *Turritella terebra* specimen (Figure 7) shows that larval settlement occurred during the rainy season (low  $\delta^{18}\text{O}$ ), and most growth was completed in the first-year dry (high  $\delta^{18}\text{O}$ ) season, followed by a significant decline in growth rate during the rainy season of the second year. By comparison, specimens of modern *Turritella duplicata* were observed by Waite and Allmon (2016) to grow more evenly throughout their lifespan, adding ~4–4.5 cm of shell length during both the first and second year of growth over a maximum observed lifespan of three years, but with very rapid growth during the first half-year of life. Using the theoretical apex system (Johnson et al., 2017) to complete the missing apical portion of the shells, this suggests *Turritella abrupta* grew approximately 7.5–8 cm in axial length during the first year and *Turritella terebra* grew approximately 9 cm in axial length during year one. *Turritella duplicata* is more similar in pleural angle and shell thickness (~3.2 mm) to *T. abrupta* than *T. terebra*. *T. duplicata* is unlikely to be closely related to *T. abrupta*, but in size and shell shape may be the closest ecological analogue among living turritellids. It is therefore interesting to observe that *T. duplicata* achieves its large, carinate, heavy shell through a different growth pattern than *T. abrupta*.

### 4.2. Estimation and comparison of calcification rates

The conic approximation method resulted in an estimated 35.4 g of first-year shell deposition by *Turritella abrupta*. Direct measurement of shell thickness in specimens with lateral breakage (facilitating removal of any compacted sediment) confirms the general reliability of this approximation. These directly massed specimens, from collections STRI 3168 and UF 221233, have maximum whorl diameters indicative of less than one year's growth (as determined from isotopically sampled individuals), significant apical material missing, and substantial lateral material missing in the case of UF 221233. These were measured to be 23 g and 18.7 g (implying original mass ca. 25 g, as approximately ¼ of the shell was missing), respectively (Figure 8). This suggests that a minimum estimated annual deposition of ~35 g is reasonable, if not conservative, as this estimate ignores both 1st-year secondary thickening and the prominent carinae.

The co-occurring species *Turritella (Torcula) atilira* is estimated to construct approximately 5.7 g of shell material in the first year of growth. Recent *T. bacillum*, which is found in a modern tropical environment with strong seasonal freshwater input (Hong Kong), produces 5 g of shell material during the first year of growth, as assessed by direct massing of live-collected shells.

### 4.3. Predation frequency and prey effectiveness

*Turritella abrupta* has a comparatively low Drilling Frequency (DF) (Table 2), 0.07 in bulk-collected specimens from Panama, compared with 0.18 for bulk-collected *Turritella atilira* and 0.14 for bulk-collected *Turritella gatunensis* (Anderson et al., 2017). In Venezuelan specimens, both *Turritella abrupta* and *Turritella venezuelana* had the same low DF (0.07). In Venezuelan specimens from the Hodson collection at PRI, 14 drillholes or attempted drillholes were observed in *T. abrupta*. This was the only collection of *T. abrupta* with a sufficient number of drillholes to calculate prey effectiveness (0.64). Whenever substantial numbers of individuals were able to be examined, *T. abrupta* demonstrated an impressive ability to resist drilling predation, as would be expected from

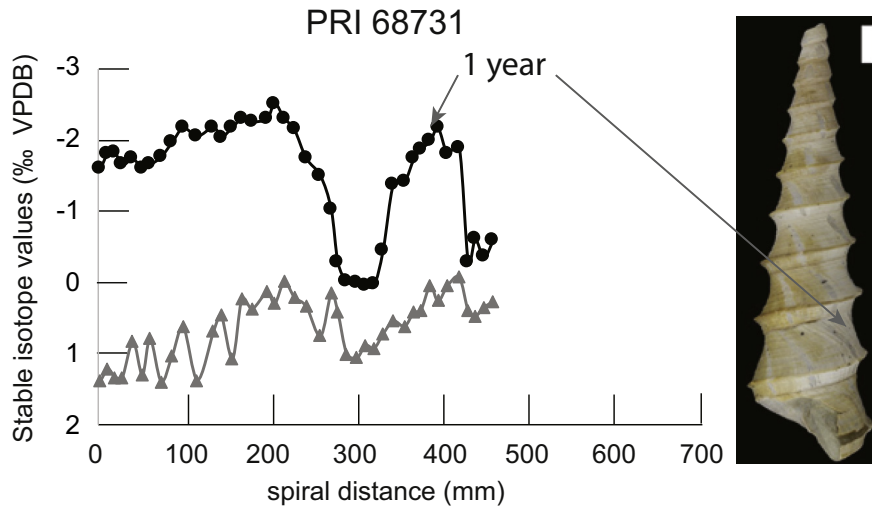


Fig. 5. Isotopic sclerochronology of smaller *Turritella abrupta* Spieker, 1922 specimen PRI 68731 from Rio Tupisa, Panama. Scale bar is 1 cm. Values for oxygen are in black circles, values for carbon are in grey triangles. VPDB is Vienna Pee Dee Belemnite Standard.

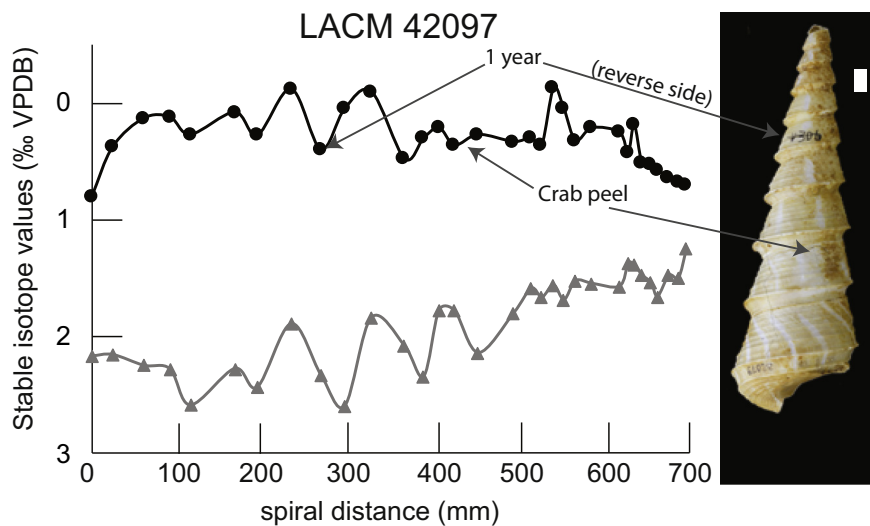


Fig. 6. Isotopic sclerochronology of larger *Turritella abrupta* Spieker, 1922 specimen LACM 42097 from Isla Cubagua, Venezuela. Scale bar is 1 cm. Values for oxygen are in black circles, values for carbon are in grey triangles. A peel-repair scar between 420 and 444 mm likely removed the wet-season deposited shell during this year of the organism's life. VPDB is Vienna Pee Dee Belemnite Standard.

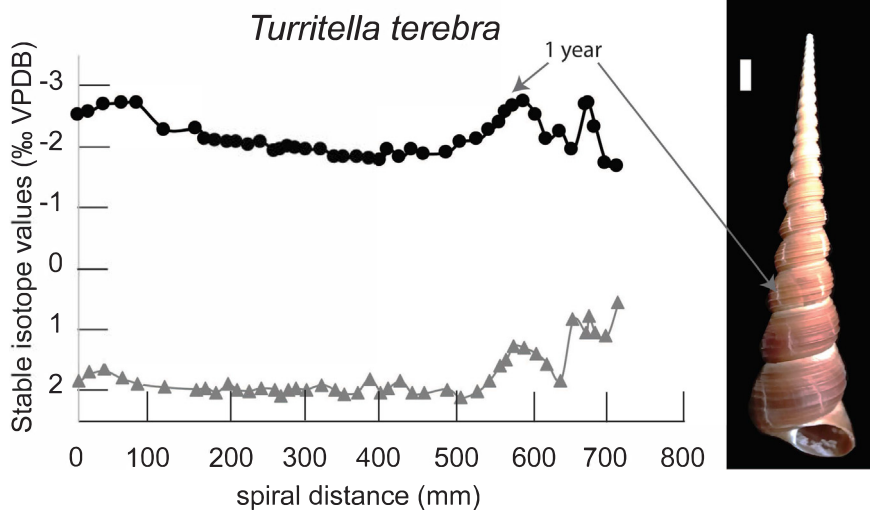
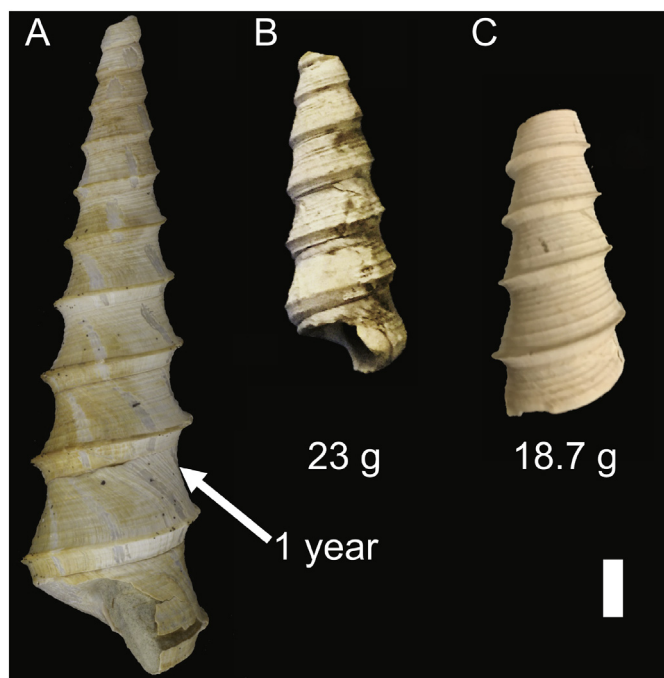


Fig. 7. Stable isotope analysis of *Turritella terebra* Linnaeus, 1758, one of the longest (axially) modern turritellid species (specimen sampled is 13 cm). Values for oxygen are in black circles, values for carbon are in grey triangles. Seasonality in this specimen is dominated by wet-dry cyclicity as indicated by the strong positive correlation between oxygen and carbon isotopic fractionation. This sclerochronology indicates a lifespan of 2 years, and that most growth took place during the first year, with a drastic decline in growth rate during the subsequent year. VPDB is Vienna Pee Dee Belemnite Standard.



**Fig. 8.** Miocene specimens of *Turritella abrupta* Spieker, 1922 that were not impacted with sediment or secondarily filled permitting direct measurement of mass. A. PRI 68731 for growth comparison. B. STRI 38168; specimen is 23 g and bears an aperture scar C. UF 221233; specimen is broken on reverse side and contains approximately ¾ of all whorls totaling a mass of 18.7 g. Scale bar is 1 cm.

its thickly constructed shell (Figure 9).

Peeling-repair is a less direct proxy for frequency of predation than DF because successful predation can result in the complete destruction of the shell (Smith et al., 2018). Peeling-repair frequencies therefore represent a combination of frequency of attack and frequency of survival. In species with differing lifespans, more attacks survived may also represent more time exposed to attack (Table 3). In Panama, the proportion of individuals that had been attacked and survived (specimens bearing any predation scar) was similar between *T. abrupta* (0.28) and *T. altilira* (0.22–0.30), and higher than *T. gatunensis* (0.15). In Venezuela, the frequency of attacks on individuals was higher for *T. venezuelana* (0.40) than *T. abrupta* (0.17). The highest number of peeling-predation attempts survived during an individual *T. abrupta*'s lifetime was 5 in Panama and 6 in Venezuela. The highest number of attempts survived by an individual *T. altilira* in Panama or *T. venezuelana* in Venezuela was 3.

**Table 2**

Drilling predation data for *T. abrupta* and co-occurring medium to large turritelid species. Minimum number of individuals calculated following the procedure of Johnson et al. (2017). Prey effectiveness calculated for samples with > 10 drillholes observed. \* indicates that a single *T. altilira* is known to have been drilled above an internal septum, although the hole was complete (Anderson and Allmon, 2018).

Species	Locality	N	MNI	DF (complete/total)	Total drillholes	Failed drilling (prey effectiveness)	Reference or collection
<i>abrupta</i>	Ecuador	10	6	0	0	N/A	PRI, Systematic
<i>abrupta</i>	Panama	5	4	0.25	1	0	PRI, Systematic
<i>abrupta</i>	Panama	17	15	0.07/0.13	2	1	Anderson et al., 2017
<i>altilira</i>	Panama	20	n/a	0.25	5	0	Allmon et al., 1990
<i>altilira</i>	Panama	1263	341	0.18	61	0* (0)	Anderson et al., 2017
<i>gatunensis</i>	Panama	167	81	0.14	23	0 (0)	Anderson et al., 2017
<i>abrupta</i>	Venezuela	97	68	0.07/0.21	14	9 (0.64)	PRI, Hodson
<i>abrupta</i>	Venezuela	23	n/a	0.04	1	0	Allmon et al., 1990
<i>venezuelana</i>	Venezuela	66	55	0.05/0.07	4	1	PRI, Hodson

4.4. Distribution data

*Turritella abrupta* is present by ~17 Ma at a number of localities, including the Zorritos, Progreso, and Jimol Formations (the age of the Jimol Formation and the Jimol/Castilletes boundary have been recently revised; Hendy et al., 2015, Moreno et al., 2015). *Turritella abrupta* is widespread between 17 and 13 Ma, but after 13 Ma the species appears to have been restricted to northern South America and Panama, and the southernmost tip of the Baja Peninsula (Figure 10). *Turritella abrupta* is present in the late Miocene Trinidad Formation at the southernmost end of Baja California (Smith, 1989). This represents the highest latitude occurrence of *T. abrupta* after global cooling began ~13 Ma (Zachos et al., 2001; Cramer et al., 2011). The similarly heavy-shelled species *Turritella ocoyana* occupies a more northerly range during the middle Miocene, including southern California (based on PBDB records), with both species present in the southern portion of Baja California and southern Mexico, but *T. ocoyana* is extinct by 13 Ma (Fig. S3). The last occurrence datum of *T. abrupta* is the Pliocene Araya Formation, from Cubagua, Venezuela (Landau et al., 2008; Landau and da Silva, 2010), dated to 3.2–2.4 Ma, based on planktonic foraminifera reported by Castro and Mederos (1997). *T. abrupta*'s reliable stratigraphic range is therefore 17–2.4 Ma, but with notable changes in geographic distribution over that period.

4.5. Assessment of community composition

*Turritella abrupta* represented approximately 1% of turritelid individuals (30 MNI of 40 fragments) in bulk collected samples from Colombia (N = 2322) and Panama (N = 1447) (Figure 11). In all samples, MNI analysis (Johnson et al., 2017) increased the relative abundance of *Turritella abrupta*, and we are therefore confident that utilizing MNI for all species rather than fragment counts did not bias our conclusion regarding low relative abundance of this species. It is also notable that turritelid species of moderate length and mass are most abundant at both localities (*T. altilira* in the Panama bulk sample, *Turritella cocoditana* and *Turritella matarucana* in the Colombian bulk sample); however, larger species make up a more significant portion of the turritelid fauna in Guajira, Colombia, including the species *Turritella falconensis* (9%; 202 MNI), *Turritella larensis* (6%; 128 MNI), *Turritella montañitensis* (10%; 225 MNI) and *Turritella machapoorensis* (6%; 132 MNI). None of these species approaches the maximum size of *T. abrupta*, but they are also relatively heavy-shelled, with moderate to large maximum lengths.

5. Discussion

*Turritella abrupta*'s ecology was quite unusual for turritelids. *T. abrupta* had a relatively long lifespan (4–5 years - double the lifespan of most species; see below), low abundances (while many turritelids are known to live at high densities), and high predation resistance



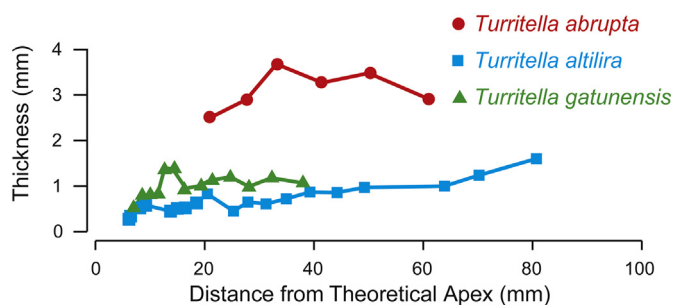


Fig. 9. Comparison of shell thickness for specimens of *Turritella abrupta* Spieker, 1922, *T. altilira* Conrad, 1857, and *T. gatunensis* Conrad, 1857 which co-occur in the Gatún Formation at the Los Lomas locality, Panama (STRI 17721). All measurements taken at the midpoint of the whorl. Apical whorls of *T. abrupta* which had been completely or substantially secondarily filled are not included.

compared with other turritellids (Allmon, 1988, 2011). It also exhibited one of the most rapid aragonitic deposition rates known among turritellids, which may have contributed to both its success and eventual extinction under changing environmental conditions.

We followed the methodology of Tao et al. (2013) to assess the degree of seasonal variation in our isotopic data collected from *Turritella abrupta* and evaluated potential seasonal sources of nutrient input (either upwelling or freshening) in their environments. We note that the positive correlation of oxygen and carbon isotopic excursions suggests both *T. abrupta* specimens come from systems with strong seasonal freshwater input (Krantz et al., 1987; Jones and Allmon, 1995; Tao et al., 2013). The more muted isotopic range of LACM 42097 is likely due to lower-resolution sampling, rather than solely being attributed to differences in local freshwater input (Ivany, 2012) or conflicting influences of both upwelling and freshening (Geary et al., 1992; Tao et al., 2013). The correlation (R) for O–C values sampled from PRI 68731 is 0.52 ( $p < 0.01$ ), indicative of a significant freshwater signal, following the methods of Tao et al. (2013). The correlation (R) for O–C values from all samples taken from LACM 42097 is 0.26 ( $p = 0.15$ ), indicative of moderate seasonal freshening (Tao et al., 2013), although it may be artificially lowered by the loss of a seasonal peak due to missing shell as indicated by a peel-repair scar. Isotopic and geologic data from La Guajira, Colombia, also suggest a much stronger influence of seasonal freshwater input in localities in northern Colombia and Venezuela (Scholz et al., 2018; Pérez-Consuegra et al., 2018), where *T. abrupta* is also present. In contrast, the Gatún Formation, Panama, where *T. abrupta* is present, appears to have nutrients from waters influenced by upwelling (Anderson et al., 2017). This suggests that *T. abrupta* may be restricted to environments with high nutrient input but had broader salinity tolerances than many turritellids (Allmon, 1988).

The typical turritellid lifespan as determined by isotopic sclerochronology is one to three years, with *Torquesia sulcifera* (Eocene; Huyghe et al., 2015) and *Turritella communis* (Recent; Baltzer et al., 2015) known to be exceptions (lifespans of four and five years,

respectively; Allmon, 2011). Therefore, the lifespan of 4–5 years (estimated here) for *Turritella abrupta* is high for the clade. If this inference is correct for fossil species, then lifespan bias (Kidwell and Rothfus, 2010; Cronin et al., 2018) may be a factor contributing to the low relative abundance of *T. abrupta* in fossil assemblages: co-occurring species appear to have had lifespans of 2–2.5 years (Anderson et al., 2017; Scholz et al., 2018), and this may have caused their abundance in death assemblages to be higher. This bias alone, however, would not be expected to drive *T. abrupta* to 1% of a bulk sample from a living population equal in number to other co-occurring turritellids. Cronin et al. (2018) documented live-dead proportional abundance discordance of only 0.20–0.25 between species with regional maximum lifespans of 11 and 46 years, a difference which is larger than that between *T. abrupta* and co-occurring turritellids for which lifespan data are available in both absolute and proportional terms. Additionally, as all fragments larger than one whorl were counted from bulk samples prior to MNI analysis (Johnson et al., 2017), taphonomy should have favored preservation of the large and heavy-shelled *T. abrupta*, compared with less robust forms.

*Turritella abrupta* exhibited a significant decline in growth rate after the first year of life, consistent with most other turritellid species (Allmon, 2011). Similar declines in growth have been tied to reproductive maturity in other molluscs, including giant clams (Jones et al., 1986). This suggests that extremely low relative abundance in the assemblages studied was due to low annual recruitment in addition to differences in the rate of contribution to the death assemblage relative to living individuals, as individuals of both *T. abrupta* and co-occurring species probably began reproducing at approximately one year in age. Life-span bias likely inflates the representation of non-*T. abrupta* turritellids in the fossil assemblage relative to their representation in the live community (Cronin et al., 2018), but if *T. abrupta* had equal recruitment rates it would be expected to be far more abundant in the fossil assemblages, even with a probable lifespan bias.

*Turritella abrupta* does not appear to be limited by energetic trade-offs among aspects of shell growth (as suggested for other molluscs; Palmer, 1979; Palmer, 1981; Voltzow, 1994); that is, the species attains high length/spiral growth during the first year of life, comparable with modern tropical species (Table 4), has the highest pleural angle (the widest whorl at a given distance from the apex), and the highest shell thickness measurements among these species. Unlike *T. terebra*, *T. abrupta* does not appear to achieve greater lengths through a trade-off with shell thickness early in life, as early whorls are not unusually thin (1.5 mm; Fig. S2) and long before reaching the first year of life, specimens begin depositing 3 mm thick growing-edge shell material (Table S1). Secondary shell thickening is also high in *T. abrupta*, as the species frequently completely fills its apical whorls (Anderson and Allmon, 2018). This is not unique among turritellids, as seen in *T. duplicata* and some other turritellid species (Andrews, 1974; Anderson and Allmon, 2018), but it illustrates that high rates of initial shell deposition are not compensated for by low rates of secondary thickening of early whorls.

This high rate of calcification must, however, have come at an

Table 3

Peeling/repair data for specimens of *T. abrupta* larger than 1.5 whorls (single whorls were not included) and co-occurring turritellid species. Peeling frequency presented both as total number of peels and a comparison of peeled and unpeeled individuals.

Species	Locality	N	#	Peeling frequency (# of peels/by individuals peeled)	Attacks on most frequently peeled individual	Reference or collection
<i>abrupta</i>	Ecuador	10	6	0.17/0.17	1	PRI Systematic
<i>abrupta</i>	Panama	5	4	0.75/0.75	1	PRI Systematic
<i>abrupta</i>	Panama	17	14	0.71/0.28	5	Anderson et al., 2017
<i>altilira</i>	Panama	20	n/a	0.30/not reported	Not Reported	Allmon et al., 1990
<i>altilira</i>	Panama	1263	18	0.22/not reported	3	Anderson et al., 2017
<i>gatunensis</i>	Panama	167	13	0.15/0.15	1	Anderson et al., 2017
<i>abrupta</i>	Venezuela	97	75	0.28/0.17*	6	PRI Hodson
<i>abrupta</i>	Venezuela	23	n/a	0/0	0	Allmon et al., 1990
<i>venezuelana</i>	Venezuela	66	66	0.74/0.40	3	PRI Hodson



Fig. 10. Distribution of *Turritella abrupta* Spieker, 1922 before (light blue) and after (dark red) global cooling ~13 Ma (Zachos et al., 2001; Cramer et al., 2011). Data derived from PBDB including the synonymous names *Turritella bösei* Hertlein and Jordan, 1927 and Miocene occurrences of *Turritella* “robusta”. The combined circle designates a locality with occurrences in formations deposited both before and after 13 Ma. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

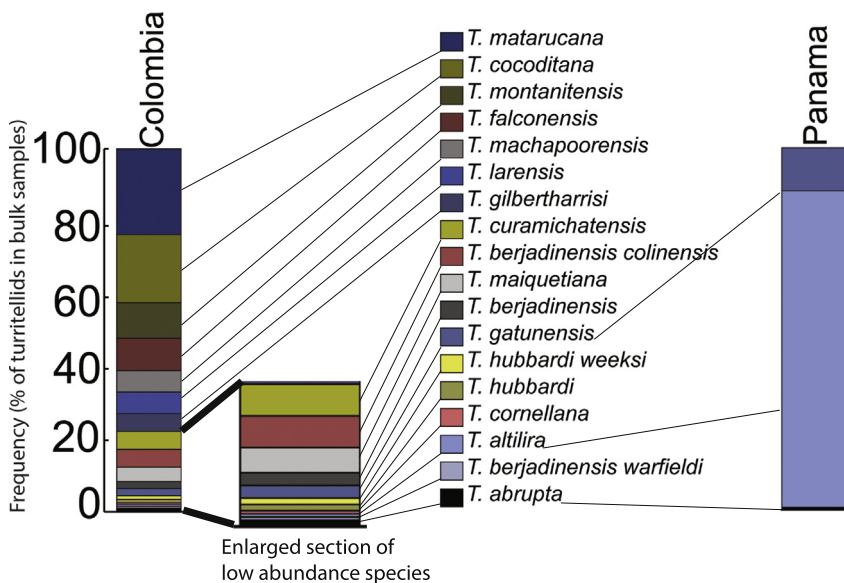


Fig. 11. Relative abundance of *Turritella abrupta* Spieker, 1922 when compared with co-occurring turritellid species in Colombia (Castilletes and Jimol Formations) and Panama (Gatún Formation). Ordering of labels corresponds to the order species are represented in the column for Colombia. Data for Panama from Anderson et al. (2017).

**Table 4**

Length of axial growth in the first year (as determined from isotopic sclerochronology) for a variety of turritellid and other tropical species. Length data for *T. abrupta* presumes settlement during dry season (heavy oxygen isotopic excursion) and incorporates missing distance to apex as inferred from the theoretical apex system (Johnson et al., 2017). NR = not reported. Data for *Turritella gonostoma* also incorporate Allmon et al.'s (1992) hypothesized missing apex height.

Species	Species pleural angle	Length (mm)	Spiral growth (mm)	Source
<i>Turritella abrupta</i>	15°	80	400+	New data
<i>Turritella atilira</i>	13°	55	212	Anderson et al., 2017
<i>Turritella bacillum</i>	14°	80	97*	Kwan et al., 2018/*new data
<i>Turritella duplicata</i>	14°	40	NR	Waite and Allmon, 2016
<i>Turritella gonostoma</i>	11°	105	NR	Allmon et al., 1992
<i>Turritella leucostoma</i>	10°	60	300	Waite and Allmon, 2013
<i>Turritella terebra</i>	11°	98	580	New data

energetic cost. Body size evolution always involves trade-offs in resource acquisition, efficiency, and allocation of metabolic energy to organismal activities, including reproductive effort (Brown et al., 1993; Kingsolver and Pfennig, 2004; Watson et al., 2017). Lower reproductive output as an energetic cost of this high rate of calcification is a reasonable hypothesis, as *T. abrupta* is consistently uncommon in assemblages in which it occurs, relative to other turritellids, and reproductive effort is one of the few activities from which a sessile filter feeder may divert resources. Lower annual fecundity is consistent with all available data, and diversion of resources is a more parsimonious hypothesis than the evolution of unique resource acquisition or metabolic pathways permitting 500–700% the shell deposition of other turritellids under similar (tropical, high-nutrient) conditions (or, indeed, other turritellids which co-occur), all of the same crossed-lamellar microstructure. Production of greater quantities of shell material by marine molluscs also appears to require high nutrient availability (Teusch et al., 2002; Peck et al., 2018), and the geographic distribution of *T. abrupta* indicates it was likely restricted to environments with high nutrient input, due to either upwelling or terrestrial runoff.

The general negative relationship between population density and body mass is a broad characteristic across taxa (Damuth, 1981; Peters and Wassenberg, 1983; Siemann et al., 1996; Blanckenhorn, 2000; Smith et al., 2016). While large size can be associated with increased fecundity in some species (Peters, 1983; Peters and Wassenberg, 1983; Blanckenhorn, 2000; Smith et al., 2016), it is also commonly associated with decreased fecundity and greater overall resource requirements (Peters, 1983; Peters and Wassenberg, 1983; Blanckenhorn, 2000; Smith et al., 2016). It would therefore be incorrect to infer that simply because *Turritella abrupta* is large, it necessarily had high annual reproductive output.

The timing of the observed latitudinal range contraction of *T. abrupta* after 13 Ma, one of the most rapid periods of global temperature change in the Cenozoic (Edie et al., 2018), suggests that global cooling was responsible for this contraction. [due to the associated increased energetic cost of calcification in cooler waters (Graus, 1974, Plummer and Busenberg, 1982, Mucci, 1983, Clarke, 1990, Watson et al., 2012, Watson et al., 2017, Lischka and Riebesell, 2017, Peck et al., 2018)]. The response to cooling observed in *T. abrupta* should not be considered typical of all turritellids. For example, Ivany et al. (2018) found that high temperature may have selected for smaller turritellid individuals at the Paleocene-Eocene boundary. Modern gastropod shell mass generally declines with latitude, [either as a result of increased cost of calcification or reduced metabolic rate, both potential effects of decreased temperature (Watson et al., 2012, 2017)], we therefore hypothesize that the response observed here for *T. abrupta* was due to the exceptional rate of shell deposition in this species.

The observed timing of the range contraction of *Turritella abrupta* also corresponded to the late Miocene East Pacific “carbonate crash” between 13 and 10 Ma, attributed to a decline in carbonate production, possibly due to decreased flow of carbonate-rich deep waters from the Atlantic Ocean through the Central American Seaway as the seaway shallowed (Lyle et al., 1995; Pälke et al., 2012). Decreased eastern

Pacific carbonate supply may have further challenged the ability of *T. abrupta* to deposit aragonite, especially in localities where nutrients were supplied primarily through upwelling waters.

Range expansion or contraction is a more common response to climate change than in situ adaptation in marine organisms (Eastman, 2005; Greenstein and Pandolfi, 2008; Krug et al., 2010; Near et al., 2012; Jablonski et al., 2013; Huang et al., 2014; Saupe et al., 2014; Saupe et al., 2015; Stuart-Smith et al., 2017; Edie et al., 2018). Several molluscan species known from the middle Miocene of southern California have ties to more tropical biogeographic provinces, with their ranges observed to retreat equatorward in the late Miocene (Addicott, 1970a), like the range of *T. abrupta*. The small population sizes of *T. abrupta* may have also limited the amount of variability presented to natural selection (e.g., variation among *T. abrupta* for substantially smaller or lighter shells). There may also be limits on turritellid maximum size at cooler temperatures related to their generally short lifespan (at 5 years, *T. abrupta* already among the longest lived turritellids), as most large cool-water molluscs attain their size through increased longevity rather than rapid growth (Moss et al., 2016, 2017).

*Turritella abrupta* had a long stratigraphic range for a neotropical American turritellid, from at least 17 Ma to as late as 2.4 Ma, exhibiting an early expansion into a broad geographic range followed by restriction to the equatorial Pacific and western Atlantic, and eventually limited to Venezuela during the Pliocene. Although temperature does not appear to have been a principle driver of Pliocene turritellid extinctions in the region (Allmon, 1992, 2001; Jackson and Johnson, 2000; Todd et al., 2002), geographic range contraction (Jablonski, 1987; Weir and Schluter, 2007; Huang et al., 2014; Congreve et al., 2018; Collins et al., 2018) due to cooling (Zachos et al., 2001; Cramer et al., 2011) and decreased eastern Pacific carbonate saturation (Lyle et al., 1995; Pälke et al., 2012) may have contributed to the extinction of *Turritella abrupta*. Low standing population sizes coupled with decreased range occupancy increased the chances that the species could have been driven to even lower total population size and ultimately extinction (Blanckenhorn, 2000; Wiens and Slaton, 2012; Congreve et al., 2018). The proximate cause of *Turritella abrupta*'s extinction was likely similar to other Western Atlantic Pliocene turritellid extinctions, including changes in regions of upwelling or fluvial nutrient input and the expansion of hardground habitats (Allmon, 1992, 2001; Jackson and Johnson, 2000; Todd et al., 2002; Sang et al., 2019; Grossman et al., 2019). Therefore, the extinction of *T. abrupta* from decline in the nutrient supply to the western Atlantic Ocean was contingent on *T. abrupta*'s prior extirpation from Pacific habitats it formerly occupied, which remained nutrient-rich, while nutrient-rich environments in the western Atlantic declined.

The extinction of *Turritella abrupta* could therefore reasonably be attributed as an eventual consequence of global climate change, despite the observed extinction lag (Jackson and Erwin, 2006; O'Dea et al., 2007) between the initial response of range contraction and their eventual extinction. Determining what factors predict eventual extinction following environmental shifts that cause decreased local abundance and/or range contraction will require both accurate assessments

of species' responses to these changes and knowledge of the mediating factors specific to these species. These would include life-history strategies and physiology of the affected organisms (Collins et al., 2018).

Analysis of *Turritella abrupta* also illustrates some potential pitfalls of extrapolating ecological or life-history information from higher taxonomic levels to individual species. The typical turritellid lives 1–2 years, inhabits cooler waters of normal marine salinity, has high and highly variable population densities, and in the presence of predation pressure is expected to evolve either a thick shell or rapid attainment of large axial length, but not both (Allmon, 1988, 1992, 2011; Allmon et al., 1992; Tull and Bohninggaese, 1993). This study highlights the importance of acquiring species-level natural history information from (at minimum) a representative sampling of diversity within a clade rather than generalizing from one or very few archetypal species (Allmon, 2011; Hendricks et al., 2014; Watson et al., 2017). While these extrapolations may capture broad trends accurately (Plotnick and Wagner, 2018), the relatively small number of detailed natural history studies is a cause for concern (Blanckenhorn, 2000; Allmon, 2011; Vermeij, 2017). Additional studies reporting species' natural history information are needed to provide more nuanced assessments of species' responses to past and future environmental change (Greene, 1986; Bartholomew, 1986; Eisner et al., 1995; Futuyma, 1998; Grant, 2000; Dayton, 2003; Greene, 2005; Allmon, 2011; Watson et al., 2017; Agrawal, 2017; Collins et al., 2018; Plotnick and Wagner, 2018).

## 6. Conclusions

The combination of relatively long lifespan (5 years) with probable low annual reproductive output, and low standing densities indicates that *Turritella abrupta* followed a strategy more reliant on individual survival (compared with reproductive output) than most turritellids. Typically, turritellids maintain large population sizes, and individual species may have evolved either rapid attainment of large lengths or thick shells to deter predation. In contrast, *T. abrupta* appears to have attained very large lengths simultaneously with large whorl widths and thick shells. This heavy investment in defense seems to have been adaptive, as *T. abrupta* had much higher survival rates from drilling and peeling attacks than co-occurring turritellids (which typically have no observed incompletely drilled individuals). The heavy shell of *T. abrupta* may have come at the cost of resources which would otherwise be allocated to reproductive effort, since *T. abrupta* is relatively rare in assemblages where it occurs when compared with other turritellids. By spreading reproduction throughout additional years and investing more energy in survival of adults and newly metamorphosed individuals, *T. abrupta* represents a rare exploration of K-selectivity (carrying-capacity driven selectivity) by the clade. *Turritella abrupta* was a successful species, despite its low population sizes, with a long stratigraphic range and broad geographic range soon after its first appearance. The eventual extinction of the species was the result of geologic factors limiting geochemically and nutritionally appropriate habitat. Initially these changes restricted the species to low latitudes, with most shallow-shelf habitat at these latitudes located in the western Atlantic. Subsequent nutrient limitation in the western Atlantic, and an inability to recolonize the eastern Pacific due to the rise of the Central American Isthmus, severely limited the species geographic range and committed the species to extinction.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2020.109623>.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Data availability

The micro-CT image used for apical thickness measurements, apertural whorl thickness measurements, and predation data are available in supplementary online material. Oxygen and carbon isotope determinations and measurements are available on Mendeley Data at DOI: 10.17632/5pyjgm8jzf.1.

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