

Paleoecology and paleoenvironmental implications of turritelline gastropod-dominated assemblages from the Gatun Formation (Upper Miocene) of Panama



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ABSTRACT

Turritelline-dominated assemblages (TDAs) frequently occur in the middle-late Miocene Gatun Formation, and are not uncommon features in the broader fossil record. By gaining a better understanding of the paleoenvironment and taphonomic processes leading to their formation we can gain insight into the conditions in the Western Atlantic (WA) during the Miocene shoaling of the Central American Seaway, as well as the conditions which may lead to TDA formation generally. TDA and non-TDA beds within the Gatun were examined for shell orientation, sclerobiont coverage, drilling predation frequency and site stereotypy, and sediment composition. The most abundant species, *T. altilira*, was also examined using oxygen isotopic sclerochronology to compare growth rate and environmental conditions during the formation of TDA and non-TDA beds. Mean annual range of temperature (MART) was found to be 6.2 °C, with a moderate associated negative O-C correlation. These data confirm the influence of Tropical Eastern Pacific (TEP) upwelling waters in the WA at this time. Upwelling conditions were found to be associated with all *T. altilira*, regardless of their source, indicating that Gatun TDAs are not the result of variation in nutrient supply. Orientation data from within a TDA, grain size, and sclerobiont coverage all suggest that TDAs in the Gatun are the result of variation in sediment supply/winning. We used the Theoretical Apex System and a calculated minimum number of individuals to determine that the frequency of drilling predation and site stereotypy within and without TDAs was statistically indistinguishable. *T. altilira* was found to live up to 3 years, growing between 50 and 60 mm in the first year of life with a subsequent decline in growth rate.

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1. Introduction

The Neogene biological and oceanographic history of the Central American Isthmus region, particularly as represented in the middle-late Miocene Gatun Formation (c. 12–9 Ma), has long been of paleontological interest (e.g. Leigh et al., 2014; Toulou, 1909; Woodring, 1957, 1966), as this formation is richly fossiliferous and provides a record of marine life prior to the closure of the Central American Seaway (CAS). The closure of the CAS produced numerous changes in the physical environment in the Western Atlantic (WA), including changes in temperature, salinity, and productivity, while upwelling and related productivity remained approximately similar in the Tropical Eastern Pacific (TEP) after closure of the CAS (Allmon, 2001; Allmon et al., 1996;

Hayes et al., 1989; Jackson and Budd, 1996; Jackson and O'Dea, 2013; Leigh et al., 2014; Lessios, 2008; Maier-Reimer et al., 1990; O'Dea et al., 2016; Todd et al., 2002). These changes were associated with substantial biological turnover in the WA demonstrating a dramatic change in nutrient regime (Allmon, 2001; Jackson and Johnson, 2000; Leigh et al., 2014; O'Dea et al., 2016; Smith and Jackson, 2009; Todd et al., 2002).

Despite the abundant evidence for these changes, details of their geographic and oceanographic context remain controversial. Recently Montes et al. (2015) have proposed that the Canal Basin adjacent to where the Gatun Formation was deposited may have been one of the only, potential shallow, marine passages between the Americas. Furthermore, Moreno et al. (2012) and Montes et al. (2015) suggested that the rising El Valle volcanic complex would have further limited seawater transport, while most of Panama was a subaerial peninsula of South America. Conversely, Kirby et al. (2008) considered the Gatun Formation to have been deposited while Panama was a mostly subaerial

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peninsula of Central America, with a substantial seaway remaining. The Middle Miocene also coincides with trans-isthmian bathyal foraminifera divergence which began ~13 Ma and with some (but not most) shallow water species divergence time estimates (Jackson and O’Dea, 2013; Lessios, 2008; Marko, 2002; Marko and Moran, 2009; O’Dea et al., 2016). Montes et al. (2015) and Bacon et al. (2013, 2016) suggest that significant terrestrial biotic interchange did not occur then due to unsuitable habitat on the land bridge, rather a marine barrier. Almost all authors agree that the flow of deep and intermediate water was cut off or very limited by 10 Ma (Collins, 1996; Leigh et al., 2014; Osborne et al., 2014; Sepulchre et al., 2014).

Present-day water in the Western Atlantic (WA) is younger, warmer, more saline (~1‰ at depths above 1000 m), and relatively nutrient-poor, while water in the tropical Eastern Pacific (TEP) is older, less saline, and relatively nutrient-rich (Allmon, 2001; Benway and Mix, 2004; Berger, 1970; Keigwin, 1982; Lessios, 2008; Reid, 1961). The modern TEP has strong upwelling in some regions where trade winds push water away from the EP coast (D’Croz and O’Dea, 2007; Lessios, 2008). In contrast, WA upwelling only occurs in small coastal regions off Colombia and Venezuela (Leigh et al., 2014; Lessios, 2008). Productivity is extremely high in the TEP during upwelling events, however TEP productivity is always higher than the WA (Lessios, 2008).

Complete closure of the CAS during the deposition of the Gatun Formation between 12 and 9 Ma remains unlikely (O’Dea et al., 2016). Caribbean salinity remained in equilibrium with Pacific waters until ~4.2 Ma (Haug and Tiedemann, 1998; Haug et al., 2001; Jackson and O’Dea, 2013; Steph et al., 2006); differences in carbonate deposition between the WA and TEP did not occur until 5–3 Ma (Haug and Tiedemann, 1998; Jackson and O’Dea, 2013); increased heat flux from low to high latitudes occurred at 3 Ma (and possibly also 2 Ma) (Cronin and Dowsett, 1996; Keigwin, 1978, 1982); and the majority of terrestrial taxa which participated in the Great American Biotic Interchange (Marshall et al., 1982) did not cross the isthmus until after 3.5 Ma (Jackson and O’Dea, 2013; Webb, 2006). Ecological structure in the Caribbean did not begin to change until ~3.5 Ma, while extinctions did not intensify until ~2 Ma (Collins, 1996, 1999; Jackson and Johnson, 2000; O’Dea et al., 2007; Smith and Jackson, 2009). This still leaves unresolved the impact of Miocene shoaling of the CAS on the paleoenvironment of the WA.

Turritelline gastropods (family Turritellidae, subfamily Turritellinae; sensu Marwick, 1957) are among the most common mollusks in the Gatun Formation and are common components of many benthic marine assemblages of Early Cretaceous to Recent age worldwide (Allmon, 1988, 2011). Most species are largely sedentary semi-infaunal suspension feeders (Allmon, 2011). They are frequently the most abundant macrofossils in assemblages in which they occur, and turritelline-rich assemblages are frequently recognized in the literature (e.g., Allmon, 2007). Such occurrences have been called “turritelline-dominated assemblages” (Allmon and Knight, 1993), herein referred to as “TDAs” and defined as “macrofaunal assemblages in which turritelline gastropods 1) comprise either at least 20% of the total actual or estimated biomass or at least 20% of the macroscopic individuals in the assemblage, and 2) are at least twice as abundant as any other macroscopic species in the assemblage” (the term “turritelline-rich assemblage” may be used for an assemblage that does not fit these quantitative requirements but in which turritellines are still the most abundant species) (Allmon, 2007). In the Gatun Formation *Turritella* is represented by at least six species: *T. abrupta* Spieker (= *T. robusta* Grzybowski (Olsson, 1964)), *T. altilira* Conrad, *T. bifastigata* Nelson, *T. gatunensis* Conrad, *T. matarucana* Hodson, and *T. mimetes* Brown and Pilsbry (Fig. 1).

TDAs in modern oceans occur mainly in cooler high-nutrient environments with normal to slightly below normal marine salinities at depths between 10 and 100 m (Allmon, 2011). Fossil TDAs occur in both cool and warm high-nutrient environments, including carbonate environments (Allmon, 2007). *Turritella* sensu lato is the most abundantly represented gastropod genus among the 156 mollusk genera

sampled by Jackson et al. (1999) in the Gatun Formation, accounting ~8.4% of >121,000 specimens analyzed. This is in striking contrast to the situation in the modern WA, where turritellines are present but rare and only include three species, *T. exoleta* Linnaeus, *T. variegata* Linnaeus, and *T. acropora* Dall. This change in turritelline abundance and diversity occurred in the Late Pliocene (Allmon, 1992, 2001), coincident with and likely caused by a decrease in shallow marine productivity is associated with the closure of the Central American Seaway (Allmon, 1992, 2001). The TEP contains at least 7 modern turritelline species: *T. anactor* Berry, *T. banksi* Reeve, *T. clarionensis* Hertlein & Strong, *T. gonostoma* Valenciennes, *T. leucostoma* Valenciennes, *T. nodulosa* King & Broderip, *T. rubescens* Reeve, several of which may be locally abundant (Keen, 1971; Allmon et al., 1992; Waite and Allmon, 2013).

The Gatun Formation provides an excellent opportunity to examine whether variations in the influence of upwelling waters contribute to the formation of TDAs, as numerous distinct TDAs may be sampled within a well-dated and paleoenvironmentally understood stratigraphic succession. One possible reason for the recurrence of TDAs in the Gatun Formation may be variation in the influence of nutrient-rich TEP upwelling waters to this location (or, alternatively, variation in terrestrial runoff). In order to test this possibility we performed combined $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopic analysis on turritelline shells from within and without TDAs. The Paleocological interactions of these organisms within and without TDAs and indicators of variable sediment supply were also explored as possible alternative explanations for the formation of these dense *Turritella* Dominated shell beds.

2. Geological setting

2.1. Stratigraphy

The study interval includes the lower, middle, and basal upper parts of the Gatun Formation in the Panama Canal Basin of Colon Province, Panama (Figs. 2, 3). Most of the TDAs we studied come from localities in the lower part of the Gatun Formation, although turritellines can be recovered from throughout the formation (Fig. 3). The Gatun Formation is exposed on the northern shores of Gatun Lake, and in roadside exposures, and quarries from Colon to Sabanitas (north-south), and from Maria Chiquita to Gobeia (east-west) (Fig. 2). The formation has an unconformable lower contact with units of different ages in different parts of the Canal Basin, unnamed Cretaceous-Paleocene volcaniclastic sediments in the east, and the Late Oligocene Caimito Formation in the west. The Gatun Formation consists of >600 m of siltstone, sandstone, conglomeratic sandstone, and tuff (Coates, 1999; Hendy, 2013) (Fig. 3). The unit encompasses the latest Middle Miocene (late Servallian) through earliest Upper Miocene (early Tortonian), with the TDAs primarily coming from strata dated between 11.5 and 9.5 Ma (based on calcareous nanofossil and planktonic foraminiferal zones; Coates et al., 2005; Collins and Coates, 1999; Collins et al., 1996; Jackson et al., 1999). Hendy (2013) reported that paleoenvironments of the Gatun Formation varied considerably, with depths ranging from nearshore (<10 m) to the lower mid-shelf (c. 100 m), with most sampled horizons representing soft-bottom habitats of normal salinity. Shallowest depths are generally represented in the lowermost part of the formation, and the deepest in the upper part (Hendy, 2013). The Gatun Formation has been correlated with other tropical Eastern Pacific and Caribbean units that contain abundant turritelline assemblages (Hendy, personal observation), including the Angostura (Ecuador), Urumaco (Venezuela), Tubará (Colombia), and Uscari (Costa Rica) formations (Coates, 1999).

2.2. Occurrence of TDAs in the Gatun Formation

Hendy (2013) presented quantitative paleoecological data from throughout the Gatun Formation, and demonstrated rapid changes in species abundance, which pointed to discrete changes in depositional

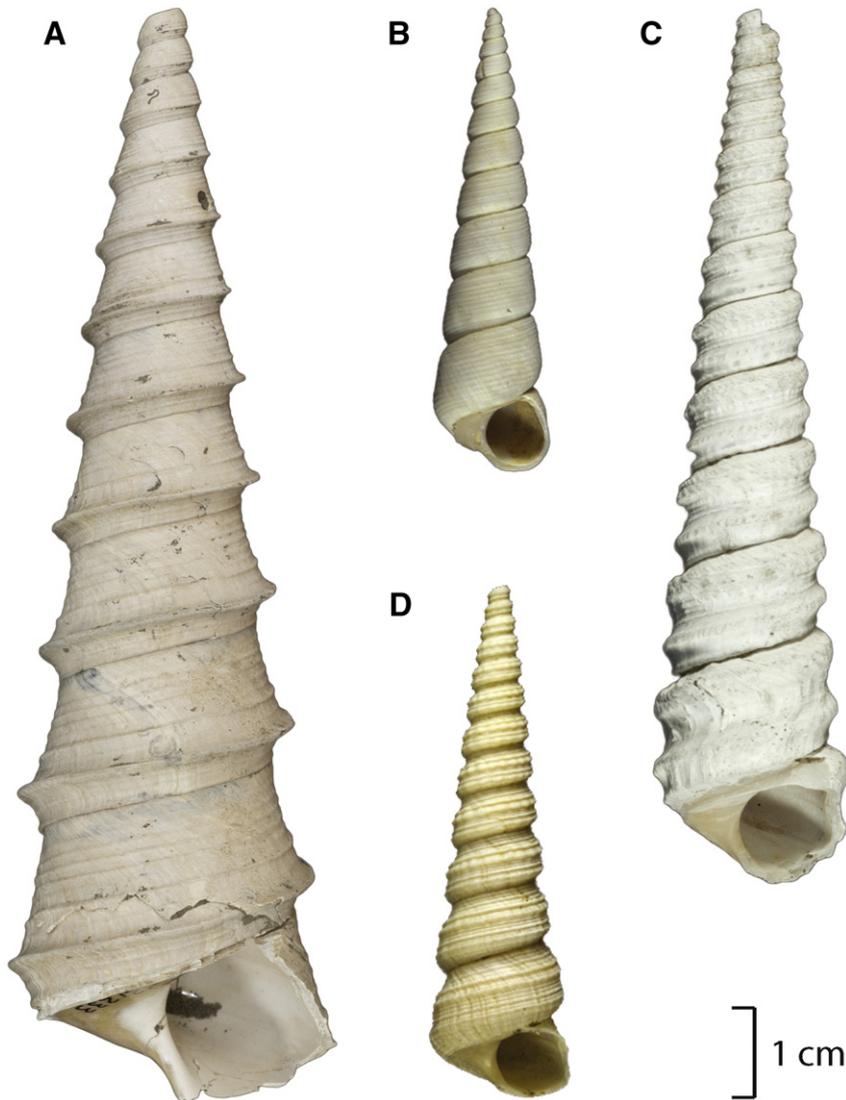


Fig. 1. Commonly sampled turrilline species from the Gatun Formation: A) *T. abrupta*, B) *T. matarucana*, C) *T. gatunensis*, D) *T. altilira*.

paleoenvironments. These data are used here to indicate the frequent occurrence of turrilline-rich assemblages (Figs. 3, 4), including three turrilline species, *T. altilira* (lower and middle members), *T. gatunensis* (middle member), and *T. matarucana* (lower member). Assemblages that fit the strict definition of TDAs (Allmon, 2007) may be observed in the following locations:

2.2.2.1. New Highway cuts at IDAAN plant (STRI Loc. 290,357; LACMIP Loc. 41,710)

The IDAAN outcrop is a fairly new roadcut approximately 3 km SE of San Judas on the newly extended Madden-Colon Highway. This section is stratigraphically the lowest of the seven discussed here, and is likely within 30 m of the base of the Gatun Formation (Hendy, 2013). Woodring's (1957) field localities 136 and 136A and Panama Paleontology Project (PPP) localities 1–11, 12 m, 218–223, 231–233, and 490 are stratigraphically closest. The sediments are primarily grey silt, with frequent concretionary beds and abundant scattered macrofossils. Turrilline-rich horizons, comprising *T. matarucana*, occur midway up this section.

2.2.2.2. San Judas (STRI Loc. 290,307; LACMIP Loc. 41,707)

This is an active quarry located NW of Cativa, and approximately 1 km SW of the Mattress Factory site (faunule 36 of Jackson et al., 1999). At least four *T. altilira* dominated assemblages are observed in

this section, along with occurrences of *T. gatunensis*, *T. abrupta*, and *T. bifastigata*. Three are located near the present floor of the quarry with the fourth located approximately 10 m higher. Woodring's (1957) field localities 139 and 139 h and PPP localities 3596–3599 are stratigraphically closest.

2.2.3. Las Lomas (STRI Loc. 290,308; LACMIP Loc. 41,708)

This locality is located 0.5 km N of the San Judas Quarry, SE of Cativa. The locality mostly consists of a deflation surface but does contain small unaltered outcrops on its borders, which yield abundant *T. altilira* and common *T. gatunensis*. It is stratigraphically below the San Judas Quarry, with the uppermost TDA at Las Lomas potentially corresponding to the lowermost TDA at San Judas. Both the San Judas and Las Lomas sections are placed in the lower member of the Gatun Formation by Hendy (2013). Woodring's (1957) field localities 139 and 139 h and PPP localities 3635–3640 are stratigraphically closest.

2.2.4. Isla Payardi (STRI Loc. 290,306; LACMIP Loc. 41,706)

This locality, known informally as "Turrillid Hill" (Fortunato, 2007), is located just outside the entrance to the formerly Texaco (now Chevron) Refinery at Isla Payardi, NE of Cativa. This locality was first described by Vokes (1969), and is proximal to Woodring's (1957) field localities 136c–d and PPP localities 1077 and 1079. The fauna from the site comprises faunule 35 of Jackson et al. (1999). It has been

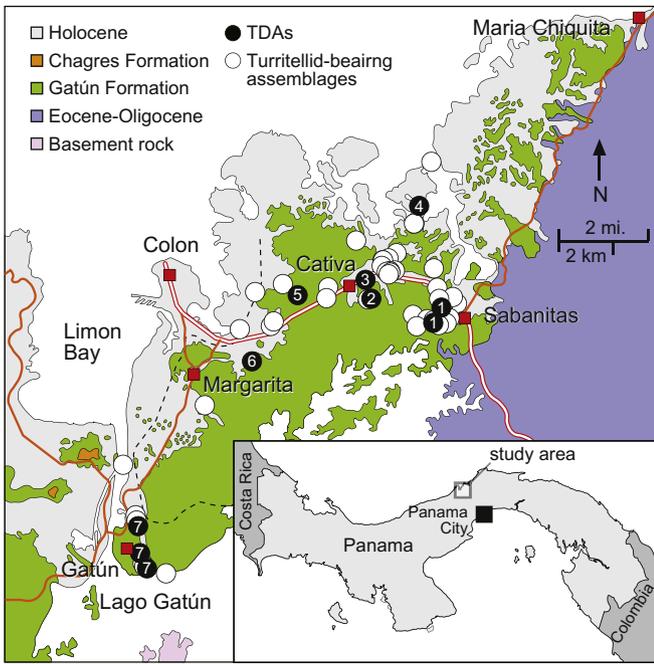


Fig. 2. Extent of the Gatun Formation and distribution of turrillid-bearing assemblages. Numbered circles indicate the location of TDA's mentioned in the text; 1. New Highway cuts at IDAAN plant, 2. San Judas, 3. Las Lomas, 4. Isla Payardi, 5. Cativa Hospital, 6. Margarita, and 7. Gatún Locks.

placed in the middle member of the Gatun Formation (Jackson et al. (1999), although Hendy (2013) regards this outcrop as belonging to the lower member. The outcrop is a hill that rises about 4 m high, consisting of grey silt and brown shelly fine sand. The top of the outcrop is a deflation lag on the exposed upper surface of an approximately 1 m thick bed containing an abundant and diverse molluscan fauna dominated by *T. altilira*.

2.2.5. Cativa Hospital (STRI Loc. 290,493)

This section was exposed for a short time during 2010–2011 during excavations for a new hospital in the town of Cativa. Field surveys were carried out on strata exposed approximately 400 m NW of the Transisthmian Highway. Woodring's (1957) field locality 141 and PPP localities 46, 484, and 485 are stratigraphically closest. These strata are placed at the base of the middle member of the Gatun Formation.

2.2.6. Margarita (STRI Loc. 290,495)

Turritella altilira-dominated assemblages occur in several roadcuts along the Madden-Colon highway near the Colon suburb of Margarita. A section (STRI Loc. 290,495) was sampled 1 km S of the northern terminus of the newly extended Madden-Colon Highway in the middle member of the Gatun Formation. Woodring's (1957) field locality 142 and PPP Loc. 36 are located nearby this section.

2.2.7. Gatún Locks (STRI Loc. 290,372; 290,490; 290,502)

Turrillid-dominated assemblages occur in a number of beds in the Gatún Third Locks section, exposed during excavations associated with widening and modernization of the Panama Canal. Multiple turrillid species are represented in TDA's that occur immediately below the Gatún Visitors Center and adjacent to the Lago Gatún shoreline (STRI Loc. 290,501) (*T. gatunensis*), and in the walls of the locks, 700 m N of the Lago Gatún shoreline (STRI Loc. 290,372) (*T. altilira*). These sections are the stratigraphically highest of those discussed here, and occur near the top of the middle member of the Gatun Formation. These sections are equivalent to Woodring's (1957) field localities 146, 153 and 153a, and PPP localities 37–41.

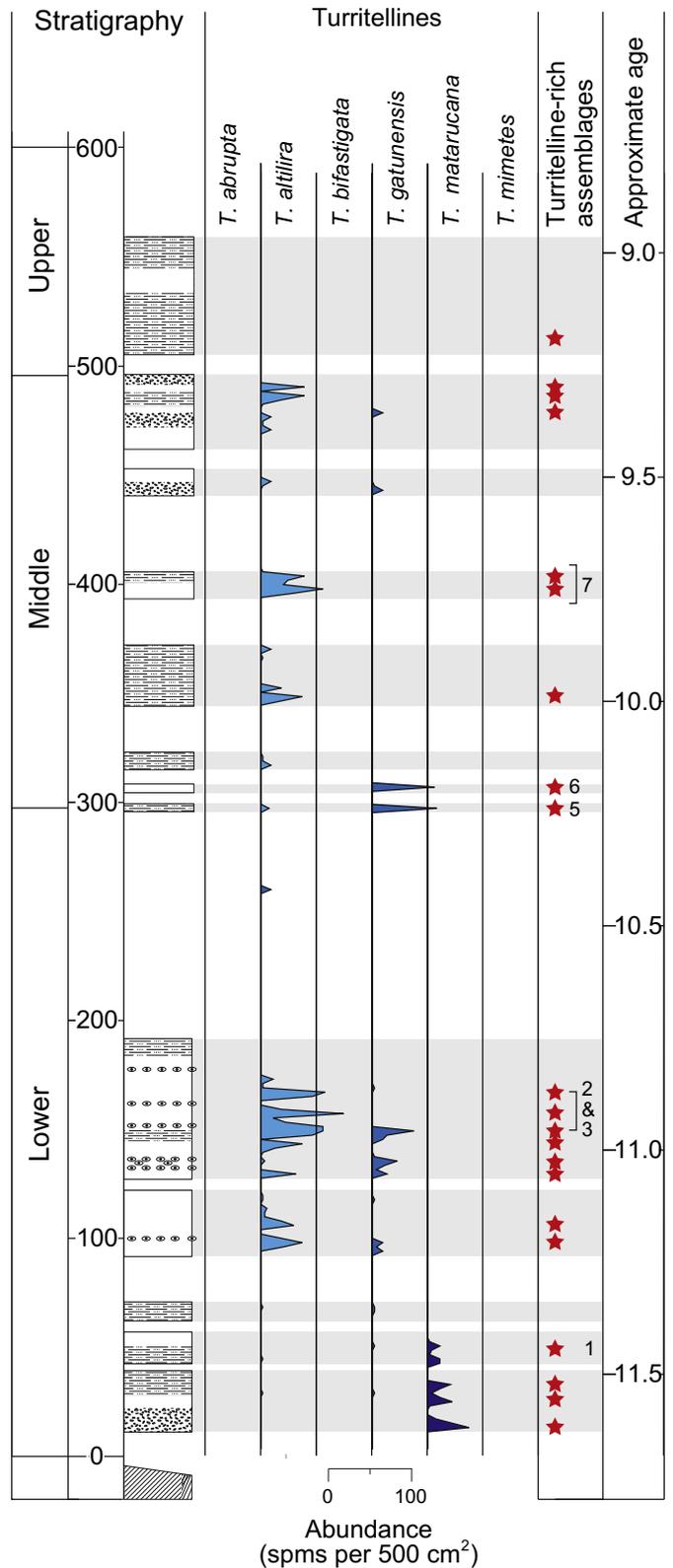


Fig. 3. Stratigraphy of the Gatun Formation (from Hendy, 2013), indicating distribution of turrillid-rich assemblages and location of sampled TDA's. Approximate ages are based on reported calcareous nanofossil and planktonic foraminiferal zones (Coates et al., 2005; Collins et al., 1996; Jackson et al., 1999) in the context of stratigraphic position within the Gatun Formation (Hendy, 2013). Abundance data from Hendy (2013) as specimens per 500 cm² measured in 2 m stratigraphic intervals.

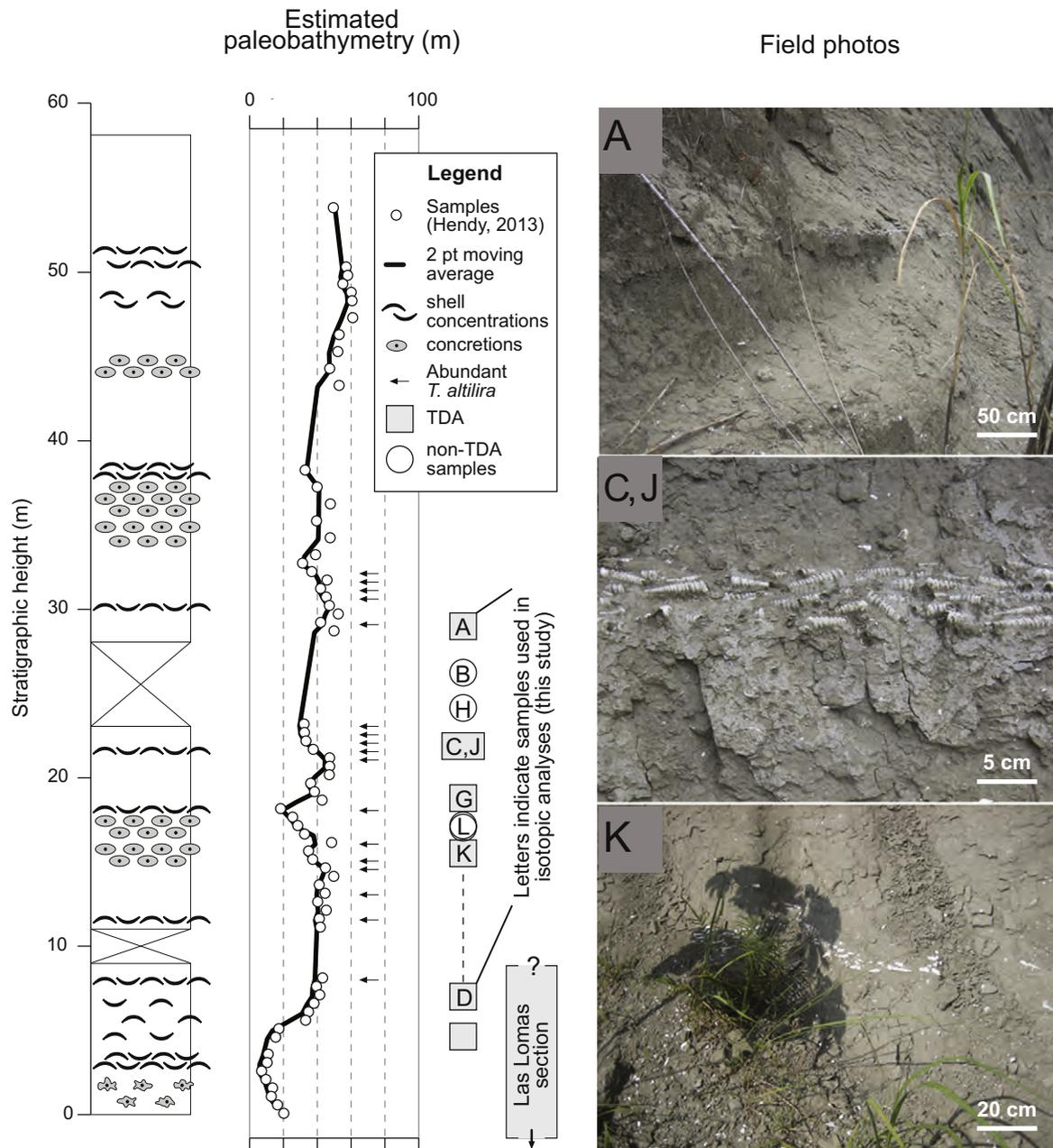


Fig. 4. Stratigraphy and paleobathymetry of the San Judas locality (adapted from Hendy, 2013), and distribution of TDAs examined from the San Judas (2) and correlative Las Lomas (3) localities (see Figs. 2, 3). Paleobathymetry was modeled at 50 cm resolution based on a 2-point moving average of Detrended Correspondence Analysis (of faunal occurrences in samples) axis 1 scores in Hendy (2013). These were shown to have high correlation ($r = 0.79$) to the mean depths of 48 species (none of which were turrillines), which were in turn either determined from bathymetric data (on still extant species) or estimated as the mean depth of all extant members of their genera (for extinct species; see Hendy, 2013 for additional details). Letters designate shells which were sampled for isotopic sclerochronologies. Isotopic samples coming from TDAs are shaded dark grey, while samples taken from background assemblages are unshaded. Field photographs of the stratigraphically lowest, 3rd lowest, and highest TDAs at San Judas, corresponding to the indicated beds.

2.3. Sampling of TDAs in the Gatun Formation

Six TDAs were sampled in the lower Gatun Formation in strata dating between 11 and 10 Ma (Hendy, 2013) (Fig. 4, dark grey). The IDAAN section was the stratigraphically lowest locality sampled. Two stringers were observed at Las Lomas, each only 1 or 2 shells thick, the higher approximately 4 m above the lower. Four in-place TDAs were observed at San Judas (Fig. 4, dark grey layers) and samples were taken both from TDAs and background assemblages. A stringer only 1 or 2 shells thick was present near the current quarry floor. This stringer may correspond to the higher TDA at Las Lomas. ~1.5 m above this TDA was an additional stringer 1 or 2 shells thick. Approximately 20 cm above this stringer was a TDA approximately 8 cm thick, the

largest observed at San Judas. The stratigraphically highest was a stringer approximately 4 cm thick located approximately 8 m above this TDA.

2.4. Physical description of fossil assemblages

2.4.1. Orientation

It was possible to observe one TDA in a bedding plane (San Judas, K) (Fig. 5A). Moving water causes turrilline shells to orient with the apex directed towards the source of the current (Allmon and Dockery, 1992; Nagle, 1967; Toots, 1965). The orientation of the apices of 83 shells were assigned to 10-degree sectors; shells which may not have been in-place were excluded. Shells showed a strong preferred orientation with apices towards the west-southwest ($N = 83$, Fig. 5B), indicating flow was

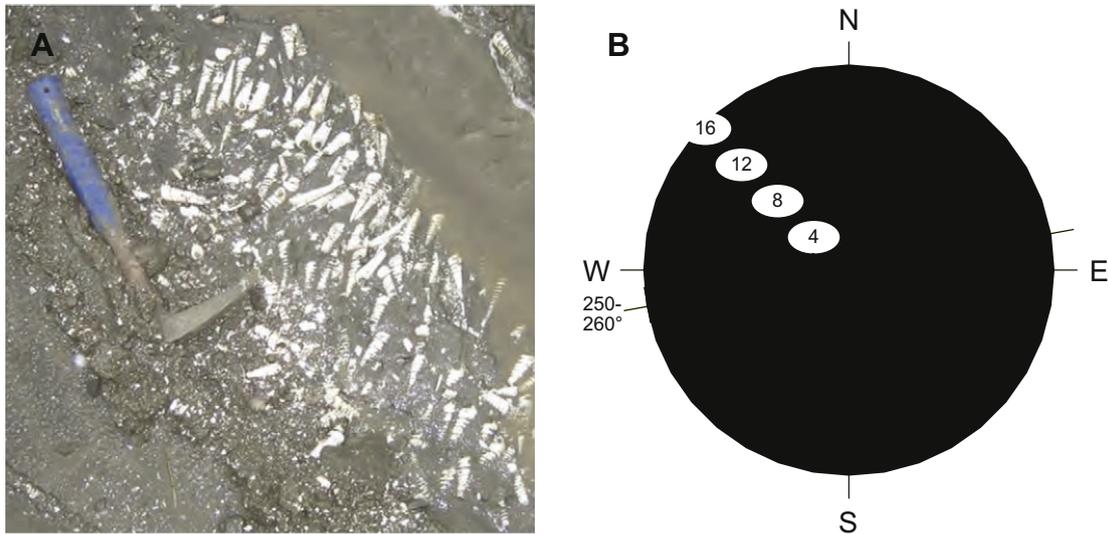


Fig. 5. A. Photograph of a portion of the lowermost TDA at San Judas, exposed on the floor of the quarry. B. Apex orientation data for in-place *T. altilira* in this photo ($N = 83$).

primarily unidirectional towards the east-northeast (Nagle, 1967; Toots, 1965). A minor subcomponent opposing this orientation may be related to the close packing of conical shells.

2.4.2. Sediment size

Sediment samples were taken from within the shells of *T. altilira* collected from the stratigraphically highest TDA and from a non-TDA bed approximately 2 m above the second highest TDA. Approximately 30 grains were chosen at random and measured under a light microscope for each sample ($N = 38$ for the TDA, $N = 28$ for the non-TDA). Sediment size ranged from medium silt to fine sand in both samples (0.04 mm to 0.18 mm and 0.03 to 0.13 mm, respectively). Mean grain size was significantly higher in the TDA bed (0.09 mm (very fine sand), and 0.06 mm (coarse silt), $p < 0.002$).

3. Paleoecology

3.1. Methods

3.1.1. Sample collection

Changes in community composition may indicate paleoecological or paleoenvironmental changes either independent of or associated with changes in the influence of upwelling waters. Paleoecological proxies which were observed in Gatun Formation turrnellines which could be compared between TDA and non-TDA beds included sclerobiont infestation rates, drilling predation rates, and drilling site stereotypy. Bulk samples of fossil-bearing sediment were collected from Isla Payardi and San Judas. Samples were washed and shells and shell fragments larger than 2 mm were retained. In addition, shells larger than 4 cm were collected from TDAs in-place at San Judas and Las Lomas and non-TDA beds at the San Judas and IDAAN localities for use in oxygen isotopic sclerochronologies. These samples were also evaluated separately when comparing encrustation/infestation frequencies and drilling frequencies as they were all large, relatively complete (>90%) shells.

3.1.2. Sclerobionts

Shells exposed at the sediment/water interface or shallowly buried are subject to colonization by a variety of organisms including some which may leave either body or trace fossils (Taylor and Wilson, 2003). In the Gatun Formation these organisms include both borers such as the sponge *Cliona* and worms, and encrustors such as the gastropod *Petalconchus* (collectively "sclerobionts"; Brett et al., 2012; Taylor and Wilson, 2003). Endobiont infestation is not restricted to empty shells (Walker, 1998), and extensive infestation can occur rapidly for

exposed shells (Brett et al., 2011). It seems likely, however, that pristine shells were more rapidly buried than those with sclerobionts (Brett et al., 2011; Geary and Allmon, 1990). Evidence from experimentally deployed shells suggests that burial need not be very deep to inhibit colonization (Brett et al., 2011, 2012; Parsons-Hubbard et al., 1999).

3.1.3. Evaluation of drilling predation

Predatory drill holes represent biotic interactions directly preservable in the fossil record (Alexander and Dietl, 2003; Carriker and Yochelson, 1968; Dudley and Vermeij, 1978; Klompmaker and Kelley, 2015; Li et al., 2011; Vermeij et al., 1980), and the frequency of drilling (DF) is often used as an indication of predation intensity (Allmon et al., 1990; Mallick et al., 2014; Vermeij, 1987). Changes in community composition during TDA intervals may result in differences in observed drilling frequencies or site stereotypy. Turrnelline shells collected from bulk samples are often broken (Fortunato, 2007), but this does not preclude evaluation of drilling predation if multiply drilled shells are rare (Johnson et al., 2017). For the evaluation of drilling predation, turrnelline shell fragments consisting of at least one complete whorl were measured. The range of widths occupied by each specimen could then be used to determine the minimum number of individuals by treating the most common width occupied by all specimens as the *minimum number of individuals* (MNI) (Johnson et al., 2017). By this method a minimum number of 341 *T. altilira* individuals were present; MNIs of 75 from Isla Payardi and 266 from San Judas, based on a total of 1263 fragments from bulk samples. Only 2 shells were observed with multiple drill holes. Therefore, the total number of drilled shells should correspond closely with the number of drilled individuals in the collection (Li et al., 2011).

3.1.4. Oxygen isotopic sclerochronology

Mollusks precipitate shell carbonate in oxygen isotopic equilibrium with seawater, and while carbon isotopes are generally noisier (Andreasson and Schmitz, 1996; Ivany, 2012; Ivany et al., 2003, 2008; Marshall et al., 1996; McConnaughey and Gillikin, 2008), within-individual variations reflect differences in seawater $\delta^{13}\text{C}$ (Ivany, 2012; Tao et al., 2013). Modern and fossil turrnellines have been the subjects of numerous stable isotope analyses (Andreasson and Schmitz, 1996, 2000; Jones and Allmon, 1995, 1999; Latal et al., 2006; Teusch et al., 2002; Waite and Allmon, 2013, 2017; Huyghe et al., 2015). The Gatun Formation was deposited in a tropical setting (ca. 9.1°N paleolatitude), and therefore oxygen isotopic excursions are presumed to be the result of either temperature changes due to seasonal upwelling or freshening, rather than seasonal temperature fluctuations (Ivany, 2012; Tao et al., 2013).

Table 1
Drilling frequencies observed in large (4 cm+ while preserving minimum widths of 2 mm) *T. altilira* sampled from TDAs and non-TDA beds and *T. altilira* recovered from bulk samples. Minimum number of individuals (MNI) calculated according to the methods outlined in Johnson et al. (2017).

Assemblage description	STRI sample #s	# drilled	# of individuals	Drilling frequency (DF)
Bulk samples	17,716; 17,721; 17,832; 17,833; 17,837	61	341 (MNI)	0.18
TDA	38,176; 38,177; 42,266; 42,270	3	19	0.16
Non-TDA	38,174; 38,175; 38,176; 38,177; 38,178	2	11	0.18

Upwelling conditions could be indicated by simultaneous negative $\delta^{13}\text{C}$ and positive $\delta^{18}\text{O}$ excursions (Geary et al., 1992; Jones and Allmon, 1995; Killingley and Berger, 1979; Tao et al., 2013). This is due to cool upwelling waters carrying isotopically light dissolved inorganic carbon as a result of preferential export of ^{12}C to deep water by photosynthesizers (Jones and Allmon, 1995; Kroopnick, 1974, 1980). In contrast freshwater typically has both isotopically light oxygen and carbon (Jones and Allmon, 1995; Krantz et al., 1987; Tao et al., 2013). In the modern TEP there is substantial seasonal variation in temperature due to seasonal upwelling which is not present in the Southwest Caribbean (D'Croz and O'Dea, 2009; D'Croz and Robertson, 1997; Tao et al., 2013).

Tao et al. (2013) evaluated the degree to which $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values correlated (R) and the sign of the correlations (positive indicative of freshening, negative indicative of upwelling), as well as the observed range in observed $\delta^{18}\text{O}$ values for species of modern *Conus* gastropods collected from the TEP and SWC to characterize whether shell carbonate could reliably indicate seawater condition. Although R values often failed to show statistically significant values or visually striking coincident $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ excursions, Tao et al. found good correspondence between observed values and expected ranges. Thus O-C relationships may not be statistically significant, but still faithfully record the relative importance of either upwelling or freshening (Key et al., 2013; Tao et al., 2013). Turritelline isotopic data from the Gatun Formation was therefore compared with values observed in these modern *Conus* from the SWC and TEP in order to evaluate whether they were influenced by upwelling waters.

Five *T. altilira* found in-place within TDAs and four *T. altilira* found in-place in non-TDA beds were serially sampled for combined ^{13}C and ^{18}O isotopic sclerochronologies (Fig. 4). Additionally 20 shells (12 from TDAs, 7 from non-TDAs, and 1 from Isla Payardi-TDA, status indeterminate), were sampled from the apical end to a width of 8 mm for comparison of average water conditions during early growth. The specimens were washed and cleansed ultrasonically for 5 min prior to sampling of the shell with a dental drill. Samples were analyzed at the University of Michigan Stable Isotopes Lab using a Finnigan MAT 251 mass spectrometer coupled to a Finnigan Kiel automated preparation device dedicated to the analysis of carbonates. Analytical error was found to be <0.1% for both carbon and oxygen.

3.2. Results

3.2.1. Sclerobiont coverage

Rates of infestation were generally low in bulk samples from both San Judas and Isla Payardi (Table S1). The most common sclerobionts were *Cliona* (represented by *Entobia* borings), worm borings, and *Petalocochus*. When comparing near-complete shells (shells larger than 4 cm), it was notable that no shells from non-TDAs were infested, while shells target sampled from TDAs had higher rates of infestation than those observed in bulk samples (21%/0% for *Entobia* and 16%/0% for worm borings for TDA and non-TDA, respectively; no other sclerobionts were present in these samples, although others were recovered in bulk samples; Table S1). In comparison, Allmon et al. (1995) found higher encrustation rates within than below a TDA, for a TDA associated with stronger upwelling, but similar encrustation rates between another TDA and the bed below for a TDA attributed to lag.

3.2.2. Drilling predation

Drill holes observed in all samples in this study were primarily beveled, indicating naticid predation was more common (Alexander and Dietl, 2003; Dudley and Vermeij, 1978; Li et al., 2011; Vermeij et al., 1980). Observed DFs for all turritelline species recovered from bulk samples are reported in Table S2. Across all localities, 62 drill holes (1 shell was drilled twice) were observed in *T. altilira*. No incomplete drill holes were observed. For *T. altilira* present in bulk samples collected from throughout the Gatun Formation, a DF of 0.18 was observed (Table 1). Individual sample data available in Tables S3 and S4 for *T. altilira* and *T. gatunensis*, respectively. This is lower than that observed for this species by Allmon et al. (1990) (0.241, Table S), and substantially lower than the average Miocene DF of turritellines (0.279). This difference is not, however, statistically significant ($p > 0.4$) and is similar to other Miocene DFs observed in turritellines (Table S5) (Allmon et al., 1990; Dudley and Vermeij, 1978; Hagadorn and Boyajian, 1997; Hoffman et al., 1974; Kojumdjieva, 1974). A minimum of 81 *T. gatunensis* were present in samples collected from San Judas with a DF of 0.136, substantially lower than DF observed by Dudley and Vermeij (1978), who found DFs of 0.617 ($n = 60$) and 0.80 ($n = 10$) for *T. gatunensis*, smaller and larger than 40 mm, respectively (Table S2).

T. matarucana was rare in our bulk samples from San Judas. Two individuals were present in one sample (STRI # 17837), the only bulk sample with multiple individuals of *T. matarucana*. The drilling

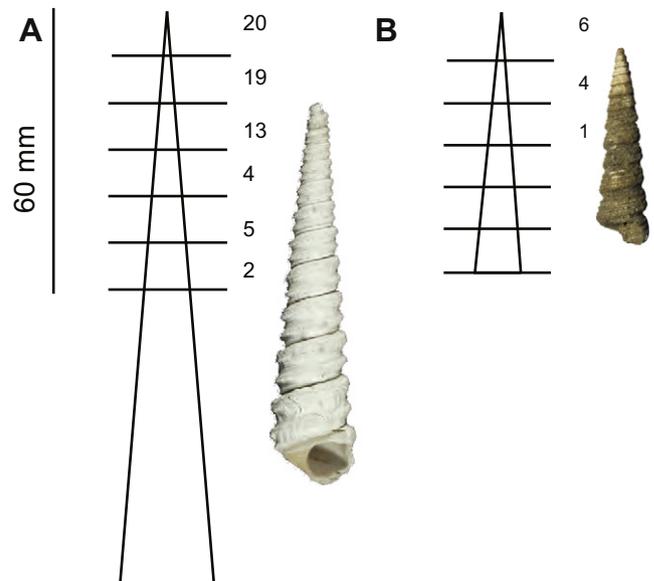


Fig. 6. Distribution of drill hole position using the Theoretical Apex System. A. Idealized isosceles triangle representing a fully grown specimen of *T. altilira*. Numbers indicate the number of drill holes located in each 10 mm bin across all specimens of *T. altilira*. A total of 63 drill holes were observed on 61 specimens out of 1263 shell fragments representing a minimum of 341 individuals. B. Idealized isosceles triangle representing *T. gatunensis*. Numbers indicate the number of drill holes located in each 10 mm bin across all specimens of *T. gatunensis*. 11 boreholes were observed on 11 specimens from 167 shell fragments representing a minimum of 81 individuals. See Johnson et al. (2017) for additional details.

frequency of 0.50 for this sample is most likely an overestimate and should be treated with caution. *T. abrupta* occurs infrequently at the Las Lomas locality as float, but was not recorded in bulk samples from this location. Several specimens (N = 15) were collected from float at this location with no regard for drilling status. The observed DF was 0.12, with one specimen bearing an incomplete drill hole, the only incomplete drill hole observed in this study.

Large *T. altilira* were collected from TDAs and non-TDA beds for isotopic analyses, however no special care was taken to exclude drilled specimens from either sample. These samples also yielded DFs of 0.16 for TDAs (n = 19) and 0.18 (n = 11) for non-TDAs, similar to those found in our bulk samples (Table 1) and comparable to frequencies calculated for non-bulk samples in museum collections (Table S2). This difference in drilling frequency was not statistically significant ($p = 0.87$, t -

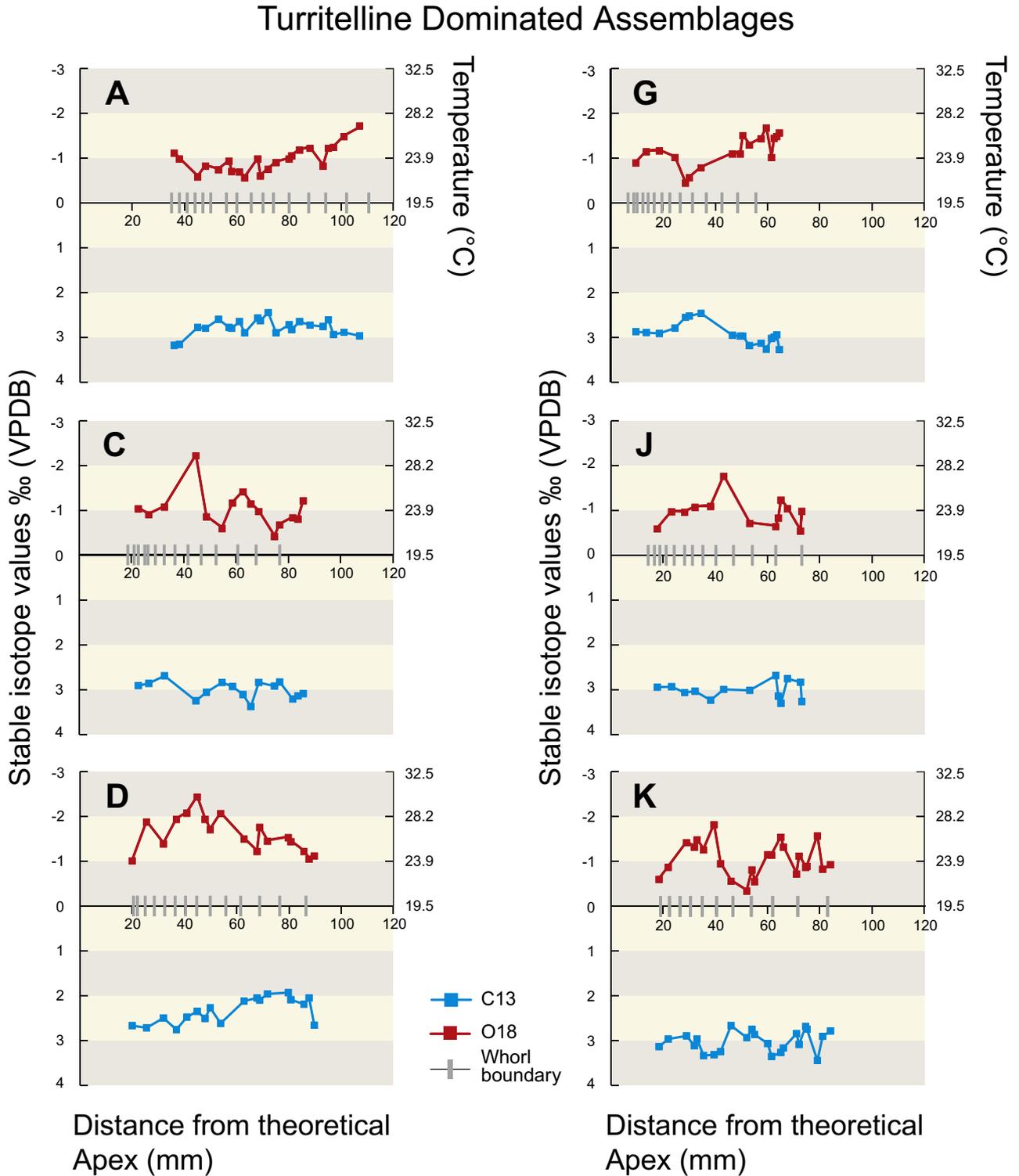


Fig. 7. Stable oxygen and carbon isotope profiles for *Turritella altilira* compared to VPDB standard for fossils collected from within TDAs and without TDAs (^{18}O values negative, ^{13}C values positive for all specimens). Stratigraphic location of San Judas and Las Lomas samples is indicated in Fig. 4. Sample E was taken from the IDAAN locality. Temperature data calculated using the equation of Grossman and Ku (1986), assuming a seawater ^{18}O value of 0.25 (Lear et al., 2000). Distances from the apex calculated using the Theoretical Apex System (Johnson et al., 2017).

Non-Turritelline Dominated Assemblages

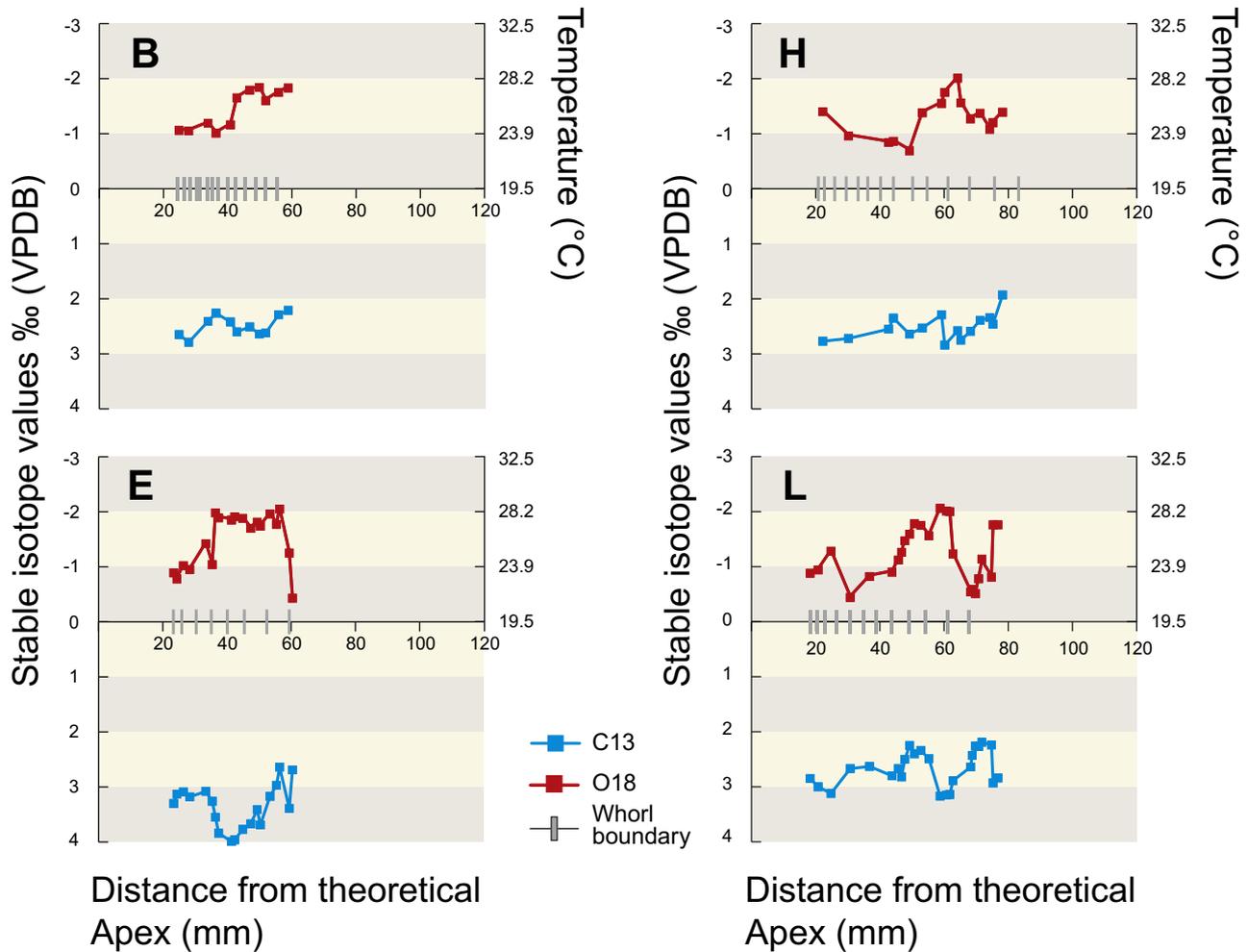


Fig. 7 (continued).

test). Allmon et al. (1995) did find lower DFs in Plio-Pleistocene TDAs compared to the beds below them (DF = 0.28 vs. 0.21 and 0.32 vs. 0.20).

In order to normalize the location of drill holes, we employed the Theoretical Apex System (TAS) described in Johnson et al. (2017) (Fig. 6). The TAS allows for an evaluation of DFs in high-spired shells without restricting the dataset to “intact” shells. As bulk samples collected from the Gatun Formation produce hundreds of *Turritella* shell fragments for every intact shell, this is a potentially vital step in evaluating the ecological interactions of this taxon. The TAS approximates the shape of the shell as a 2 dimensional isosceles triangle and a shell fragment as an isosceles trapezoid and uses the dimensions of the fragment to determine the minimum size of the individual (see Johnson et al., 2017).

The TAS can be used to determine the distance of a drill hole from the apex of the theoretical unbroken shell. The distribution of observed drill holes is indicated in Fig. 6. For *T. altilira*, the majority (62%) located within 20 mm of the theoretical apex (Fig. 6a). The average distance from the theoretical apices for *T. altilira* was 17.85 mm, with a median of 14.48 mm. 75% of all drill holes were located between 1.8 mm and 25 mm from the theoretical apex. For *T. gatunensis*, all drill holes were observed within 30 mm of the theoretical apex, with more than half observed within the first 10 mm (Fig. 6b). All drill holes observed in *T. altilira* taken from TDAs and non-TDAs (3 and 2 drilled individuals, respectively) were located within 30 mm of their theoretical apices, consistent with the data derived from this species in bulk samples.

3.2.3. Isotopic sclerochronology

Isotopic sclerochronologies are presented in Fig. 7. The TAS (Johnson et al., 2017) was used to standardize all sample distances from theoretical apices facilitating comparison among broken specimens. All *T. altilira* appear to have lived for <3 years, consistent with most other isotopic analyses of turritellines (Allmon, 2011). All individuals also appear to have grown to lengths between 50 and 60 mm in the first year, with no notable differences between samples from TDAs and non-TDAs. Whorl addition rate was also similar among all specimens, with ~10 whorls added between 20 and 55 mm. Whorl width at a given ontogenetic stage, which may indicate differences in productivity (Teusch et al., 2002), also showed no statistical difference between TDAs and non-TDAs, $p = 0.77$ (t -test), although statistical power is very low (0.05).

No significant differences were observed between TDA and non-TDA with respect to $\delta^{18}\text{O}$ minima (t -test, $p = 0.73$, maxima ($p = 0.74$), range ($p = 0.87$), $\delta^{13}\text{C}$ minima ($p = 0.34$) or maxima ($p = 0.93$) (Table 2). R values for the correlation between ^{18}O and ^{13}C (Tao et al., 2013) also did not show any statistically significant differences between TDA and non-TDA samples. Specimens C, G, and K (from TDAs) and E and L (from non-TDAs) all showed statistically significant (at $p < 0.05$) negative correlations (R) between ^{18}O and ^{13}C . The fraction of samples showing significant correlations (5/11) was higher than that observed in modern *Conus* spp. (3/13) (Tao et al., 2013). Specimen B may not preserve a full year's growth, which may have resulted in an unusually low R value;

Table 2
Comparison of mean stable isotope values for *T. altilira* shells obtained from TDA and non-TDA beds.

	TDA mean N = 7	Non-TDA mean N = 4	p-Value (t-test)
$\delta^{18}\text{O}$ max	-0.64	-0.55	0.74
$\delta^{18}\text{O}$ min	-1.99	-1.93	0.73
$\delta^{18}\text{O}$ range (seasonality)	1.38	1.35	0.87
$\delta^{13}\text{C}$ max	3.22	3.20	0.93
$\delta^{13}\text{C}$ min	2.45	2.24	0.34
R value (O vs C)	-0.48	-0.20	0.12 (0.32, excluding B)

excluding this sample also does not result in a statistically significant difference. All shells showed negative $\delta^{18}\text{O}$ - ^{13}C correlations. Analysis of shell averages from the first year of growth also does not appear to indicate any difference between shells obtained from TDAs and non-TDA beds (Fig. 8). The $\delta^{18}\text{O}$ ranges observed were similar to those observed in Lower (1.1) and Middle (1.3) Gatun Formation bivalves (n = 1 for each) (Teranes et al., 1996).

4. Discussion

4.1. Orientation

The strong orientation observed in the lowermost San Judas bed (Fig. 5) implies that winnowing likely contributed to the formation of TDAs in the Gatun Formation. At the inferred paleodepth (estimated to be 20–60 m; Fig. 4; Hendy, 2013), this orientation is likely the result of strong storm-induced currents (Peters and Loss, 2012), which typically have strong unidirectional components (Morton, 1988). Alternatively, this orientation may be consistent with distributory flow from an open seaway, although broader sedimentary evidence does not support this site as the location of the seaway itself. von der Heydt and Dijkstra (2005) modeled early Miocene ocean circulation to include a shallow wind-driven westward through the CAS, but with an eastward subsurface flow conferring a net eastward transport through the

Seaway. While shoaling began in the middle Miocene, net transport likely continued to be eastward. Nevertheless, evidence for strong current influence in the Gatun Formation is infrequent—and likely associated with short-term depositional events. Thick cross-stratified coquina beds from the overlying Chagres Formation (Hendy, 2013) are more likely indicators for any such cross-isthmian circulation.

4.2. Predation

T. altilira samples taken from within and without TDAs are statistically indistinguishable from each other and from bulk samples with respect to drilling frequencies. Naticids appear to be the dominant drillers in all samples, and site stereotypy remains markedly ad-apical in bulk samples as well as in relatively complete shells taken from within and without TDAs. These data do not indicate any significant differences in the frequency of these interactions at the time of deposition of TDA as opposed to non-TDA beds.

4.3. Paleoenvironmental implications of isotopic analyses

If the ^{18}O fraction of seawater is known, temperatures can be calculated from shell carbonate using the equation of Grossman and Ku (1986). Seawater isotopic composition can be estimated using estimates of glacial ice volume and paleolatitude (Ivany et al., 2003; Lear et al., 2000; Zachos et al., 1994). Modern (non-upwelling) SWC environments at ~20 m water depth show temperatures ranging between 24 and 29 °C and 22 and 26 °C at ~50 m water depth (World Ocean Atlas 2001, Conkright et al., 2002, Tao et al., 2013). In modern upwelling TEP waters (Gulf of Panama) temperatures range between 20 and 28 °C at 20 m water depth and 16 to 22 °C at 50 m water depth (Tao et al., 2013). Using a seawater ^{18}O fraction of -0.25 for ~10 Ma (Lear et al., 2000), we can calculate that seasonal temperatures ranged from 21.9 °C to 27.9 °C in TDAs and from 22.3 °C to 28.2 °C for non-TDA samples. These are larger temperature ranges than observed in the modern SWC, which may indicate input from TEP upwelling across the CAS.

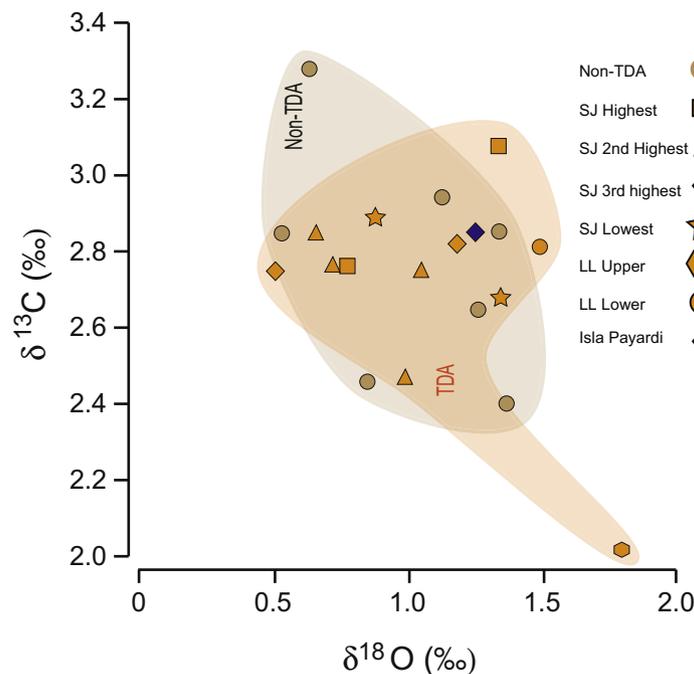


Fig. 8. Average $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values (VPDB) by locality. Shells were sampled from the apical end until a width of 8 mm. No trend was observed distinguishing non-TDA shells (brown circles) from TDA shells (Isla Payardi TDA status indeterminate; all others from TDAs designated with orange icons). Variability within individual TDAs exceeded between TDA variability, with the possible exception of the uppermost Las Lomas sample. SJ: San Judas, LL: Las Lomas. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

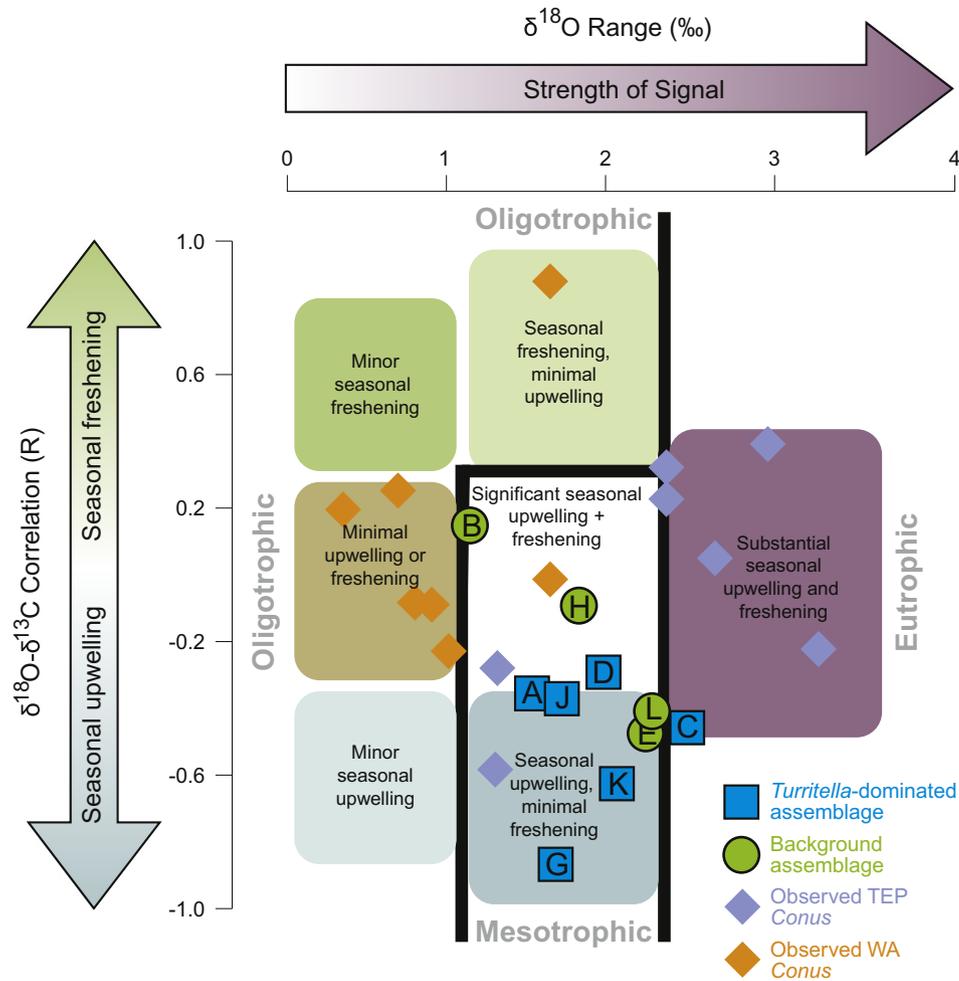


Fig. 9. Relationship of $\delta^{18}\text{O}$ ranges and $\delta^{18}\text{O}$ - $\delta^{13}\text{C}$ correlation (R) observed in samples from TDAs (squares) and background assemblages (circles) in the Gatun Formation. Diamonds indicate values obtained from modern *Conus* spp. from the WA (orange) and TEP (purple) (modified from Tao et al., 2013). Note that turritelline specimen B likely has a lower R value because it did not survive a full year. Specimen H is the only sample in the present study which fell within the ranges observed for modern SWC; all other samples fell within ranges observed for TEP *Conus* or exhibited stronger $\delta^{18}\text{O}$ - $\delta^{13}\text{C}$ correlations (although some modern *Conus* had broader ranges in $\delta^{18}\text{O}$). Divisions between regions indicating likely oligotrophic, mesotrophic, and eutrophic conditions (sensu Tao et al., 2013) are demarcated by bold lines. All turritellines which survived at least 1 year fell within the likely mesotrophic range (sensu Tao et al., 2013).

We do infer significant upwelling influence in the Gatun Formation (11–10.5 Ma, Fig. 9). Samples from TDAs all fall within the $\delta^{18}\text{O}$ - $\delta^{13}\text{C}$ correlation (R) and $\delta^{18}\text{O}$ ranges observed for modern *Conus* from the TEP, or had R values even more strongly negative than those observed in *Conus* (Tao et al., 2013). Samples from non-TDAs largely overlapped with those from TDAs, with the exception of specimen B, likely due to this specimen not having preserved a full year's growth. Even including specimen B, no significant differences were observed in $\delta^{18}\text{O}$ - $\delta^{13}\text{C}$ correlation (R) between TDAs (-0.48) and non-TDAs (-0.2) $p = 0.12$ (0.32 , excluding B). $\delta^{18}\text{O}$ ranges were also highly similar between TDA and non-TDA samples (Fig. 9). Bivalve shells from the Gatun Formation have also shown evidence of seasonal upwelling influence, although sampling was limited to 2 shells, one in the lower Gatun Formation and one in the middle Gatun Formation, and only oxygen isotopic ranges were reported (Teranes et al., 1996).

Average shell oxygen and carbon isotopic values during early ontogeny were also obtained for 12 *T. altilira* from TDAs, 7 from non-TDAs and one from Isla Payardi and no trend was observed distinguishing TDA from non-TDA shells (Fig. 8). Mean $\delta^{13}\text{C}$ was 2.73 for TDA and 2.78 for non-TDA, a difference which was not statistically significant (t -test, $p = 0.72$). Mean $\delta^{18}\text{O}$ was -1.07 for TDA and -1.01 for non-TDA, which was also not statistically significant (t -test, $p = 0.72$).

Mean annual range in temperature (MART) was found to be 5.99 °C for TDA, and 5.85 °C for non-TDA shells. Excluding sample B, non-TDA

MART was 6.6 °C and the MART observed across all samples was 6.2 °C. These values are consistent with those found by Okamura et al. (2013), who reported a MART of 6.1 °C, and Jackson and O'Dea (2013), who found MARTs around 6 °C throughout the Miocene based on a bryozoan zooid size proxy. These values are also similar to the MART of 6 °C found at 50 m water depth in modern upwelling TEP waters, while SWC waters have a MART of 4 °C (World Ocean Atlas 2001, Conkright et al., 2002; Tao et al., 2013). Conditions were likely non-analogous to either modern SWC or TEP (O'Dea et al., 2012), reflecting the flow of TEP water (influenced by local upwelling) travelling East across shallow straights into the SWC, rather than local SWC upwelling.

5. Conclusions

5.1. Interpretation of TDAs in the Gatun Formation

Modern turritellines have been found to live at high densities, with several species observed at densities higher than 1000 individuals per m^2 (Allmon, 1988, 2011; Gaymer and Himmelman, 2008), and 15 cm thick *Turritella* beds can represent <100 years of time averaging (Baltzer et al., 2015). Therefore it is possible that TDAs represent actual communities of turritellines from highly productive environments (Allmon, 1988, 1992, 2001, 2011; Gaymer and Himmelman, 2008). Environments where turritellines reach very high abundances are linked

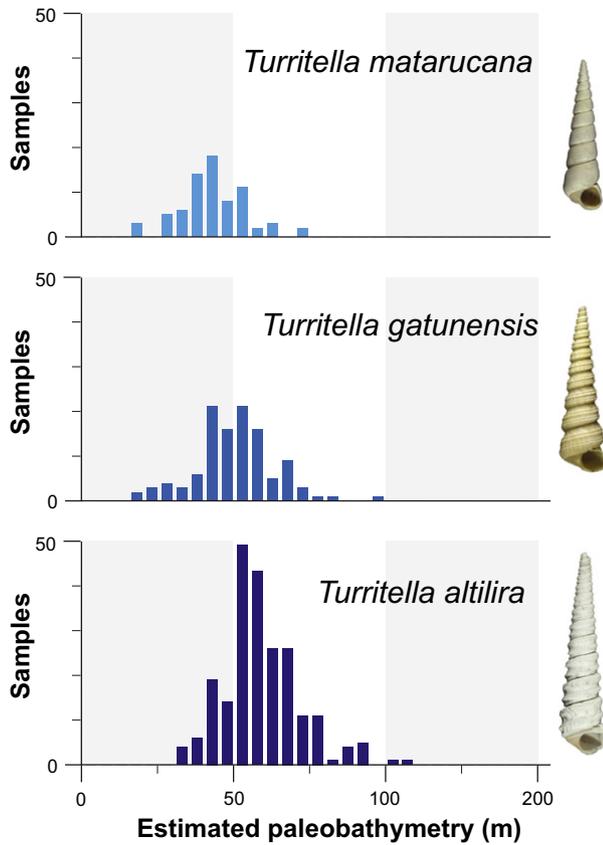


Fig. 10. Occurrence frequency of three species of *Turritella* along a paleobathymetric gradient modeled for Gatun Formation assemblages (Hendy, 2013). Note differences in peak occurrence and relative breadth of paleobathymetric range.

to high-nutrient conditions, related either to upwelling or terrestrial runoff (Allmon, 1988, 2011; Jones and Allmon, 1995). Based on the analysis presented in this paper, TDAs of *T. altilira* in the Gatun Formation seem, in general, indicative of the influence of TEP upwelling, but specific TDAs in the Gatun Formation do not appear to indicate environmental conditions significantly different from beds that contain conspecifics at lower densities. There are no significant differences in drilling predation rates or drilling site stereotypy between TDAs and non-TDAs, suggesting similar community composition.

Table 3

Summary of factors which may contribute to the formation of TDAs in contrast to beds where turrillines are present, but at lower density (“non-TDA” herein).

Factor	Description	Support: Gatun Fm.	Support: general
Variation in nutrient supply	Differing living densities may have been supported by variations in productivity.	Not supported for the Gatun Fm. (All influenced by TEP upwelling).	Not systematically tested elsewhere.
Variation in other environmental conditions	Preference for particular depths, salinities, or temperatures may variously exclude turrillines or other taxa (potentially including their predators).	Not supported for the distribution of TDAs in the Gatun Fm.	Plausible for other TDAs (Allmon and Dockery, 1992; Baltzer et al., 2015).
Allee effect	The Allee effect, also known as inverse density dependence, suggests benefits from the presence of conspecifics (Kennedy, 1995; Stephens et al., 1999; Allmon, 2011).	Plausible, but cannot be tested experimentally in an extinct taxon. It is unknown if this affects extant <i>Turritella</i> species.	Plausible, but cannot be tested experimentally in an extinct taxon. It is unknown if this affects extant <i>Turritella</i> species.
Sedimentation rate	Low sedimentation rates can condense shell beds (and conversely high sedimentation rates can dilute shell beds) if the input of shells is constant in time.	Low rates of colonization or sclerobiont damage suggest that shells in non-TDAs were coated in sediment more rapidly than those which formed TDAs. However, even limited sediment cover may limit subsequent colonization.	Likely important but not sufficient to generate other TDA accumulations (unrealistic sedimentation rates/hiatuses) (e.g., Allmon et al., 1995)
Winnowing	Removal of fine sediments by currents, leaving coarse particles such as shells.	Supported for the Gatun Fm., by both orientation and grain-size data.	Turrilline shells are often recognized as indicators of paleocurrents, but reports of preferred orientations in TDAs are mixed (e.g. Allmon and Dockery, 1992; Allmon et al., 1995)

While similar biologically, taphonomy does suggest differences between TDA and non-TDA beds. No sclerobionts were found on shells collected from non-TDAs, and TDA shells presented more damage from clionids and worm borings. This suggests that sedimentation rates may have been higher when non-TDAs were formed (sedimentation rates may have been highly variable at this time; Cantalamessa et al., 2007; Hendy, 2013; Kirby et al., 2008; Montes et al., 2015; Strong et al., 2009), possibly diluting the density of *T. altilira* relative to TDAs, but higher sedimentation rates or slower current speeds may also have been unfavorable for filter-feeding turrillines. As even limited burial appears to give substantial protection from sclerobiont infestation (Brett et al., 2011, 2012), this is not itself sufficient to establish whether variation in sedimentation rate alone could be responsible for TDAs. Further, TDAs showed evidence of reworking, suggesting that winnowing was important for the formation of these deposits.

These TDAs therefore indicate the consistent importance of TEP upwelling waters in the Southwest Caribbean during the Middle Miocene, associated with high variability in sediment deposition rates rather than intermittent restriction or cessation of communication between the TEP and WA. This is consistent with a traditional interpretation that while the CAS may have substantially shoaled during the Middle Miocene, depth remained sufficient for TEP upwelling waters to be transported to the Atlantic side of the Panama Arc providing substantial seasonal nutrient input.

5.2. General model of the formation of TDAs

Two factors are prerequisites for the formation of TDAs; a nutrient-rich environment and otherwise appropriate environmental conditions for the species in question. Any particular TDA might be the result of a combination of high live abundance and physical concentration. Jones and Allmon (1995), for example, found broadly similar isotopic values and patterns between TDAs and non-TDA horizons in the Pliocene of Florida and attributed one TDA to strong upwelling and another to upwelling, but also increased time-averaging. Similarly, Allmon and Dockery (1992) reported a TDA which did not appear related to higher-than-background nutrient conditions.

All *T. altilira* shells examined herein (which lived at least one year) show similar upwelling isotopic signals, consistent with previous research linking TDAs with such environments (or to substantial terrestrial runoff) (Allmon, 1988, 2011; Allmon et al., 1995; Allmon and Knight, 1993; Fallon et al., 2014; Jones and Allmon, 1995). TDAs of *T. matarucana* appear to be associated with shallower water conditions,

while those of *T. altilira* and *T. gatunensis* are more likely to occur in sediments generated further offshore (Hendy, 2013; Fig. 10).

These conditions are not themselves sufficient for TDA formation. Additional factors (Table 3) including variation in environmental conditions (including nutrient input), and Allee effects could contribute to variation in the size of live turrilline communities. Variations in nutrient supply are not supported for the Gatun Formation, as both TDAs and non-TDAs showed similar levels of influence from upwelling waters. Variations in other environmental conditions such as temperature or salinity may be important in other TDAs, but are not supported for the Gatun Formation. Interactions between drilling predators and turrilline prey also appear to be maintained within and without Gatun Formation TDAs. The Allee effect, suggests that individuals may benefit from the presence of conspecifics, and it has been suggested that this could be an important factor contributing to the generation of TDAs (Allmon, 2011; Kennedy, 1995; Stephens et al., 1999). This remains a possibility but has not been examined in living populations of *Turritella*.

Further, variations in sediment supply or removal could contribute to the dilution or condensation of shells in the sedimentary record. Low rates of colonization or sclerobiont damage suggest that shells in non-TDAs were more rapidly buried than those which formed TDA. A larger mean grain size within TDAs compared with non-TDA beds and some evidence for strong currents are consistent with winnowing as a factor contributing to the formation of these deposits. Allmon et al. (1995) also noted that badly abraded shells and pristine shells had been found together, indicative of some level of concentration for TDAs observed in the Pliocene Pinecrest Sand of Florida, however the level of concentration necessary to form one bed was a factor of 61.5, suggesting real changes in the abundance of live organisms.

As filter feeders turrillines may also respond to different levels of sediment input. It is possible that *T. altilira* preferred environments with lower sedimentation rates or stronger currents and therefore were present at lower abundances in environments where they were also likely to be diluted by sediment. TDAs are much more common in coarse sands and limestones than very fine siliciclastic sands, silts or muds (Fig. S1; 75% of occurrences in sand or limestone rather than clay or silty substrates, although if limestone and sands are considered separately there is no statistical difference among all three; Tukey *p*-values > 0.65; sedimentologic data from Allmon, 2007). This is consistent with their need to exclude fine siliciclastic particles from their mantle while filter feeding from a semi-infaunal life position (Allmon, 1988, 2011). In at least one other case where TDAs were present associated with silt, shells also appeared to be strongly oriented (Allmon and Dockery, 1992).

TDAs, therefore, represent paleoenvironments with high nutrient input (typically sourced from upwelling as most turrillines require fully marine salinities), likely without fine siliciclastic bottom sediments. Distinct TDA shell beds, such as those observable throughout the Gatun Formation, typically represent the combined effects of concentration, either through low sediment input or winnowing by storms or currents, and very high-density live communities (e.g. Allmon et al., 1995), due to the gregarious nature of turrillines (Allmon, 2011; Kennedy, 1995).

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2017.01.026>.

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