Taphonomy and paleoenvironment of two turritellid-gastropod-rich beds, Pliocene of Florida

WARREN D. ALLMON, MATTHEW P. SPIZUCO AND DOUGLAS S. JONES

LETHAIA


Two beds containing large numbers of turritellid gastropods (Family Turritellidae) occurring in the densely fossiliferous Upper Pliocene Pinecrest Sand of Florida formed as a result of upwelling and consequent high biological productivity, together with some degree of physically mediated time averaging. Analyses of size-frequency distribution and shell surface condition, combined with isotopic data on chronological age of individual shells, water temperature and upwelling intensity, suggest that both beds formed relatively quickly, probably in less than 100–200 years. The upper bed, occurring within Petuch’s (1982) unit 2 (3.5–2.0 Ma) and containing abundant Turritella apicalis Heiprinn, appears to have formed largely as a result of upwelling; the lower bed, occurring in upper unit 6/7 (3.5–2.5 Ma) and containing abundant Turritella glauconis Mannfield, appears to have formed over a longer period, as a result of upwelling, increased time-averaging, and perhaps cooler overall water temperatures. This study highlights the potential to isolate and examine separately some of the biological and physical factors affecting shell bed formation, and especially to address the role of biological productivity in this process. Pinecrest Beds, Pliocene, upwelling, turritellid gastropods, taphonomy.

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Fossil assemblages containing very large numbers of turritellid gastropods (Family Turritellidae) are common features of the Cretaceous and Cenozoic stratigraphic record around the world (Allmon & Dockery 1992; Allmon & Knight 1993), yet the paleoenvironmental significance of such assemblages remains unclear. Recent turritellids are most abundant in relatively shallow marine depths (<50 m), cool temperatures (<20°C), and high nutrient conditions, often associated with coastal upwelling (Allmon 1988). Living turritellids occur in a range of densities, however, and in a range of environmental conditions (Allmon et al. 1992, 1994). It is furthermore not clear that the group has had the same range of environmental tolerances or preferences throughout its history (Allmon 1992).

The discovery of two separate turritellid-rich horizons, each dominated by a different turritellid species, within the Upper Pliocene Pinecrest Beds in a quarry complex on the central west coast of Florida offers an opportunity to examine the range of environmental conditions that may have led to the formation of such assemblages. The possibility that turritellid-rich beds are indicative of upwelling is, additionally, of particular interest in this case, as high biological productivity, potentially associated with upwelling, has been discussed as an important factor in the development of these extraordinarily dense fossil accumulations (e.g., Stanley 1986; Allmon 1993; Jones & Allmon 1993; Allmon et al. 1995).

Geological setting

The two turritellid-rich horizons considered here were formerly exposed in two pits in the quarry complex of Quality Aggregates, Inc., just east of the city of Sarasota, on the central west coast of Florida (Fig. 1). Most of the stratigraphic section exposed at Sarasota is assignable to the Upper Pliocene Pinecrest Beds (Fig. 2). The Pinecrest is well known for its abundant and diverse mollusk fauna (Petuch 1982; Stanley 1986; Jones et al. 1991; Scott & Allmon 1992; Allmon 1993; Allmon et al. 1993). At Sarasota, it consists of a complex series of horizons characterized by dominance of one or more macroscopic taxa, usually mollusks. Petuch (1982) established a system of numbered stratigraphic units for the Sarasota sequence based on macrofaunal content; this system is employed here. Although some of these faunal units are discontinuous or show marked facies changes, their
Fig. 1. Map of the central west coast of Florida, showing the location of study sites. □, 2. Quality Aggregates University Parkway (QAUP); □3. Quality Aggregates Phase 6 (QA6).
stratigraphic order is consistent and most units are recognizable across the several quarries at Sarasota, over an area of at least 10 km² (Fig. 1).

Absolute age assignments for the Pinecrest remain controversial (see Allmon 1993 for discussion). Petuch’s units 10–15 are often referred to as ‘Lower Pinecrest’ and dated at between 3.5 and 2.5 Ma; units 4–2 are often referred to as ‘Upper Pinecrest’ and dated at between 2.5 and 2.0 Ma (Cronin 1991; Jones et al. 1991; Zullo & Harris 1992; Allmon 1993). Some of these upper units may correlate to some or all of units previously referred to the Caloosahatchee Formation (e.g., Hazel 1983; Cronin 1991; Lyons 1991; Ketcher 1994), which overlies the Pinecrest at Sarasota and is generally held to be of latest Pliocene age (Lyons 1991).

The lower turritellid bed (Fig. 3B) was approximately 30–40 cm thick and was exposed over a lateral distance of approximately 100 m in the southeastern corner of the Phase 6 (QA6) pit (now completely excavated), in the southwestern part of the complex (Fig. 1). Based on the sequence of faunal assemblages below it, it was correlated with ‘unit 2’ (Fig. 2) within the ‘Upper Pinecrest’. Its macrofauna is characterized by an abundance of *Turritella gladeensis* Mansfield, 1931.

The upper turritellid bed (Fig. 3A) was also approximately 30–40 cm thick and was exposed over a lateral distance of approximately 100 m in the southeastern corner of the Phase 6 (QA6) pit (now completely excavated), in the southwestern part of the complex (Fig. 1). Based on the sequence of faunal assemblages below it, it was correlated with ‘unit 2’ (Fig. 2) within the ‘Upper Pinecrest’. Its macrofauna is characterized by an abundance of *Turritella gladeensis* Mansfield, 1931.

**Methods**

Bulk samples were collected from within and approximately 0.5 m below each of the two beds. Sample sizes are given in Table 1. All identifiable turritellids, in all degrees of fragmentation, were picked from each sample. ‘Whole’ shells were considered to be those of more than five whorls for those with maximum whorl diameter of >1 cm, and those of more than three whorls for those with maximum whorl diameter of <1 cm. All other shells were considered ‘fragmentary’. All shells, ‘whole’ and otherwise, were examined and scored for a number of taphonomic attributes (Table 2). Data are
summarized in Table 1. A total of 4119 'whole' and 2283 'fragmentary' shells were examined and graded.

Because of their very narrow, elongate shape, turritellids are almost always broken in fossil assemblages. The evenly tapering shape of these fragmentary specimens makes them very difficult to sort into unambiguous individuals. In our analysis, 'whole' shells, as defined above, were considered to be individuals, and their size was taken as maximum whorl width. Although this procedure inevitably overestimates the true number of individual animals represented by fossils, it seems a reasonable compromise that yields usable comparative data.

Taphonomic analysis

Size frequency

Samples from within the two turritellid beds show different size-frequency distributions (Fig. 4). The upper (*T. apicalis*)
Fig. 4. Size-frequency distributions for the four samples examined in this study. □A, B. Upper bed containing abundant Turrillella apicalis, QA6; A, within bed; B, ca. 0.5 m below bed. □□C, D. Lower bed containing abundant T. gladeensis, QAUP. C, within bed; D, ca. 0.5 below bed. Numbers of individuals not standardized to sample volume (see Table 1).

Fig. 5. Percentage of fragmented vs. whole turrillellid shells (see text for definition) in four samples.

bed shows a bimodal distribution (Fig. 4A), whereas the lower (T. gladeensis) bed shows a unimodal distribution (Fig. 4C). Samples from outside the turrillellid beds show unimodal distributions (Fig. 4B, D).

Shell condition

Fragmentation. – Degree of fragmentation (i.e. abundance of 'fragmentary' shells, as defined above) was similar within and without the upper (T. apicalis) bed and within the lower (T. gladeensis) bed, and less than in the sample taken below the lower turrillellid bed (Fig. 5).

Abraision. – The least abraded level of the four degrees of abrasion recognized (Table 2) showed the greatest values in the lower (T. gladeensis) bed (Fig. 6). Intermediate and greatest degrees of abrasion peaked in the sample taken below the upper (T. apicalis) bed, and were slightly less in the sample taken below the lower bed.

Encrustation. – The two turrillellid beds show approximately the same levels of in-aperture encrustation (Fig. 7A), whereas the samples taken below each bed show higher and approximately equal levels, respectively. A different pattern is shown by on-shell encrustation (Fig. 7B), which is less for samples within and below the lower bed and greater for samples within and below the upper bed.

Bioerosion. – Frequency of bioerosion (Fig. 8) is greater in the upper turrillellid bed than in any of the other three samples, which all show approximately the same level of bioerosion.

Predation. – Drilling predation by naticid and muricid gastropods (cf. Allmon et al. 1990) (Fig. 9) shows a pattern similar to in-aperture encrusting; samples taken below the two turrillellid beds show greater, and approximately similar, frequency of drilling, whereas samples taken within the two beds show lesser, and approximately similar, frequency. (Predation values for T. apicalis observed here are somewhat lower than those reported by Allmon et al. 1990, whereas those observed for T. gladeensis are approximately the same.)

Discussion

Neither of the beds discussed here is a 'turrillelline-dominated assemblage', as defined by Allmon & Knight (1993), i.e. a dense macrofossil assemblage of low total diversity (<20 species) in which turrillelines are more than two to three times as abundant as the next most common species. Rather, they can both be referred to as 'turrillellid-rich assemblages' in which turrillelines are the most abundant macrofaunal taxon but are not dominant to the exclusion of most other macrofaunal species.
As is the case for all dense fossil accumulations, these two turritellid beds formed as a result of some combination of processes of physical accumulation, sediment winnowing, biological production, and diagenesis (Kidwell et al. 1986). Ignoring diagenesis, which appears to be of minor importance in this situation, we should thus ask what physical and biological processes have been most important in forming these beds.

At least five scenarios seem possible for the formation of the two beds:

1. High turritellid abundance in both beds is the result of high biological productivity, perhaps associated with strong coastal upwelling. The differences in the two beds are due largely to the differing life-spans of the two species.

2. High turritellid abundance in both beds is the result of high biological productivity, perhaps associated with strong coastal upwelling, but differences between the two beds indicate different levels of productivity.

3. High turritellid abundance in both beds is due to environmental variables other than productivity, such as temperature, depth or current energy.

4. High turritellid abundance in both beds is due more to processes of physical accumulation, reworking, and time-averaging than to high abundance of living snails.

5. High turritellid abundance in both beds is due to a combination of high biological productivity and differential reworking and/or time-averaging.
We believe that scenario 5 best describes the factors responsible for the formation of these two beds.

Physical reworking/time-averaging. - Because active infaunal taxa are commonly inhibited from burrowing in densely shelly sediments (Kidwell & Jablonski 1983), the densely shelly nature of the Pinecrest Beds suggests in general that physical accumulation and condensation were important mechanisms in their formation (Geary & Allmon 1990; Allmon 1993). Turritellid gastropods are, at least occasionally, active burrowers in soft sediments; they may also, however, live in or on gravelly or rocky substrates, and in extremely high abundances stacked on top of one another (Allmon 1988), and might have done so in the Pinecrest. Throughout the Pinecrest Beds at Sarasota, furthermore, shell beds contain badly abraded, encrusted and bioeroded shells (indicative of long exposure at the sediment–water interface) as well as pristine shells together in varying proportions (Geary & Allmon 1990; Allmon 1993). Time averaging and physical accumulation and concentration therefore almost certainly have occurred during deposition of the Pinecrest; the intensity of these processes in different units within the sequence, however, may have varied considerably.

Differential physical accumulation seems unlikely as an exclusive explanation for these two turritellid beds for two reasons: (1) to winnow an assemblage such as those represented by the two samples taken below the turritellid beds and to produce an assemblage such as those represented by the samples within the turritellid beds would require differential concentration of turritellids by a factor of between 4.7 (upper _T. apicalis_ bed) and 61.5 (lower _T. gladeensis_ bed) (Table 1); although the lower end of this range is imaginable, the upper end seems unrealistically high. (2) Although the turritellids in the lower bed show significantly greater physical abrasion levels (Fig. 6), and so may have been subject to more physical transport and/or reworking, the assemblage is dominated by smaller individuals (Fig. 4C), an unlikely outcome of prolonged physical winnowing.

If physical reworking and/or time-averaging played a significant role in the formation of these assemblages, therefore, other factors were also probably important.

The physical taphonomic data described above suggest that these two beds formed over different lengths of time. The most conspicuous evidence of this difference is the size-frequency distributions. The upper (_T. apicalis_) bed appears to include individuals belonging in more than a single age class (Fig. 4A, B), whereas the lower (_T. gladeensis_) bed appears to include only a single age class (Fig. 4C, D). The upper bed contains many individuals in the oldest age classes, whereas the lower bed does not.

Comparison of these size and abundance data with known densities of living turritellids allows us to constrain the time scale of accumulation of these beds in absolute terms. A similar technique was used by Geary & Allmon (1990) for a strombid gastropod–rich layer in lower unit 7 in the Sarasota Pinecrest sequence. The volumes of the two bulk samples taken from the turritellid beds are 0.024 m³ and 0.012 m³, respectively. Given an average thickness of both beds of 0.35 m, the volume of the turritellid beds under 1 m² of Pliocene seafloor was ca. 0.35 m³. Therefore each bulk sample represents an accumulation under ca. 0.024/0.35 and 0.012/0.35, or 1/14.58 m² and 1/29.17 m², respectively. The observed abundance of turritellids in each sample should, therefore, be multiplied by these values for comparison with modern abundances of turritellids per m². Our samples thus represent cumulative densities of 41,028 (= 14.58x2814) and 31,037 (= 29.17x1064) shells per m², respectively.

Available data on live turritellid abundance (Allmon 1988, Table 2) yield a range of 1–10,000 individuals per m², with a mean of 745. Data on age of individual turritellids in these Pliocene fossil beds (Jones & Allmon 1995) allow us to estimate annual mortality. Based on δ¹³C analysis of the shell, _T. apicalis_ appears to have lived 1.5–2.0 years; thus between three-fourths and one-half (i.e. ~0.63) per year of the living individuals might be expected to have died and, if all were preserved and retained in the area, to have been buried. _T. gladeensis_ appears to have lived only one year; thus virtually all of the living density might have died and been buried per year. To accumulate 41,028 shells of _T. gladeensis_, if they lived at modern densities, would therefore require ca. 55 years (= 41,028/745) (range 4–41,028 years). To accumulate 31,037 shells of _T. apicalis_, if they lived at modern densities, would require ca. 66 years (= 31,037/0.63x745) (range 3–53,498 years). Higher living densities of these species would reduce the duration of bed formation; lower living densities would increase it. These estimates are comparable to those obtained by Geary & Allmon (1990) for the strombid layer (49–220 years).

Whatever the absolute time duration of accumulation, the bulk of the taphonomic data are thus consistent with the hypothesis that the upper bed took longer to form than the lower bed and was subject to more physical reworking. Although physical abrasion is lower in the upper bed (Fig. 6), both bioerosion and on–shell encrustation are higher (Figs. 7, 8), suggesting that turritellid shells in the upper bed lay exposed on the seafloor for a longer period than those in the lower bed. The similarity of levels of in–aperture encrustation (Fig. 7A) in the two beds suggests that comparable proportions of individuals in the two assemblages were dead on the surface and that the differences are not due to different rates of burial. We conclude that most of the turritellids in both beds were alive for most of the time they were exposed on the seafloor.

Temperature. – Allmon & Dockery (1992) concluded that a turritellid–dominated bed in the Oligocene of Mississippi resulted from locally cool water temperatures, rather than especially high nutrient conditions. Based on pollen, ostracodes and benthiic foraminifera, Willard et al. (1993) suggest that water temperatures in unit 2 at Sarasota were lower than those in unit 6/7. To the degree that Pliocene turritellids shared with Recent turritellids a preference for low tempera-
tures (Allmon 1988), it is therefore possible that low temperatures in unit 2 were partly responsible for the high abundance of turritellids. Based on oxygen-isotope analysis of shells of turritellids and other mollusks from the Pinecrest section at Sarasota, Jones & Allmon (1995) conclude that temperatures in the upper turritellid bed were, if anything, slightly warmer than temperatures in the lower turritellid bed. Temperatures in the lower turritellid bed, however, are approximately the same as or (more probably) somewhat lower than temperatures lower in unit 6/7 (Jones & Allmon 1995; Willard et al. 1993).

Productivity. – Analysis of carbon- and oxygen-isotopic records in turritellid and other mollusk shells from the Pinecrest Beds at Sarasota (Jones & Allmon 1995) suggests that upwelling was occurring throughout the section, and particularly during the formation of the two turritellid beds considered here. As indicated by enrichments in the oxygen isotopic profiles coincident with depletion episodes in the carbon isotopic record, upwelling is evident in analyses of turritellids from both turritellid beds, and from ca. 2 m below the lower bed in the middle of unit 6/7 (Jones & Allmon 1995). The strongest upwelling ‘event’ detected in these records is in a single turritellid specimen from the upper turritellid bed; the small sample size may, however, suggest that this result should be accepted with caution.

Comparison of the isotopic temperature estimates obtained by Jones & Allmon (1995) with those of Willard et al. (1993), which were based on faunal and floral analysis, is also consistent with a hypothesis of upwelling. Temperature estimates derived from turritellids within the lower turritellid bed are considerably cooler (by 1–5°C) than those obtained from lower in unit 6/7, as would be expected if upwelling was stronger during formation of the bed than before or after (although it should be noted that the ‘upwelling signal’ is not otherwise particularly strong within the lower turritellid bed; Jones & Allmon 1995). ‘Background’ temperatures (Willard et al. 1993) are cooler in unit 2, but are approximately the same as those obtained within the upper (unit 2), as well as the lower, turritellid bed. If upwelling was occurring at this time, it produced less temperature contrast.

Paleoenvironmental conclusions. – We conclude that these two turritellid beds formed under conditions of higher biological productivity than existed during the formation of other biofacies within the Pinecrest Beds at Sarasota, and that these conditions were probably associated with upwelling. Other processes, however, also were important in the formation of these assemblages, particularly in the upper bed.

The upper (T. apicis) bed formed under relatively cool ‘background’ temperatures (14–24°C; Willard et al. 1993), which may have been conducive to high turritellid abundance. As indicated by the differential surface condition and size-frequency distributions in the two beds, as well as the relatively low degree of physical concentration that would be required to produce it from its immediate precursor assemblage, the upper bed formed over a longer time period, and its turritellid shells were subjected to a greater degree of time-averaging, probably involving winnowing of sediment by waves or currents and concentration of multiple generations of turritellids more or less parautochthonously (cf. Geary & Allmon 1990), than were the turritellids in the lower bed. Although there is a strong upwelling signal evident in isotopic analyses from the upper bed, sample size is limited and upwelling may have been no stronger in the upper than in the lower bed.

The lower (T. gladeensis) bed has higher turritellid density than the upper bed. It formed under warm ‘background’ (18–25°C; Willard et al. 1993), but locally cool (11–23°C; Jones & Allmon 1995), temperatures, suggesting the effects of upwelling. Based on both density and life span of the turritellids dominating it, the lower bed appears to have formed over a shorter period of time than the upper bed. The surface condition of the turritellid shells in the lower bed, as well as the enormous degree of concentration that would be required to produce it from its immediate precursor bed, suggest that time-averaging was of relatively less importance in forming the lower assemblage. High biological productivity was therefore probably a major causal factor.

Geographic distribution. – The rudimentary state of understanding of Florida Plio–Pleistocene stratigraphy prevents our obtaining an accurate geographic perspective on the scale of turritellid-rich assemblages from this time and region. One indication of their potentially broad extent, however, is available in the literature. The upper (T. apicis) bed at Sarasota appears to be similar in faunal composition and stratigraphic position to the ‘Turritella Facies’ described by DuBar (1958, p. 95), and earlier by Dall & Harris (1891, p. 147) and Mansfield (1931, p. 20). DuBar characterized this assemblage as containing abundant T. apicis and placed it at the bottom of the Caloosahatchee Formation, in his Cyto-

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<th>Table 3. Mollusk species listed by DuBar (1958) as characterizing his Cyrtopleura costata biozone within the Caloosahatchee Formation.</th>
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pleura costata zone. The mollusk species he listed as characteristic of this zone (Table 5) suggest that it is equivalent to "Zone E" of Ketcher (1993) and to the uppermost units (Petuch's units 1 and/or 2) at Sarasota, and so of approximately the same biostratigraphic age as the upper turritellid bed discussed here. DuBar stated that the 'Turritella facies' was 'known from only a small area' near his station A23, near the town of LaBelle in Hendry County on the Caloosahatchee River (see Fig. 1). At Sarasota the known outcrop area of the lower (T. gladeensis) bed was much larger than that of the upper (T. apicalis) bed. Yet if the Sarasota and LaBelle T. apicalis assemblages are approximately isochronous, this later area of high turritellid abundance (and so the area of upwelling) could thus have extended over a distance of as much as 120 km. Puri & Vanstrum (1971) also noted a turritellid concentration from late Plio-Pleistocene strata of this area. They reported on ostracodes from the 'Turritella facies' in the Caloosahatchee River area, probably in sediments equivalent to the Caloosahatchee Formation as used here, and suggested that salinities during its formation may have been low and/or variable.

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References


