DRILLING AND PEELING OF TURRITELLINE GASTROPODS SINCE THE LATE CRETACEOUS

by WARREN D. ALLMON, JAMES C. NIEH *and* RICHARD D. NORRIS

ABSTRACT. Frequencies of predation on turritelline gastropods by drilling and peeling predators have not changed significantly during the course of the Cenozoic. Rates of drilling in the Cretaceous are lower than Cenozoic rates, but not significantly so. Conversely, rates of peeling and repair in the Late Cretaceous reach or exceed Cenozoic values.

Turritelline shell form is not correlated with predation intensity. Highly sculptured species are not more immune to drilling and peeling predation than are less sculptured taxa. Shell geometry in these gastropods does not show progressive trends during the Cenozoic. Sculpture strength and most aspects of shell form and sculpture strength are evidently not adaptations to resisting peeling and drilling predation in turritellines. Turritellines have not evolved during the Cenozoic in an arms race to build more predation-resistant shells, although behavioural or other non-shell characteristics may have changed over time. Thus, in this group, any 'marine revolution' and adaptive response of prey to the evolution of durophagous predators must have occurred prior to the Late Cretaceous.

THE notion that predation influences the evolution of prey has been widely discussed (e.g. Vermeij 1977, 1978, 1982*b*, 1983, 1987; Hughes 1980; Bayne 1981; Kitchell *et al.* 1981; Bakker 1983; Taylor 1984) but has seldom been tested within a single prey clade. Turritelline gastropods (i.e. members of the family Turritellidae, subfamilies Turritellinae and Protominae, *sensu* Marwick [1957]) are common to abundant fossils in many Cretaceous and Cenozoic horizons, and many bear the marks of attack by drilling and shell-peeling (i.e. aperture-breaking) predators. Previous studies (e.g. Dudley and Vermeij 1978; Vermeij and Dudley 1982) have discussed trends in predation in this group, at least as represented by these traces. In this paper we expand this earlier work by (1) considering a much larger data set, (2) making use of more adequate views of both turritelline ecology (Allmon 1988*a*) and of the stratigraphic and systematic relationships of species from the southeastern United States (Toulmin 1977; Allmon 1988*b*), which have figured prominently in previous work, and (3) exploring possible evolutionary consequences of predation on turritelline shell form.

Vermeij (1987, and references therein) has long argued that durophagous predation has been at least partly responsible for some trends in gastropod shell morphology. Whether this has been the case for turritellines is of particular interest since almost nothing is known about the functional significance of most features of their shells. Correlation or lack of correlation between predation intensity and shell form over the history of this group may indicate evolutionary origins of particular features. Although their origin is obscure, turritellines appear to have arisen in the Late Jurassic or Early Cretaceous (Merriam 1941), a time of rapid morphological and taxonomic diversification among gastropods (Vermeij 1977; Taylor *et al.* 1980, 1983). An understanding of the factors controlling the occurrence and significance of predation in turritellines may thus also contribute to a better understanding of the evolutionary dynamics of this interval.

MATERIALS AND METHODS

New data presented here are derived from examination of specimens in the collection of the Department of Invertebrate Paleontology of the Museum of Comparative Zoology (MCZ), Harvard University. All are from

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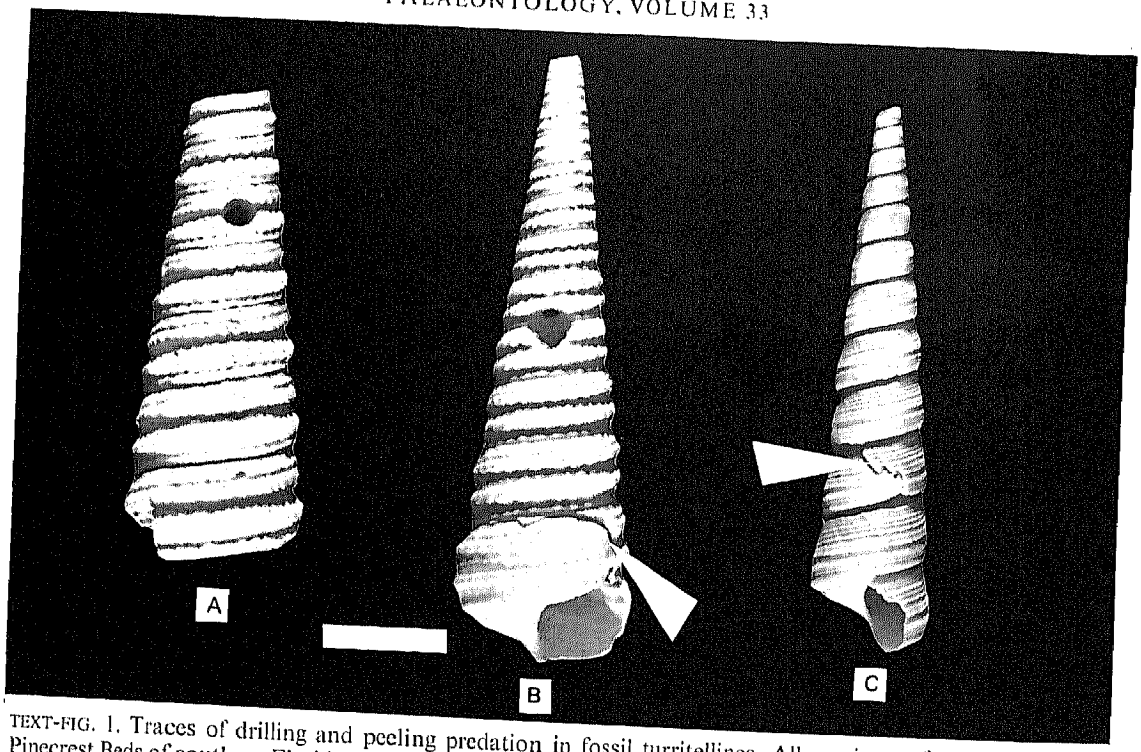
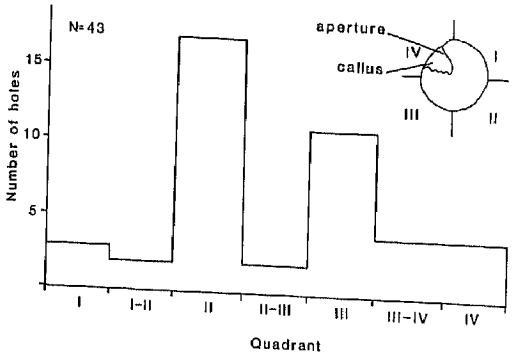


TEXT-FIG. 1. Traces of drilling and peeling predation in fossil turritellines. All specimens from the Pliocene Pinecrest Beds of southern Florida. A. *Turritella* cf. *T. apicalis* Heilprin, showing naticid drill hole in the middle of the whorl. B. *Turritella* cf. *T. apicalis* Heilprin, showing the less common positioning of a drill hole astride a suture between whorls. Peeling/repair scar indicated by arrow. C. *Turritella pontoni* Mansfield, showing peeling/repair scar, indicated by arrow. Scale bar = 1 cm.



TEXT-FIG. 2. Longitudinal distribution of drill holes on intact turritelline shells of all species in our data set (Appendix 1). Figure in upper right shows the base of a turritelline shell looking toward the apex parallel to the axis of coiling, indicating division into quadrants for recording the longitudinal position of drill holes. Intact bases and apertures are distinguished from broken and incomplete specimens by the presence of parietal callus on outside of last whorl.

Cenozoic deposits of the New World and most were personally collected by one of us (WDA). A total of 1097 specimens representing 27 species were examined. For each specimen the following observations or measurements were made: length (or estimated length if broken), maximum whorl diameter, presence/absence of drill holes (text-fig. 1A, B), hole diameter, position of the hole vertically on the whorl and relative to the aperture if this could be determined (text-fig. 2), diameter or drilled whorl, presence/absence and number of repaired shell breaks (text-fig. 1C), and diameter of broken-and-repaired whorl. All measurements were made with digital calipers to the nearest 0·1 mm. Frequency of drilling in each species is the number of drilled shells divided by the total number of shells of that species examined, expressed as a percentage. Frequency of peeling/repair is the total number of scars divided by the number of shells examined, expressed as a decimal

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value. These data (Appendix 1), together with additional observations from the literature (Appendix 2) represent a total of 10,387 specimens of 68 species, ranging in age from Early Cretaceous to Recent.

As noted by Dudley and Vermeij (1978), the generic and subgeneric taxonomy of turritellines is unresolved, particularly for fossil species (Marwick 1957; Allmon 1988*b*). Consequently we refer all species to *Turritella sensu lato*. Despite this remaining uncertainty, however, it is reasonable to make use of recent and relatively uncontroversial opinions on the position of some taxa, and we have therefore excluded from consideration three Recent species included in the genus by Dudley and Vermeij (1978). '*T. erosa* Couthouy' and '*T. reticulata* Mighels' belong to the genus *Tachyrhynchus* Mörch (e.g. Abbott 1974), which Marwick (1957) places in the subfamily Pareorinae. '*T. duplicata* Linnaeus' is the type species for the genus *Zaria* (Marwick 1957). We have also excluded fossil and living species assigned to the genus *Mesalia* Gray, including the Eocene species *M. regularis* Deshayes and *M. amekiensis* Eames, both of which were considered by Dudley and Vermeij. *Mesalia* and *Zaria* are placed in Pareorinae by Marwick. Whatever the generic placement of species within Turritellinae, these taxa are almost certainly only distantly related to the other species considered here.

In their study of turritelline specimens in the collection of the U.S. National Museum, Dudley and Vermeij (1978) assigned several strictly Palaeocene species (e.g. *T. mortoni*, *T. praecincta*) to the Eocene (see Toulmin [1977] and Allmon [1988*b*] for further discussion of stratigraphic relations of early Tertiary species). Reassignment of these species and examination of others provide the first estimates of drilling frequencies in turritellines from the Palaeocene of the southeastern U.S.

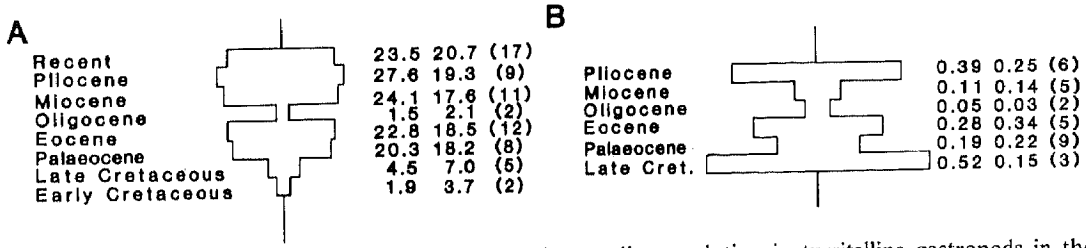
Drilled and undrilled shells may exhibit differential preservation potential (Dudley and Vermeij 1978; Taylor *et al.* 1983), but biases may operate in both directions. Drilled shells may be more easily fragmented or transported or, because many naticid predators pull their prey into the sediment to feed, they may increase the probability of preservation of drilled shells (Edwards 1974). Here we assume that all shells have equal preservation potential.

Most of the holes observed in these turritelline shells resemble the 'truncated spherical paraboloid' typically produced by naticacean gastropods (text-figs. 1A, B), rather than the usually more straight-sided holes characteristic of muricaceans (e.g. Sohl 1969; Carriker 1981). The great majority of holes examined here fall into types C, E and F of Arua and Hoque (1989), which these authors suggest as belonging to naticids. Specification of an exact percentage is difficult since many holes are eroded and cannot be assigned to one type over the other. Probably no more than 5–10% of the holes we examined are attributable to muricids, and we assume that the majority of drilling predators were naticids. We have also assumed that most of the observed breakage/repair scars were produced by shell-peeling predators, such as calappid crabs (cf. Vermeij 1982*a*, 1983), rather than accidental breakage not associated with predation (cf. Vermeij 1987, p. 227).

RESULTS

Temporal patterns

Early and Late Cretaceous drilling frequencies are not significantly different (*t*-test, $P = 0{\cdot}32$), although both are well below almost all Cenozoic values (text-fig. 3A). Drilling frequency for all Cretaceous species taken together is significantly lower than that for Palaeocene, Miocene or Plio-Pleistocene species (Mann–Whitney *U*-tests, $0{\cdot}025 > P < 0{\cdot}05$), but not significantly different from



TEXT-FIG. 3. Distribution of rates of A, drilling, and B, peeling predation in turritelline gastropods in the Cretaceous and Cenozoic. First of three numbers on right is mean frequency (in % for drilling) of all samples for each time interval; second number is one standard deviation; third number is number of species sampled. Figures derived from all data presented in Appendices 1 and 2.

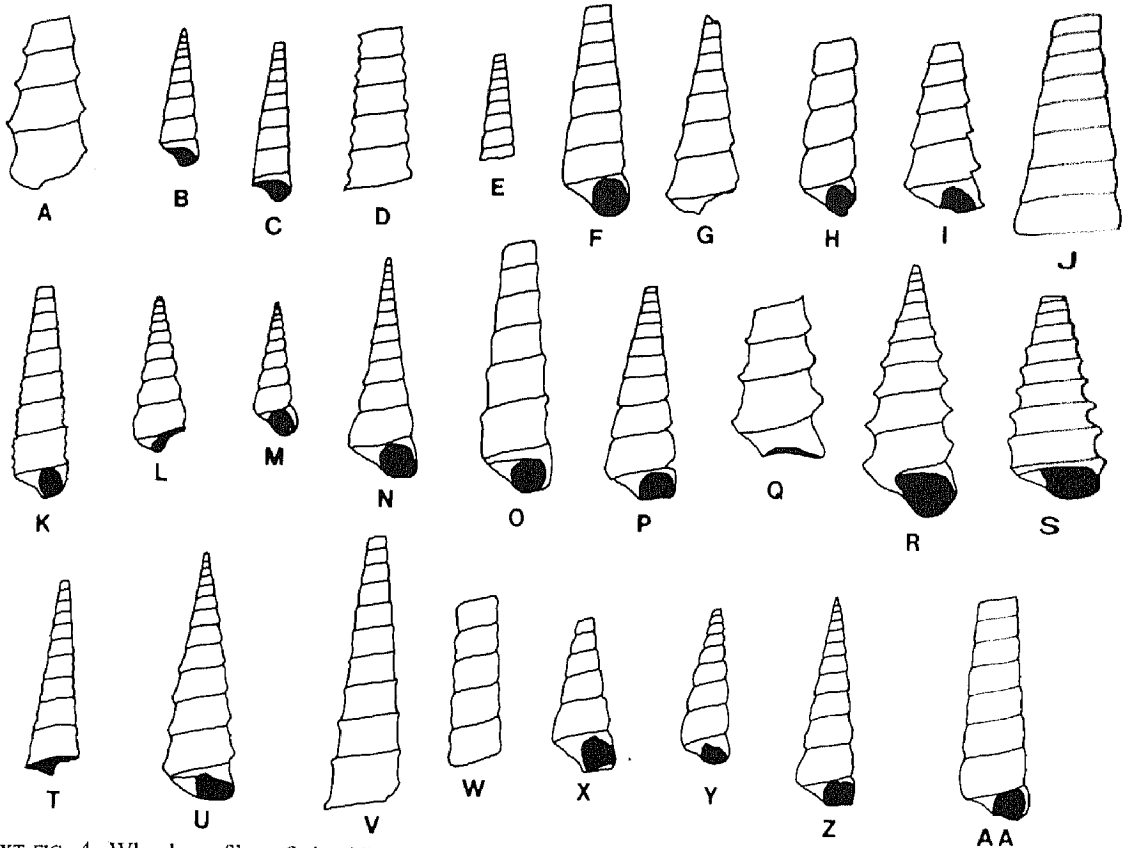
that for Eocene species ($P = 0{\cdot}25$). Drilling frequency for the Oligocene is lower than that for either the Eocene or the Miocene (probably a result of small sample size), but the differences are not significant. In fact, no epoch of the Cenozoic shows a drilling frequency significantly different from any other (Mann–Whitney U-tests, $0{\cdot}10 < P > 0{\cdot}05$).

Late Cretaceous values for peeling/repair frequency, are higher, but not significantly so, than those of any epoch of the Cenozoic (text-fig. 3B). As is the case for drilling, peeling/repair values for each Cenozoic epoch are not significantly different from any other (Mann–Whitney U-tests, $0{\cdot}10 > P > 0{\cdot}05$).

Geographic patterns

Dudley and Vermeij (1978) stated that their data showed 'a distinct latitudinal trend in drilling predation for Recent species of *Turritella*', with tropical and subtropical shells showing drilling frequencies roughly three times those of temperature shells. Exclusion of the temperate *Tachyrhynchus* species from the group in our data set does not greatly alter this pattern. Of 212 shells collected above 30° latitude, 33 (15·6 %) were drilled; of 766 shells collected below 30°, 226 (29·5 %) were drilled.

Among fossil species only limited latitudinal comparisons are possible because of a paucity of

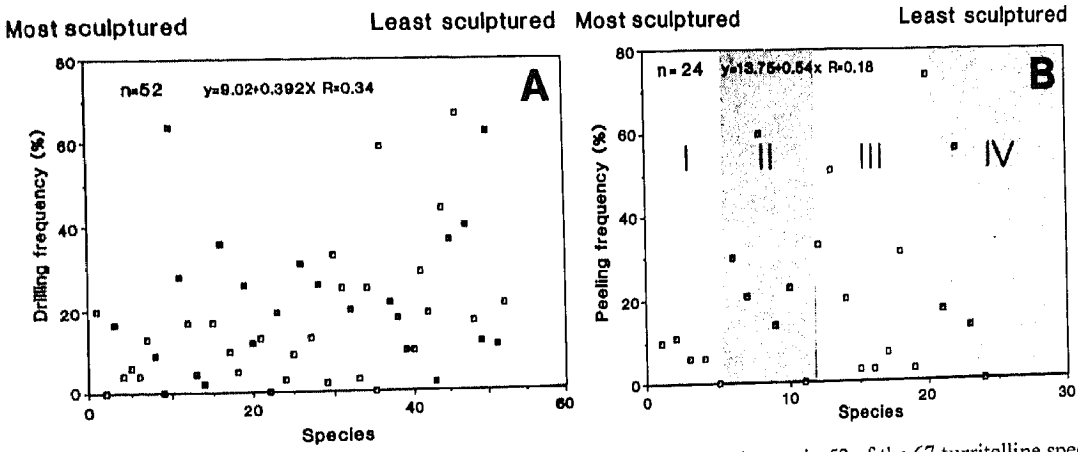


TEXT-FIG. 4. Whorl profiles of the 27 species examined in the present study (Appendix 1). A. *T. abrupta*, B. *T. alabamiensis*, C. *T. aldrichi*, D. *T. altilira*, E. *T. alveata*, F. *T. apicalis*, G. *T. carinata*, H. *T. cumberlandia*, I. *T. rina*, J. *T. rubicollis*, K. *T. eurynome*, L. *T. femina*, M. *T. gilberti*, N. *T. gladeënsis*, O. *T. humerosa*, P. *T. indenta*, Q. *T. larensis*, R. *T. postmortoni*, S. *T. praecincta*, T. *T. mississippiensis*, U. *T. mortoni*, V. *T. multilira*, W. *T. perattenuata*, X *T. perdita*, Y. *T. plebeia*, Z. *T. pontoni*, AA. *T. wagneriana*.

approximately isochronous and geographically widespread samples. *Turritella mortoni*, *T. praecincta* and *T. humerosa* from the Palaeocene Aquia Formation of Maryland and Virginia lived at approximately the same time as *T. praecincta*, *T. postmortoni*, *T. multilira* and *T. eurynome* from the Palaeocene Tuscahoma and Nanafalia Formations of Alabama (e.g. Hazel *et al.* 1984; Ward 1985). All of these species are relatively large forms with moderate to well-developed spiral sculpture (text-fig. 4). Of 137 shells of the four lower latitude Alabama species, 11 (8·0%) were drilled and the peeling/repair frequency was 0·299. Of 179 shells of the three higher latitude Aquia species, 33 (18·4%) were drilled and the peeling/repair frequency was 0·078. The single species in common to the two areas, *T. praecincta*, showed a lower frequency of drilling (17% vs. 38%) and higher frequency of peeling/repair (0·36 vs. 0·035) in Alabama than in Virginia.

Predation and shell form

When ranked on a subjective scale of strength of sculpture, highly and moderately sculptured species show relatively low frequencies of drilling (text-fig. 5A). Sculpture and drilling frequency are significantly negatively correlated (t-test, $0{\cdot}025 > P < 0{\cdot}05$). Despite this relationship, the nine most highly sculptured species as a group are not significantly less frequently drilled than all other species

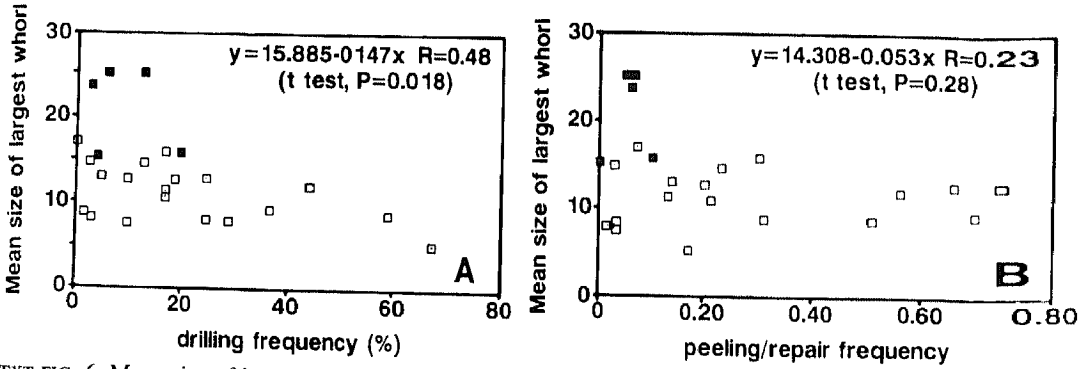


TEXT-FIG. 5. A. Drilling frequency vs. development of external spiral sculpture in 52 of the 67 turritelline species listed in Appendices 1 and 2. Species are arranged subjectively from least to most sculpture development along the horizontal axis as follows: 1. *T. praecincta*, 2. *T. postmortoni*, 3. *T. mauryana*, 4. *T. mortoni*, 5. *T. larensis*, 6. *T. abrupta*, 7. *T. rina*, 8. *T. berjadinensis*, 9. '*T. carinifera* Lamarck' (Recent, South Africa), 10. *T. gatunensis*, 11. *T. bicarinata*, 12. *T. altilira*, 13. *T. exoleta*, 14. *T. pagoda*, 15. *T. apicalis*, 16. *T. mariana*, 17. *T. eurynome*, 18. *T. multilira*, 19. *T. leucostoma*, 20. *T. variegata*, 21. *T. carinata*, 22. *T. trilira*, 23. *T. symmetrica*, 24. *T. femina*, 25. *T. vertebroides*, 26. *T. badensis*, 27. *T. cumberlandia*, 28. *T. nodulosa*, 29. *T. perattenuata*, 30. *T. pontoni*, 31. *T. gladeënsis*, 32. *T. variabilis*, 33. *T. mississippiensis*, 34. *T. humerosa*, 35. *T. rubricollis*, 36. *T. aldrichi*, 37. *T. subangulata*, 38. *T. imbricataria*, 39. *T. banksi*, 40. *T. alabamiensis*, 41. *T. gilberti*, 42. *T. wagneriana*, 43. *T. howelli*, 44. *T. alveata*, 45. *T. bieniaszi*, 46. *T. indenta*, 47. *T. gonostoma*, 48. *T. perdita*, 49. *T. acropora*, 50. *T. annulata*, 51. *T. communis*, 52. *T. plebeia*. Open squares represent our observations (Appendix 1); solid squares represent previously published data (Appendix 2).

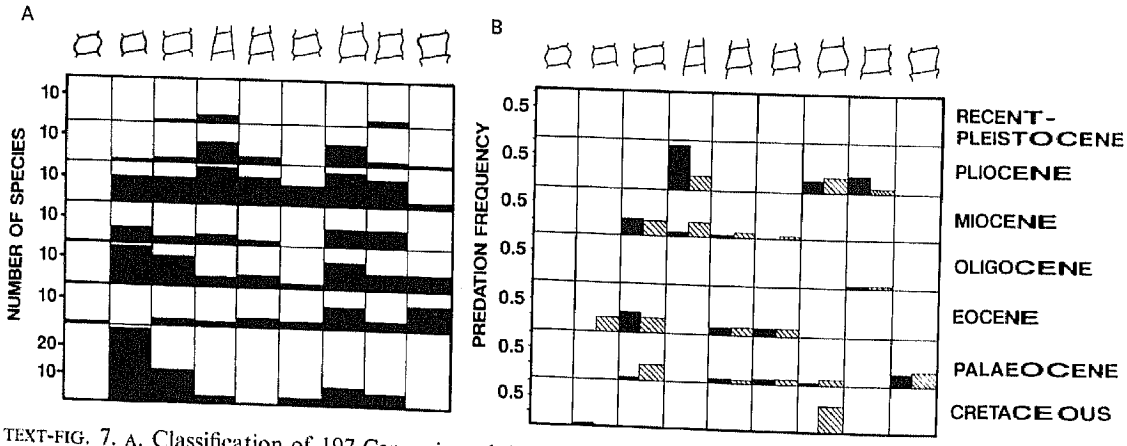
B. Peeling frequency vs. development of external spiral sculpture in the 27 turritelline species we have examined. Species are arranged subjectively along the horizontal axis, and numbered as follows: 1. *T. praecincta*, 2. *T. postmortoni*, 3. *T. mortoni*, 4. *T. abrupta*, 5. *T. larensis*, 6. *T. rina*, 7. *T. altilira*, 8. *T. apicalis*, 9. *T. eurynome*, 10. *T. multilira*, 11. *T. carinata*, 12. *T. femina*, 13. *T. cumberlandia*, 14. *T. perattenuata*, 15. *T. pontoni*, 16, *T. gladeënsis*, 17. *T. mississippiensis*, 18. *T. humerosa*, 19. *T. rubricollis*, 20. *T. aldrichi*, 21. *T. alabamiensis*, 22. *T. gilberti*, 23. *T. wagneriana*, 24. *T. alveata*, 25. *T. indenta*, 26. *T. perdita*, 27. *T. plebeia*. In an attempt to increase interpretability, groups of species indicated by Roman numerals were designated *a priori* on the basis of general similarity of degree of sculpture development; I = highly sculptured, II = moderately sculptured, III = weakly sculptured, IV = unsculptured.

together (Mann–Whitney U-test, $P = 0{\cdot}48$). Similarly, the five most highly sculptured species as a group show lower peeling/repair frequency, although not significantly so (Mann–Whitney U-test, $P = 0{\cdot}45$; text-fig. 5B). Peeling/repair frequency declines with increased sculpture, but not significantly so (t-test, $P = 0{\cdot}135$). Frequencies of peeling/repair and drilling among less sculptured species range from very high to very low. (WDA and RDN independently arranged the 27 species in text-figure 5B according to their own judgments of 'strength of sculpture'; results for peeling/repair and drilling frequencies were essentially identical for both arrangements, suggesting confidence in the patterns despite subjectivity of the method.)

To assess the influence of spire height on peeling/repair frequency we computed length : width ratios for each shell and compared the distribution of peeled shells with the total sample. The two distributions are not significantly different (G-test, $P = 0{\cdot}15$). Drilling frequency and peeling/repair frequency decline with increasing size of the largest whorl (text-fig. 6).



TEXT-FIG. 6. Mean size of largest whorl measured for each species plotted against frequency of A, drilling and B, peeling/repair. Size is negatively correlated with predation frequency in both cases, but not significantly so with peeling/repair. The five most strongly sculptured species are represented by solid squares. Elimination of these species does not change the correlation between size and drilling ($P = 0{\cdot}027$), but does further reduce the significance between size and peeling/repair ($P = 0{\cdot}48$).



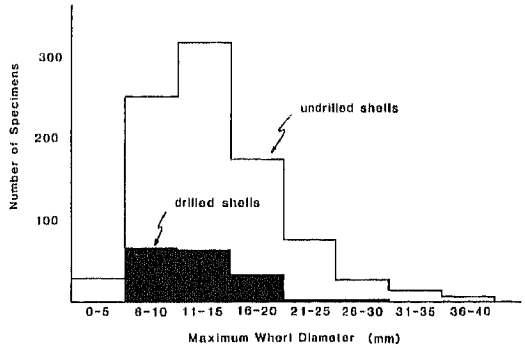
TEXT-FIG. 7. A. Classification of 197 Cenozoic and 43 Cretaceous turritelline species from North, South and Central America and the Caribbean into nine whorl profile types proposed by Ida (1952) and used by Marwick (1971). This figure includes approximately 75% of the described species of *Turritella* from the New World. B. Predation frequencies (drilling in dark shading, peeling/repair in lighter shading) for turritelline species according to whorl classification used in text-fig. 4. Text-figure based on only those species in common between the compilation used in text-fig. 4 and Appendices 1 and 2.

In turritellines, whorl profile can be examined separately from the external, mostly spiral sculpture (Marwick 1971; Allmon 1988*b*). In a sample of New World species, both the distribution of whorl profile types (text-fig. 7A) and the distribution of predation frequencies (text-fig. 7B), show little or no temporal pattern in drilling and peeling/repair data.

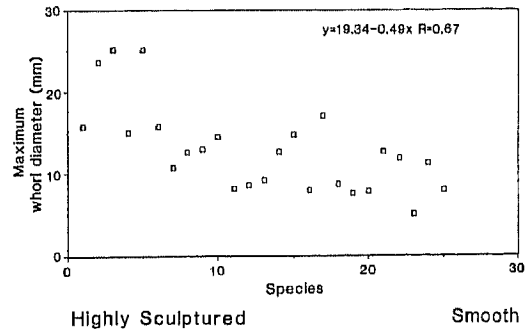
Size

Size distributions of drilled and undrilled shells in our data set are basically similar (text-fig. 8). For the 27 species we examined (although not for turritellines as a whole) size and sculpture development are significantly positively correlated (*t*-test, $P < 0{\cdot}001$) (text-fig. 9).

TEXT-FIG. 8. Comparison of size distribution of drilled and undrilled shells in 1097 shells examined in the present study.



TEXT-FIG. 9. Plot of size (represented by maximum whorl diameter on Y axis) against the subjective ranking of sculpture development used in text-fig. 5B.

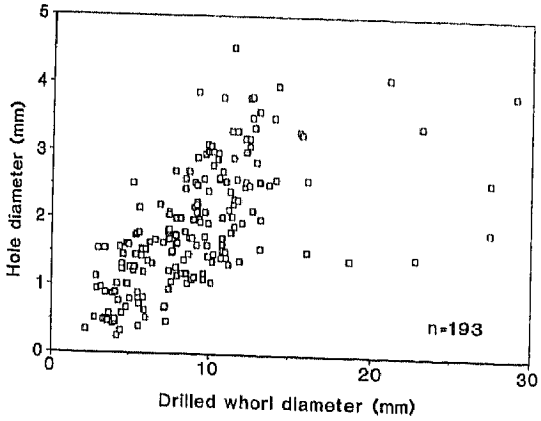


Incomplete drill holes

Only nine incomplete drill holes were observed in our sample: three each on specimens of *T. abrupta* and *T. eurynome*, and one each on specimens of *T. praecincta*, *T. larensis* and *T. humerosa*.

Predator and prey behaviour

Data on position of the drill hole relative to intact apertures indicate a high degree of selectivity on the part of the predators (text-fig. 2). Most holes are located on the half of the shell just behind the aperture (quadrants numbered II and III). This pattern is significantly different from the null hypothesis of a uniform distribution of holes around the circumference of the shell (*G*-test, $P < 0{\cdot}01$). Drill holes vary in their vertical position on the whorl, but most (54%, $N = 170$) are located near the centre, rather than closer to either upper or lower sutures. Occasional holes are observed straddling a suture (text-fig. 1B). Diameter of the drill hole (a measure of predator size [e.g. Wiltse 1980]) plotted against maximum whorl diameter (a measure of prey size) shows that size of predator and prey are highly correlated (text-fig. 10).



TEXT-FIG. 10. Plot of drill hole diameter against diameter of drilled whorl.

DISCUSSION

Problems of pattern recognition

Studies of predation in the fossil record are potentially biased by a large number of factors. In any ecosystem, predation frequency on a given species will vary with abundance of predators, number of alternative prey, and the ranked preference relative to other prey. Only some of these factors can be assessed in the fossil record (e.g. Stanton and Nelson 1980; Stanton *et al.* 1981); for those that can be studied (e.g. abundance of naticids vs. potential prey species), few data are so far available from the coastal plain.

Preservable traces of predation may represent only a small fraction of actual predation on preservable prey species (Signor 1985; Vermeij 1987). Ansell and Morton (1987) have shown, for example, that some bivalves may be suffocated by naticid predators, leaving an incomplete borehole or no trace at all. Naticids are also known to attack gastropods through the aperture (Edwards 1969; Hughes 1985). Bottom-feeding fishes and asteroid echinoderms may be locally important predators of Recent turritellines (Allmon 1988*a*, and references therein), and will leave little or no record of such behaviour in the fossil record.

Interpreting possible evolutionary consequences of predation can be complicated in turritellines by the potential importance of non-shell characters in resisting predation. These include: (1) deep withdrawal into the high-spired shell (Vermeij *et al.* 1980; Vermeij 1982*b*, p. 708; 1987, pp. 195ff.; Allmon 1988*a*), (2) active escape by burrowing or crawling (Allmon 1988*a*), (3) seeking shelter among rocks (e.g. *T. banksi* – Dudley and Vermeij 1978) or in sponges (e.g. '*T. carinifera* Lamarck' – Kilburn and Rippey 1982), and (4) predator avoidance by small, patchily distributed populations or predator saturation by very large populations (Allmon 1988*a*).

Sample size must also be considered. Although our total data set is large, the sample of Oligocene and Cretaceous species is small. Both of these time periods are characterized by the lowest drilling frequencies we observe. Clearly one must wonder if these periods of reduced drilling intensity are real or are sampling artefacts.

Some or all of these factors may be responsible for the high variability in most of our results. Variability occurs within single species from the same area (e.g. *T. plebeia* from the Miocene of Maryland and Virginia, which shows drilling frequencies of 0–30%), within single species from different areas (e.g. *T. badensis* is 17% drilled in a Polish sample and 40·4% in a Bulgarian sample), among species within single time periods (e.g. high standard deviations in text-fig. 3), and among species within the group as a whole (text-fig. 5). Substantial variability also exists between species occurring in the same formation, and even the same outcrop.

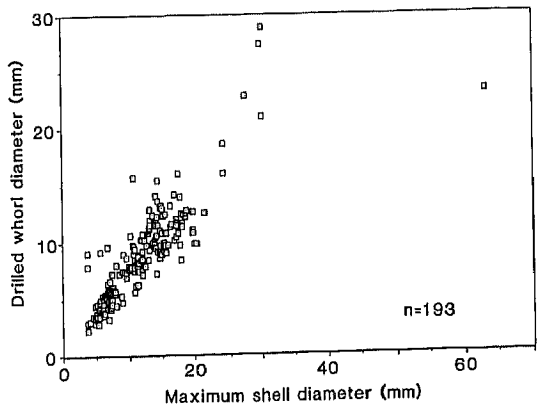
Traces of drilling and peeling can represent two different phenomena (Vermeij 1982*b*, 1987). Frequency of incomplete drill holes (on shells without complete holes; see Kitchell *et al.* 1986; Vermeij *et al.* 1989) and frequency of peeling/repair represent frequency of unsuccessful predation.

On the other hand, frequency of complete drill holes represents the frequency of successful predation. High frequency of unsuccessful predation indicates that predators are exerting strong selection pressure on prey, and that prey are successfully resisting most attacks (Vermeij 1982*a*, *b*). Low frequency of unsuccessful predation indicates either that few prey are being attacked (either because there are few predators or because by hiding or escape the prey avoid even the initiation of attack), or that most attacks are lethal. Low frequency of successful predation could indicate either that predators are rare or that prey avoid detection and capture. It is important to add that high frequency of successful predation may be evidence of intense demographic pressure (high predation-induced mortality) on a prey population, but not necessarily intense selective pressure for antipredatory adaptations (Vermeij 1982*b*).

Predator and prey behaviour

Although much is known about how naticids attack other molluscs (e.g. Ziegelmeier 1954; Sorensen *et al.* 1955; Fretter and Graham 1962; Gonor 1965; Edwards 1969; Taylor 1970; Berry 1982; Hughes 1985) naticid predation behaviour on turritellines is unknown. Observations of living turritellines (Allmon 1988*a*) show that the half of the shell comprising the two most-drilled quadrants in this study (II and III, text-fig. 2) is normally uppermost when the animal is actively crawling (aperture parallel to the substrate); quadrants I and II are normally uppermost when the animal is in a sedentary feeding position (aperture perpendicular to the substrate). Studies with living naticids and turritellines are required to determine whether naticids prefer the dorsal side of the turritelline shell, and actively manipulate them to this end, or whether the dorsal side is drilled because turritellines are frequently active crawlers.

The vertical distribution of holes over the whorls suggests that predators actively select the thinnest part of the shell for drilling. The correlation between size of drilled whorl and maximum whorl size of the drilled shell (text-fig. 11) suggests that for prey of any size, drilling predators tended to choose a whorl that was in the same relative position, usually two to three whorls behind the aperture (text-fig. 1A).



TEXT-FIG. 11. Plot of diameter of drilled whorl against maximum shell diameter of the drilled shell.

Geographic patterns

Geographic patterns in predation are more difficult to study in the fossil record than in Recent assemblages (e.g. Dudley and Vermeij 1978; Vermeij *et al.* 1989). In the case of the Palaeocene species from Virginia and Alabama discussed above, the situation is exactly the reverse from that seen among living species, with lower rates of drilling. Other factors may be involved in this case, including a relatively small latitudinal difference between the two areas ($< 10°$), a weaker latitudinal temperature (and predation?) gradient during the early Tertiary compared to today (cf. Vermeij *et al.* 1980), and the small number of species considered.

Evolutionary significance

The idea that predation intensity in some way affects gastropod shell morphology has been considered by many authors (e.g. Vermeij 1978, 1982*a*, *c*, 1987; Raffaelli 1978; Hughes and Elner 1979; Palmer 1979; Hughes 1980; Bertness and Cunningham 1981; Johannesson 1986; Thomas and Himmelman 1988), but we know little about the actual involvement of predation in the morphological evolution of a single prey clade. In the case of turritellines, Dudley and Vermeij (1978) have suggested that extreme development of carinae in *T. postmortoni* and *T. praecincta* from the Palaeocene of Alabama conferred protection from predation, since these species showed low drilling frequencies in their data. Our results show that well-developed sculpture confers only slight, if any, protection from either drilling or peeling attacks. While a significant negative relationship exists between sculpture and drilling frequency overall (text-fig. 5A), the most highly sculptured species are not significantly less drilled as a group than are less sculptured species as a group. Furthermore, the weak relationship that is observed between sculpture and drilling intensity can be explained as an effect of prey size.

The most sculptured species are larger than less sculptured species (text-fig. 9). The larger size of strongly sculptured taxa contributes to their lower frequencies of drilling and peeling (text-fig. 6). Since large size is correlated with reduced predation intensity, any correlations between sculpture development and predation are confounded by size effects (A. R. Palmer, pers. comm.). The size effect, however, should strengthen the correlation between highly sculptured, large species and low levels of predation. In fact, this correlation is quite poor, and shows that despite the help size effects proved to boost the fit, sculpture development is very poorly related to predation frequency.

Anecdotal indications of a relationship between sculpture and predation come from examination of co-occurring species. *T. mortoni* and *T. humerosa*, for example, occur in the Upper Palaeocene Aquia Formation of Maryland and Virginia. *T. mortoni* has more pronounced sculpture, consisting of several carinae, the largest of which is very strong and occurs near the base of the whorl. *T. humerosa* has fainter sculpture, consisting of fine spiral lines over the entire whorl and a pronounced but rounded subsutural collar. *T. humerosa* shows a drilling frequency of 25% and a peeling/repair frequency of 0·03, while *T. mortoni* shows 5·5% drilling and a peeling/repair frequency of 0·115. In the Matthews Landing Member of the Upper Palaeocene Porters Creek Formation in Alabama, *T. alabamiensis* shows a drilling frequency of 10% and a peeling/repair frequency of 0·03, while *T. aldrichi* is 59% drilled and has a peeling/repair frequency of 0·78. These two species are of similar size, but late whorls of *T. alabamiensis* are basally convex while those of *T. aldrichi* are more straight-sided and usually bear a weak adapical carina. Neither species shows pronounced spiral sculpture.

These individual examples (all of which need more detailed study) notwithstanding, there is little convincing evidence that sculpture yields any consistent advantages in resisting predation on turritellines.

Shell geometry is also uncorrelated with peeling and repair frequencies in turritellines; slender and robust species suffer statistically equivalent frequencies. This finding is contrary to Signor's (1985) results for Recent terebrid species in Guam, where robust forms sustained not only much higher rates of both successful and unsuccessful predation than did slender forms, but also higher rates of repair. Slender species are somehow better able to avoid detection or capture by peeling predators. Signor tentatively concludes that smaller aperture size in slender forms is responsible, by preventing access to a crab's cheliped.

It is possible that the turritellid shell shape itself is an adaptation against peeling predation (since it allows deep withdrawal of the body mass); this might help explain its recurrence in a variety of gastropod groups since the Devonian (e.g. Signor 1984).

Two temporal patterns stand out in our results. The first is the Cenozoic and apparent Late Cretaceous stability in predation frequencies. The second is the timing of establishment of this stability. While frequencies of drilling and peeling/repair do fluctuate from the Late Cretaceous to the Recent, none of these changes is significant at the five percent level of confidence. Late

Palaeocene drilling frequencies are approximately as high as those at any other time in the Cenozoic, and modern peeling frequencies are no different from those in the Late Cretaceous. If predation on turritellines did substantially increase, as suggested by previous workers, this increase must have happened prior to the Late Cretaceous.

The low incidence of incomplete drill holes in our total sample (9 of 1097 specimens) is consistent with previous findings (e.g. Vermeij and Dudley 1982), and suggests that, as in most other gastropods, turritellines are not very successful at resisting drilling once subjugated (cf. Vermeij 1982*b*, 1987, p. 210). Late Cretaceous peeling/repair values (text-fig. 3B) are higher than mean values for any epoch in the Cenozoic. This agrees with earlier findings for turritellines and other Cretaceous gastropod groups (Vermeij and Dudley 1982; Vermeij 1987, p. 229).

The overall temporal patterns we see in turritellines agree with patterns observed in some gastropod groups but not in others. As in turritellines, Terebridae show little or no temporal trend in predation frequency during the Cenozoic (Vermeij *et al.* 1980). On the other hand, Conidae display increased incidence of peeling and repair from the Eocene to the Miocene (Vermeij 1987, p. 231). Neither Conidae nor Terebridae have a Cretaceous record (Taylor *et al.* 1980), so if predation significantly affected the evolution of these groups, it did so at varying rates and times.

Vermeij (1977) proposed the 'Mesozoic marine revolution' as an arms race between newly evolved durophagous predators and their prey, and an explanation for the largely Mesozoic appearance of anti-predatory shell structures in many groups of marine invertebrates. Our results for turritellines (and Vermeij's own findings for terebrids) suggest that after the appearance and initial diversification of a prey group, there may be few long-term trends in shell form or structure aimed at resisting drilling or peeling predators. The evolution of anti-predatory shell structures may have occurred relatively rapidly in some prey groups and then advanced no further. In the case of turritellines, any gradual evolution of anti-predatory shell structures, or increase in predation intensity, must have been a completely Mesozoic phenomenon because long-term trends in shell form, sculpture, and predation intensity are absent in the Cenozoic. Any 'arms race' appears to be at a standstill in so far as turritelline shell design is concerned. These conclusions are consistent with previous results (Vermeij *et al.* 1981; Vermeij 1987, pp. 227ff.) that suggested that predation intensities attained essentially modern levels near the end of the Mesozoic, and remained essentially unchanged thereafter.

None of these results contradicts the basic notion of the marine revolution. The history of drilling and peeling/repair in turritellines may suggest that they switched from shell-based defence to behavioural or soft-anatomy defences against predators. Alternatively, both predators and prey may have reached an impasse early on, with neither group able to achieve a morphological breakthrough that might permit a renewal of the race. Although the 'marine revolution' has resulted in many highly armoured prey species, not all of these species have gradually evolved greater predation resistance after their initial appearance.

CONCLUSIONS

We find remarkable stasis in the overall spectrum of shell design in turritellines, a situation mirrored in the absence of temporal trends in the frequency of drilling and peeling attacks on these gastropods. Frequencies of drilling and peeling/repair have not changed significantly since the Late Cretaceous. Unfortunately, low sample sizes in the Cretaceous prevent us from determining exactly when these frequencies reached Cenozoic levels. The strength of shell sculpture is uncorrelated with drilling and peeling/repair frequencies, suggesting that sculpture itself is currently of little value as a predator defence. The lack of correlations between shell form and predation, and the absence of temporal trends in predation intensity, suggest that turritelline shell structure has not evolved continuously in response to predation, at least not during the Cenozoic. Any gradual evolutionary trends in turritelline shell evolution that may have occurred could only have taken place in the Mesozoic.

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APPENDIX 1

Frequencies of drilling and peeling in 27 fossil species of Cenozoic turritellines. All specimens are in the collection of the Department of Invertebrate Paleontology of the Museum of Comparative Zoology.

Species (Age)	Locality	Formation	*N*	Frequency	
				Drilling (%)	Peeling/ repair
T. abrupta Spieker Miocene	Venezuela	?	23	4	0·00
T. alabamiensis Whitfield Palaeocene	Alabama	Porters Creek	30	10	0·03
T. aldrichi Bowles Palaeocene	Alabama	Porters Creek	32	59	0·31
T. altilira Conrad Pliocene	Panama	Gatun	20	25	0·30
T. alveata Conrad Eocene	Mississippi	Moodys Branch	15	13	0·93
Eocene	Louisiana	Moodys Branch	30	60	0·37
T. apicalis Heilprin Pliocene	Florida	Pinecrest	58	17	0·21
T. carinata I. Lea Eocene	Alabama	Gosport	30	13	0·23
T. cumberlandia Conrad Miocene	Maryland	Calvert	15	13	0·33
T. eurynome Whitfield Palaeocene	Alabama	Nanafalia	30	10	0·60
T. femina Stenzel Eocene	Texas	Weches	30	3	0·00
T. gilberti Bowles Palaeocene	Alabama	Bashi	45	29	0·02
T. gladeënsis Mansfield Pliocene	Florida	Pinecrest	22	27	0·00
			22	23	0·41
T. humerosa Conrad Palaeocene	Virginia	Aquia	32	25	0·03
T. indenta Conrad Miocene	Maryland	Calvert	18	67	0·17
T. larensis Hodson Miocene	Venezuela	?	50	6	0·06
T. mississippiensis Conrad Oligocene	Mississippi	Byram	30	3	0·03
T. mortoni Conrad Palaeocene	Virginia	Aquia	80	4	0·03
			15	17	0·20

APPENDIX 1 (*cont.*)

Species (Age)	Locality	Formation	*N*	Frequency	
				Drilling (%)	Peeling/ repair
T. multilira Whitfield					
Palaeocene	Alabama	Tuscahoma	30	7	0·30
Palaeocene	Alabama	Nanafalia	16	0	0·25
			18	6	0·22
T. perattenuata Heilprin					
Pliocene	Florida	Pinecrest	48	2	0·51
T. perdita Conrad					
Eocene	Mississippi	Moodys Branch	30	7	0·13
T. plebeia Conrad					
Miocene	Maryland	Calvert	30	0	0·00
T. pontoni Mansfield					
Pliocene	Florida	Pinecrest	49	31	0·25
			27	37	0·70
T. postmortoni Harris					
Palaeocene	Alabama	Nanafalia	15	0	0·20
T. praecincta Conrad					
Palaeocene	Virginia	Aquia	30	40	0·07
			22	36	0·00
Palaeocene	Alabama	Tuscahoma	7	0	0·29
			4	50	0·75
			19	0	0·05
T. rina Palmer					
Eocene	Alabama	Lisbon	38	13	0·05
T. rubricollis MacNeil					
Oligocene	Mississippi	Mint Spring	15	0	0·07
T. wagneriana Olsson & Harbison					
Pliocene	Florida	Pinecrest	72	19	0·74

APPENDIX 2

Data from previously published sources on drilling and peeling frequencies in fossil and living turritellines.

Species	Age	Locality	*N*	Drilling (%)
T. acropora Dall	Recent	Bermuda[1]	41	12
T. annulata Kiener	Recent	Ghana[2]	436	62·6
T. badensis Sacco	Miocene	Poland[3]	1229	17·0
	Miocene	Bulgaria[4]	1921	40·4
T. banksi Reeve	Recent	Panama[1]	12	16·7
	Recent	Ecuador[1]	9	0
T. berjadinensis Hodson	Miocene	Venezuela[1]	35	9·0
T. bicarinata (Eichwald)	Miocene	Poland[3]	112	28·0
T. bieniaszi Friedberger	Miocene	Bulgaria[4]	532	36·6
'*T. carinifera* Lamarck'	Eocene	France[5]	51	14·1

APPENDIX 2 (*cont.*)

Species	Age	Locality	*N*	Drilling (%)
'*T. carinifera* Lamarck'	Recent	South Africa[1]	6	0
T. communis Risso	Recent	Shetlands[1]	107	11·0
T. erronea Cossmann	Miocene	Poland[3]	120	25·0
T. exoleta (Linnaeus)	Recent	Tobago[1]	48	4·3
T. funiculosa Deshayes	Eocene	France[5]	77	58·4
T. gatunensis Conrad	Pliocene	Panama[1]	70	64·0
T. gonostoma Valenciennes	Recent	Mexico[1]	70	40·0
T. granulata Sowerby	Cretaceous (Albian)	England[6]	704	3·7
T. howelli Harbison	Cretaceous (Campanian)	Mississippi[1]	83	1·0 (0)*
	Cretaceous (Campanian)	Mississippi[7]	16	6·3 (0·47)*
T. imbricataria Lamarck	Eocene	France[5]	45	17·8
T. leucostoma Valenciennes	Recent	Mexico[1]	35	26·0
T. mariana Dall	Recent	Mexico[1]	36	36·0
T. mauryana Newton	Eocene	Nigeria[8]	6	16·7
T. mortoni Conrad	Palaeocene	Virginia[1]	14	7·0
T. nodulosa King & Broderip	Recent	Panama[1]	151	26·0
T. pagoda Reeve	Recent	New Zealand[1]	50	2·0
T. perdita Conrad	Eocene	Mississippi[1]	70	21·0
T. plebeia Conrad	Miocene	Maryland[1]	101	27·7
	Miocene	Maryland[9]	416	21·0
T. postmortoni Harris	Palaeocene	Alabama[1]	12	0
T. praecincta Conrad	Palaeocene	Alabama[1]	27	0
T. subangulata d'Orbigny	Miocene	Bulgaria[4]	189	21·7
T. symmetrica Hutton	Recent	New Zealand[1]	57	19·3
T. tricarinata	Pliocene	Italy[10]	19	52·6
T. trilira Conrad	Cretaceous (Campanian)	Alabama[1]	13	0
T. triplicata (Brocchi)	Recent	Libya[1]	34	47·1
T. unisulcata Lamarck	Eocene	France[5]	14	50·0
T. variabilis Conrad	Pliocene	Florida[1]	40	20·0
T. variegata (Linnaeus)	Recent	Gulf of Mexico[1]	53	12·0
T. vertebroides Morton	Cretaceous (Campanian)	Mississippi[1]	11	9·0
T. sp.	Recent	Mozambique[1]	47	19·0
T. sp.	Recent	Philippines[1]	138	68·0
T. sp.	Recent	India[1]	61	10·0
T. sp.	Cretaceous (Campanian)	Mississippi[7]	17	12·0 (0·41)*
T. sp.	Cretaceous (Campanian)	Mississippi[7]	13	7·8 (0·69)*
T. sp.	Cretaceous	England[6]	2	0

Key: [1]Dudley and Vermeij (1978); [2]Buchanan (1958); [3]Hoffman *et al.* (1974); [4]Kojumdjieva (1974); [5]Fischer (1966) [6]Taylor *et al.* (1983); [7]Vermeij and Dudley (1982); [8]Arua (1982); [9]Kelley (1982); [10]Robba and Ostinelli (1975);

* Percent peeling.

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