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Daily growth lines in some living Pectens (Mollusca: Bivalvia), and some applications in a fossil relative: Time and tide will tell

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Abstract

Laboratory experiments on two species from the *Pecten (Pecten)* subgroup of pectinids indicated that they form growth lines with a true (solar) daily periodicity. Experimental subjects that formed growth lines in numbers equal to their days of growth were consistently those with uniform, apparently continuous shell growth, and subjects that formed fewer lines than days were those with stress marks, or disturbance lines. No subjects formed more growth lines than days. Furthermore, those specimens forming stress marks had those marks spaced out in very similar patterns, apparently in response to stressful events in their aquarium, such that the patterns could be correlated, not only between the specimens with interrupted growth, but with the others as well.

In the original experiments, a natural light–dark stimulus had been present (transparent aquaria near an outside window). To test whether the subjects were responding to this stimulus, another experiment was conducted in which several individuals were subjected to an accelerated light–dark regime. These subjects responded by increasing production of their growth lines to approach the number of cycles to which they had been exposed.

An opportunity to extend this work into the fossil record came with the collection of a number of Pliocene pectinids, closely related to one of the species used in the experiments, from a thin horizon that almost certainly represents a catastrophic event. Measurements of the intervals between growth lines were made across hundreds of increments on many paired (and presumably untransported) valves. Comparison of these growth rate records suggested that many, and perhaps all of these individuals died at the same time. Moreover, frequency analysis of these records revealed a regular fluctuation of about 15 days, suggesting a tidal cycle marked off by solar increments. When the growth rate patterns were compared with nearby tidal regimes, the best fit was for a regime matching the currently accepted paleogeography of the collecting site in Pliocene time. This strongly supports the experiments on the living species, for tidal patterns in the fossil group could not have been revealed without an accurate solar marker.

Keywords: Growth; Periodicity; Tidal currents; Pliocene; Gulf of California

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1. Introduction

As discussed in an earlier review article (Clark, 1974b), periodic growth lines can be valuable sources of information about fossil organisms and their environments. This is especially so when the periodicity represents intervals on the order of days or less, and when the growth rates change in response to environmental variations. Under favorable conditions, long sequences of this sort could permit identification of seasonal variations in growth, disturbances by storms or by other organisms, the ages of particular individuals, and the approximate time of year that the individual died. Moreover, comparisons of individuals within a fossil assemblage could lead to conclusions about contemporaneity, much like the examination of tree rings in dendrochronology.

Such sequences of growth lines can also be examined from the perspective of paleoecology. Just as matching patterns of disturbance zones can give evidence for contemporaneity within a population, so would they suggest an environment, such as shallow water, where extreme conditions occur. In similar manner, seasonal halts in growth would suggest cold winters or hot summers, or perhaps both. In exceptional cases (e.g., Evans, 1972), the very position of an organism within the tidal zone can be determined, or (as reported here) the relationships between ancient tides and the basin that contained them can be inferred.

Fundamental to all this is the assumption that the growth lines to be examined are truly periodic, and that the periodicity is known. Unfortunately the entire field of growth line studies has been confused by the great variety of organisms studied, by the significant differences in study methodologies, and, sadly, by a few studies driven more by wishful thinking than by objectivity. This, in turn, has led to criticism by several scholars, a few of whom seemed to find satisfaction in rejecting the whole concept.

Ordinarily I would prefer to begin this report with new information, regarding an assemblage of Pliocene pectinids bearing growth line sequences of remarkable interest; but if those results are to be taken seriously I must first establish the basis for accepting the daily periodicity of these growth lines. The best evidence, of course, would come from observations on living specimens, preferably of the same or a closely related species. I have conducted such experiments, but the results were not as straightforward, and my reports (Clark, 1968, 1975) not as complete, or well explained, as some critics would have liked (see, for example, Crisp, 1989). I lack the means to run new experiments, but I will begin this report with a more exacting recital of the evidence and reasoning behind my interpretation of these earlier results: that this group of pectinids forms external growth ridges with a daily periodicity.

2. Experimental evidence for a daily periodicity

2.1. Experimental subjects

The most consistent experimental evidence for daily growth lines comes from two species within the *Pecten (Pecten)* subgroup (see Hertlein, 1969): *Flabellipecten diegensis* and *Oppenheimopecten vogdesi*. Short-term observations on a third species, *Euvola ziczac*, suggested daily growth line formation, but I was unable to complete any experiments on this form. These represent three of the four extant genera in the subgroup; the other is *Pecten* itself. I have done no experimentation with species of *Pecten*, although *Pecten maximus* has received attention from a number of workers (for example, Gruffydd, 1981, and Owen et al., 2002), with generally negative results.

F. diegensis, *O. vogdesi*, and *E. ziczac* all have nearly flat left (upper) valves, and excavate shallow pits in the sediment in order to lie with these valves even with the substrate surface. They achieve this excavation by jetting water from alternate sides of their shells, both downward to excavate sediment and upward to rotate themselves into the depression, and in the process stir up enough sediment for a layer to accumulate on their upper surfaces, effectively concealing them when closed (Fig. 1). It may be significant to this habit that the two species with the greatest convexity on the right (lower) valves have very smooth surfaces there, with fine concentric ridges on their left valves only. Only *F. diegensis*, with little convexity on the right valve, has raised ridges on both.

What might be the function of these fine concentric ridges? One thought is that they might discourage larvae of encrusting organisms from settling, for