Shell color and predation in the Cretaceous oyster *Pycnodonte convexa* from New Jersey

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Introduction

Original shell coloration, preserved as radial bands in a gryphaeid oyster species from the Upper Cretaceous Navesink Formation in New Jersey, record a history of predation attempts by durophagous predators through the life of the oyster. A majority of left valves of the oyster *Pycnodonte convexa* preserve original shell coloration in the form of reddish brown radial bands, similar to those reported in other species of gryphaeidae. The bands vary greatly among individual oysters both in number and thickness. Of particular interest is the observation that the color bands are discontinuous, being laterally offset along multiple shell growth lines. Growth lines associated with the offsets usually show evidence of disruption in the form of abrupt thickening, healed, crenelated breaks, and localized, abrupt changes in the slope of the outer shell surface.

Color-band offsets do not appear to be a diagenetic feature. There is no evidence of disruption or damage on the valve interior, nor are any of the valves crushed or damaged as a result of shell dissolution. Apparently, the offsets were generated by repeated disruptions of the valve margin during growth. My working hypothesis is that the color-band offsets record unsuccessful predation attempts resulting in damage to the shell margin along the plane of commissure. Injury to the mantle tissue along the plane of commissure or extreme withdrawal of the mantle away from the commissural shelf could have resulted in a repositioning of the regions of the mantle secreting pigmented shell. If so, then band offsets provide a new metric for assessing the intensity of durophagous predation on *Pycnodonte*.

Figure 1. Left valve of *Pycnodonte convexa* showing color bands extending from umbo at top left to plane of commissure at bottom. Three distinct lines of color-band offset are apparent. (Click on thumbnail for larger image.)

Shell Color in Fossil Oysters

Navesink Formation exposures on the northern New Jersey coastal plain contain large specimens of the gryphaeid species *Pycnodonte convexa* preserved in muddy glauconitic sands representing outer continental shelf environments (Owens and Sohl, 1969). In the Navesink Formation shell preservation can be exceptional, to the extent that bands of original shell color are preserved in many specimens of *Pycnodonte* collected from the creek beds of central New Jersey. Coloration in *Pycnodonte* occurs as brownish to reddish radial bands in the outer calcite shell layer that extend from the umbo to the plane of commissure on the coiled left valve (Fig. 1).

The chemical nature of the pigment is unknown, however, mollusks are known to incorporate a variety of organic pigment molecules in their outer shell layer, the most common being uroporphyrin-1 (Fox, 1966). The pattern of banding is highly variable from individual to individual, ranging from thick bands that cover most of the shell to a few grouped bands or a single thin band (Fig. 2). Color bands in *Pycnodonte convexa* have been reported previously in specimens from Utah and New Jersey (Stokes and Stifel, 1964) but their ubiquity in the Navesink Formation is previously unrecognized. In many specimens biocorrosion and impregnation of the shell by clay particles obscures the color bands. Even on well-preserved shells the bands can be missed if the shell is dry and is not examined carefully. Fortunately, the banding pattern is greatly enhanced when viewed under long wave UV radiation (black light). Under black light, the calcite oyster shell fluoresces with a pale glow and the bands appear dark against the light background (all specimens shown in Fig. 2 were photographed under black light). Although shell coloration is rarely preserved in most fossil species, radial color bands have been noted in a variety of fossil gryphaeids and in one gryph-shaped ostreid (Stenzel, 1971), suggesting that this may have been a common color pattern in these oysters.

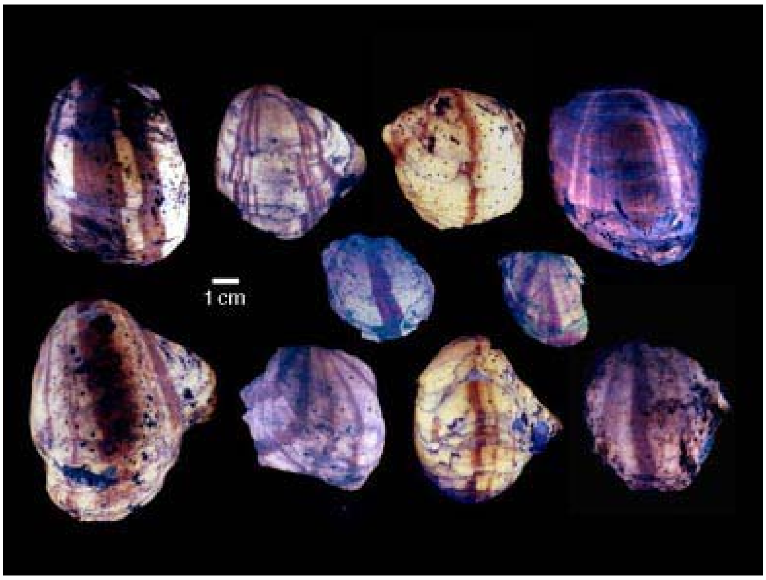

Figure 2. Montage of ten valves showing the variation in color-band pattern between individual oysters. All specimens photographed under longwave UV (black light). (Click on thumbnail for larger image.)

Color Band Disruptions

In almost all *Pycnodonte* valves preserving color, the color bands are periodically shifted to one side or the other, as if displaced along tiny faults (Fig. 3). An episode of offset usually affects all bands on the valve, but in some cases only one side of the valve shows offset. Offset occurs equally as left lateral and right lateral relative to the umbo, with both types of offset occurring on the same valve, and in a few cases, along the same growth line. There is no evidence of compression of the shell wall or of disruption of the shell because of compaction. Indeed, the inner surfaces of the valves are smooth and undisturbed, showing that the oyster fossils are undamaged by diagenetic processes such as compaction and dissolution. Instead of forming after burial, the color-band displacements must have occurred during growth of the shell. In animals that grow by lateral accretion of the valve margin, pigment in the outer shell layer can only be incorporated into the shell as it is secreted along the margin of the valve by the mantle tissue. An abrupt shift in the position of the color bands implies an abrupt shift in the position of the mantle tissue secreting the shell. The question then becomes; what would cause such a shift in the position of the mantle tissue? A possible answer may be found in the observation that color-band shifts are also commonly marked by prominent disruptions in the growth lines of the shell. Growth lines along displaced bands usually show evidence of disruption in the form of abrupt thickening, healed, crenelated breaks, and localized, abrupt changes in the slope of the outer shell surface. On many specimens it appears as if the shell margin was broken irregularly and then later repaired, but with the mantle in a slightly different position, leaving the newly formed shell bands, although of the same number and width as before, in a different position along the margin of the shell after the break (Fig. 3). On some valves color-band shifts are associated with v-shaped indentations in the margin of the shell that have been identified by other workers as the scars of unsuccessful predation attempts (Fig. 4).

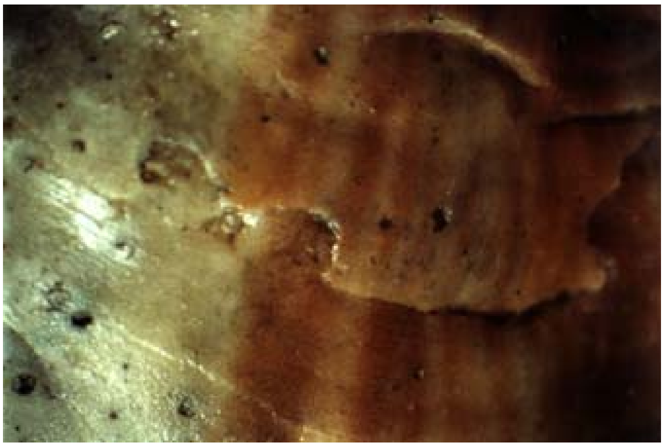

Figure 3. Growth line along color-band shift showing jagged indentations indicative of damage during growth along the valve margin. (Click on thumbnail for larger image.)

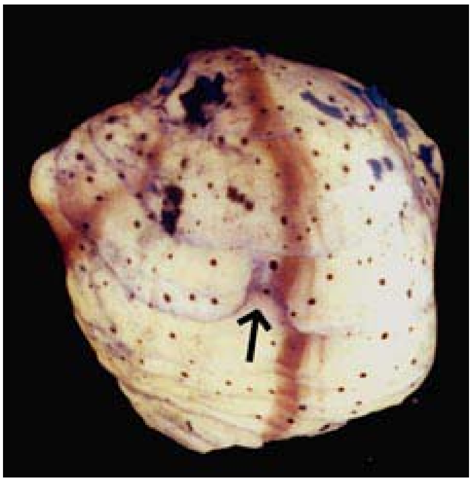

Figure 4. Left valve of *Pycnodonte convexa* showing v-shaped indentation characteristic of damage due to crustacean predator. Note that the damage point is associated with a shift in the position of the shell color band. (Click on thumbnail for larger image.)

Oyster Predation

Modern oysters have many predators, but they commonly fall victim to the feeding activities of durophagous crustaceans (crabs and lobsters) and drilling gastropods (such as the infamous *Urosalpinx* or "oyster drill"). Gastropod attacks are easy to spot as they result in the creation of a small but distinctive drill hole in the shell of the prey. Crustaceans such as crabs manipulate bivalve prey with their legs and claws, attempting to use the larger claw to snip away at and to crush the shell margin (Hickman, 1972; LaBarbera, 1981). If a crab attack is successful, the shell may be broken into pieces, obscuring the nature of its demise. If the attack is unsuccessful, the shell margin will heal as the oyster continues to grow by accretion. A deep enough break in the shell will permanently alter the shape of the shell margin, resulting in a prominent breakage scar, and Cretaceous oysters commonly bear indentations and other signs of breakage-induced shell repair (Dietl, et al., 2000). In a remarkable study, LaBarbera (1981) demonstrated that modern crab species (blue crabs and stone crabs) will attack and attempt to consume resin models of extinct gryph-shaped oysters. These observations and the association of color band shifts with healed shell damage suggest that the color-band displacements and accompanying growth line disruptions seen in the Navesink *Pycnodonte* may have resulted from unsuccessful predation attempts by durophagous crustaceans. These attacks, although not lethal, may have damaged the shell margin sufficiently to shift the position of the mantle tissue and change the position of the color bands secreted after the attacks. If this hypothesis is correct, then the preserved shell color in *Pycnodonte* provides a unique window into the predation pressure exerted on a population of Upper Cretaceous gryphaeid oysters. The Upper Cretaceous has been argued to be a critical period in the evolution of gryphaeid oysters - the time when their evolutionary radiation became increasingly influenced and checked by the concurrent radiation of their marine predators (Dietl, et al., 2000; LaBarbera, 1981; Vermeij, 1977). By tabulating the number of predation events recorded by individual oysters, questions of prey selectivity and predation survivability can be addressed and the role of durophagous predators in the eventual decline of the gryphaeidae can be better understood.

Acknowledgements

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