

The Role of Spinose Ornament in Predator Deterrence and Epibiont Colonization: The Bivalve *Arcinella*,
Pinecrest (Pliocene) of Florida

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THE ROLE OF SPINOSE ORNAMENT IN PREDATOR DETERRENCE AND EPIBIONT COLONIZATION: THE BIVALVE *ARCINELLA*, PINECREST (PLIOCENE) OF FLORIDA

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The spinose shells of the sessile, epifaunal bivalve *Arcinella cornuta*, from the fossiliferous Pliocene Pinecrest and Caloosahatchee beds of Florida, provide evidence of ecological interactions with both boring predatory gastropods and commensal bivalves. The number, sizes, and positions of borings in *A. cornuta* were compared to parameters such as size of the valve and density of spines at the boring site to determine to what extent spines influenced the borers.

Records of attacks by naticid and muricid gastropods are preserved as borings in the shells of their putative prey. Gastropods can exhibit stereotyped attack patterns and can be highly selective with regard to prey size and boring site in order to optimize net energy return.

Although some site and size selectivity was evident, attack strategies toward *A. cornuta* shifted over time. Spine density at boring sites was negatively correlated with boring frequency, demonstrating that spines hindered predatory attacks. Smaller predators were selective and most often bored at the thinner posterior region of the shell. Larger predators were less selective and most often bored at the lunule; the thickest portion of the shell, but the only area unobstructed by spines. Larger predators apparently accepted longer boring times in order to increase chances at success. Over time, establishing two preferred boring sites enabled predators to optimize their attacks. This direct link between prey morphology and predator

adaptation signals that an arms race between these two species may have been underway.

A. cornuta shells were also the preferred habitat of boring gastrochaenid bivalves, signaling a shift in the borer's habitat. Some species of the bivalve family Gastrochaenidae dwell in semi-endolithic boreholes partially covered by secreted calcareous envelopes or crypts.

Gastrochaenids selectively colonized shells of *A. cornuta* to exploit the feeding currents, armor, and raw materials provided by the host. The distribution of borings and crypts indicates that gastrochaenids colonized and grew within the spines of *A. cornuta*, orienting their siphons to exploit feeding currents created by the host. As the gastrochaenids matured and outgrew the space available within the spines, they incorporated them into their crypts.

Foreword

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INTRODUCTION

Interaction between species, both cooperative and competitive, facilitates an evolutionary dynamic that offers species the opportunity to adapt to increase their potential for success. Understanding this dynamic is vital to gaining insight into the development of any ecosystem over evolutionary time. While ecologists have the opportunity to observe such interactions firsthand, paleoecologists are often forced to rely on inferred relationships between long-extinct species since symbionts are rarely preserved with their hosts, and predator and prey are seldom found preserved in a death struggle. Any encounter between species that leaves a clear trace in the fossil record is, therefore, valuable to paleoecologists. One such encounter is a predatory attack by a carnivorous gastropod that penetrates the shell of its victim by a process of physical and chemical abrasion, leaving behind a characteristically shaped borehole (Carriker, 1981; Kabat, 1990; Kowalewski, 1993; Sohl, 1969). Another encounter is the colonization of a shell by one of a number of boring bivalves that also employ physical and chemical means to construct domiciles (Savazzi, 1999). Traces of shell borers have been recorded as far back as the Cambrian, traces of endolithic bivalves back to the Triassic, and reliable traces of gastropod attacks to the Jurassic (Savazzi, 1999; Sohl, 1969). Because of their preservation potential and extensive fossil record, these mollusk borings provide a rare opportunity to study interactions between species over evolutionary time.

Evidence from the Pliocene shell beds of Florida suggests the spinose tropical bivalve *Arcinella cornuta* was simultaneously involved in competitive interactions with boring

gastropod predators and commensal interactions with boring bivalves. The evidence raises questions regarding the role of spinose ornament in interspecific encounters. Did the spines of *A. cornuta* deter or hinder predatory attacks? How did predators react to the defensive challenges posed by spines? Did the ornament of *A. cornuta* offer epibionts advantages not available from other hosts? The goal of this study is to answer these questions by examining the traces left by borers for clues to their behavior. Patterns and shifts in boring strategies will reveal the degree to which spinose ornament affected these borers and provide greater insight into the ecological interactions of epifaunal organisms and the forces that influence their evolution.

COEVOLUTION AND THE "ARMS RACE"

Responses to environmental threats, both physical and biological, have been a major driving force of adaptation throughout the history of life (Vermeij, 1987). Species that are successful over evolutionary time adapt in an effort to bridge the gap between the capacity of the individual to survive and the challenges posed by its environment. To do this, species must make compromises among numerous possible adaptations that, when combined, will place the individual in the best economic position to survive, reproduce, and increase the representation of its descendants in the next generation. Species that cannot bridge the gap either become extinct or are forced to limit themselves to less challenging environments (Vermeij, 1987). As successful species become better adapted to their environment interspecific competition and exploitation become more intense, prompting the need for more efficient adaptations to those stressful interactions. The "nearly universal" (Dietl and Kelley, 2002) threats from predators are important catalysts for such adaptations, as prey species are forced to adapt to protect themselves from attack. They can also be the first salvos in a battle driven by coevolution, or reciprocal adaptation of species, with predator and prey each influencing the evolution of the other (Dietl and Kelley, 2002). This coevolutionary scenario is known as an arms race. It is similar to a military arms race between two nations that challenge each other with increasingly destructive weapons and impregnable defenses, prompting the creation of more devastating weapons and stronger fortifications. Over time, a predator involved in an arms race becomes more efficient at capturing and killing its prey. The prey adapts to survive or avoid attacks by

predators. The predator then counters with an adaptation of its own that increases its effectiveness against the new defense. The prey counters with another adaptation, and so on. Adaptations on both sides may continue until the costs of, or trade-offs with, competing functions override selection for greater offensive or defensive capabilities. The pressure to continue the arms race need not be equal for both sides—the consequences of failure are far greater for the prey than for the predator.

Intrafamilial behavior patterns tend to remain stable over evolutionary time, but species-level behavioral changes may occur with greater frequency. Such behavioral changes can also occur more rapidly than changes in morphology (Boucot, 1990). Behavioral adaptations may then be the more likely manifestations of inter-species arms races, as morphological adaptations are less likely to develop in time to effectively respond to the threats posed by competitors.

While the arms race analogy has been widely employed to describe predator-prey systems, scant evidence suggesting that predators respond evolutionarily to their prey has been observed. Adaptations by predators are more likely to be "unilateral"; caused by escalation pressure from the predators' own enemies and competitors (Dietl and Kelley, 2002, Vermeij, 1987). Shifts in predatory behavior have been observed in response to so-called "dangerous" prey—species with the ability to turn on their attackers (Dietl and Alexander 2000). The potentially injurious behavior of the prey may have forced the predator to adapt in response. For a true arms race to occur, both predator and prey must adapt reciprocally, in direct response to each other.

BORING GASTROPOD PREDATORS

Most groups of predatory gastropods emerged during the Mesozoic (Taylor, Morris, and Taylor, 1980), their origin a part of the predatory advances of the Mesozoic marine revolution (Vermeij, 1977). Some of these new predators adopted the strategy of penetrating calcium carbonate shells through chemical and physical attacks. Shell-borers developed among the Mesogastropods, Neogastropods, nudibranchs, and pulmonates (Kabat, 1990). Today, most boring species are subtropical to tropical and range from intertidal zones to depths of 2,700m (Carriker, 1981). Of these, the most frequently studied and best-known are the Naticacea (Mesogastropoda) and Muricacea (Neogastropoda).

Among gastropods, the strategy of shell penetration by chemical dissolution and physical abrasion first appeared in the late Cretaceous (Cenomanian) in the superfamily Naticacea (Sohl, 1969). Although they were anatomically different, the borers of the distantly related Naticacea and the superfamily Muricacea (which appeared later in the Cretaceous (Campanian) (Sohl, 1969)) converged on a single attack strategy. Each possessed an accessory boring organ (ABO) that secreted enzymes and acids to soften the prey shell. The radula was used to rasp away at the weakened shell material and create a borehole to gain access to the prey's soft tissues. This type of attack left characteristic traces in the prey shell that increased in frequency from the Cretaceous through the Tertiary as borers diversified (Sohl, 1969). The total number of muricid and naticid species that possessed the ability to bore has yet to be determined (Carriker, 1981).

The known predatory behavior of naticid and muricid gastropods was thoroughly described by Carriker (1981) and Kabat (1990). A summary of attack behavior from those studies, with pertinent additions, follows.

Hunting and Attack Behavior of Naticacean Predators

Naticids are restricted to soft substrates and primarily hunt infaunally in coarse, clean to slightly muddy sands, avoiding compacted sediments (although subaerial hunting has been observed in at least one naticid species, *Natica gualteriana*) (Kabat, 1990; Savazzi and Reyment, 1989; Taylor, Morris, and Taylor, 1980). Their hunting strategy most likely evolved in response to the retreat of many bivalves to infaunal habitats during the Mesozoic. Naticids commonly prey on infaunal bivalves, gastropods, scaphopods, and ostracods. They are sometimes cannibalistic (Dietl and Alexander, 2000; Kabat, 1990). When hunting, it is likely that naticids seek out both chemical effluents and vibrational signals from burrowing prey. When a prey animal is detected, the naticid predator burrows into the sediment toward it. After locating the prey, the naticid grasps the shell with its exceptionally large foot and immobilizes it with a coat of mucus. The prey is then manipulated into a preferred position for boring. The typical position of the borehole varies with both predator and prey species, but naticids usually bore at a specific position on a preferred valve. The naticid alternately applies its ABO (located under the ventral lip of the proboscis) and radula to the boring site. The proboscis is rotated through ninety-degree sectors, rasping one quadrant of the borehole at a time, from its center to its edge. This leaves an elevation in the center of the hole where the least rasping occurs, a prominent feature in incomplete boreholes. Loose fragments of

the bored shell are ingested by the naticid and excreted. After an entire cycle of rasping, the proboscis is replaced by the ABO, which dissolves another thin layer of shell to be rasped away (Carriker, 1981; Savazzi and Reyment, 1989). Once the shell is breeched, the naticid feeds on the flesh of the prey animal through the hole. The detection, subjugation, and boring of prey usually occur entirely within the sediment. Some naticid borers are known to pursue and immobilize bivalve prey with the large foot until the shell gapes and the predator can feed directly on the soft tissues, eliminating the need for boring (Frey, Howard, and Hong, 1986).

Hunting and Attack Behavior of Muricacean Predators

Muricids live on firm or hard substrates and prefer to hunt epifaunal prey, such as oysters, barnacles, gastropods, bryozoans, and small crabs (Carriker, 1981, 1998; Taylor, Morris, and Taylor, 1980). Due to their economic impact, the hunting behaviors of muricids such as *Urosalpinx cinerea*, the oyster drill, have been well documented. When hunting, a muricid seeks out chemical cues from the exhalent water of living organisms. Once the muricid locates a prey animal, it begins a period of exploration across the shell and intermittently passes the proboscis over the shell surface. How the predator determines the specific site for boring is unclear (Carriker and Van Zandt, 1972). Most muricids bore through one valve, although some bore at the ventral shell margin (Carriker, 1998). The snail positions itself on the prey shell with the ABO (located in a pore in the mid-anterior ventral region of the foot) over the prospective boring site, clinging to the shell with its foot (Carriker, 1998). After the ABO is applied for a period of shell dissolution, the posterior part of the foot remains firmly attached to

the shell, while the anterior portion forms a tube down which the proboscis is extended. The radula rasps at the weakened shell, and is then retracted to allow the ABO to dissolve another thin layer at the bottom of the borehole. This process is repeated until the borehole breaks through to the interior of the shell and is large enough to admit the proboscis, which the snail inserts into the cavity to feed on the flesh (Carriker and Van Zandt, 1972).

Description and Identification of Gastropod Boreholes

Gastropod boreholes are generally circular in plan view, perpendicular to the shell surface and have diameters that decrease slightly with depth (Carriker, 1981, 1998). In shells composed of homogeneous material borehole walls are macroscopically smooth. Shell layers of different hardness or composition, however, give rise to irregularities in the borehole diameter. The inner edge of the borehole (nearest the soft tissues) may be sharp, smooth, or jagged (Carriker, 1998; Carriker and Van Zandt, 1972). The external diameter of a borehole is generally determined by the size of the predator (Carriker, 1998; Carriker and Van Zandt, 1972; Kitchell et al. 1981).

Naticid boreholes have a spherical parabolic shape that is truncated at the point of shell penetration. The outer opening is usually enlarged with a wide beveled rim that gives the borehole a countersunk appearance (Kabat, 1990; Kowalewski, 1993). Incomplete naticid boreholes are often characterized by a central boss or rounded elevation (Kabat, 1990; Thomas, 1976).

Muricid boreholes vary in cross section, but are typically subcylindrical to cylindrical (Carriker, 1981; Carriker and Van Zandt, 1972; Kowalewski, 1993). Muricid boreholes

may also appear to be countersunk (Carriker, 1981), but incomplete boreholes show no evidence of a central boss (Fretter and Graham, 1962; Thomas, pers. com. 2002).

Naticid and muricid boreholes cannot be accurately distinguished merely by their appearance. Indeed, the shape of a gastropod borehole may be affected by a number of factors other than taxonomy of the boring predator, such as borehole site and prey morphology, thickness and structure of the bored shell, and taphonomic alteration (Kowalewski 1993). Because naticids and muricids hunt in nearly exclusive environments habitat of the prey animal may be the deciding factor in determining the putative predator.

Stereotyped Attack Behavior

Specialized attack behavior has been recorded for both fossil and recent gastropod predators. Kitchell et al. (1981) concluded that recent naticid predators selected their prey nonrandomly and employed a predictable cost-benefit hunting strategy designed to deliver maximum energy return for minimum energy output. Through tactile manipulation, predators consistently identified prey that was small enough to be easily subdued, but large enough to make the attack worthwhile from an energetic standpoint. Comparisons of borehole diameters (a proxy for predator size) and prey lengths showed positive correlation. This indicated naticids practiced size stereotyped behavior, i.e., behavior in which predators of a certain size preferred prey of a certain size. They also demonstrated site stereotyped behavior, or nonrandom selection of the boring site. Studies of naticid attacks in both the fossil record and the recent show similar stereotyped cost-benefit-based hunting strategies (Allmon, Nieh, and Norris, 1990;

Anderson, 1992; Anderson et al. 1991; Berg and Nishenko, 1975; Dietl and Alexander, 1995, 2000; Kelley, 1988; Kelley and Hansen, 1993, 1996; Kitchell et al. 1981).

Muricids have also anecdotally demonstrated selective attack behavior. Individual *Urosalpinx cinerea* have the ability to change and improve their attack techniques over time (Wood, 1968). Stone (1998) recorded stereotyped attacks by muricid predators while testing their response to heavily ornamented prey. The muricid *Thais luteostoma* was observed to manipulate its prey into a preferred orientation during subjugation and displayed extreme site selectivity, refusing to attack smooth valve surfaces when its preferred attack site, the byssal gape, was blocked by artificial spines. Its rejection of spinose prey animals was determined to be, in part, a result of unfavorable tactile stimuli. In the same study, the muricid predators *Chicoreus microphyllus* and *Thais clavigera* preferentially selected prey animals with little or no ornament over those that were spinose. They also preferentially attacked the nonornamented attachment surfaces of *Chama reflexa*, a normally cemented bivalve dislodged for the experiment. Taylor (1990) and Harper & Skelton (1993) suggested that the spines of the intertidal oyster *Saccostrea cucullata* also deterred boring by muricids.

Predictable stereotyped behavior provides the basis for studying perturbations in gastropod attacks. If spines or other heavy ornament were effective deterrents to gastropod predators, stereotyped behavior should be disrupted. Spines could disguise the true size of a prey animal thus disrupting the selection of appropriate prey or providing the prey a "virtual size refuge". If spines hindered a predator's ability to manipulate prey or bore at a preferred location site selectivity could be muted.

Alternately, borings could be confined to nonornamented regions of the shell. If a true arms race had occurred, a shift in the predators' attack strategies should be observed over time.

BORING GASTROCHAENID BIVALVES

Some bivalves actively excavate domiciles in a variety of solid substrates by chemical etching, mechanical abrasion, or a combination of the two. They invaded the endolithic habitat in successive adaptive radiations during the Triassic, the Jurassic and Cretaceous, and the Cenozoic. Over time, they have adapted to live in a variety of materials, including coral, mollusk shells, rock of varying lithology, wood, bone, brickwork, concrete, metal, and plastic (Kelly and Bromley, 1984; Savazzi, 1999). Some maintain mutualistic relationships with living hosts (Vance, 1978). Groups of obligatory borers gave rise to tube-dwellers that adapted to living in soft sediments by enclosing themselves in a secreted calcareous crypt. Most recent tube-dwellers are also facultative borers (Savazzi, 1999).

The Gastrochaenidae emerged in the Jurassic as borers of calcareous substrates; generally tropical corals (Carter, 1978; Savazzi, 1982). Their boring strategy combined chemical and mechanical processes that gave them the flexibility to occupy habitats containing larger amounts of sand or silt than those occupied by other borers such as *Lithophaga*. Some gastrochaenids adapted primarily to boring, whereas others adapted to tube-dwelling.

Gastrochaenid borings are classified as the ichnotaxon *Gastrochaenolites dijugus* (Kelly and Bromley, 1984). The borehole is divided into two well-defined parts: a posterior siphonal borrow and an anterior shell chamber. The entire structure may be several times longer than the borer itself and can be straight or curved. The shell chamber is only slightly larger than the borer in every dimension and is circular to

slightly elliptical in cross-section. A smooth calcareous layer lines the shell chamber, sealing pores in the substrate and strengthening it against breakage and erosion. The calcareous lining can also be used to repair portions of the borehole that have been accidentally exposed because the lining is secreted as a self-sustaining mucous membrane that wrinkles and calcifies soon after it forms (Savazzi, 1982).

As they grow, gastrochaenids periodically extend the anterior portion of their shell chambers. Some borings contain signs of tiny tubules that penetrate the anterior shell chamber lining. These tubules are numerous when borings approach each other or edges of the substratum, suggesting they are part of a probing system that guides the borer. This probing system may allow gastrochaenids to bore without perforating the shell of a living host or the chamber of another borer (Carter, pers. com. 2001).

Gastrochaenids are also capable of extending their siphonal chambers when necessary, especially in instances when the borer is threatened with coral overgrowth (Carter, 1978).

Members of four genera of the family Gastrochaenidae (*Gastrochaena*, *Cucurbitula*, *Eufistulana*, and *Kummelia*) primarily inhabit soft sediments inside unattached tubes or crypts (Savazzi, 1982). The crypt of the tube-dwelling gastrochaenid is homologous with the calcareous lining of endolithic borers, and is similarly formed by a calcifying mucous membrane. Sediment particles and shell fragments may be incorporated into the crypt (Savazzi, 1982). The foot of the tube-dwelling gastrochaenid makes no contact with the sediment. Because of this, the structure of the crypt itself has adapted to maintain the organism in a suitable life position. When its crypt is overturned, the

tube-dweller can also extend its posterior siphonal chambers above the sediment (Savazzi, 1982).

Crypt-building Strategies

It has been theorized that the ability to generate a self-sustaining calcareous envelope as a means of repairing a damaged boring was the adaptation that allowed gastrochaenids to shift habitats from calcareous substrates to soft sediments.

Gastrochaenids have been known to switch from boring to crypt-building habit as the need arises (Carter, 1978 and pers. com. 2001). Specimens of *Gastrochaena rueppelli* extracted from their borings in a coral substrate were observed to build complete calcareous envelopes cemented to an aquarium wall over the span of several days (Savazzi, 1982), and a specimen of *Gastrochaena* (*s. s.*) sp. from the Pliocene of North Carolina that had originally bored into a pectinid shell for support formed an aragonitic crypt after it had outgrown the substrate (Carter, 1978). This versatility allowed gastrochaenids to adopt a semi-endolithic habit in substrates too thin to contain a complete adult borehole, build free crypts in environments where no suitable substrate could be found, or revert to boring other shells to stabilize their crypts if necessary (Savazzi, 1982). Reports of such behavior are anecdotal, and a comprehensive study of the colonization strategies of gastrochaenids has yet to be undertaken.

THE NATURAL HISTORY OF *ARCINELLA*

Little has been written regarding the natural history and ecology of the bivalve genus *Arcinella*. The most recent comprehensive review of the genus (formerly known as *Echinochama*) was presented by Nicol in 1952. This is a summary of that review, with additions of more recent material, as noted.

The genus *Arcinella* contains tropical bivalves whose shells are often studded with an imposing battery of spines (Figure 1). They are the youngest and most extremely ornamented members of the Chamidae, a family that shows a tendency toward increasingly exaggerated ornament over time. The genus first appeared in the fossil record in the early Miocene, and probably originated in Florida. Today, *Arcinella* can be found in the tropical waters of the southeastern United States, northern South America, Central America, and Baja California. The species *Arcinella cornuta* encompasses all specimens of the genus from the Miocene through the Recent collected in the United States

Description and Systematics

Genus *Arcinella* Schumacher, 1817

Type species *Chama arcinella* Linné 1767

[=*Echinochama* Fischer, 1887, non *Arcinella* Oken, 1815] (Cox et al. 1969)

The valves are convex and slightly unequal in size. Both valves are covered by radiating rows of hollow, cylindrical spines. Spines sometimes overlap the margin, especially at the posterior end. Between spine rows, the shell is covered by a secondary nodose ornament, giving the surface a rough, crosshatched texture. The

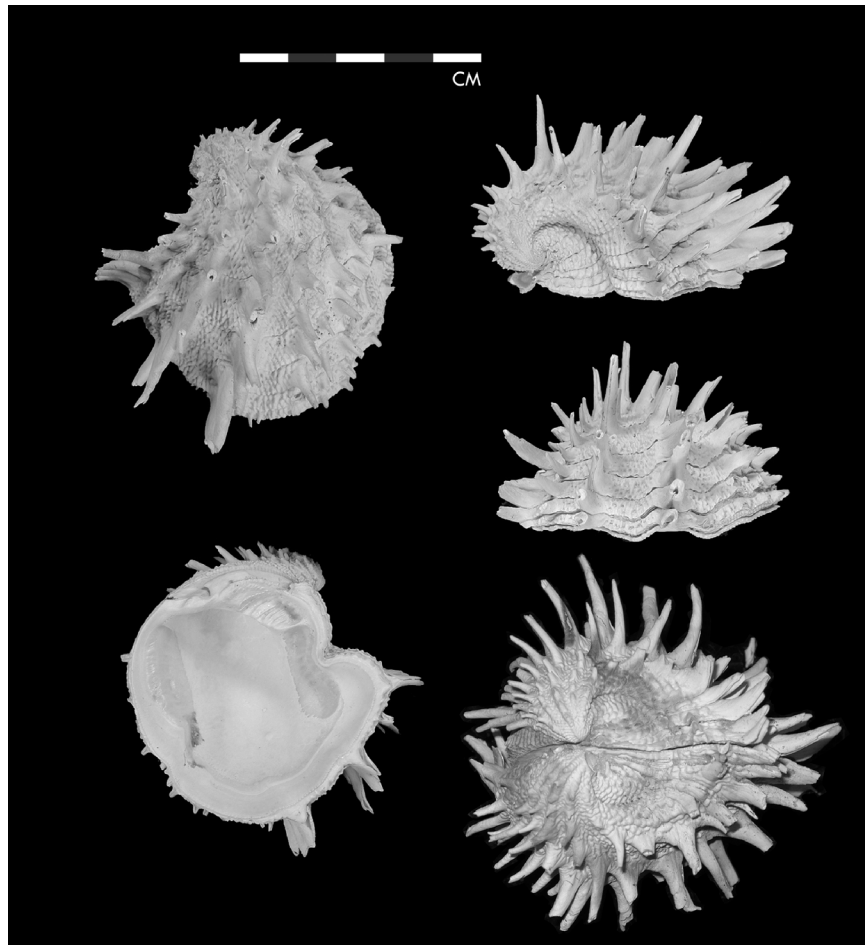


Figure 1. The bivalve *Arcinella cornuta* from the Pinecrest beds of the SMR Aggregates property near Sarasota, Florida.

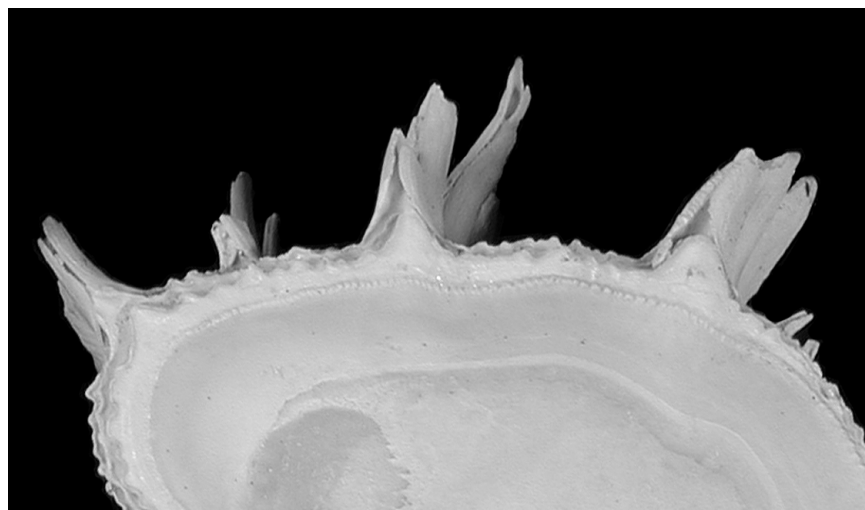


Figure 2. An interior view of *A. cornuta* showing the spines. New spines begin as leafy projections at the margin. As the spines grow, their edges curl toward each other to form hollow tubes.

valves are prosogyrate, and a large, round, depressed lunule is present anterior of the beak of each valve. The lunule is covered by nodose ornamentation, but lacks spines. The juvenile stage is attached, and most individuals carry an attachment scar at the beak of the right valve. The ventral margin is crenulated. The anterior muscle scar is elongated; the posterior scar is more rounded.

Arcinella cornuta Conrad 1866

The species *Arcinella cornuta* includes all the specimens of the genus from the United States. The average ratio of height to convexity is about 0.84, the largest ratio of any species of *Arcinella*. Recent specimens average eight spine rows; Pliocene and older specimens average nine or ten. Larger specimens with eighteen spine rows have been documented.

Geologic age—Miocene to Recent

Geographic distribution—Recent: Cape Hatteras to Yucatan. Fossil: North Carolina, South Carolina, Georgia, Florida.

Ecology

Soon after an abrupt early ontogenetic change in ornamentation, *Arcinella* attaches itself to a rocky or shelly hardground, commonly by the right valve. Some elements of the nodose ornament form a pattern on the shell surface, others elongate and form ribs that give rise to spines. As the spines grow, their sides curl ventrally toward each other, forming elongate tubes (Figure 2). The sides of some spines are only slightly curled; others curl until they overlap each other. Spine growth appears to be episodic and corresponds to growth at the ventral margin. Spine length has been shown to vary with

water temperature (Nicol, 1965). As it matures and no longer requires attachment for stability, *Arcinella* lies freely on the surface, resting on one valve, stabilized by the spines. Its semi-spherical form and extreme ornament suggest that *Arcinella* does not burrow. Indeed, observations of living *Arcinella* confirm that it prefers to lie on firm substrata of broken shells, coral, or gravel rather than soft sediment. Aquarium specimens make no attempt to burrow into sand. *Arcinella* is most often found in warm waters, on shells or gravel, at depths ranging from 18 to 45 m. Extant species range from the Carolinas to northern South America in the western Atlantic and from Baja California to Panama in the eastern Pacific.

Fossil Record and Geographic Range

Arcinella first appeared in the early Miocene, probably originating near Florida (Nicol, 1952). By the middle Miocene, the genus had spread to the Dominican Republic, Mexico, Costa Rica, Panama, Colombia, and Ecuador. During the Pliocene, it moved as far north as Cape Hatteras.

The ancestor of the genus was a species of *Pseudochama*, possibly *Pseudochama draconis* (Dall) from the lower Miocene of Florida. The morphologies of *P. draconis* and *Arcinella* are nearly identical, especially in early ontogeny. The development of an unattached spinose stage and a nearly equivalve shell distinguished *Arcinella* from its ancestor (Nicol, 1952).

By the Pliocene, two main lines of *Arcinella* had been established in the western Atlantic, with *A. cornuta* extending from Florida northward to North Carolina and *A. arcinella* (a larger species with a greater number of spine rows) extending southward

from Cuba to Venezuela. *A. cornuta* can be found among the fauna of several of the Plio-Pleistocene fossil beds of southern Florida.

Today, *A. cornuta* is found in the waters along the coast of North America from Cape Hatteras southward to Florida, west around the Gulf of Mexico to the Gulf of Campeche. At the eastern edge of the Yucatan Peninsula, *A. arcinella* replaces *A. cornuta* and extends southward and eastward through Central America, South America, and the West Indies.

THE PINECREST SHELL BEDS OF FLORIDA

Shells of *A. cornuta* were collected for this study at the Phase Nine pit of the SMR Aggregates (formerly Quality Aggregates) property near Sarasota, Florida, where approximately 5 m of shell beds from the upper Pinecrest beds (Portell, pers. com. 1999) are exposed (Figure 3). Bored shells were also selected from the collections of Dr. Harold Rollins, the University of Pittsburgh, and the Florida Museum of Natural History. In total, 1172 valves of *A. cornuta* from the Pinecrest beds and the overlying Caloosahatchee Formation were examined (Table 1).

The "Pinecrest beds" are a group of shelly quartz sands with many exposures near Sarasota (Figure 4). They are composed of densely packed, poorly sorted, aragonitic and calcitic invertebrate shells in a clean quartz sand matrix, with minor appearances of other lithofacies (Allmon, 1992; Geary and Allmon, 1990; Zullo and Harris, 1992). Despite their faunal richness and geological importance, many details of the lateral extent, stratigraphic correlation, and formation of the Pinecrest shell beds and other Plio-Pleistocene shelly sands in the region remain unclear. Specific compositional details vary from exposure to exposure (Zullo and Harris, 1992), and a numbered scheme that divides the Pinecrest into units based on macrofaunal content (a scheme first utilized by Petuch in 1982) is not always easily applied.

The Pinecrest beds at Sarasota were likely deposited in at least two distinct phases between 3.5 and 2.0 Ma (Allmon, 1993). They are generally grouped into upper and lower units, divided by a disconformity. Both are members of the upper Pliocene Tamiami Formation of southern Florida (Zullo and Harris, 1992) (Figure 5). It has been



Figure 3. The Pinecrest beds at the SMR Aggregates Phase Nine pit near Sarasota, Florida. The bucket is the foreground in approximately 12 inches in height.

Table 1. Pinecrest and Caloosahatchee Formation collection sites.

Site	Unit	Single valves	Paired valves	Total valves	Complete borings	Incomplete borings
Phase Nine pit	Pinecrest	536	94	630	9	8
Phase Six pit	Pinecrest	75	2	77	10	0
Macasphalt shell pit	Pinecrest	315	0	315	16	3
Fort Basinger	Pinecrest	5	0	5	1	0
Mule Pen	Pinecrest	4	0	4	2	0
<i>Total Pinecrest</i>		935	96	1031	38	11
Cochran shell pit	Caloosahatchee	72	0	72	16	2
Desoto shell pit	Caloosahatchee	66	0	66	1	1
Labelle	Caloosahatchee	1	2	3	1	0
<i>Total Caloosahatchee</i>		139	2	141	18	3
<i>Total</i>		1074	98	1172	56	14

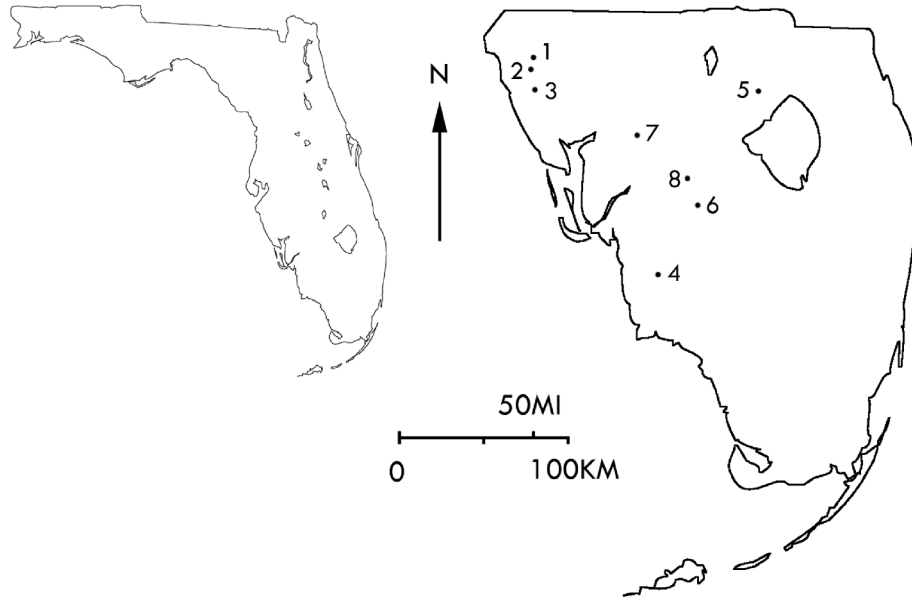


Figure 4. A map of southern Florida collection sites. 1. SMR Aggregates Phase Nine pit. 2. SMR Aggregates Phase Six pit. 3. Macasphalt shell pit. 4. Fort Basinger. 5. Mule Pen. 6. Cochran shell pit. 7. Desoto shell pit. 8. Labelle.

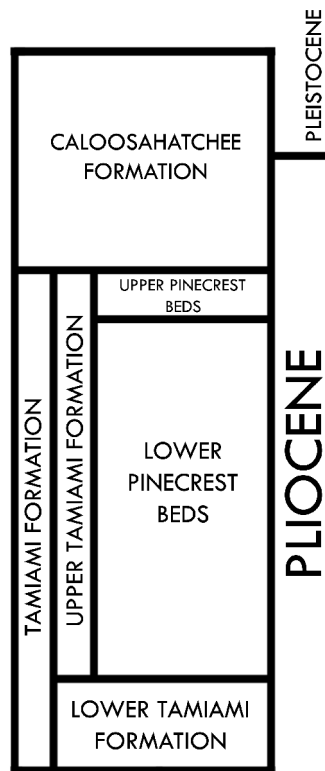


Figure 5. A highly schematic stratigraphic section of the Plio-Pleistocene units exposed near Sarasota, Florida (adapted from Allmon, 1992 and Zullo and Harris, 1992).

suggested that some units of the Upper Pinecrest may correlate with units of the Caloosahatchee Formation, a fossiliferous quartz sand that disconformably overlies the Tamiami Formation (Allmon et al. 1995; Scott, 1992). Because the Caloosahatchee Formation is lithologically similar to the underlying Tamiami Formation, units are often distinguished biostratigraphically (Zullo and Harris, 1992). The exact age of the Caloosahatchee remains unclear; Allmon et al. (1995) consider it latest Pliocene in age.

The beds were deposited in a complex sequence of habitats, from brackish to deep subtidal, during one or more transgressive events (Allmon, 1992, 1993; Jones, 1997). The fauna represents a mix of both tropical and temperate taxa, and varies from site to site (Jones, 1997). Water temperatures were slightly cooler than those found on the modern shelf due to a combination of generally cooler temperatures and upwelling of cool, nutrient-rich waters that fueled high biological productivity in the region (Allmon, 1993).

Evidence suggests the shell beds accumulated through a combination of high biological productivity and physical accumulation by storms or currents, although which process was dominant at any given time remains unclear. This was followed by rapid burial, sediment winnowing, shell condensation, and time averaging (Allmon 1993; Allmon et al. 1995; Geary and Allmon, 1990). Much of the reworking of shells appears to have occurred "in place", with repeated episodes of rapid burial and sediment winnowing, but without much exposure or lateral transport (Allmon, 1992, 1993; Geary and Allmon, 1990).

At the Phase Nine pit, shell beds were densely packed, poorly sorted, and bioclast-

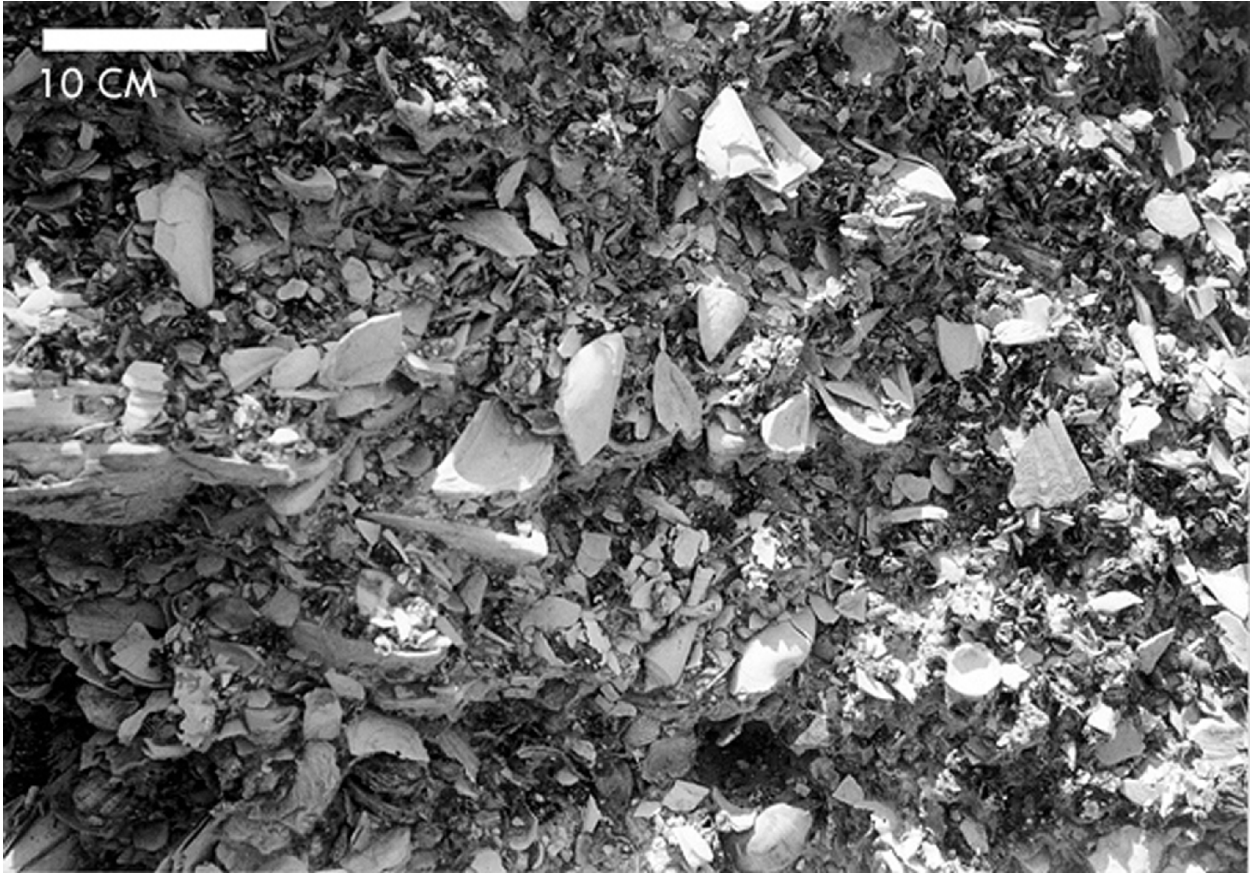


Figure 6. A close-up view of the Pinecrest beds at the Phase Nine pit.

supported (sensu Kidwell, 1991) in a matrix of slightly muddy sand (Figure 6). Some calcite recrystallization and cementing of clasts was observed. Overall, the invertebrate fauna at this site was well preserved, and many delicate specimens were collected. Fifteen percent of *A. cornuta* shells collected at the Phase Nine pit were articulated, suggesting they were buried rapidly (Brett and Baird, 1986). A mix of organisms from both epifaunal and infaunal habitats, such as *Arcinella cornuta*, *Hytissa haitensis*, *Mercenaria mercenaria* and *Chione cancellata*, was observed. Both naticid and muricid gastropods were collected.

METHODOLOGY

Sample Collection at the Phase Nine Pit

At the Phase Nine pit, all valves of *A. cornuta*, both individual and paired, that were observed in the pit walls and adjoining spoil were collected, regardless of completeness or condition. Shells of other taxa and a 0.015 m³ bulk sample were also collected. The individual shells were washed and cleared of matrix. Approximately 2/3 of the bulk sample was wet-sieved for taphonomic analysis. From this portion, size fractions greater than 0.150, 0.710, and 4.0 mm were separated and examined. Identifiable invertebrates, whole and fragmented, were sorted by taxon.

Taphonomic Analysis

The extent of taphonomic alteration at the Phase Nine pit was ascertained by selecting whole and fragmented shells of *A. cornuta* and two species of muricid gastropod (designated "gastropod A" and "gastropod B") from the bulk sample (Figure 7). The muricids were selected for study as potential predators of *A. cornuta*. Each specimen was examined under a binocular microscope and assessed according to a list of taphonomic characteristics. Following the method of Geary & Allmon (1990), shells were examined for evidence of chemical and physical shell damage, borers, encrusters, and predators. The amount of shell damage was assessed by assigning a numerical value to each shell indicating the extent of coverage by encrusters, borers, and carbonate precipitation according to the following system:

0 = pristine or trace coverage

1 = light coverage (less than 25% of the shell affected)

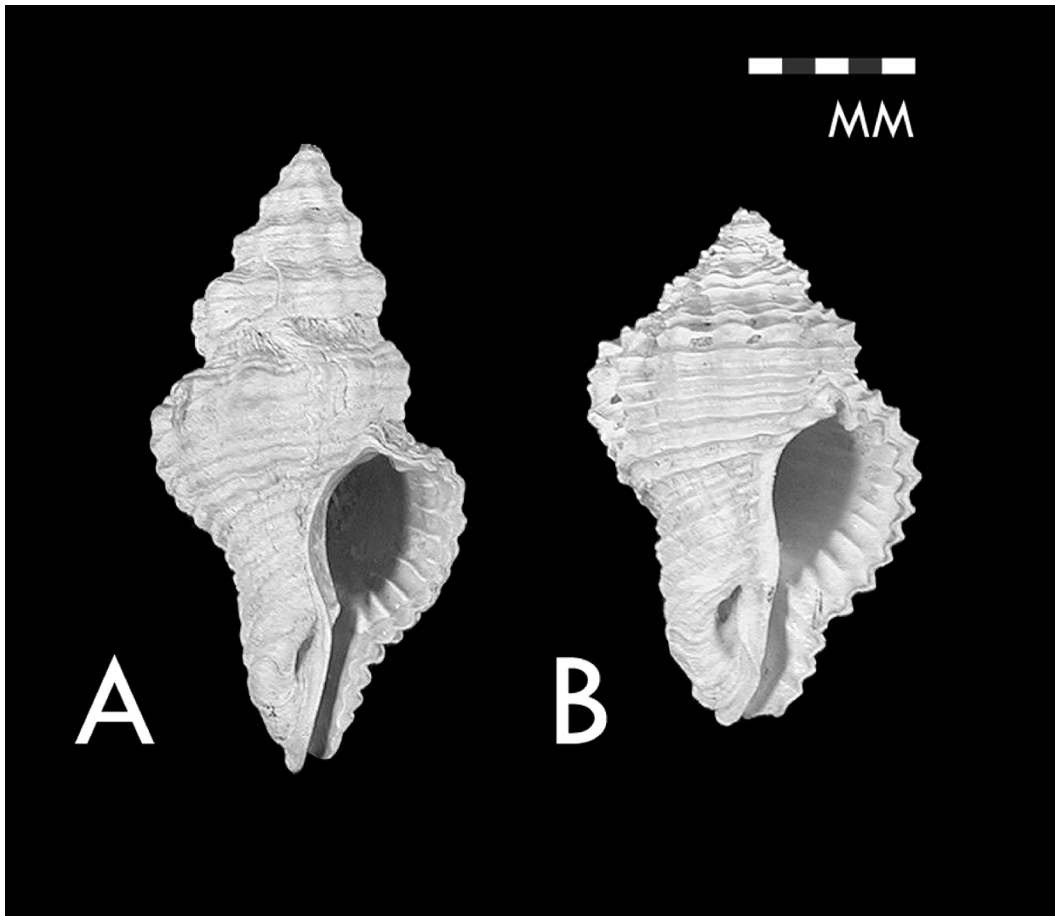


Figure 7. Gastropod taxa “A” and “B” selected from the bulk sample for taphonomic analysis.

2 = moderate coverage (less than 50% of the shell affected)

3 = heavy coverage (50-75% of the shell affected)

4 = very heavy coverage (more than 75% of the shell affected)

Values were assigned for internal, external, and total coverage. The timing of encrustation was also considered. Epi- and endobionts restricted to the exterior of the shell that did not pierce its interior were considered to have infested before the death of the host. Those that pierced the shell or occupied a portion of the shell's interior behind the pallial line were considered to have infested after the death of the host.

Borehole Classification

All valves were examined under magnification for the presence of both predatory and domicile borings. Although predatory borings are readily distinguished from the domicile borings of sponges and worms, they can be similar in size and shape to the domicile borings of bivalves, especially when incomplete or in an irregular, ornamented substrate. The following criteria, based on observations of easily identifiable borings in the shells of *A. cornuta*, were employed when the identity of the borer was not evident:

Gastropod borings:

1. are generally perpendicular to the shell surface and circular in plan view,
2. occur between spine ribs or on other low-relief surfaces,
3. and are usually represented by a single occurrence per shell.

Gastrochaenid borings:

1. are generally at oblique angles to the shell surface and elliptical in plan view,
2. occur anywhere on the shell, including on spine ribs or through spines,

3. can show evidence of crypt building or repair,
4. and often occur in groups in a host shell.

If the shell in question was infested by gastrochaenids, any borings not easily identified were considered to have been created by gastrochaenids.

Photography

Once valves with predatory borings were identified, they were photographed with a Nikon 990 digital camera. Obtaining morphometric and other data from digital images eliminated the need for measuring the cumbersome shells by hand. Three views of each valve containing a gastropod borehole were captured (Figure 8):

1. an exterior view with the plane of the commissure parallel to the plane of the photograph (view A)
2. an interior view with the plane of the commissure parallel to the plane of the photograph (view B),
3. an exterior view with the plane tangent to the boring site parallel to the plane of the photograph (view C)

A scale was photographed along with each sample. The resulting images were analyzed using "Digital Ruler", a customized C++ and OpenGL-based program developed for this project. Digital Ruler was designed for pixel-exact measurement of digital photographs, recording borehole locations, and collecting spine density data. The program is cross-platform and is available from the author.

The location of each borehole was initially recorded by superimposing an eight-sector grid onto view A of each valve (Figure 9). Each sector covered an approximately equal

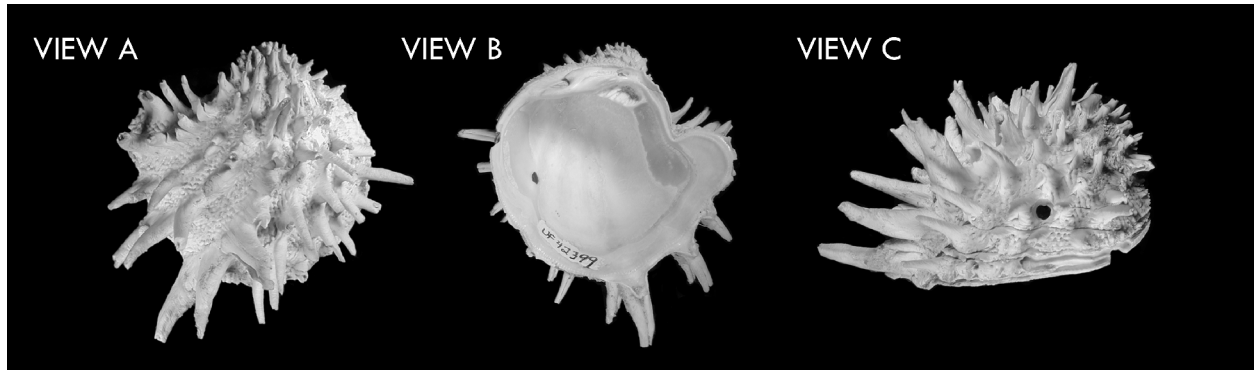


Figure 8. The three views captured as digital images.

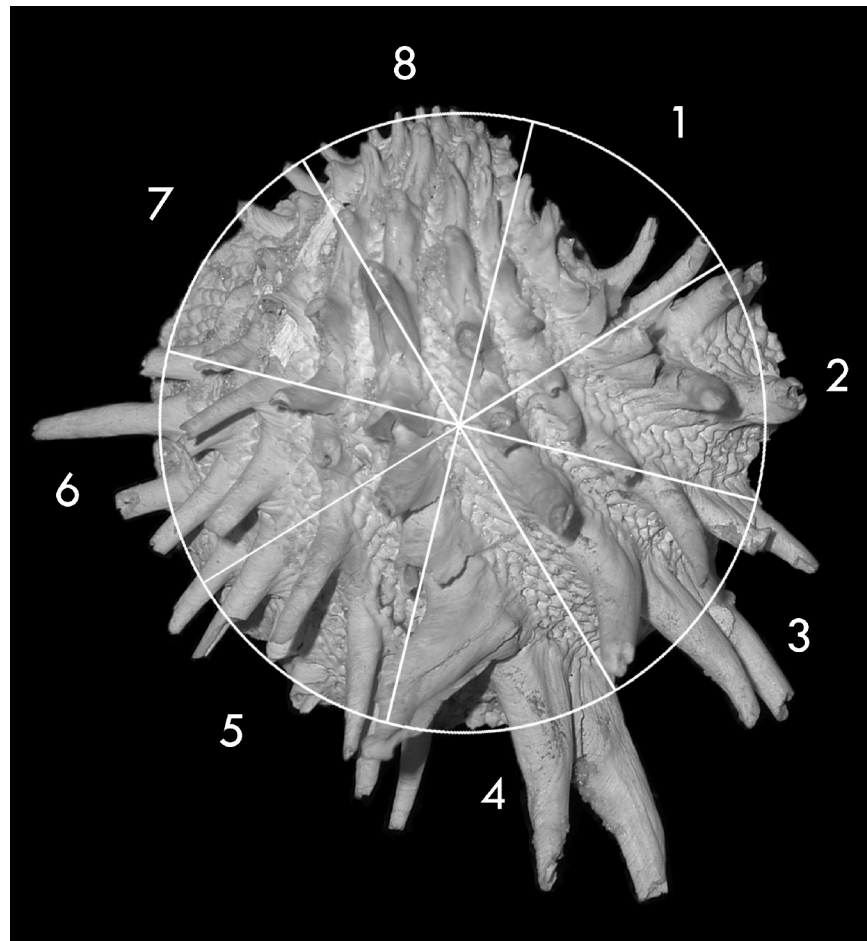


Figure 9. Shell sector designations projected onto a right valve. Sector 1 was positioned over the lunule, sector 8 was positioned over the beak.

area of the spherical valve, with sector 1 positioned over the lunule and sector 8 over the beak. When a borehole fell on a line dividing two sectors, one half counted toward each of the adjacent sectors.

Because the irregular and complex morphology of the shell severely limited the use of surface landmarks, the precise positions of boreholes were mapped with respect to interior landmark points. Three “type one” landmarks, representing juxtapositions of tissues or centers of inclusions (*sensu* Bookstein, 1991), were selected: the intersection of the pallial line with the anterior and posterior muscle scars (landmarks 1 and 2 respectively), and the borehole center (landmark 3) (Figure 10).

A reference for measurement was established by selecting two points 1 mm apart on the scale included in each image. Digital Ruler recorded the number of pixels between the two points and converted subsequent measurements accordingly.

Landmarks 1 and 2 were located on view B, and the distance between them (x) served as a proxy for prey length. This was considered more reliable than a traditional measurement of valve length due to the crenulated and variable nature of the margin. Following Bookstein (1991), Digital Ruler established a Cartesian coordinate system with its origin at landmark 1 and x as its unit value. Landmark 3 was located on the image, and the software recorded its coordinates (Figure 11). This process allowed the positions of boreholes to be normalized across the range of samples. When landmark 3 was not visible in view B, its location was recorded on view A. View A was then inverted and superimposed onto view B. The position of landmark 3 was established on view B, and its coordinates recorded by analyzing the resulting image with Digital Ruler.

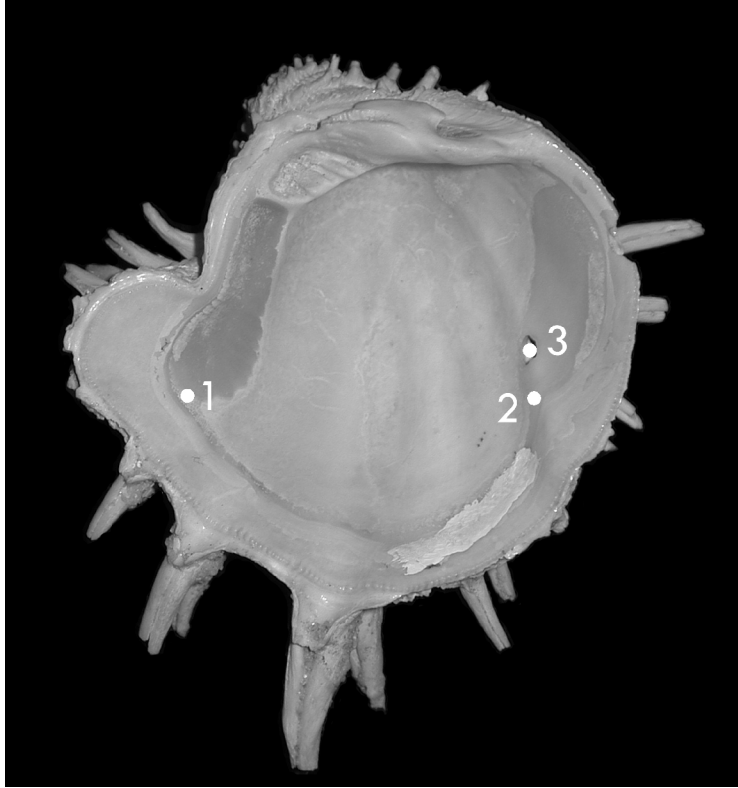


Figure 10. Interior landmark points.

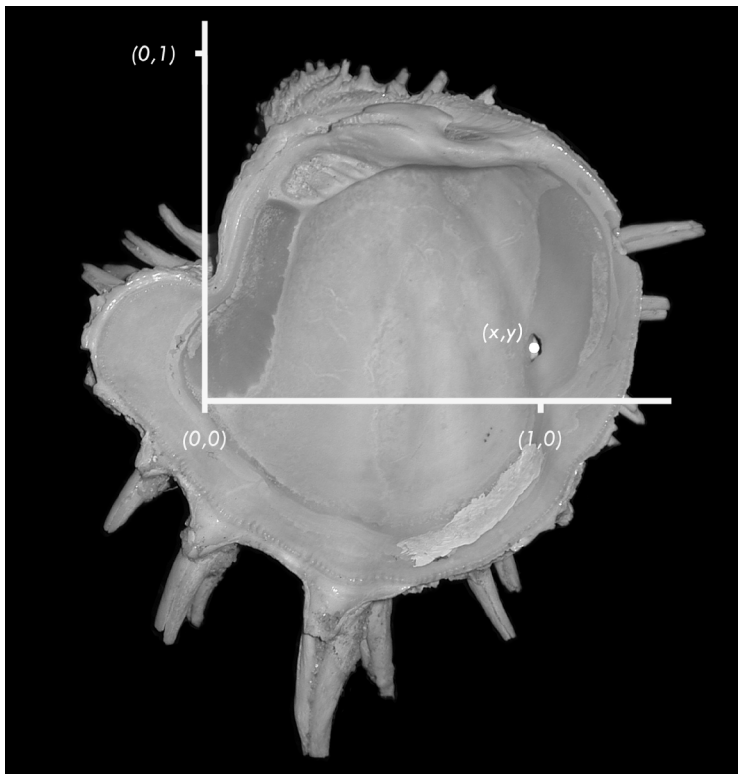


Figure 11. The Cartesian coordinate system based on landmark data.



Figure 12. A screen capture of spine density measurement using Digital Ruler. Circles of radius nr were projected onto the image, and spines falling within each concentric zone were marked and counted.

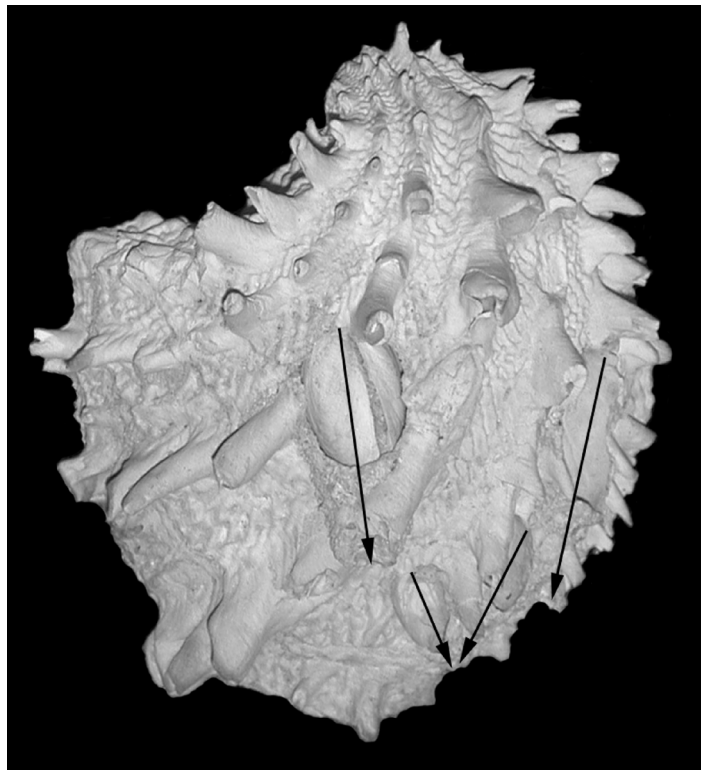


Figure 13. Vectors were superimposed onto view A recorded the sizes, positions, and orientations of gastrochaenid crypts.

Landmark data were not collected for broken valves that were missing at least one landmark location.

Borehole diameter and spine density at boring sites were measured using view C. Points on the image marking the maximum outer borehole diameter (*obd*) were selected. Digital Ruler then calculated the location of the borehole center, recorded the borehole radius (*r*), and projected circular zones of radius nr ($n = 1, 2, 3, \text{etc.}$), radiating out from the borehole center, onto the image (Figure 12). Spines (both broken and unbroken) that fell within each concentric zone were selected and their number recorded. Zones that stretched beyond the valve surface were not counted. Spine data were not collected for valves that suffered serious taphonomic deterioration.

After analyzing the images, Digital Ruler wrote the resulting data to a text file that was easily imported into spreadsheet software.

View A was also captured for each valve collected at the Phase Nine pit that contained a visible gastrochaenid crypt. A vector representing the size, position, and orientation (SPO) of each crypt was superimposed onto the image to record relevant crypt data (Figure 13).

RESULTS

Taphonomic Analysis of the Phase Nine Pit

A wide range of shells and shell fragments were recovered from the bulk sample from the Phase Nine pit, including whole and fragmented shells of *A. cornuta*, Gastropod A and Gastropod B (Table 2). Sixty to seventy-five percent of shells examined were considered whole. Some chipped or worn edges can be observed, but no samples of any taxon, whole or fragmented, show major wear or rounding. Broken spines were investigated as an indicator of abrasion, but determining the severity of breakage proved to be difficult and somewhat subjective.

Most shells are white or off-white, and all have lost their original color. Many are discolored in some manner, often by iron stains. Occasionally a gray discoloration can be observed. Nearly half of *A. cornuta* shells experienced some major dissolution, most often manifested as erosion of the outermost shell layer revealing a partially dissolved interior structure (Table 3). Dissolution is often concentrated at areas where spines had been broken at their base. Gastropod shells show evidence of some chalkiness, and some experienced extreme dissolution.

Carbonate concretions and calcite recrystallization are common in the bulk sample. Ten shells of *A. cornuta* and one shell of Gastropod A display thick carbonate crusts with shell debris (Table 4, Figure 14). The extensive carbonate precipitation on some samples prohibited further taphonomic evaluation. Similar carbonate concretions have been attributed to localized supersaturation caused by the anaerobic decay of organic matter (Brett and Baird, 1986; Canfield and Raiswell, 1991), suggesting the organisms

Table 2. Summary of physical damage to shells of *A. cornuta* and Gastropods A and B.

Physical shell damage					
	Whole	Broken	No abrasion	Minor abrasion	Major abrasion
<i>A. cornuta</i>	25	15	21	19	0
<i>% of total</i>	62.5	37.5	52.5	47.5	0.0
Gastropods	12	5	7	10	1
<i>% of total</i>	70.6	29.4	41.2	58.8	5.9

Table 3. Summary of chemical damage to shells of *A. cornuta* and Gastropods A and B.

Chemical shell damage						
	No damage	Chalkiness	Pitting	Corrosion	Sculpture enhancement	Extreme dissolution
<i>A. cornuta</i>	21	3	0	0	0	18
<i>% of total</i>	52.5	7.5	0.0	0.0	0.0	45.0
Gastropods	6	8	1	1	0	2
<i>% of total</i>	35.3	47.1	5.9	5.9	0.0	11.8

Table 4. Summary of shell coverage.

	Exterior carbonate precipitation	Interior carbonate precipitation	BD encrustation	AD encrustation	Total encrustation	Mean Exterior coverage	Mean Interior coverage	Mean coverage
<i>A. cornuta</i>	1.08	0.79	0.88	0.37	1.03	0.52	0.26	0.36
Gastropods	0.24	0.24	1.25	0.25	1.31	1.06	0.25	0.62

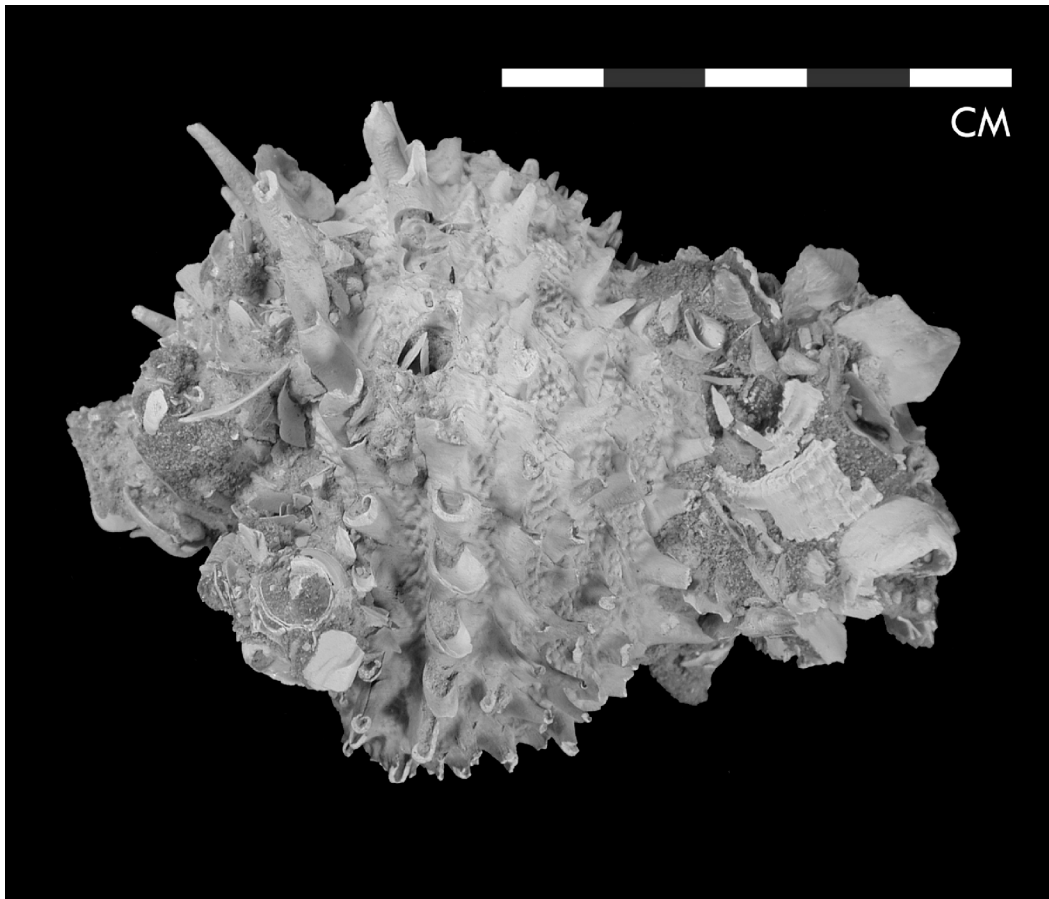


Figure 14. An example of the carbonate precipitation found on some samples from the Phase Nine pit.

Table 5. Summary of encrusting and boring.

	Growth disturbance	Barnacle	Coral	Bryozoan	Oyster	Peeling	Encrusting pelecypod	Encrusting crepulid
<i>A. cornuta</i>	0	0	0	3	0	0	0	0
Gastropods	0	1	0	0	0	0	0	0

	Lithophagid	Hole	Sponge	Drillhole	Tube impression	Vermetid gastropod	Worm tube	Total encrustation
<i>A. cornuta</i>	9	8	3	2	9	1	4	39
Gastropods	0	10	3	3	6	0	0	23

were rapidly buried

Some type of biogenic shell damage occurs on many samples (Table 5). The diversity of biogenic damage is lower than that recorded by Geary and Allmon (1990), and is mostly restricted to lithophagid bivalve borings, worm tubes, clionid sponge borings, and gastropod boreholes. Few samples show any clear evidence of post-mortem encrustation.

The close-packed, bioclast-supported nature of the Pinecrest beds at the Phase Nine pit suggests taphonomic concentration. Most shells show no evidence of major abrasion and none exhibit edge rounding, even when fragmented. Encrustation is minor and shows low diversity. These observations are consistent with the conclusions of Geary and Allmon (1990), and suggest that shells at the Phase Nine pit were rapidly buried, experienced little transport, and spent only a brief time in the taphonomically active zone (TAZ) at and just below the sediment-water interface, where most dissolution, abrasion, and bioerosion takes place (Davies, Powell, and Stanton, 1989; Meldahl, Flessa, and Cutler, 1997).

Predatory Borings

Description of borings: Fifty-six complete predatory boreholes were identified (thirty eight from the Pinecrest beds and eighteen from the Caloosahatchee formation), ranging from 1.65 mm to 6.73 mm maximum outer diameter (Table 6). Fourteen incomplete boreholes were identified, ranging from 0.93 mm to 6.35 mm maximum outer diameter.

Complete borings are generally circular in plan view and cylindrical in cross section .

Table 6. Locations of complete predatory boreholes in shells of *A. cornuta*.

Site	Image number	Valve	Borehole sector	Normalized x coordinate	Normalized y coordinate
Phase Nine pit	Dscn1188	L	5–4	0.64	-0.03
	Dscn1191	R	5	0.90	-0.14
	Dscn1194	L	1	0.27	0.59
	Dscn1197	L	5–6	0.96	0.01
	Dscn1200	L	6	0.74	0.39
	Dscn1329	L	1	0.27	0.48
	Dscn1344	L	5	1.03	-0.13
	Dscn1347	L	1	0.21	0.42
	Dscn1350	L	6–7	0.68	0.22
Phase Six pit	Dscn1202	R	2	Na	Na
	Dscn1205	L	5	0.70	0.01
	Dscn1208	R	6	1.04	0.34
	Dscn1304	L	6	0.89	0.40
	Dscn1307	R	4–5	0.57	0.09
	Dscn1310	L	7	0.75	0.41
	Dscn1313	R	5–6	0.83	0.16
	Dscn1316	L	3–4	0.36	-0.09
	Dscn1320	R	4	0.62	-0.24
Dscn1323	L	4–5	0.79	-0.04	
Macasphalt shell pit	Dscn1092	L	5–4	0.63	-0.11
	Dscn1341	L	6	1.05	0.29
	Dscn1068	L	7	0.68	0.43
	Dscn1071	R	6	1.07	0.46
	Dscn1121	R	6–7	0.92	0.60
	Dscn1124	L	1	0.27	0.64
	Dscn1176	L	8	0.46	0.91
	Dscn1179	R	6	0.97	0.39
	Dscn1182	R	5–6	0.90	0.22
	Dscn1080	R	6	1.01	0.17
	Dscn1089	L	7	0.58	0.45
	Dscn1151	L	6–7	0.74	0.49
	Dscn1332	L	6	0.93	0.27
	Dscn1166	R	6	1.28	0.57
	Dscn1130	R	5–6	0.58	0.20
	Dscn1133	L	5	0.74	0.04
Dscn1157	L	5	0.70	-0.02	
Mule Pen	Dscn1097	R	4	Na	Na
	Dscn1102	L	6	0.98	0.13
Fort Basinger	Dscn1172	R	7	0.81	0.74
Cochran shell pit	Dscn1136	R	1	0.07	0.41
	Dscn1139	R	8	0.62	0.81
	Dscn1142	R	6	1.02	0.49
	Dscn1298	L	6	0.99	0.26
	Dscn1301	L	6	0.81	0.30
	Dscn1077	R	1	0.15	0.32
	Dscn1083	R	1	0.39	0.62
	Dscn1086	R	6	1.05	0.24
	Dscn1105	R	5	0.85	-0.05
	Dscn1108	L	6	0.99	0.32
	Dscn1113	R	7	0.67	0.77
	Dscn1116	R	1	0.30	0.48
	Dscn1127	R	1	0.33	0.58
	Dscn1145	R	6	0.85	0.50
	Dscn1148	R	1	0.39	0.55
Dscn1154	L	7–8	Na	Na	
Desoto shell pit	Dscn1095	L	5	1.03	-0.01
Labelle	Dscn1326	R	3	0.17	-0.12

Some appear to have wide beveled outer rims (Figure 15). The inner rims range in appearance from smooth to jagged. Incomplete borings have smooth bowl-shaped bottoms and show no evidence of a central boss.

Data from complete borings were grouped in two ways: sites that contained more than two completely bored valves (the Phase Nine pit, Phase Six pit, Macaspalt shell pit, and Cochran shell pit) were analyzed individually, and all completely bored valves were analyzed as grouped Pinecrest and grouped Caloosahatchee Formation data.

Predation intensity: The intensity of predation was calculated for the Phase Nine pit, the site at which sampling was most complete. Although the accuracy of such a calculation may be questioned due to issues of spatial and temporal mixing, it is included here for comparison with similar studies.

Because most valves are disarticulated, a correction is necessary to accurately estimate the number of individuals sampled. Each individual can contribute two valves to the total number of valves sampled. The probability of sampling a bored valve from a bored individual is half as likely as the probability of sampling either of its two valves. Accordingly, predation intensity is calculated as:

$$PI = b/(0.5 v) = 2b/v$$

where PI is intensity of predation, b is the number of specimens with complete borings, and v equals the total number of valves (Hoffmeister and Kowalewski, 2001). Predation intensity at the Phase Nine pit was calculated to be 2.8%.

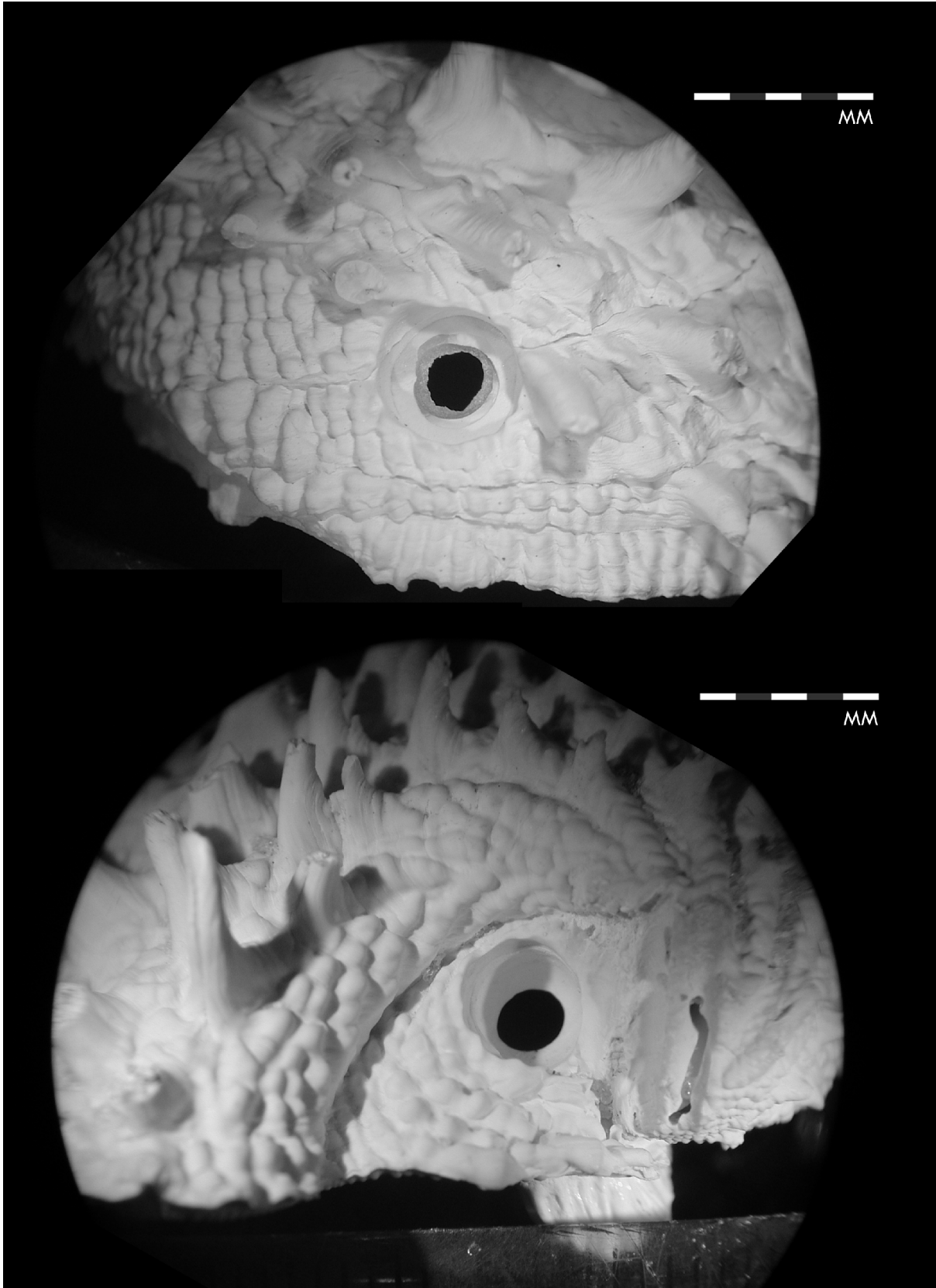


Figure 15. Gastropod boreholes in shells of *A. cornuta*.

Valve preference: Preference for attacking left or right valves was mixed. At the Phase Nine pit, left valves were preferentially attacked; at the Cochran shell pit, right valves were preferentially attacked. At the Phase Six pit and Macaspalt shell pit, attacks showed no clear preference. In the grouped Pinecrest, left valves were preferentially attacked 1.6 to 1, in the grouped Caloosahatchee Formation, right valves were preferentially attacked 2.6 to 1.

Borehole site distribution: Chi-square analysis confirms that boreholes at all four major sites, and in the grouped Pinecrest and Caloosahatchee Formation samples, were distributed nonrandomly and do not follow the Poisson distribution (Figure 16, Table 7). Significance levels for all sites and grouped data are below 0.029. The distribution of borings is unimodal at both the Phase Six pit and the Macaspalt shell pit. At the Phase Nine pit and the Cochran shell pit, borings are distributed bimodally, with modes in sectors 1 and 5 at the Phase Nine pit and sectors 1 and 6 at the Cochran shell pit.

Borings for grouped Pinecrest sites are distributed unimodally with mode at sector 6 and a slightly elevated tail at sector 1. In the grouped Caloosahatchee Formation, borings are distributed bimodally, again with modes at sectors 1 and 6.

Normalized borehole loci for the grouped Pinecrest and Caloosahatchee Formation were superimposed onto a single valve (Figure 17). A weakly bimodal distribution of attack sites is seen in the grouped Pinecrest data, with 81% of attacks scattered posterior of the center line of the valve. Many of the remaining attacks are concentrated near the anterior muscle scar. The distribution of borehole loci for grouped Caloosahatchee Formation attacks is strongly bimodal, with attacks clustered near the

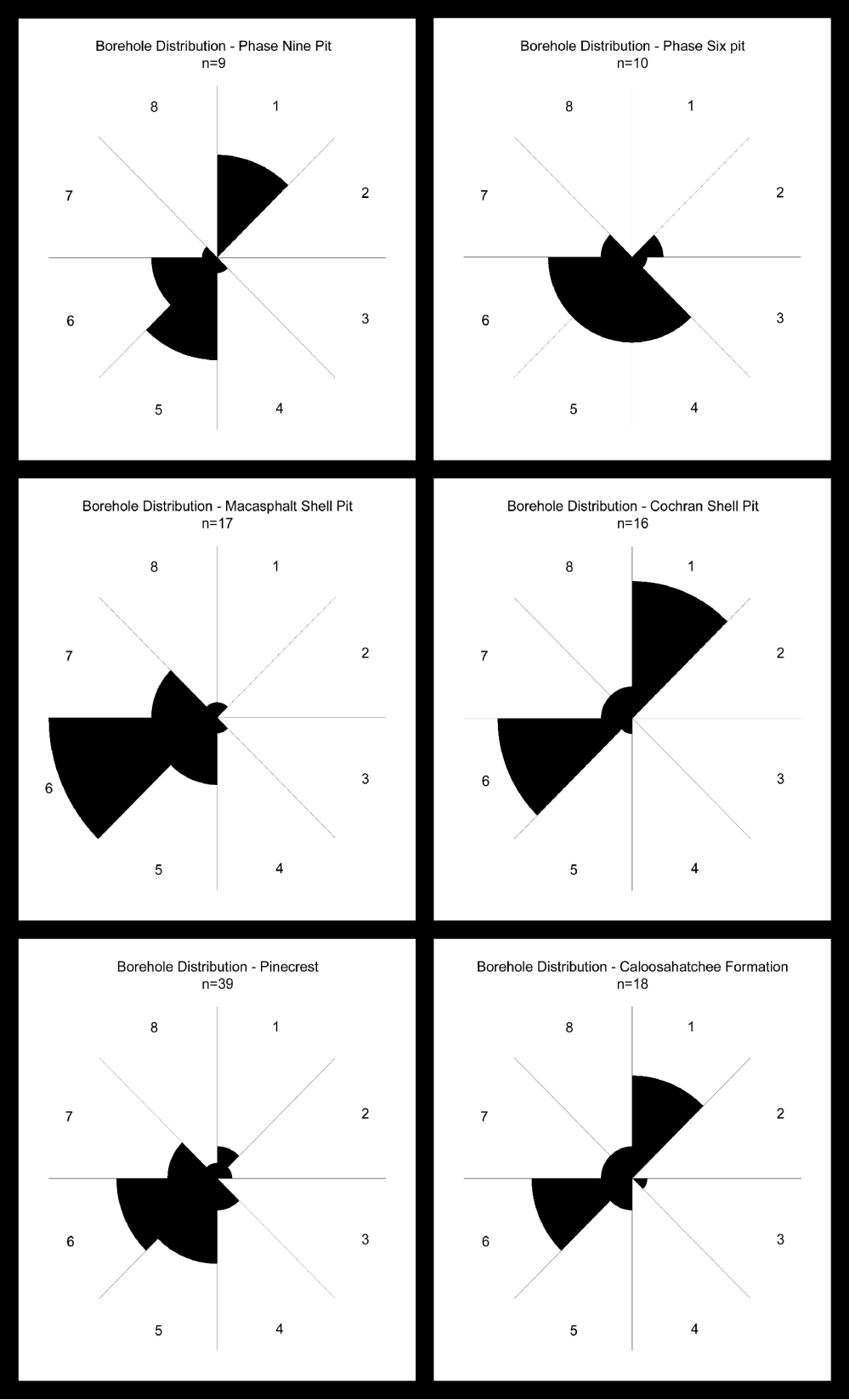


Figure 16. Distribution of boreholes at four individual sites and in the grouped Pinecrest and grouped Caloosahatchee Formation samples.

Table 7. Calculation of χ^2 significance for goodness of fit of observed borehole distributions to Poisson distributions.

Site	Number of borings per sector	Observed distribution	Expected distribution	Significance
Phase Nine pit	0	5	1.322	0.00873
	1	0	2.380	
	2	1	2.142	
	3	1	1.285	
	4	1	0.578	
Phase Six pit	0	3	0.657	0.02891
	1	2	1.642	
	2	1	2.052	
	3	2	1.710	
Macasphalt shell pit	0	3	1.210	0.00000
	1	2	2.285	
	2	0	2.158	
	3	1	1.359	
	4	1	0.642	
	5	0	0.242	
	6	0	0.076	
	7	0	0.021	
Cochran shell pit	0	3	0.814	0.00003
	1	2	1.860	
	2	1	2.125	
	3	0	1.619	
	4	0	0.925	
	5	0	0.423	
	6	2	0.161	
Grouped Pinecrest	0	1	0.493	0.00000
	1	2	1.375	
	2	0	1.915	
	3	0	1.778	
	4	2	1.238	
	5	1	0.690	
	6	0	0.320	
	7	0	0.127	
	8	0	0.044	
	9	0	0.014	
	10	0	0.004	
	11	1	0.001	
	12	0	0.000	
13	1	0.000		
Grouped Caloosahatchee	0	2	0.611	0.00379
	1	2	1.572	
	2	2	2.021	
	3	0	1.733	
	4	0	1.114	
	5	0	0.573	
6	2	0.245		

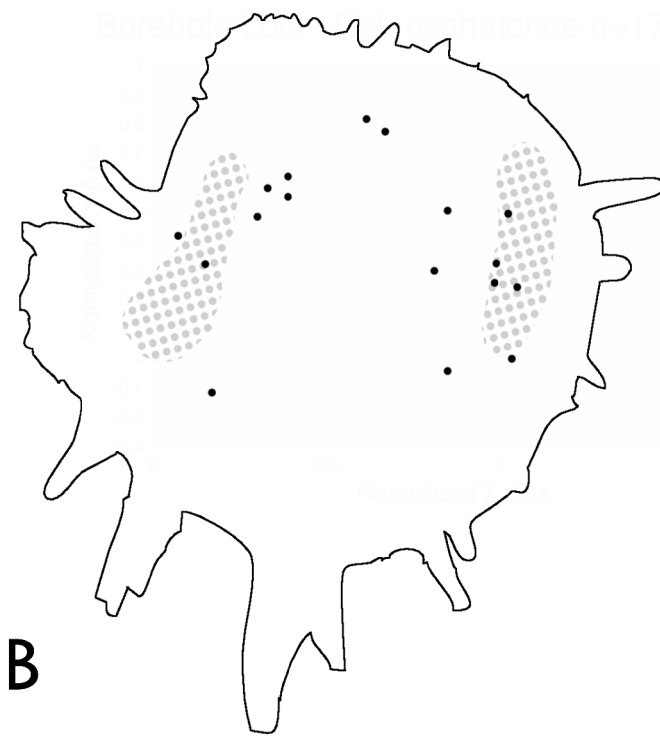
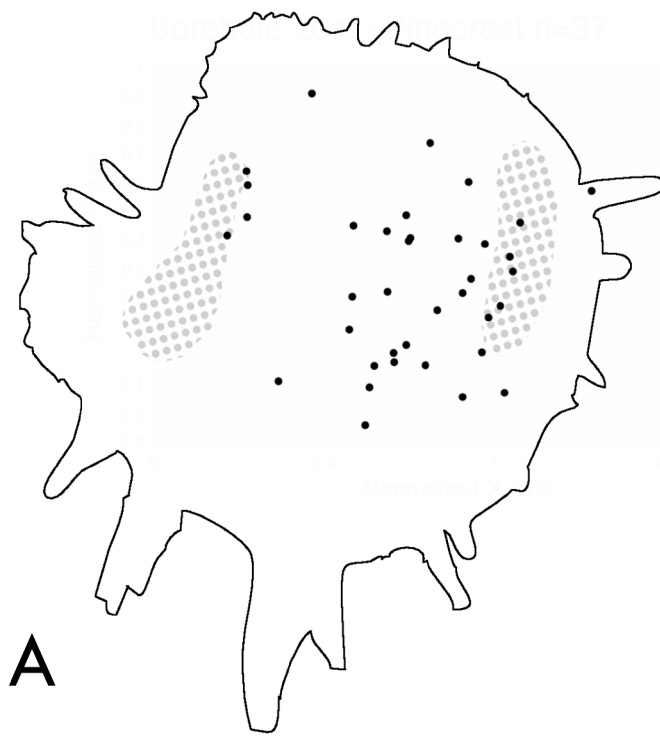


Figure 17. Normalized borehole loci for grouped Pinecrest (A) and grouped Caloosahatchee Formation (B) samples. Stippled areas represent the anterior and posterior muscle scars.

muscle scars.

Predator and prey size distribution: Correlation of *obd* (a proxy for predator size) and *x* (a proxy for prey length) also varies from site to site (Table 8, Figure 18). There is no correlation at the Macasphalt shell pit, and very poor positive correlation at the Phase Nine pit ($r = -0.06$ and $r = 0.25$ respectively). Correlation is slightly stronger at the Cochran shell pit ($r = 0.57$) and very strong at the Phase Six pit ($r = 0.83$).

No correlation is seen in the grouped Pinecrest samples ($r = 0.06$), but boreholes of smaller predators ($obd < 4.7\text{mm}$) weakly correlate positively with prey size ($r = 0.52$), while those of larger predators ($obd > 4.0\text{mm}$) weakly correlate negatively with prey size ($r = -0.63$) (Figure 18). Grouped Caloosahatchee Formation sites show a weak positive correlation ($r = 0.45$).

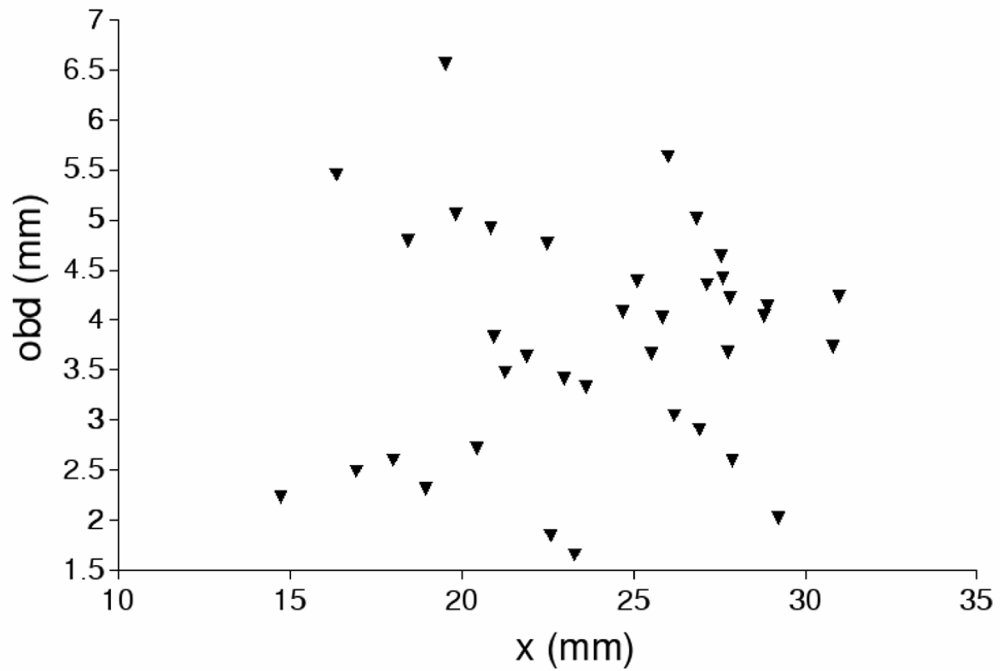
The size ratio of prey length proxy to outer borehole diameter ($SR = x/obd$) was calculated to measure variations in prey size selection (Table 8). Small *SR* values indicate larger predators were attacking smaller prey, while large *SR* values indicate smaller predators were attacking larger prey. If size selection was exceptionally strong, the value of *SR* would be equal in all cases, regardless of borehole location. The mean value of *SR* for each bored shell sector was calculated at each site (Table 9).

At the Phase Nine pit and Macasphalt shell pit, the mean value of *SR* is low for borings in sector 1 and much higher for borings in sectors 3-8, indicating the borings in sector 1 were often made by larger predators on smaller valves. This pattern is repeated in the grouped Pinecrest samples, where borings in sector 1 are on average 41% larger than those in all other sectors.

Table 8. Prey and predator size proxies, size ratios (*SR*) and size correlations.

Site	Image number	x (mm)	obd (mm)	SR	x/obd correlation
Phase Nine pit	Dscn1188	25.99	5.64	4.61	
	Dscn1191	28.89	4.13	6.99	
	Dscn1194	16.33	5.45	2.99	
	Dscn1197	27.54	4.64	5.93	
	Dscn1200	25.83	4.02	6.42	
	Dscn1329	18.43	4.79	3.85	
	Dscn1344	20.92	3.83	5.46	
	Dscn1347	19.81	5.06	3.92	
	Dscn1350	14.72	2.23	6.59	0.25
Phase Six pit	Dscn1202	Na	5.52	Na	
	Dscn1205	28.80	4.04	7.13	
	Dscn1208	27.59	4.41	6.25	
	Dscn1304	27.80	4.22	6.58	
	Dscn1307	21.88	3.64	6.02	
	Dscn1310	27.73	3.68	7.54	
	Dscn1313	21.25	3.48	6.11	
	Dscn1316	25.10	4.39	5.72	
	Dscn1320	24.68	4.09	6.04	
Dscn1323	16.92	2.49	6.81	0.83	
Macasphalt shell pit	Dscn1092	22.97	3.41	6.73	
	Dscn1341	30.80	3.74	8.24	
	Dscn1068	23.27	1.65	14.09	
	Dscn1071	23.60	3.33	7.09	
	Dscn1121	26.83	5.02	5.35	
	Dscn1124	19.52	6.56	2.97	
	Dscn1176	27.12	4.35	6.23	
	Dscn1179	27.87	2.59	10.75	
	Dscn1182	20.84	4.92	4.24	
	Dscn1080	22.57	1.85	12.23	
	Dscn1089	18.95	2.31	8.19	
	Dscn1151	26.17	3.04	8.60	
	Dscn1332	29.21	2.02	14.44	
	Dscn1166	26.91	2.90	9.27	
	Dscn1130	17.98	2.60	6.92	
	Dscn1133	25.52	3.67	6.96	
Dscn1157	20.43	2.72	7.52	-0.06	
Mule Pen	Dscn1097	Na	4.80	Na	
	Dscn1102	30.98	4.24	7.31	
Fort Basinger	Dscn1172	22.47	4.76	4.72	
Cochran shell pit	Dscn1136	14.20	4.11	3.45	
	Dscn1139	16.87	3.97	4.25	
	Dscn1142	18.21	2.48	7.35	
	Dscn1298	16.62	2.61	6.36	
	Dscn1301	16.99	4.23	4.02	
	Dscn1077	26.90	5.51	4.89	
	Dscn1083	22.19	4.43	5.01	
	Dscn1086	23.16	5.44	4.26	
	Dscn1105	22.65	5.78	3.92	
	Dscn1108	24.76	5.90	4.20	
	Dscn1113	24.94	4.74	5.27	
	Dscn1116	23.38	3.90	6.00	
	Dscn1127	23.18	4.66	4.97	
	Dscn1145	22.28	2.61	8.52	
Dscn1148	23.19	6.69	3.47		
Dscn1154	Na	5.13	Na	0.57	
Desoto shell pit	Dscn1095	22.70	2.30	9.89	
Labelle	Dscn1326	21.83	6.73	3.24	
Grouped Pinecrest					0.06
Grouped Caloosahatchee					0.45

Outer Borehole Diameter vs. Valve Length Proxy
Pinecrest n=37



Outer Borehole Diameter vs. Valve Length Proxy
Caloosahatchee Formation n=17

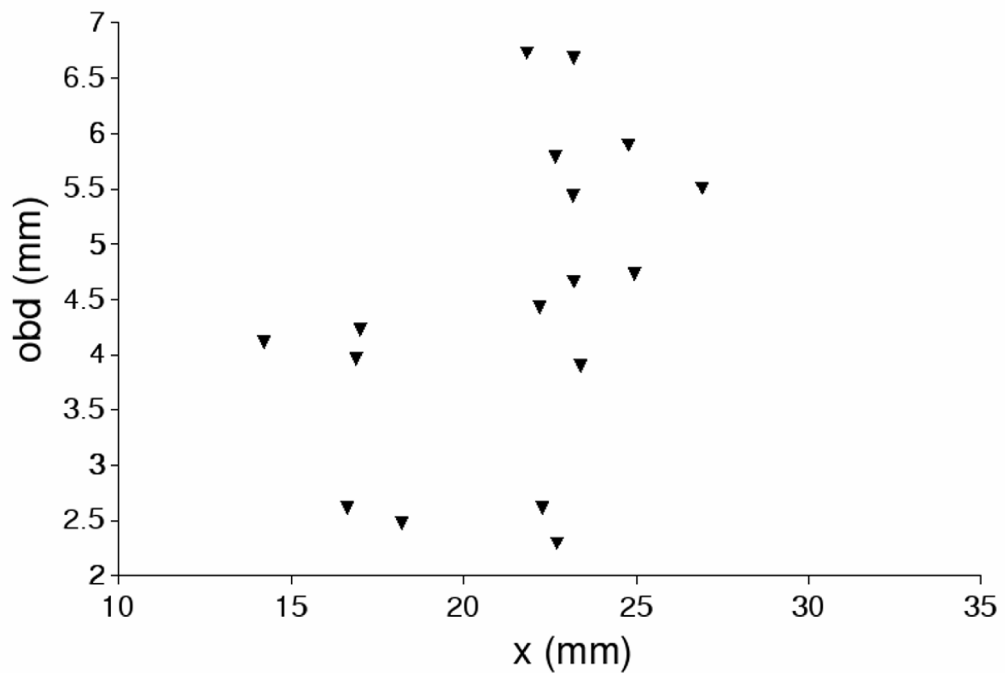


Figure 18. The relationship of outer borehole diameter (*obd*) to prey size proxy (*x*).

Table 9. Borehole distributions, spine densities, and size ratios arranged by shell sector.

Site	Sector 1	Sector 2	Sector 3	Sector 4	Sector 5	Sector 6	Sector 7	Sector 8	Borehole dist./spine density correlation
Phase Nine pit									
<i>Borehole distribution</i>	3	0	0	0.5	3	2	0.5	0	
<i>Mean spine density</i>	2.00			8.80	5.43	5.35			-0.861
<i>Mean SR</i>	3.57			4.61	5.66	6.25	6.60		
Phase Six pit									
<i>Borehole distribution</i>	0	1	0.5	2.5	2.5	2.5	1	0	
<i>Mean spine density</i>		5.50		2.82	3.17	4.38			-0.837
<i>Mean SR</i>			5.72	6.07	6.52	6.33	7.54		
Macasphalt shell pit									
<i>Borehole distribution</i>	1	0	0	0.5	3.5	8	3	1	
<i>Mean spine density</i>	2.00			3.50	3.41	2.96			0.111
<i>Mean SR</i>	2.97			6.73	6.22	7.90	7.92	6.23	
Cochran shell pit									
<i>Borehole distribution</i>	6	0	0	0	1	6	1.5	1.5	
<i>Mean spine density</i>	0.93				6.00	4.64	10.00		-0.769
<i>Mean SR</i>	4.54				3.92	5.24	5.06	4.25	
Grouped Pinecrest									
<i>Borehole distribution</i>	4	1	0.5	4.5	9	13.5	5.5	1	
<i>Mean spine density</i>	2.00	5.50		4.68	3.85	3.47	7.33		-0.282
<i>Mean SR</i>	3.39		5.72	5.82	6.10	7.23	7.05	6.23	
Grouped Caloosahatchee									
<i>Borehole distribution</i>	6	0	1	0	2	6	1.5	1.5	
<i>Mean spine density</i>	1.30		8.33		3.57	4.64	10.00		-0.729
<i>Mean SR</i>	4.54		3.24		5.61	5.24	5.27	4.25	

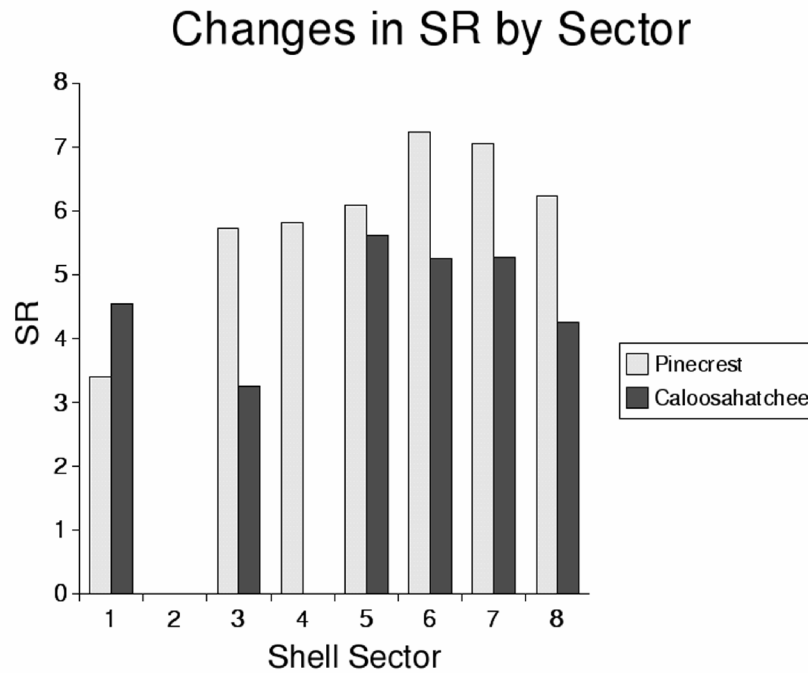


Figure 19. Changes in the mean value of SR in each shell sector between the Pinecrest and the Caloosahatchee Formation.

Trends in the distribution of prey size to predator size change from the Pinecrest beds to the Caloosahatchee Formation. The mean value of *SR* for borings in sector 1 of grouped Caloosahatchee Formation samples is greater than that of grouped Pinecrest samples, and the mean values of *SR* for borings in all other sectors of grouped Caloosahatchee Formation samples are smaller than those of the grouped Pinecrest (Figure 19). This suggests that, over time, ratios of prey size to predator size in different sectors were trending toward a uniform value. The distribution of prey size to predator size ratios also shifted from the Pinecrest to the Caloosahatchee Formation (Figure 20). The mean value of *SR* is lower for grouped Caloosahatchee Formation samples than for grouped Pinecrest samples. The variance of *SR* also decreases over time, suggesting prey size to predator size ratios in different sectors are trending toward uniformity. These changes suggest that attacks were changing, and possibly becoming more uniform, over time.

Spine density: Spine density data were obtained for each bored shell by counting the number of spines located within concentric zones of increasing radius around the borehole (Table 10). Spines within a radius of seven times the outer borehole diameter were counted. Borings were grouped by sector and mean spine densities were calculated by sector (Table 8). The mean spine density for each sector was then compared to the number of borings in that sector.

At the Phase Nine pit, the Phase Six pit, and the Cochran shell pit, mean spine density by sector is negatively correlated with the number of borings occurring in that sector ($r = -0.86, -0.84, \text{ and } -0.77$ respectively) (Figure 21). There is no correlation

Distribution of Prey Size/Predator Size Ratio (SR)

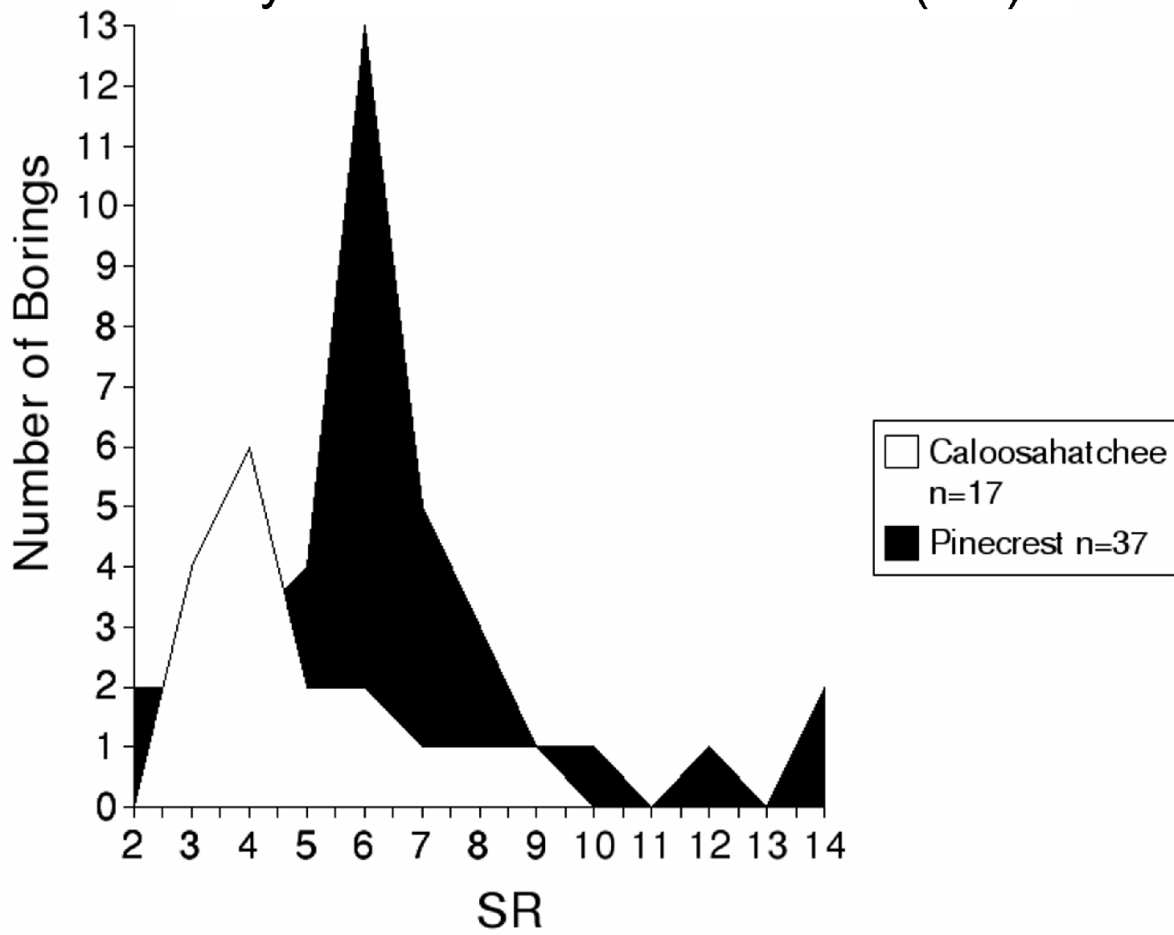


Figure 20. Distribution of prey size to predator size ratios (*SR*).

Table 10. Spine density measurements.

Site	Image number	Spines within annulus r=1	r=2	r=3	r=4	r=5	r=6	r=7
Phase Nine pit	Dscn1188	0	2	3	6	16	17	
	Dscn1191	0	3	2	5	3	4	
	Dscn1194	0	3					
	Dscn1197	0	4	4	6			
	Dscn1200	0	1	1	5	4	7	9
	Dscn1329	0	0	2	4	3		
	Dscn1344	0	1					
	Dscn1347	0	0					
Phase Six pit	Dscn1202	0	5	3	4	10		
	Dscn1208	0	4	0	11			
	Dscn1304	0	3	3	7	2	5	
	Dscn1307	0	0	3	1	3	7	5
	Dscn1313	0	2	2	2	3	7	7
	Dscn1320	0	0	4	3	4	3	
	Dscn1323	0	1	2	1	3	3	5
Macasphalt shell pit	Dscn1092	0	0	5	1	3	6	6
	Dscn1341	0	2	2	1	5		
	Dscn1071	0	3	0	6	2		
	Dscn1124	0	2					
	Dscn1182	0	4	6	7	12		
	Dscn1080	0	0	2	2	0	3	3
	Dscn1166	0	0	1				
	Dscn1130	0	2	1	2	3	5	3
	Dscn1157	0	0	3	1	1	1	3
Mule Pen	Dscn1097	0	2	4	4	10	11	15
	Dscn1102	0	2	1	1	4	4	3
Fort Basinger	Dscn1172	0	6	5	11			
Cochran shell pit	Dscn1136	0						
	Dscn1139	0	0					
	Dscn1142	0	3	0	6	3	1	4
	Dscn1298	0	2	3	3	3	2	5
	Dscn1301	0	6	10	14	12		
	Dscn1077	0	0					
	Dscn1083	0	0	0				
	Dscn1086	0	3	2				
	Dscn1105	0	5	4	9			
	Dscn1108	0	4	3	10	11		
	Dscn1113	0	5	6	14	15		
	Dscn1116	0	0	1	5			
	Dscn1127	0	0	0				
	Dscn1145	0	2	3	1	5	5	4
Dscn1148	0	1	6					
Desoto shell pit	Dscn1095	0	0	1	5	1		
Labelle	Dscn1326	0	6	9	10			

between the number of spines and the number of borings at the Macasphalt shell pit. The grouped Pinecrest data displays weak negative correlation ($r = -0.28$) and the grouped Caloosahatchee Formation samples show stronger negative correlation ($r = -0.73$).

Incomplete borings: Two distinct types of incomplete borings can be observed (Figure 22). Half are larger borings with outer borehole diameters ranging from 2.1 to 6.35 mm, and the rest are small borings with outer borehole diameters ranging from 0.93 to 2.1 mm. Larger incomplete borings typically occur in sectors 7 and 8. Smaller borings are restricted to the area of the lunule. Small predators apparently lacked the capacity to bore through the thick shell of the lunule and abandoned boring after some period of time. Whether the smaller predators were juvenile members of the same species as the larger predators or mature members of another, smaller species is unknown.

Domicile Borings

Description of borings and crypts: Sixty-one valves containing gastrochaenid borings and crypts were collected at the Phase Nine pit (11 from the bulk sample, 50 individually collected shells). Three bored valves of the infaunal bivalve *Chione*, one bored shell of the gastropod *Strombus*, and the unattached posterior portion of a crypt were also discovered in the bulk sample. All other gastrochaenid borings and crypts are associated with valves of *A. cornuta*. Gastrochaenid borings and crypts also occur in shells of *A. cornuta* from the Phase Six pit and the Florida Museum of Natural History collections.

Several manifestations of boring and crypt building can be observed (Figure 23).

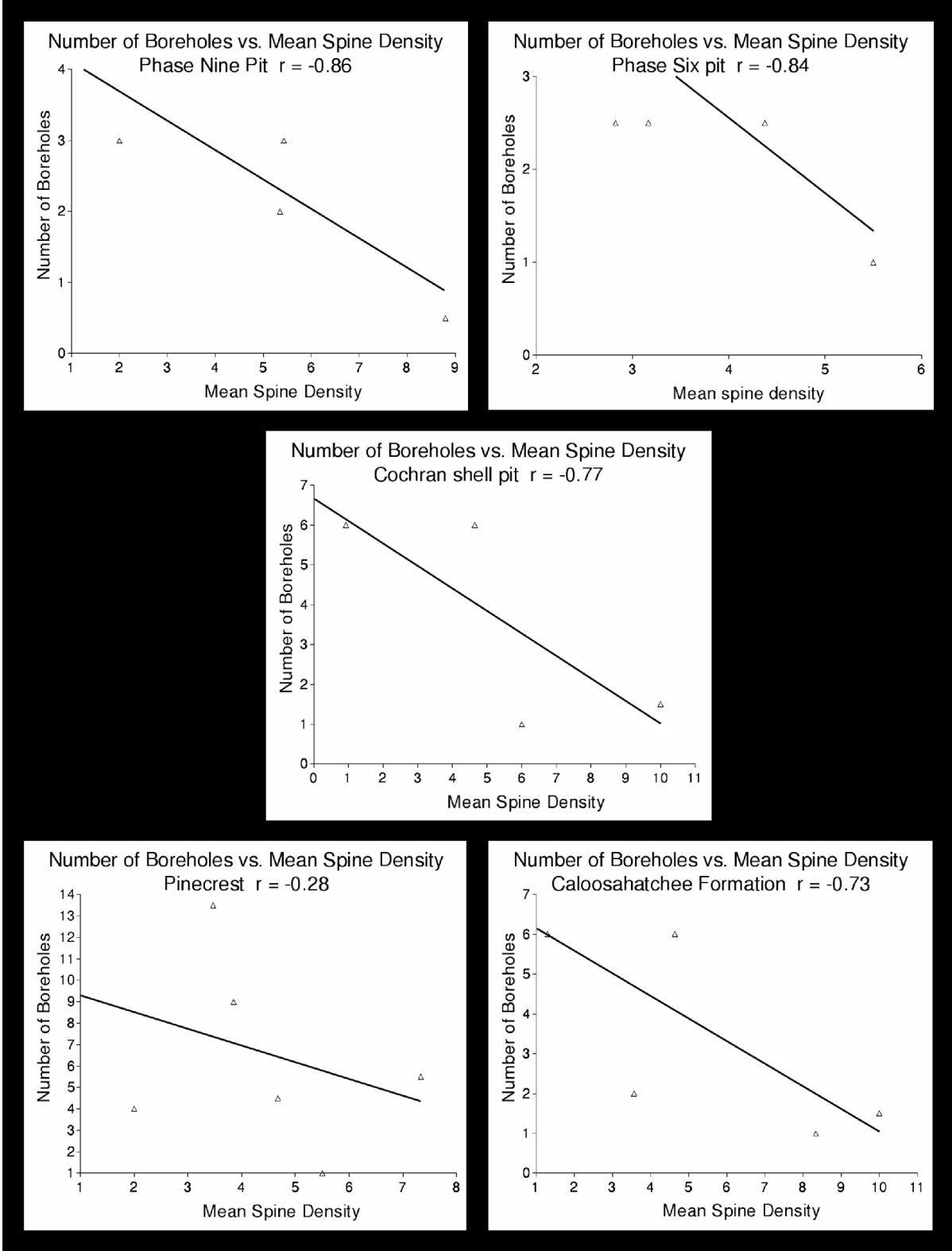


Figure 21. The relationship between the number of successful boreholes and the mean spine density near the borehole for individual sites and the grouped Pinecrest and Caloosahatchee Formation samples.

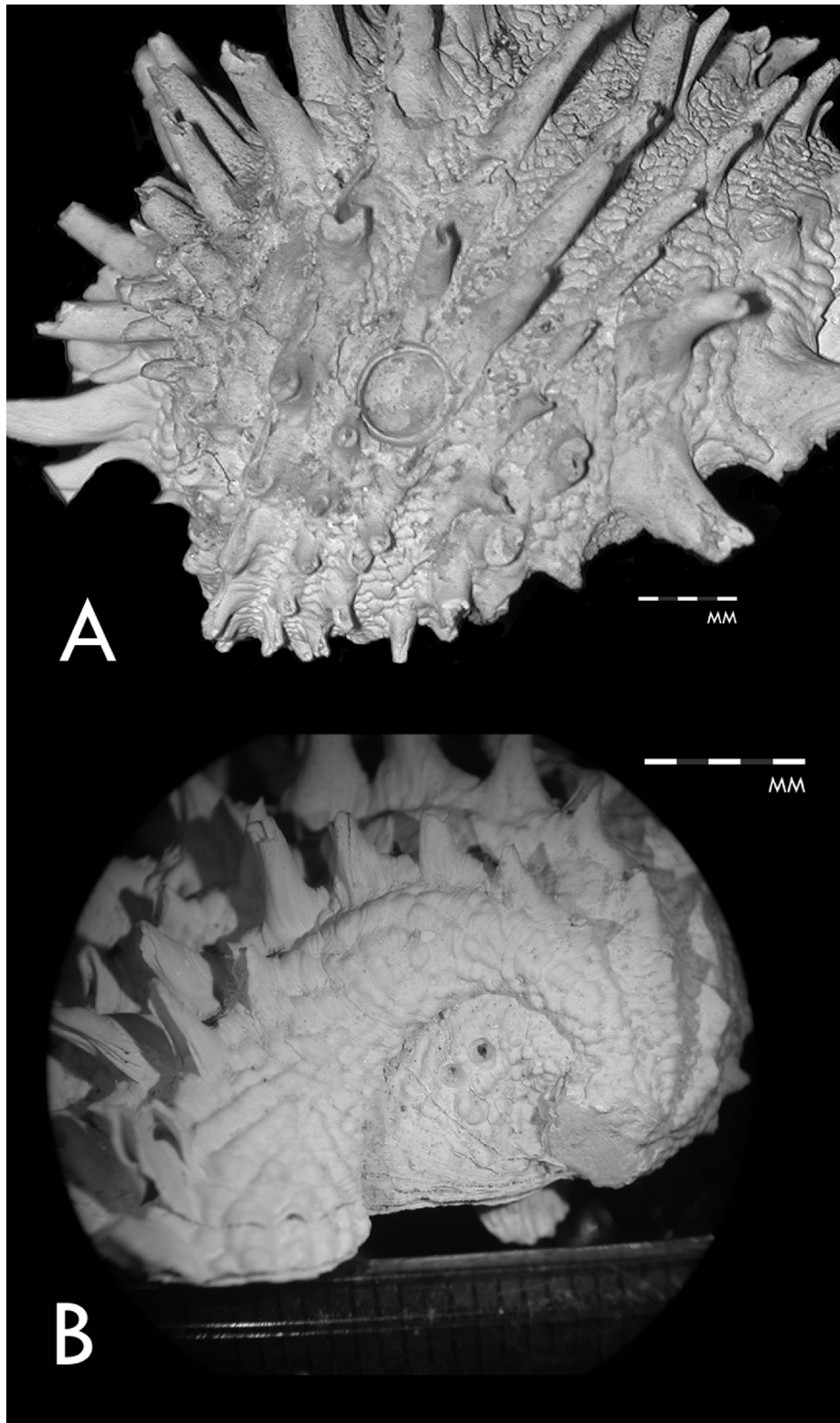


Figure 22. Incomplete gastropod borings. A: larger incomplete borings that often occurred in spinose areas. B: smaller incomplete borings that were restricted to the lunule.

These include:

1. small conjoined boreholes representing the siphonal openings
2. clavate, lined boreholes (some containing shells) with narrow apertures characterized by parallel, conjoined tubes
3. clavate borings as described above with a precipitated carbonate envelope covering part or all of the exposed surface of the borehole
4. and carbonate envelopes attached to the surface of a shell, with little or no apparent boring into the substrate.

Crypts are semicircular in cross-section and have smooth, lined interiors. Some crypts are semi-endolithic and show evidence of minor repair by carbonate precipitation where the borehole breached the substrate valve; others are much larger, extending from the surface of the host shell and incorporating the spines in their construction. Some crypts contain the shells of their inhabitants (Figure 24). The anterior portions of some crypts show evidence of small tubules (Figure 25). Some crypts occur in clusters, but do not intersect each other (Figure 26). No evidence of shell repair by the host was observed, suggesting that borers avoided perforating the shells of their living hosts. Crypt surfaces have the appearance of solidified carbonate bubbles, many of which are punctured by small holes (Figure 27). Some incorporate sand grains or small shell fragments. Crypts show no evidence of growth lines or periodic growth stages. Some crypts are preserved intact; others are partially or fully broken down to the surface of the host shell. The short-siphoned crypts and the shells extracted from them closely resemble those of *Gastrochaena (Rocellaria) ovata*, a gastrochaenid commonly found in

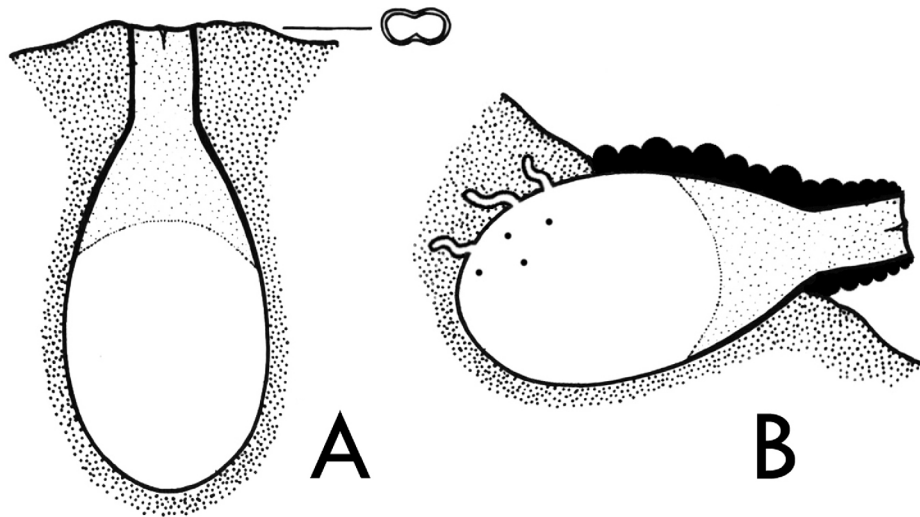


Figure 23. A schematic diagram of the two main types of gastrochaenid domiciles observed in shells of *A. cornuta*. A: a fully endolithic boring with siphonal openings that break the surface. B: a semi-endolithic carbonate crypt with anterior tubules. Adapted from Warne (1975).

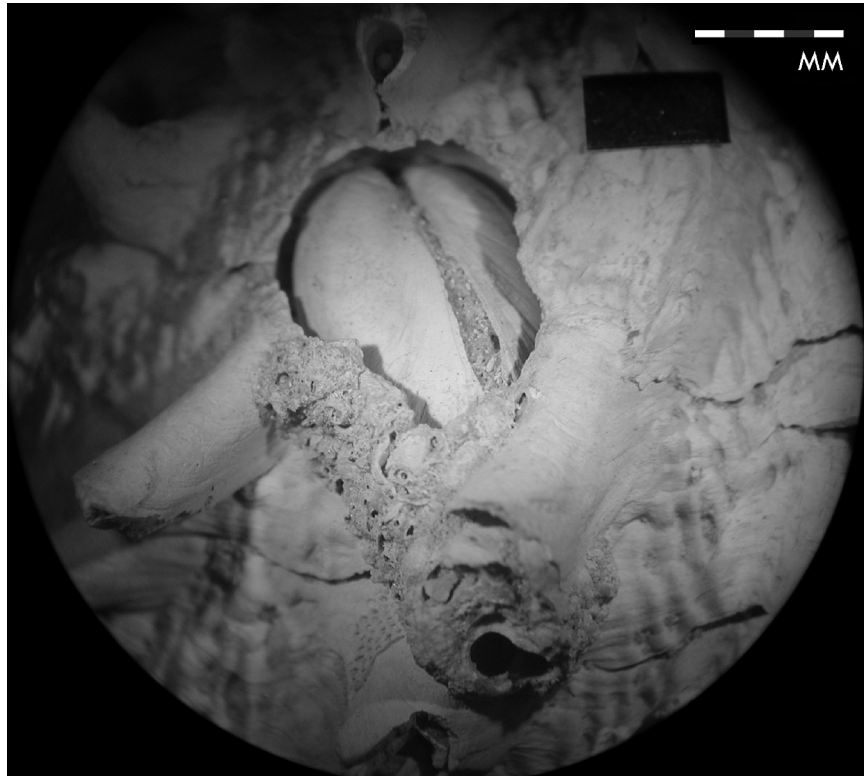


Figure 24. A gastrochaenid bivalve inside its crypt. The siphonal openings are near the bottom of the photo. Growth of the borehole would have proceeded toward the top of the photo.

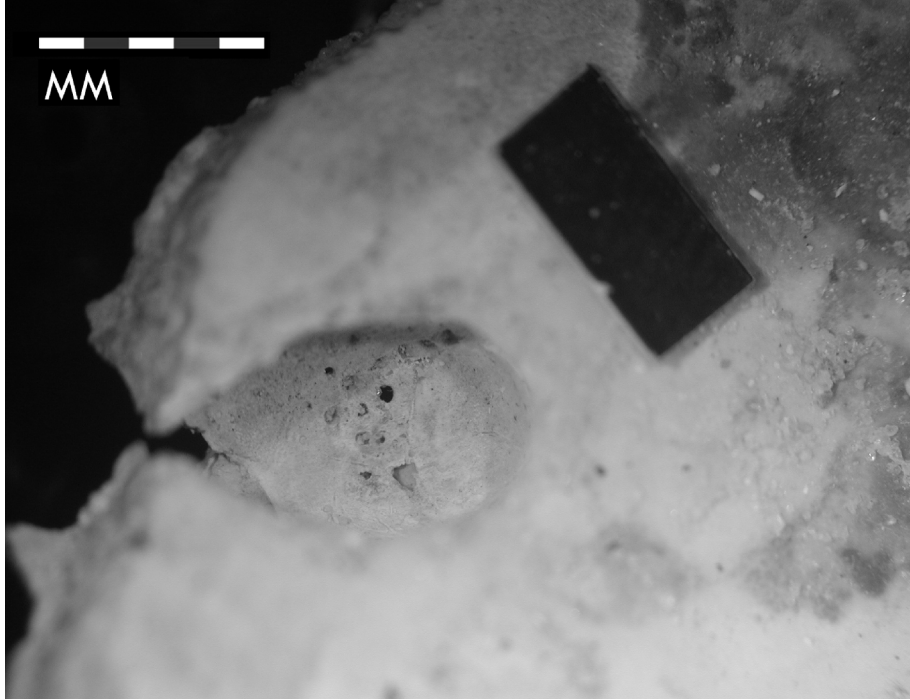


Figure 25. Small tubules perforate the anterior portions of several crypts.



Figure 26. Three crypts with aligned siphonal openings. The anterior tubules may have acted as a probing system, allowing gastrochaenids to bore without intersecting other crypts.

the Florida Keys and Caribbean of the Recent (Carter, 1978; Warne, 1975) (Figure 28).

Each of the crypts associated with *A. cornuta* is attached to or incorporates one or more of the calcareous spines in its construction. Small borings can be observed at the ventral margin of the host, where new spines are formed. Some crypts nestle inside the hollow spines (Figure 29). Others grow outward beyond the confines of the ornament (Figure 30). One crypt passes through a spine (obliterating the lower part of the spine and leaving its end perched atop the crypt)(Figure 31), and another crypt completely replaces a spine (Figure 32). One gastrochaenid crypt was found to intersect the borehole of a predatory gastropod (Figure 33).

Crypt orientation: Trends in crypt construction were examined by scaling and layering images of individual shells containing crypts. The composite image displayed the SPO vectors of thirty-five gastrochaenid crypts (Figure 34). Marking the intersections of the SPO vectors with the circular portion of the ventral margin revealed that the siphonal openings of all photographed crypts were oriented in a 98° arc with siphons directed toward the posterior ventral shell margin, and 57% of those were clustered in a 20° arc along the margin (Figure 35). This area of the margin corresponds to the region of the inhalent and exhalent apertures of the Chamidae *Chama* and *Pseudochama* (Yonge, 1966). Assuming the internal arrangement of *A. cornuta* is similar to other Chamidae, gastrochaenids colonized living *A. cornuta* and aligned their borings to exploit the inhalent and exhalent currents created by their hosts.



Figure 27. The surface of a gastrochaenid crypt.



Figure 28. The shell of a gastrochaenid borer of *A. cornuta*.



Figure 29. Siphonal openings protruding from the spines of *A. cornuta*.

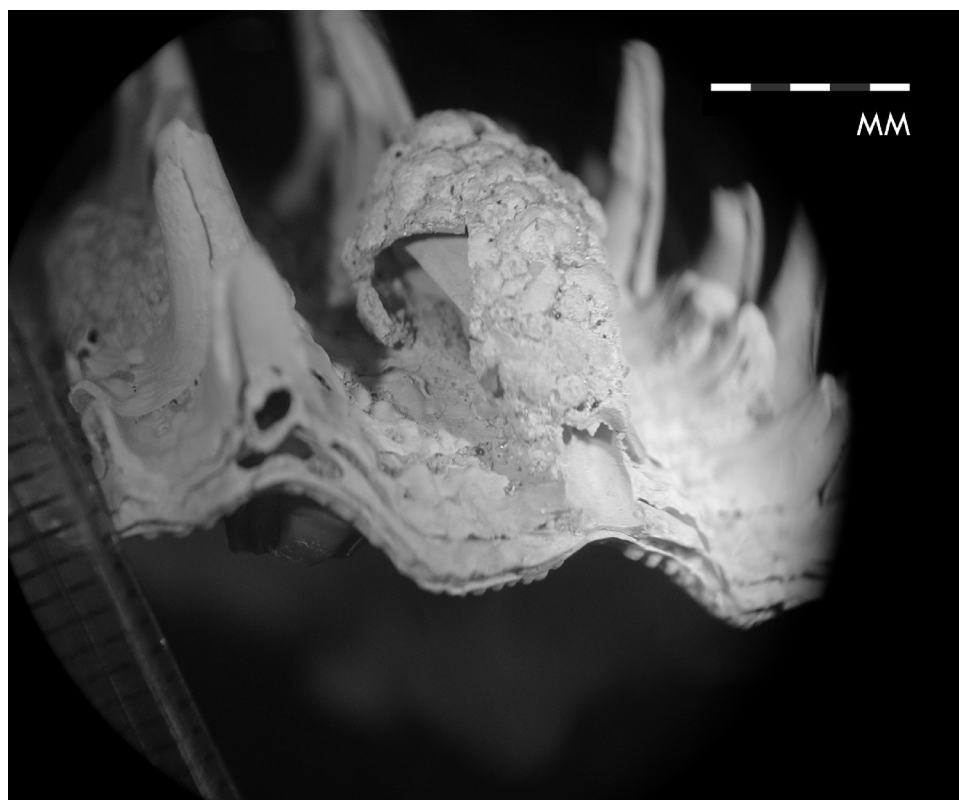


Figure 30. A crypt that had grown along a spine row. The broken left side of the crypt reveals the gastrochaenid shell inside.

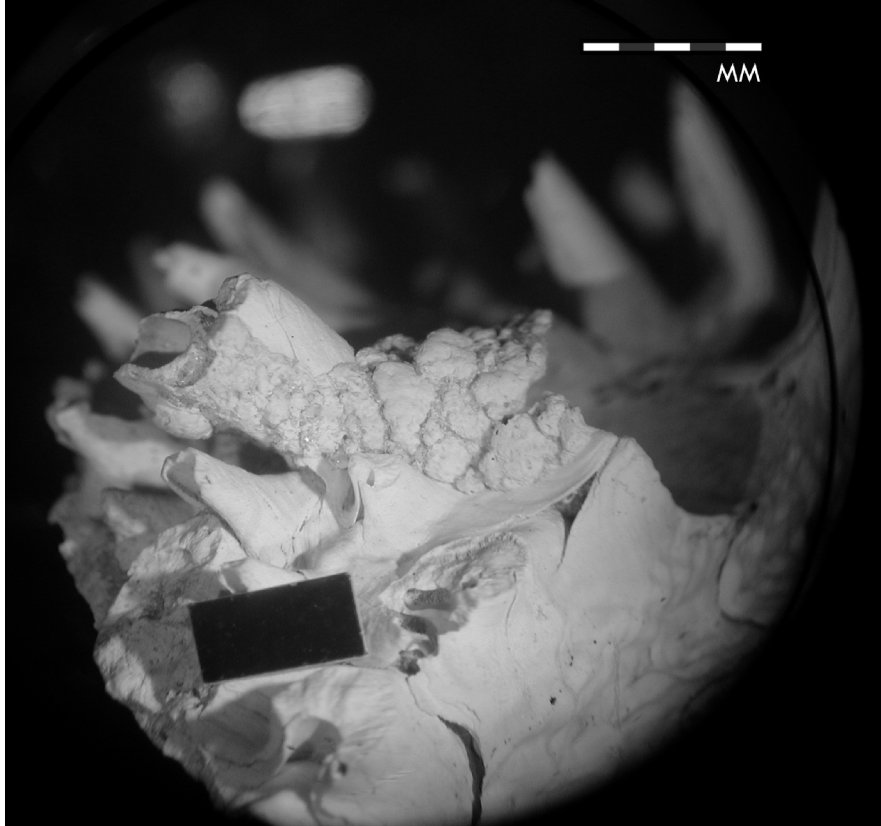


Figure 31. A crypt that had cut a spine in two. The spine tip was left perched atop the crypt.

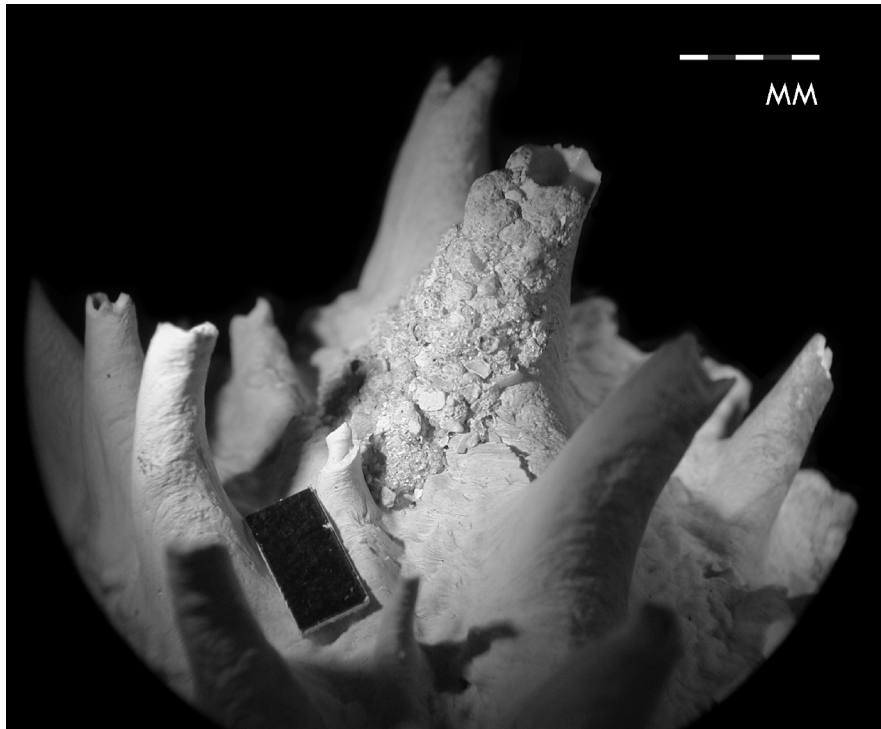


Figure 32. A crypt that occupied the interior of a spine.



Figure 33. A gastrochaenid crypt (left) passing through a predatory gastropod borehole (right).



Figure 34. Relative size, position and orientation (SPO) vectors representing gastrochaenid crypts superimposed onto a single shell of *A. cornuta*. Stippled areas represent the anterior and posterior muscle scars.

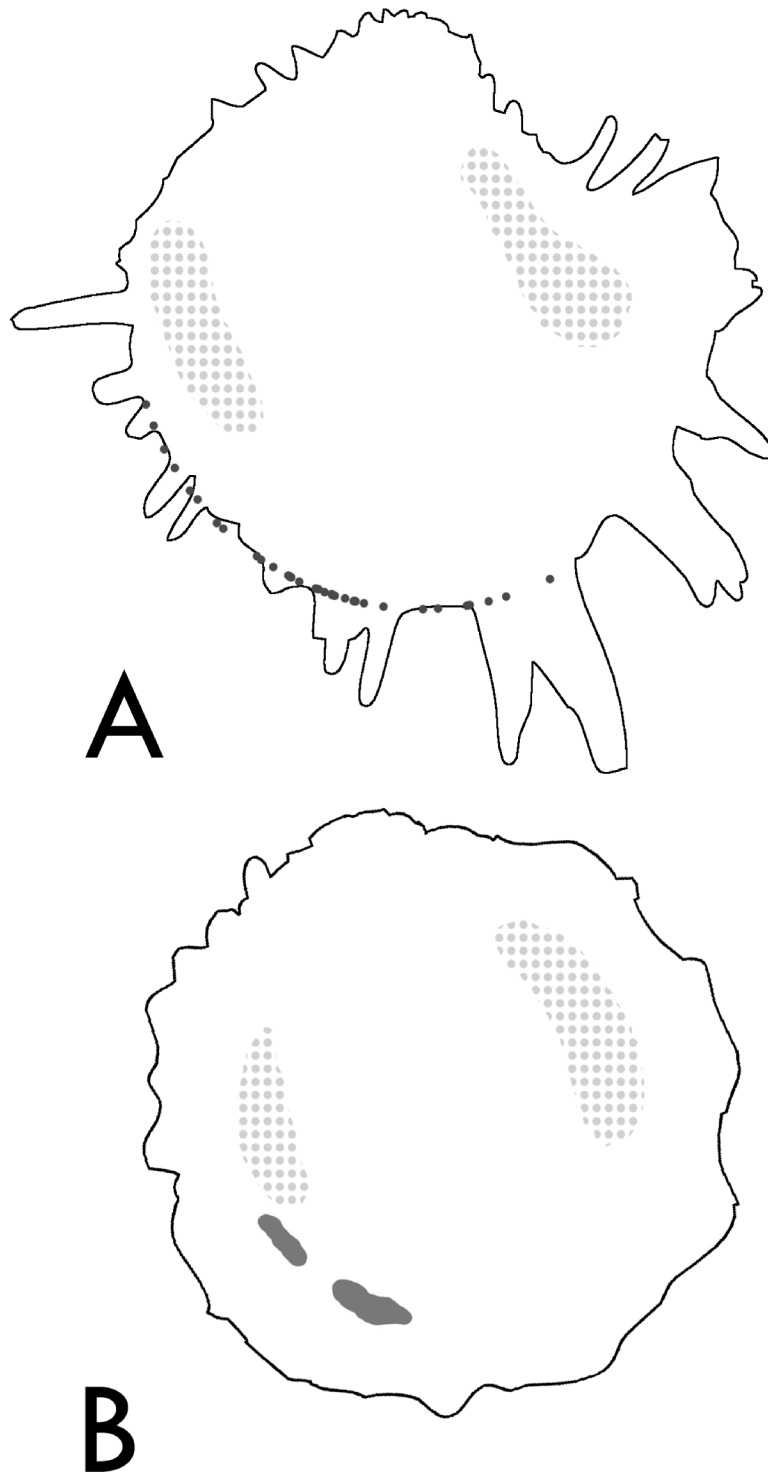


Figure 35. Comparison of gastrochaenid crypt orientations in shells of *A. cornuta* with the morphology of *Chama*. A: dots represent the intersections of SPO vectors with the semicircular ventral margin. B: the morphology of *Chama*. The gray patches represent the inhalent and exhalent apertures. Stippled areas represent the anterior and posterior muscle scars.

DISCUSSION

The Identity of the Predator

A muricid predator was most likely responsible for the boring attacks on *A. cornuta* in the Pinecrest beds and Caloosahatchee Formation. The preferred habitat of *A. cornuta*, a substrate of gravel or broken shells, is the preferred hunting ground of muricid predators. Recent muricids are important predators in the shallow, warm-water environments populated by heavily ornamented epifaunal organisms like *A. cornuta*. It has been suggested that more than half of fatalities among spinose bivalve in recent Jamaican reefs are the result of muricid predation (Jackson, 1977). Although most borings are large and several appear to be wide-rimmed or countersunk, they are similar in size and shape to borings by the recent muricids *Murex fulvescens* and *Murex brevifrons* (Carriker and Yochelson, 1968). None of the incomplete borings shows evidence of the central boss characteristic of unsuccessful naticid attacks. As most Pinecrest samples show little evidence of post-mortem transport or mixing, any of the large muricids found among that fauna, including *Murex*, *Hexaplex*, and *Muricanthus* (Jones, 1997; Petuch, 1992), could have been the putative predator.

A Shift in Attack Strategy in Response to Spinose Ornament

Gastropod attack strategies vary both temporally and geographically, and were impacted by the spinose ornament of *A. cornuta*. Evidence from borings points to some degree of size and site selective behavior, and indicates the borers employed a type of cost-benefit strategy similar to that practiced by other gastropod predators (Allmon, Nieh, and Norris, 1990; Anderson, 1992; Anderson et al, 1991; Berg and Nishenko,

1975; Dietl and Alexander, 1995, 2000; Kelley, 1988; Kelley and Hansen, 1993, 1996; Kitchell et al., 1981; Stone, 1998). Borehole sites were selected nonrandomly, and showed preference for boring at the thin posterior region of the shell (sectors 5, 6, and 7). In the Pinecrest beds, predator size and prey size are positively correlated when the predators are smaller. The strongest correlations occur at the Phase Six pit, where the largest borehole that can be compared to prey size is 4.41 mm in diameter, and in the grouped Pinecrest data when boreholes are less than 4.7 mm in diameter. This implies that smaller predators practiced energy-maximizing tactics by identifying and selecting appropriately-sized prey, then boring at a preferred site.

Bivalve spines have been traditionally regarded as a means of stabilization or structural support, an attractive hardground for epibionts, or a network of stilts to prop the ventral margin above soft sediments (Leighton, 2000; Nicol, 1952; Stone, 1998; Vance, 1978). The spines of *A. cornuta*, however, seem to have disrupted selective attack behavior, strengthening the suggestion that spines developed, in part, as a defensive adaptation (Leighton, 2001; Stone, 1998).

Spines disrupted selective attacks in several ways. The number of bored valves recovered from the Phase Nine pit was low, suggesting *A. cornuta* was rarely selected as prey, possibly because it provided unfavorable tactile stimuli to predators. Successful attacks often targeted areas of relatively low spine density. At both the Phase Nine pit and the Cochran shell pit a second, equally preferred boring site was established at the unornamented lunule. Recent muricid predators have been observed to abandon preferred boring sites obstructed by ornament for those without (Stone,

1998), and the same behavior appears to have occurred in the Pinecrest beds and the Caloosahatchee Formation. Spines hindered boring at the preferred site, the thin posterior of the shell, and prompted predators to shift their attacks to the thicker but unornamented lunule.

Larger predators were apparently under the greatest pressure to shift to another boring site. Borings in sector 1 of the grouped Pinecrest shells were, on average, 41% greater in diameter than those from all other sectors. The efficiency of attacks by larger predators in the Pinecrest was low. Larger borehole diameters correlate negatively with prey size, a reversal of energy-maximizing tactics, and size ratio results show that predators attacking in sector 1 selected relatively smaller prey than those attacking elsewhere. Although larger predators altered their strategy, they failed to consistently select appropriate energy-maximizing prey.

Several factors could be responsible for the change in attack efficiency with predator size.

1. The data may represent two different species of predator with different predatory strategies.
2. Larger predators may have experienced less pressure from competitors or other predators and may have had no need to employ an energy maximizing strategy; their size may have afforded them the opportunity to become lax in their approach to selecting prey and take as much time as necessary when boring.
3. Spines could have provided the prey animal a "virtual size refuge", making it difficult for the predator to accurately select appropriate prey.

4. The spinose ornament could have created a physical barrier to boring: larger predators might not have been able to properly position the ABO or radula between spine rows to effectively excavate a borehole.

The linear distribution of borehole diameters suggests a single attacking species. It is likely that this species found it difficult to successfully bore in regions with spines, as shown by the negative correlation of number of borings and number of spines. The alternative, boring at the lunule where the valve was thickest but obstruction to the valve surface was minimal, meant trading longer boring times for greater chances at success. This trade-off appears to have been an acceptable one for the predators. Larger predators may have even deliberately selected relatively smaller prey to minimize the time required for boring at the lunule. Poor size selection in the grouped Pinecrest samples may be a reflection of this change in attack behavior.

The relationship of prey size to predator size appears to shift between the Pinecrest and the Caloosahatchee Formation samples. Correlation of prey length to outer borehole diameter becomes stronger in the grouped Caloosahatchee Formation samples, indicating site selection was stronger. The grouped Pinecrest data show a low mean value of SR in sector 1 and high mean values of SR in all other sectors. That trend reverses in the grouped Caloosahatchee Formation data, with the mean value of SR increasing in sector 1 and falling in all other sectors. This suggests that prey size to predator size ratios in different sectors were becoming more uniform, a sign of increasingly size-selective behavior. The mean and variance of SR for the grouped Caloosahatchee Formation samples are also lower than those of the grouped Pinecrest

samples, again indicating increased selectivity. Stronger correlation of prey size to predator size, greater uniformity of prey size to predator size ratios for attacks in different shell sectors, and stronger manifestation of two preferred boring sites suggests that the predators were refining their hunting behavior during the latest Pliocene.

The spinose ornament of *A. cornuta* caused gastropod predators to alter their attack strategy for increased success, an adaptation previously observed only in response to "dangerous prey" (Dietl and Alexander 2000). It is possible that spines caused some injury to the predator during subjugation that prompted the shift. Geographic variations in attack strategy and efficiency may be manifestations of "coevolutionary hot spots", subsets of communities where reciprocal adaptation was locally strong (Dietl and Kelley, 2002). In certain locations, predators were able to adapt quickly. In other locations, predators may have had to deal with different pressures or tradeoffs and did not adapt. The strategic shift may reveal the adaptive plasticity of the predator in response to local challenges from prey, or it may signal the first steps toward an evolutionary canalization of adaptive behavior over time in response to spinose prey.

That spinose ornament developed in response to predatory attacks remains unclear. Harper (1991) suggested that the development of cementation in bivalves was influenced by predation, because it reduced the predator's ability to manipulate the prey shell. Similar pressures could have played a role in the development of spines. It is clear that, in encounters with predatory gastropods, spinose ornament was a useful exaptation, disrupting the preferred behavior of gastropod predators and forcing them to respond by adapting their attack strategy. The shift to a "two-pronged" assault in

response allowed gastropods to refine size and site selectivity over time. The link between prey morphology and predator adaptation indicates that an arms race between these two species may have been underway in the Late Pliocene of southern Florida.

Selective Colonization by Gastrochaenids

Observations of *A. cornuta* and its gastrochaenid borers suggest a previously undescribed selective association between the two species that is linked to spinose ornament. Selective colonization of *A. cornuta* by juvenile gastrochaenids implies the borers were rugophilic. The scarcity of corals, the preferred domicile of boring gastrochaenids, at the Phase Nine pit most likely prompted a habitat shift that caused the borers to seek out new hosts with extreme ornament. Juvenile gastrochaenids appear to have settled along the host's margin, where new spines were forming, then grew inside the spines. The spinose shell of *A. cornuta* would have provided several advantages to larval gastrochaenids. The hollow calcareous spines formed natural crypt-like structures that may have offered not only shelter, but a framework for future construction. They would have also offered protection from predators that would find removing a small bivalve from within a thicket of spines a daunting task. Vance (1978) observed that the heavily ornamented shells of *Chama* attracted more epibionts than smooth shells, and that those epibionts inhabiting *Chama* experienced lower mortality rates than those inhabiting other substrates. By colonizing *A. cornuta*, gastrochaenids appear to have actively selected a host that would afford them similar protection.

As the gastrochaenid borer matured and outgrew the space available within the spine, it simply incorporated the remains of its previous domicile in its new crypt. The spine

itself may have been a source of calcium carbonate that facilitated the secretion of larger crypts. Similar semi-endolithic crypt construction has been observed in Indo-Pacific species of *Gastrochaena* (*Cucurbitula*) boring into the spinose shells of *Spondylus* (Carter, 1978). Juvenile borers penetrate the outer calcitic layer of the host shell and partly enter the aragonitic layer beneath. As it matures, the gastrochaenid often emerges and secretes a protective crypt. That many spines of *A. cornuta* were destroyed by or incorporated into the construction of crypts suggests that construction began inside the spines themselves and proceeded outward.

The nonrandom alignment of crypt siphonal openings with the siphons of the host infers that gastrochaenids were also rheophilic, or current-seeking. Juvenile gastrochaenids settling inside newly forming spines near the margin would have access to inhalent and exhalent currents created by the host that would have provided a steady stream of nutrient-rich water for the borer. As the host grew and new shell material was added to the margin, the source of the currents would have moved away from the borer. Crypt growth allowed the borer to extend its siphons and continue to exploit those feeding currents. Gastrochaenids that colonized shells of *Chione cancellata* at the Phase Nine pit displayed a similar strategy, settling near the siphons. Although nonrandom crypt alignment implies that both host and borer lived simultaneously, some crypts penetrate the interiors of their host shells. This suggests that gastrochaenids possibly outlived their hosts or sometimes colonized empty shells that passively channeled nutrient-rich waters

What benefit, if any, the gastrochaenid borers provided their hosts remains unclear.

Vance (1978) established that the bivalve *Chama* was less susceptible to attack by the predatory starfish *Pisaster* when covered by epibionts. Only one *A. cornuta* with gastrochaenid borers was successfully attacked by a boring gastropod predator, but there is no evidence to suggest that gastrochaenids helped to camouflage their hosts, either physically or chemically. Gastrochaenids at the Phase Nine pit selectively colonized shells of *A. cornuta* to exploit the feeding currents, armor, and raw materials provided by the host. Colonization did not provide any clear advantage or detriment to the host. The relationship between the two is best described as commensal.

CONCLUSION AND FUTURE RESEARCH

During the Pliocene, in southern Florida, the spinose ornament of *A. cornuta* disrupted gastropod attacks and prompted a shift in attack strategy to improve their efficiency, suggesting a true arms race may have occurred. The spines of *A. cornuta* also attracted gastrochaenid bivalve epibionts by providing protection and an attractive foundation for boring and crypt building. What prompted the development of such extreme ornament is still unclear, but spines undoubtedly affected the manner in which other organisms interacted with *A. cornuta*.

Shells collected on the beaches of Captiva Island along Florida's Gulf Coast show that the ecological relationships between *A. cornuta* and boring predators and epibionts continue into the recent. Evidence of gastropod predation and gastrochaenid colonization was observed in *A. cornuta* shells collected in March of 2003. The morphologies and locations of borings appear to be similar to those from the Pliocene. Further investigation of recent shells may determine if these relationships have persisted since the Pliocene or are linked, temporally or geographically, to other environmental factors such as habitat loss or diversity of prey species.

Investigation of the competitive and commensal interactions of ornamented mollusks will continue to shed light on the evolutionary forces that shape the morphologies and behaviors of other organisms. Expanding the scope of the current study, by examining greater numbers of shells and investigating more shell beds, will provide insights in to the temporal and geographic variations of coevolution. Aquarium experiments with live specimens would not only complement observations from the fossil record but also

provide insights not available from shells alone. Observing the selection, manipulation, and boring of ornamented prey would augment current understanding of predatory behavior. Documenting the manner in which boring epibionts select and modify their hosts would be useful in testing the limits of adaptive response to the destruction of preferred habitats. Continued study of mollusk borers will strengthen and expand the understanding of the nature of interspecific interactions and the manner in which they influence evolutionary dynamics.

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