PALEOECOLOGY OF *CREPIDULA* (MOLLUSCA:GASTROPODA) BEDS, JAMES CITY FORMATION (PLEISTOCENE), NORTH CAROLINA

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CONTENTS

I. ABSTRACT

Masses of life-oriented valves of the marine gastropod *Crepidula fornicata* (Linne, 1758) form lenses in the James City Formation (Pleistocene) of North Carolina. The units are exposed along the banks of the Neuse River estuary in Craven County, near Johnson Point. Three other types of lithologic units, which occur in the bluffs at Johnson Point and differ (to various degrees) with respect to taxonomic composition and sedimentology, are *dense clay layers, shell-hash layers,* and *dispersed shell beds*. The primary distinguishing characteristics of the *Crepidula* beds include high shell/matrix ratio, high abundance of *C. fornicata,* and high relative proportion of epifaunal suspension feeders. The *Crepidula* beds may be classified as "minor simple shell beds" (terminology of Kidwell, 1982) produced through the biologic activity of epifaunal organisms.

Taxonomic analysis of the *Crepidula* beds shows them to contain over 30 species of Mollusca, which are predominantly small, vagrant, carnivorous and grazing gastropods, and infaunal, siphon-feeding pelecypods. The *Crepidula* bed communities were physically controlled communities whose compositions fluctuated in response to physical factors in the environment.

Populations of *C. fornicata* from different *Crepidula* beds show similar size-frequency distributions and survivorship curves. A high rate of mortality for juveniles is indicated, followed by lower, but consistently increasing mortality throughout adulthood. This pattern suggests that after the attainment of a threshold size, the onset of old age was the major determiner of mortality in the populations. Differences in size data between samples may be related to differences in environmental stability during the periods
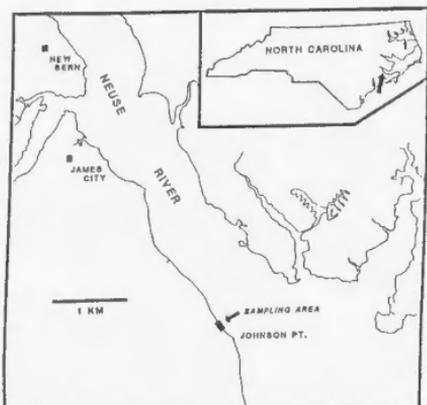
Figure 1. Locality map, Neuse River estuary of eastern North Carolina.

when the populations were living on the sea floor.

The *Crepidula* beds were deposited within a shallow, semi-restricted basin. The origin of the beds appears to be tied to the current regime and pattern of natural disturbances in the bay. Strong currents, produced through intermittent activation of tidal channels, initiated production of the units. Resurgence of *Crepidula fornicata* populations, in response to increased nutrients in the environment, resulted in the rapid accumulation of shell material. At the same time, a reduced rate of sedimentation abetted the proliferation of epifaunal species. Termination of *Crepidula* bed production in the James City Formation is attributable to changes in hydrography of the basin.

II. INTRODUCTION

The James City Formation (DuBar and Solliday, 1963) is the oldest stratigraphic unit recognized in outcrops along the Neuse River estuary, in Craven County of eastern North Carolina. Its deposits are exposed for approximately 6.5 km along the banks of the Neuse River, downstream from the town of New Bern (Fig. 1). Outcrops of the formation are in the extreme northwestern end and on the south bank of the estuary. The type locality is located 2.1 km downstream (east) from the town of

James City (DuBar and Solliday, 1963), and strata containing dense *Crepidula* layers are a few kilometers farther downstream, in the vicinity of Johnson Point. The measured lateral extent of outcrop containing *Crepidula* layers at Johnson Point is approximately 150 m.

In the type area, the James City Formation is unconformably overlain by the Flanner Beach Formation and has a gentle regional dip to the southeast (Fig. 2). The base of the James City is not exposed in the type area, and the total thickness of the unit is uncertain; but it is not thought to exceed 15 m (DuBar, Solliday, and Howard, 1974).

The James City Formation is one of a series of coastal plain units that were depo-
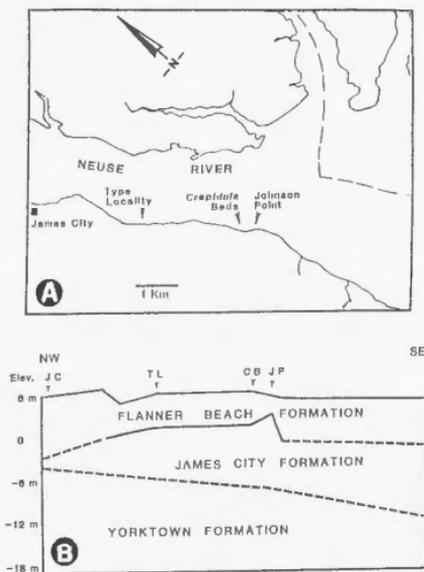

Figure 2. A. Locality map, Neuse River estuary. B. Generalized geologic cross-section of the study area (after DuBar, Solliday, and Howard, 1974). Arrows point to approximate locations, along a traverse from northwest to southeast, of the town of James City, JC; the James City type locality, TL; the James City *Crepidula* beds (sampling area), CB; and Johnson Point, JP.

sited during Pleistocene high-stands of sea level. Blackwelder (1981) estimated the age of the unit to be between 1.2 and 1.8 million years old; however, the results of more recent investigations into Atlantic Coastal Plain stratigraphy suggest a considerably younger age (0.7 - 1.3 million years) for the James City (Cronin *et al.*, 1984).

The *Crepidula* beds occur as discrete sedimentologic or biologic units, which are interbedded with three other types of lithologic units that show repeated and somewhat predictable patterns of occurrence in the outcrops. These other unit types are *dense clay layers, shell-hash layers* and *dispersed shell layers*.

The dense clay layers are usually 5 to 10 cm thick and consist of moderately indurated blue clay, with few scattered fossils. They occur both as thinner, discontinuous interbeds between *Crepidula* beds, and as thicker (*e.g.*, 0.4 m), more laterally extensive layers in the lower regions of some bluffs. The sparse fossil content of these units is mainly isolated single valves or small stacks (two or three individuals) of *Crepidula fornicata*, or valves of *Anadara aequicostata*. Sedimentary structures are generally absent, and trace fossils are limited to a few thin, sand-filled burrows that contain small pelecypod shells (*e.g.*, *Nuculana acuta*) and shell fragments.

The shell-hash layers tend to be irregular in shape, with a general thickness range of 10 to 20 cm. They are composed mainly of slightly indurated, silty mud and shell hash, and are situated at about the same stratigraphic level as the *Crepidula* beds (relative to the ground surface) or slightly lower. Their fossil contents are predominantly small specimens of *Mulinia lateralis* and *Nuculana acuta*, with relatively few broken and disarticulated adult specimens of *Anadara aequicostata* and *Crepidula fornicata*. The shell-hash layers contain the most sand of any of the lithologic units and probably were deposited under turbulent conditions.

The *Crepidula* beds are discontinuous, vertically repeating, in some places interfingering shell beds, approximately 7.5 to 12 cm thick, and situated below the more continuous dispersed shell layers. They are composed mainly of large (*e.g.*, 6 to 12 individuals in a stack), densely packed stacks of *Crepidula fornicata* (Fig. 3) in slightly indurated, silty mud matrix, in which there are also a few sand-filled burrows. The stacks appear to be randomly oriented and most are rotated out of life positions. *Crepidula* shells are bored and encrusted to varying degrees, but most are fairly well-preserved. Most other fossils in these units are epifaunal species.

The dispersed shell beds range in thickness from 0.4 to 0.75 m and occupy the highest stratigraphic positions in the bluffs of the four unit types (immediately below the soil and root zone). The faunas of these units are generally more diverse than those of the *Crepidula* beds, but not as diverse as those of the shell-hash layers. The orientation of shells within the dispersed shell beds indicates a depositional setting of relatively low turbulence. Large clams and oysters, and small stacks (four or fewer individuals) of *C. fornicata* remain articulated and are often *in situ*. The matrix is grey-brown, moderately indurated, clayey mud. Sand-filled burrows of the sort found in the dense clay layers and *Crepidula* beds were not observed in the dispersed shell layers.

III. METHODS

Samples were collected during two trips to the field area. The first trip was essentially a reconnaissance expedition surveying faunal content and sedimentology of shell beds along the 150 m extent of outcrop containing *Crepidula* beds. Twelve six-liter bulk samples were collected, and at each sampling station notes were recorded regarding shell density, preservation, dispersion, orientation, relative abundance of epi-bionts, and approximate size and number of individuals in *Crepidula* stacks. These samples were useful for establishing the general faunal and sedimentologic compositions of the different shell bed types, but represented too great a span of time to be useful in detailed analysis of preserved community attributes of the assemblages. During the second trip, samples were collected from three well-preserved *Crepidula* beds that would allow for higher resolution analysis of faunal content and size-frequency distribution of *C. fornicata* within those units.

Figure 3. A. Densely-packed *Crepidula* stacks and silty mud matrix of a James City *Crepidula* bed. (Scale divisions are 5.0 cm) B. Faunal assemblage of a dispersed shell bed.

The fossil material was sorted and counted at the Tulane Geology Department. Faunal lists, including the number of specimens in each listing (absolute abundance) were compiled for each sample. This information has since been published by Miller and DuBar (1988) and Miller (this volume) and will not be repeated here. Size-frequency data for *C. fornicata* were obtained by measuring all specimens found in each of the three higher resolution samples.

Gross separation of sand-, silt- and clay-sized material in sediment samples was accomplished through modified sieving and decantation procedures of Folk (1965, pp. 18-24, and p. 40) and Blatt (1982, p. 520). Percent calcium carbonate in the samples was determined by weighing before and after digestion in dilute hydrochloric acid.

All but two of the survey samples were composed predominantly of very fine-grained material with the average proportion of silt and clay being about 55% for the 12 samples. The sand-sized material was mainly medium to fine-grained, subangular quartz and calcium carbonate shell fragments. X-ray diffraction analysis of the James City clay minerals by DuBar, Solliday, and Howard (1974) showed them to be predominantly mixed-layer illite-montmorillonite, with minor amounts of kaolinite. The relatively high proportion of coarser-grained material in the shell-hash samples is probably indicative of a higher energy depositional environment. The higher resolution *Crepidula* bed samples were less variable than the survey samples, and averaged 30.5% sand-sized, 42.9% clay-sized, and 25.7% clay-sized material.

The biolithic content of sediments reflects "dead shell" abundance on the sea floor, which influences such community attributes as number and diversity of epifaunal species (see Driscoll and Brandon, 1973), and may indicate the ancient community's residence time in the environment. The survey sediment samples ranged from 13% to over 30% calcium carbonate. Analysis of sediment (material less than approximately 1 mm in diameter) from the *Crepidula* bed samples showed substantially less calcium carbonate (between 7 and 11%), the bulk of which was contained in the coarsest size fractions.

IV. BIOLOGY OF *CREPIDULA FORNICATA*

Crepidula Lamarck (Gastropoda:Calyptraeidae) is a genus of marine Mesogastropoda found in modern shallow-water environments. Hoagland (1977) states that this genus dominates many marine communities in both biomass and energy cycling, relative to other filter-feeding organisms present. There are 40 valid species known worldwide, ten of which are extinct (Hoagland, 1977).

Feeding in *Crepidula fornicata*, a prosobranch mesogastropod, is by filtering particulate food matter (in the form of marine plankton) from the sea water. Loomis and Van Nieuwenhuyze (1985) observed a feeding behavior in *C. fornicata* that they suspect may enhance its chances for survival under conditions of low current velocity and high turbidity. Postural changes of snails in direct contact with muddy sediments allowed them to resuspend particulate matter and then filter it from the water. Filter-feeding efficiency in *C. fornicata* decreases under conditions of high turbidity (Johnson, 1971), but Loomis and Van Nieuwenhuyze feel that the ability to feed at all under circumstances that would clog the filtering apparatus of most other filter feeders is a selective advantage.

Adults of the species are sedentary and normally found in stacks composed of twelve or more individuals (Fig. 4), in which females are situated toward the bottom and the younger males toward the top. The following is a summary of proposed functions of the stack in *C. fornicata.*

1. It allows for formation of a breeding unit. Thus, stacking insures the availability of one or more suitable breeding partners. In addition, it minimizes the threat of predation on motile males who would otherwise be required to wander in search of the sedentary females (Hoagland, 1979).
2. It allows for production of feeding currents. By alignment of the right anterior shell margins of members within the stack, the inhalent water current entering the mantle cavity is maximized. At the same time, the excurrent flow of feces and pseudofeces
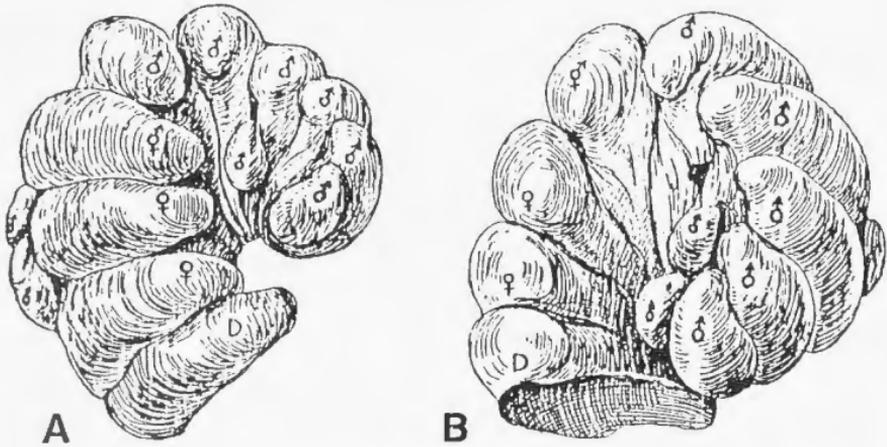
Figure 4. Two views (A and B) of a large *Crepidula* stack, consisting of one (dead) supporting shell (D), two females, one transitional individual, six non-motile males and three motile (supplementary) males. (From Coe, 1936)

is augmented by subtle changes in stack shape (Hoagland, 1979).

3. It provides suitable substrate for settling larvae. The preferred substrate of *C. fornicata* is a smooth, convex surface (Hoagland, 1978, 1979). This shape exposes individuals to greater currents and less sedimentation than either flat or concave surfaces. Stacking offers unlimited substrate of this type for new members of the population.

Members of the family Calyptraeidae exhibit protandry: a complicated form of hermaphroditism in which the young individuals always develop first into functional males, progress through a intermediate phase, and later mature into functional females. *Crepidula fornicata* and other species within this genus differ from the rest of the family in that the change from male to female does not occur at the same time (age) for all individuals. Instead, the length of time spent in each sexual phase is governed by specific factors in the individual's immediate environment (Purchon, 1977). Many studies (*e.g.*, Coe, 1936, 1938a and b, 1942; Hoagland, 1979) have been aimed at determining the nature of factors responsible for change of sex in *Crepidula fornicata*. In general, the type and length

of association of an individual with other members of the population appears to be the most important controlling factor.

Recruitment effort in populations of *C. fornicata* appears to be intrinsically related to their residence time in the environment. Total egg output per adult tends to decrease as the density of the population increases (Hoagland, 1978). This is because a larger proportion of each individual's lifetime is spent in the male phase for non-colonizing populations.

Growth and variability in *Crepidula fornicata* are mediated by conditions in the environment, and by the life history of the individual. Growth rate is higher in isolated males than in mated males, and is most rapid during the intermediate stage occurring between the male and female phases. Widely deviating growth forms are seen in nature, including large and dwarfed individuals, and variability in shape, color, and texture. Two basic shell morphologies are commonly exhibited (Coe, 1942). The first is a narrow growth form, found on muddy or sandy substrates. It results from surface limitation for foot attachment, imposed by the stacking behavior. Shells of this type are smooth, narrow and highly arched (Fig. 5A), and usu-
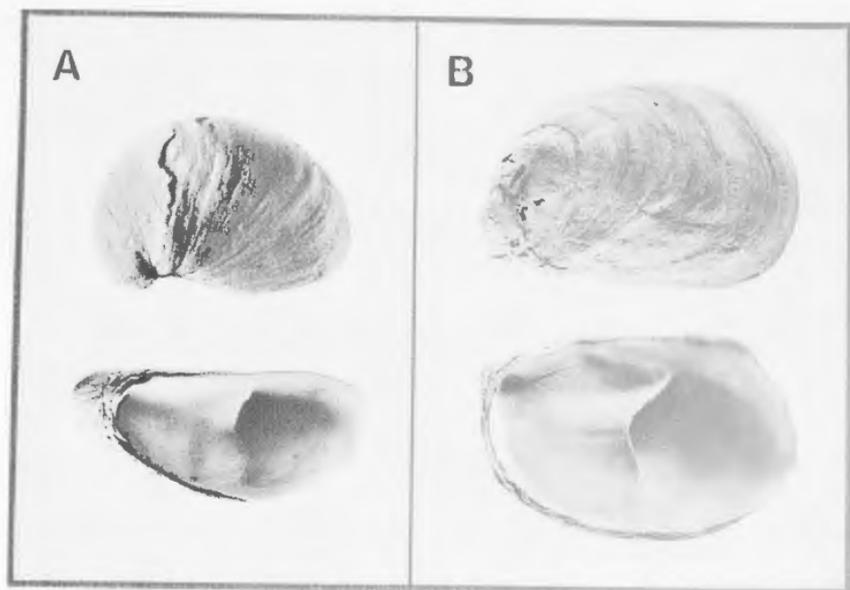
Figure 5. Growth forms in specimens of *Crepidula fornicata* from the James City *Crepidula* beds. The narrow form (A) resulted from limited growth surface (within a stack). The broad, flat form (B) was attained through growth on an unrestricted surface.

ally occur in large stacks of as many as sixteen individuals. The second growth form is a flat, oval shell (Fig. 5B), which may be found singly or in small groups of two or three individuals. In this case, substrate is an unrestricted surface upon which maximum shell size may be attained. If a young or half-grown individual is transferred from a convex surface to one that is flat, the narrow growth form can be halted and replaced by broad, flat shell growth. Coe (1942) noted that sex transformation usually accompanied the onset of a new growth form in experiments of this nature. Young individuals that attach themselves to very small pebbles or shells develop into highly arched dwarfs. Other highly variable shell shapes are produced by growth on irregular surfaces. For instance, if an individual attaches itself to the shell of a scallop, the crenulated surface will be re-

flected in the texture of the snail's shell as it grows (Hoagland, 1977).

Figures 5 and 6 show some of the various shell shapes observed in specimens of *C. fornicata* from the James City *Crepidula* layers. The highly arched shell form (Fig. 5A) predominated in the collections, which is understandable, because most of the individuals occupied positions in stacks. Irregular shapes (Fig. 6d and e) were also common in the samples. Constrictions on some shells (Fig. 6a, b, and c), which indicate a change in growth form (from narrow to broad) during the life of the individual, have been called "mate marks" (Hoagland, 1977). They are usually caused by a change in substrate from a more restricted surface (*i.e.*, the shell of a female), to a less restricted surface, which probably coincided with sex transformation (Coe, 1942; Hoagland, 1977).
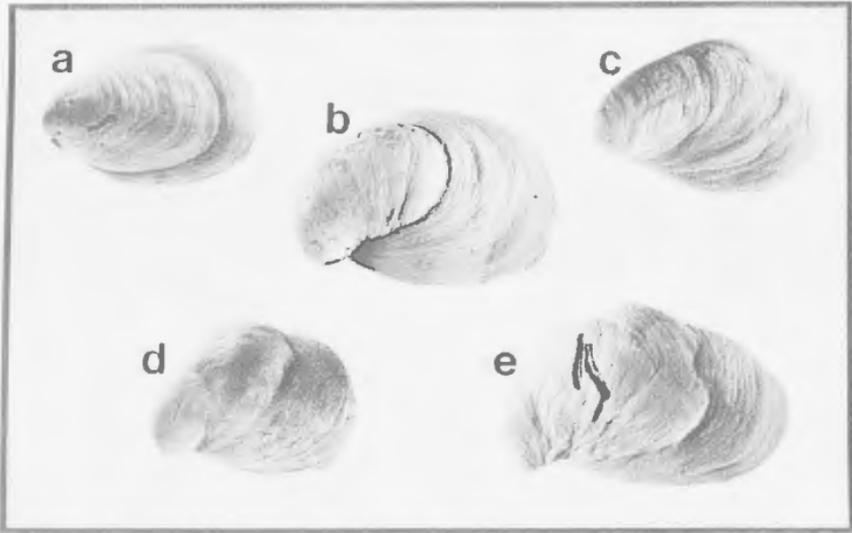
Figure 6. Morphologic variability in specimens of *Crepidula fornicata* from the James City *Crepidula* beds. "Mate marks" (a, b and c) indicate a change in growth surface from more to less restricted; irregular shell growth (d and e) is due to uneven growth surfaces.

V. PALEOSYNECOLOGY OF *CREPIDULA* BEDS

Crepidula fornicata is a common faunal element in outcrops of the James City Formation along the northwest bank of the Neuse River estuary. It is prevalent in the other types of shell beds, as well as in the *Crepidula* beds upon which this study is focused. For this reason, it may be useful to outline specific attributes of "*Crepidula* Beds" that distinguish them from the other fossiliferous units at Johnson Point.

The most obvious features of the James City Crepidula beds (Fig. 7) are:
(1) high density of shells (high shell/matrix ratio);
(2) numerical abundance of *Crepidula fornicata;*
(3) highly visible as discrete layers, particularly when viewed from a distance; and
(4) evidence of post-depositional disturbance generally limited to reorienta-

tion of stacks, with fossils mainly whole and well preserved and *Crepidula* stacks not disaggregated.

Secondary features that can be recognized in conjunction with, or directly resulting from the primary features include:
(1) relatively fewer specimens of *Anadara aequicostata,* or other infaunal bivalves *(e.g., Mulinia lateralis* and *Nuculana acuta);*
(2) common occurrence of epifaunal and encrusting species *(e.g., Balanus* sp. and *Ostrea sculpturata);*
(3) larger stacks of *C. fornicata* (usually more than 6 individuals); and
(4) lower stratigraphic position in the bluffs than the less compact, quiet water assemblages.

The James City *Crepidula* beds fit the criteria of Kidwell (1982) for being classified as "minor simple shell beds." Attributes that describe this general class of shelly accumulation are: (1) relatively thin (cm to 10's of cm); (2) contained within the
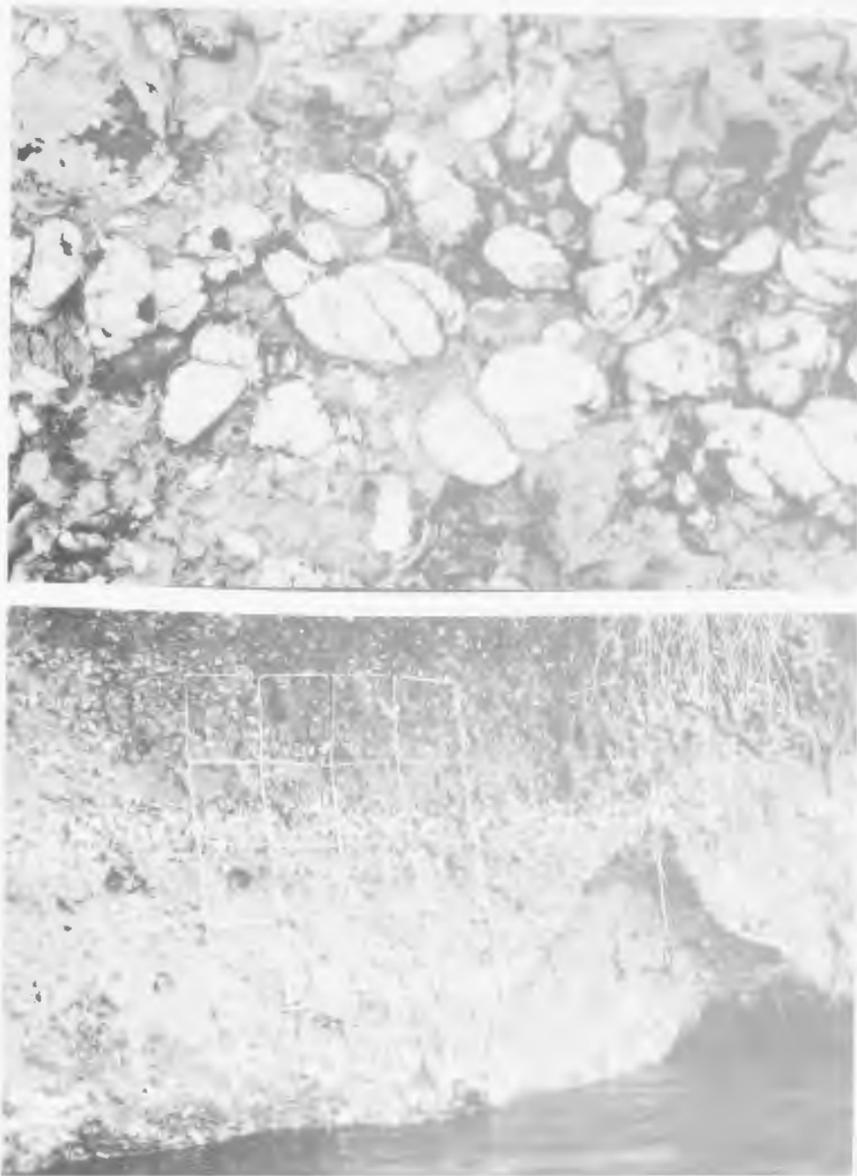
Figure 7. Characteristics of *Crepidula* beds: composed mainly of densely-packed, aggregated stacks of *C. fornicata* in slightly disturbed orientations (A); form discrete layers in the bluffs B).

bounds of a single facies; (3) geometry ranging from irregular pods and layers of pods, to single valve stringers and thicker beds; (4) usually lacking lateral or vertical variation in composition or taphonomic character of fossil assemblages and sedimentary matrices; (5) may or may not be associated with depositional discontinuities; and (6) relatively simple taphonomic histories. Kidwell defines "minor simple shell beds" as generally short-term events resulting from biologic and physical processes capable of concentrating shells over a period of time that may range from months to tens of years, or the portion of the absolute time scale designated "ecologic time" (see Kidwell, 1982, text-fig. 1).

The *Crepidula* beds at Johnson Point range from 7.5 to 12.0 cm in thickness, and individual beds can not be traced laterally for more than a few meters. All beds are contained within the lateral bounds of a massive mudstone unit, and tend to vary slightly in taxonomic and sediment matrix composition. The beds exhibit a roughly lensoidal geometry, being slightly thicker towards the middle of the layers and tapering at the outer edges.

Fossil preservation within the layers is mainly related to only two factors: length of exposure on the sea bottom, prior to being buried; and post-burial oxidation and erosion due to groundwater infiltration. Some indicators of longer residence times on the sea bottom include higher incidence of encrusted, bored and fragmented shells and possibly, local hardground development. Assemblages that existed for relatively short periods of time before being buried are more likely to contain "clean" whole shells. In regard to the effects of groundwater, whether or not a layer has been altered appears to depend upon its proximity to the overlying soil layer. Shell beds situated near the bottoms of bluffs have been generally spared chemical alteration by migrating fluids. Those nearer the tops of bluffs have sustained more oxidation and post-depositional erosion.

Biogenic reworking of the sediment by infaunal organisms is apparent from the absence of bedding within or between the units, and some within-habitat disturbance

is evident. However, there is no evidence of large-scale transport processes, therefore the bulk of the fossil material is probably indigenous. The *Crepidula* beds are not associated with unconformities at either their upper or lower bed contacts and have the appearance of simply "floating" in the outcrops.

Community Structure of Crepidula *beds*

The James City *Crepidula* beds are composed predominantly of molluscan species, but also contain species of Crustacea, Bryozoa, Annelida, Porifera and Cnidaria (see Miller, this volume). Table 1 lists the niche characteristics of molluscs from the units.

Specimens of *Crepidula fornicata,* a sessile, epifaunal suspension feeder, composed the bulk of the shell material in samples from the beds. With the exception of *Crepidula plana,* the remainder of the gastropods were small, vagrant carnivores, grazers and parasites (see Table 1). *Boonea seminuda,* an ectoparasite that lives on *C. fornicata,* was numerically abundant in the samples. *Anachis lafresnayi* and *A. obesa,* two carnivorous species, were also recovered in large numbers.

Pelecypods found in the units were predominantly infaunal siphon feeders. The most common burrowing species were *Nuculana acuta* and *Mulinia lateralis.* More significant in terms of actual biovolume, however, were *Anadara aequicostata* and *Ostrea sculpturata,* two epifaunal suspension feeders. Rapid burrowers *(e.g., Tellina texana* and *Ensis directus)* were scarce and commonly fragmented in the samples.

Johnson wrote (1972, p. 151):

The environment of benthic communities on clastic substrate is usually gradational. Muds grade into muddy sands and these, in turn, into sands. Depth, light, salinity and water motion tend to vary in a continuous fashion. As a consequence, benthic communities on clastic substrates tend to be continuous and intergrading, both in shallow and deep water.

The James City *Crepidula* beds are typical of Johnson's (1972) benthic com-

TABLE 1. Niche Characteristics of Molluscan species from the James City *Crepidula* Beds. Key: SF, Suspension Feeder; DF, Deposit Feeder; C, Carnivore; G, Grazer; EP, Ectoparasite; SC, Scavenger; SI, Siphon Feeder; E, Epifaunal; I, Infaunal. (Information is from Stanley, 1968, 1970; and Driscoll and Brandon, 1973.)

Taxa	Feeding Mode	Substrate Relationship	Locomotion-Attachment
Gastropoda			
Crepidula fornicata	SF	E	Foot attached
Crepidula plana	SF	E	Foot attached
Boonea seminuda	EP	E	Vagrant
Anachis lafresnayi	C	E	Vagrant
Anachis obesa	C	E	Vagrant
Nassarius albus	SC	E	Vagrant
Nassarius consensus	SC	E	Vagrant
Natica pusilla	C	E	Vagrant
Urosalpinx cinera	C	E	Vagrant
Eupleura sulcidentata	C	E	Vagrant
Fasciolaria lilium	C	E	Vagrant
Turbonilla sp.	EP	E	Vagrant
Melanella sp.	EP	E	Vagrant?
Marginella (Prunum) sp.	C	E	Vagrant
Busycon canaliculatum	C	E	Vagrant
Seila adamsi	G	E	Vagrant
Epitonium humphreysi	C	E	Vagrant
Pelecypoda			
Anadara aequicostata	SF	E	Slow Burrower*
Nuculana acuta	DF	I	Active Burrower
Nucula proxima	DF	I	Active Burrower
Mercenaria campechiensis	SI	I	Shallow Burrower
Mulinia lateralis	SI	I	Burrower
Ostrea sculpturata	SF	E	Cemented
Argopecten irradians	SF	E	Nektic, Recliner
Tellina texana	SI	I	Rapid Burrower
Corbula conradi	SI	I	Slow Burrower
Chione cancellata	SI	I	Burrower
Yoldia limatula	DF	I	Active Burrower
Ensitellops protexta	SI	I	Burrower
Ensis directus	SI	I	Rapid Burrower
Polyplacophora	SC	E	Vagrant
Chaetopleura apiculata	G	E	Vagrant

*occasional byssal attachment

munities on clastic substrates, in that their faunal compositions reflect the gradational nature of the environment. Three types of species that occur in the beds are (see Johnson, 1972, p. 157): (1) characteristic species - the most obvious faunal elements, which tend to occur in the greatest numbers; (2) intergrading species - those species characteristic of another, usually adjacent environment; and (3) ubiquitous species - species that occur in several settings, but are not characteristic of any one environment. *Crepidula fornicata* is the obvious characteristic species of the *Crepidula* beds. It dominates the faunas both numerically and in bulk volume. *Boonea seminuda* which lives specifically in association with *C. fornicata,* is also prevalent,

and can be classified as a secondary characteristic species of the *Crepidula* bed communities. Most of the pelecypod taxa found in the units are considered to be intergrading species, associated with either higher or lower energy environments than what is optimal for *Crepidula* bed formation. Species thought to be intergradational toward a typically higher energy environment include rapid burrowers such as *Tellina texana, Ensis directus,* and *Yoldia limatula.* An intergrading species leaning toward the lower-energy end of the environmental gradient is *Ostrea sculpturata. Anadara aequicostata* and *Mulinia lateralis* can be considered ubiquitous species, since they are common in units suggestive of quiet water deposition (i.e., dispersed shell beds), as well as in the higher energy shell-hash and *Crepidula* layers.

The James City *Crepidula* beds are thought to represent low grade communities whose occurrence and compositions were under the direct influence of the physical environment (see Margalef, 1968; Johnson, 1972). Regular fluctuations in certain key parameters in the environment (discussed in subsequent sections) resulted in density variability of the characteristic species *(Crepidula fornicata)* over time.

Spatial Distribution Within C. fornicata *Populations*

Three types of spatial distribution that can occur within populations are random, regular or overdispersed, and clumped or underdispersed (Dodd and Stanton, 1981). As evidenced by the preserved stacks of the James City *Crepidula* beds, individuals within the *C. fornicata* populations were underdispersed or spatially clumped during life; but a further question with respect to scale should be considered. Clumps of a given species may occur in an area, but the clumps themselves may be randomly distributed (Dodd and Stanton, 1981). The question of whether the situation in the James City *Crepidula* beds was one of randomly spaced clumps (stacks), or one of stack clustering is pertinent to a complete understanding of the population structure, and a reasonable interpretation of the origin of the beds. A primary distinguishing feature of the *Crepidula* layers (with re-

spect to the other types of shell beds in the James City Formation) is the manner in which large stacks are closely packed together. It appears likely that the stacks composing the original *Crepidula* populations were also underdispersed on the substrate, and that the discontinuous, roughly lensoidal beds represent original patches of sea floor that contained many clustered stacks. Inhomogeneities in the distribution of suitable habitat, and positive interaction between individuals of the species are proposed reasons for clumping in populations (Dodd and Stanton, 1981). Biological evidence suggests that these two factors are interrelated in populations of *Crepidula fornicata.* In regard to substrate preference of settling spat, Hoagland (1978) found that the newly metamorphosed young are attracted to adults and juveniles of their own species, and particularly to females. Under laboratory conditions, substrates with adult snails received more than three times the number of spat of substrates without adults. Apparently, the presence of adults increases the likelihood of young settling on the same substrate in nature as well, but the influence is simply a presence or absence effect. No relationship between density of adults and density of settling spat has been indicated (Hoagland, 1978).

Biological means by which clumped populations may be produced are: postponement of larval metamorphosis until a suitable substrate is found; survival of only those larvae that settle within the clumps; concentration of food supply in only certain areas; and development of the young from eggs deposited near the parent (Dodd and Stanton, 1981). Food supply and larval settling behavior are thought to have been the major determiners of dispersal in the *Crepidula* beds. Live and/or dead individuals can also be physically concentrated in an area through the action of strong currents, but this is not thought to have had a significant influence in the *Crepidula* beds.

Age and Size Distribution of Population Members

Rates and patterns of mortality in populations of *Crepidula fornicata* were assessed through analysis of size-frequency data from three *Crepidula* bed samples.
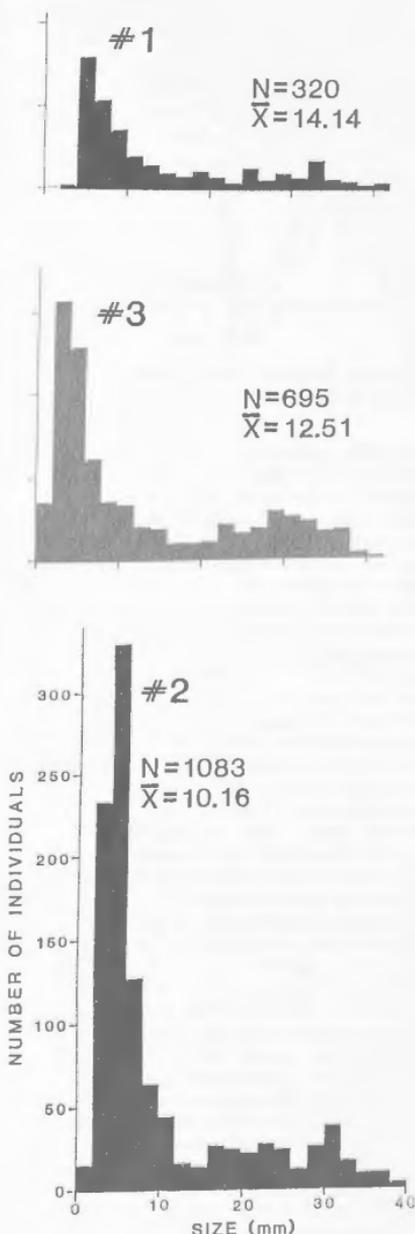
The lengths of specimens of *C. fornicata* in the samples ranged from less than 2 mm to about 42 mm. Although the numbers of individuals in the three samples varied greatly, the tendency toward large numbers of small specimens was exhibited in each case (Fig. 8). In all three samples more than half of the individuals were less than 10 mm long. Sample 1, however, contained appreciably fewer specimens of the smallest size categories than the other two samples. No shells of *C. fornicata* less than 2 mm in length were recovered, and only about 1% of the total number of individuals in that sample fell into the 2-4 mm category, compared to 22% for samples 2 and 3.

Sample 1 had the largest mean specimen size of the three groups (probably due to the relative absence of individuals in the first two size categories), and sample 2 had the smallest (see Fig. 8).

Size-frequency curves for the three samples were constructed in the manner prescribed by Folk (1965, p. 43). The size-frequency data for the three groups were converted into cumulative curves. Then, slopes of tangents to the cumulative curves were plotted at 1 mm intervals. Size-frequency curves enables distribution to be more readily observed and interpreted, by illustrating overall trends (modes) in the populations.

The curves for the sampled *Crepidula* populations are strongly right (positive) skewed (see Fig. 9). Large, well-defined peaks occur at about 5 mm for all three populations. Less conspicuous inflections appear at approximately 31 mm in samples 2 and 3, and at 34 mm in sample 1. It is rare for assemblages to show more than one or a few strong peaks in their size frequency curves, and polymodality in sufficiently large samples has been related to successive annual broods in populations (see Craig and Hallam, 1963). The peaks occurring at 31 and 34 mm in the *Crepidula* populations probably represent mortality

Figure 8. Size-frequency data for specimens of *C. fornicata* from *Crepidula* bed samples 1, 2 and 3. N is the number of specimens measured in each sample. $\bar{x}$ is the mean size for specimens in each sample. Scale is the same for all three histograms.
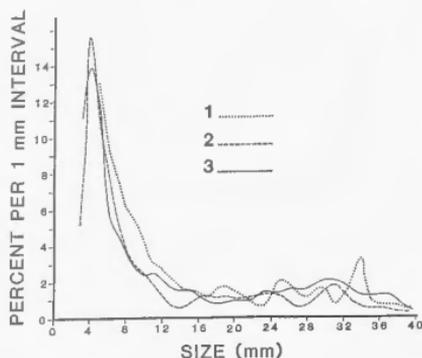
Figure 9. Size-frequency curves for *C. fornicata* in *Crepidula* bed samples 1, 2 and 3.

in an older generation of snails (*i.e.*, one or more seasons) than the individuals represented by the large spikes at 5 mm. The other small, irregular inflections in the curves (particularly in sample 1) may be spurious, or the result of size variability within the species. In addition to mortality rates, size-frequency distributions are dependent upon growth, so it is understandable that data for populations of *C. fornicata* might produce relatively complex curves. The fossil populations, although extremely short-term geologically, are thought to represent recruitment and natural mortality in *C. fornicata* populations over a period of time (*i.e.*, years), rather than mass-kill censusing (see Hallam, 1972; Dodd and Stanton, 1981). The general trend illustrated is for a high rate of mortality in the infant sizes, more or less constant mortality throughout youth and adulthood, and a renewed high rate of mortality in old age.

Survivorship curves (Figs. 10B, 11B and 12B) were plotted by the method prescribed by Hallam (1972). The number of survivors is expressed as percent of the total population sampled, and is plotted on a logarithmic scale along the ordinate. Length from the size-frequency histograms (Fig. 8) was converted to relative age, and plotted along the abscissa. Relative age was determined from size by assuming that the largest individuals in the three samples (42 mm) were the oldest. This size was then designated maximum age for members of all three populations. All other

sizes are expressed as percentages of the maximum age. This technique is somewhat problematic for stacked populations of *C. fornicata*, because shell length only roughly correlates to true body mass in the highly arched growth form. Also, older individuals in the population can be much smaller than younger individuals, depending upon stack constraints (*e.g.*, a small basal shell) (Hoagland, written comm.).

Specific patterns of mortality in populations are enhanced in survivorship curves. Mortality rate is indicated by slope. Changes in slope along the length of the curve reflect the mortality patterns in the populations. Three basic curve shapes may occur (MacArthur and Connell, 1966; Hallam, 1972): (1) convex to the upper right, signifying increasing mortality with age; (2) approximately linear, reflecting constant mortality; and (3) concave to the upper right, indicating decreasing mortality with age. Survivorship curves for species living on firm substrates and/or in environments that are relatively turbulent are characteristically convex (Richards and Bambach, 1975). Apparently, once individuals in those settings have survived long enough to begin producing calcified shells, the predominant factor that will ultimately affect survival of their size class is the onset of old age. On the other hand, species in muddy environments typically suffer extremely high juvenile mortality due to predation and difficulties in feeding, breathing, and maintaining position on the muddy substrate. These groups characteristically have concave survivorship curves, and the decrease in mortality rate corresponds to attainment of size capable of maintaining a stable position on the sea floor.

The survivorship curves for the three *Crepidula fornicata* populations are more complex than the general cases described above (see Figs. 10B, 11B and 12B). They are linear to weakly concave up to about 30% of the maximum age, then become convex through the remainder of the age classes. Sample 2, in particular, exhibits an extremely high rate of mortality in the youngest age classes (Fig. 11B). This may reflect particularly harsh environmental conditions for that population during the time of spatfall (see Richards and Bambach, 1975). It appears that up to a point (a
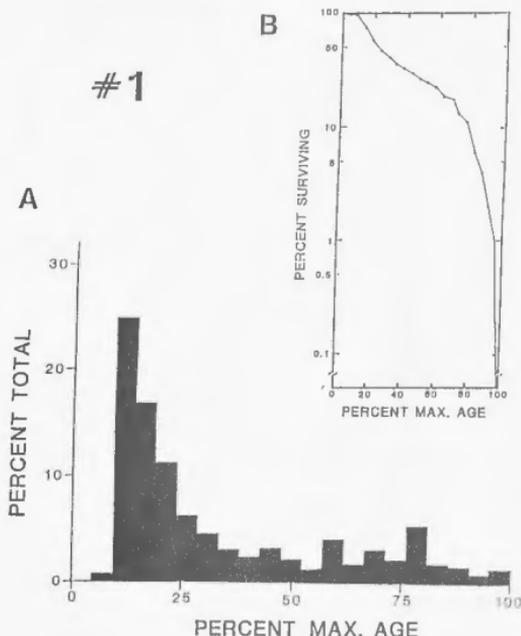
Figure 10. Age-frequency histogram (A), and survivorship curve (B) for *C. fornicata* in *Crepidula* bed sample 1.

threshold size), smaller individuals in the *Crepidula* populations tended to experience higher mortality than larger individuals. The threshold size, which is approximately 14 mm in the sampled populations, may correspond to the end of the motile male phase, during which individuals were more susceptible to predation. After reaching sedentary adulthood, gerontic factors took over as the main influences on death or survival. Since growth in *C. fornicata,* as in many molluscan species, continues throughout the lifetime of the organism (albeit, more slowly after attaining maturity), individuals over the threshold age (size) had a progressively higher chance of dying.

The survivorship curves for the three *Crepidula* populations, although similar in overall shape, vary somewhat with respect to (apparent) ages at which specific changes in slope occur. In particular, smaller sizes at points of change in mortality are indicated by the curve for sample 2 (see

Fig. 13). An overall smaller size of individuals is characteristic of *Crepidula* populations that are new settlements or colonizing populations. Sex change in such populations tends to occur at a smaller size and younger age, due to a lower proportion of females (Hoagland, 1978). Growth rate is reduced following sexual maturity in *C. fornicata* (Hoagland, 1978), so the curve for sample 2 may also record a drastically reduced rate of growth.

VI. DISCUSSION

Depositional Setting

Based on sedimentologic and faunal (molluscan and foraminiferal) data, DuBar, Solliday, and Howard (1974) interpreted the depositional environment of the James City Formation as having been a shallow, semi-restricted embayment. The generalized faunal and sedimentologic data produced by the reconnaissance sam-
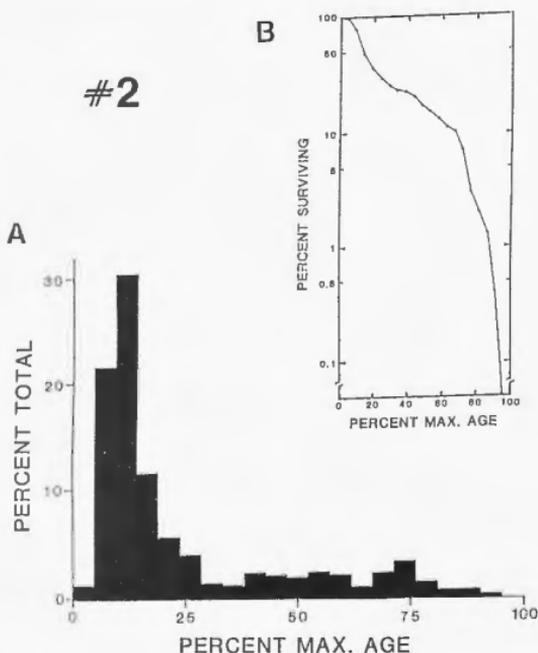
Figure 11. Age-frequency histogram (A), and survivorship curve (B) for *C. fornicata* in *Crepidula* bed sample 2.

pling for this study is consistent with this interpretation. A few species (*C. fornicata, Anadara aequicostata,* and *Nuculana acuta*) comprised upwards of 75% of the preserved faunas of the non-biostromal deposits and *C. fornicata* comprised up to 87% of the *Crepidula* bed fossils. This characteristic is indicative of a somewhat restricted depositional setting. Because the faunas are so similar between the non-biostromal and *Crepidula* biostromal deposits at Johnson Point (including the abundance of *C. fornicata)*, the question that begs to be answered is: what were the unique physical or biological factors that supported development of the biostrome? Unfortunately, studies relating the occurrence of living *Crepidula* beds with densities of *C. fornicata* approaching those of the James City strata to physical factors in the environment are scarce. Parker's (1959) classic study of coastal bays in central Texas investigated the distribution of

molluscs in ecologic environments for the explicit purpose of providing criteria by which ancient settings could be interpreted. The taxa and sediments of the James City Formation are characteristic of Parker's high salinity bay environments. The faunas of those environments can be grouped into two assemblages: the bay margin assemblage and the bay center assemblage (Parker, 1959). Substrate and circulation are the most important factors separating the two environments. Parker has described "solid *Crepidula* deposits" along the margin of a shallow bay near Rockport, Texas, that receives a steady influx of water from the Gulf of Mexico (1960, written comm. to J. DuBar). Later studies on assemblages faunistically similar to the James City strata have also linked development of high density shell beds dominated by epifaunal suspension feeders to environments having relatively high current velocities.
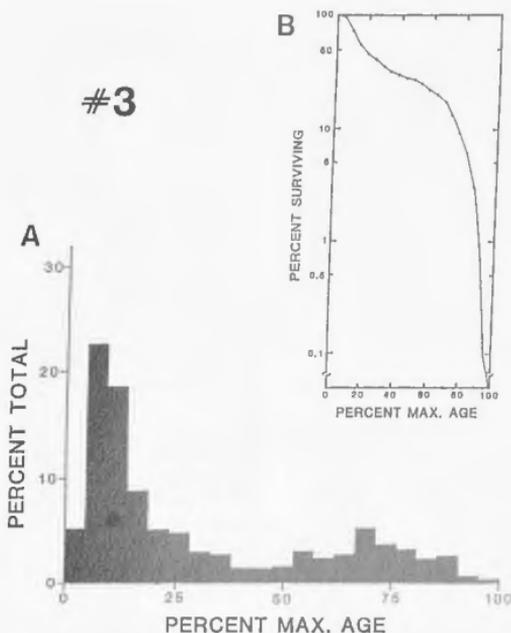
Figure 12. Age-frequency histogram (A), and survivorship curve (B) for *C. fornicata* in *Crepidula* bed sample 3.

Driscoll (1967) found that the hydrography of a shallow protected cove within Buzzards Bay, (Massachussetts), which yielded the greatest densities of *C. fornicata*, was suggestive of the presence of tidal currents strong enough to provide an abundant food supply. The fine sediments in the cove were somewhat more consolidated than those elsewhere in the bay.

Preliminary investigation of a fossil *Vermicularia* biostrome within the Pinecrest beds at Sarasota, Florida (Stanley; in progress) also points to inlet influence within a lagoonal setting.

Contrary to the evidence for inlet influence, Hoagland (1989, written comm.) states that she has observed the densest *Crepidula* beds in Long Island Sound and Vineyard Haven in bays where current velocities were low. So far, no studies have supported a relationship of increased density of *C. fornicata* populations with decreased current velocity, but there is clearly a need for further work in this area.

Origin of Crepidula *Beds*

Although the case for inlet circulation playing the crucial role in determining the presence or absence of *Crepidula* beds in the James City Formation is not conclusive, it is certainly feasible based on the existing evidence from living *Crepidula* beds and the nature of shallow coastal environments. Also, the recurrent nature of *Crepidula* beds at Johnson Point and their alternating occurrence with the barren clay layers tends to suggest a periodic natural distrubance event, such as tidal channel activation, in the ancient environment.

Tidal channels form through bars and barriers as a result of episodic events such as the deep scouring action of storm generated waves. While the channels are active, sedimentation to areas of the bay floor proximal to the inlets tends to be extremely slow, or pre-existing sediments may be eroded (Shepard 1953; Davis, 1983). Inlets are short-lived geologically and inevitably fill up with sediments. When this occurs,
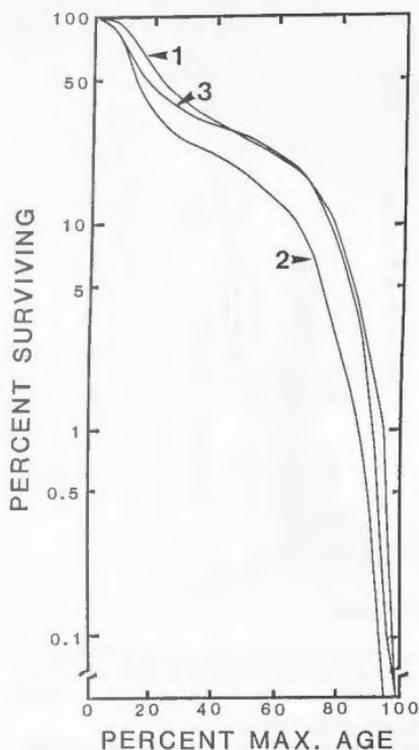
Figure 13. Survivorship curves for the three *Crepidula* populations, which are similar in shape, but differ with respect to apparent ages (sizes) at which changes in mortality occur.

circulation within the basin may revert to a pattern similar to that occurring before the channel opened. Physical consequences of altered current regime, which may bring about the collapse of a biocoenosis, would include a sudden or gradual change in salinity, grain size and/or composition of the sediments caused by a change in the direction of currents, and the onset of sedimentation in areas that previously received no sediment, due to a change in current direction (Schafer, 1972). Biological consequences of a shift in circulation pattern might be: fouling by increased levels of excretory substances (*i.e.*, feces) among the dense populations due to a decrease in the velocity of bottom currents, and rapid or gradual starvation due to a decrease in the velocity of feeding currents.

Termination of *Crepidula* biostromal production in the James City Formation was probably related to changes in hydrography (*e.g.*, migration of the inlet) of the basin.

Two possible consequences of tidal channel activation proposed herein as mechanisms in the formation of the James City *Crepidula* beds are population resurgence, and reduction in sedimentation. R. G. Johnson's study (1960) was one of the first promoting the concept of fossil density as a function of relative rates of hardpart input and sedimentation. He described three basic ways by which richly fossiliferous deposits might be produced. They are: (1) if hardpart input were to increase against a background of constant sediment supply; (2) if sedimentation decreased while the rate of hardpart input remained constant; or (3) if both rates varied in such a way as to result in net increase in hardpart input relative to sediment supply.

The James City *Crepidula* layers possess a strongly biogenic signature, due to the spatial distribution of skeletal elements within them. Accumulations of this type are produced by the intrinsic gregarious behavior of the organisms whose skeletons make up the units (Kidwell, Fursich and Aigner, 1986). As previously stated, stacking and the preferential colonization of substrates already occupied by adults of their species by *C. fornicata* larvae are the primary factors responsible for the distribution pattern in the *Crepidula* beds.

In modern settings, drastic increases in numbers of certain species of invertebrates have been observed over relatively short periods of time (*e.g.*, a few years). Groups that exhibit this type of behavior have been termed "resurgent populations" by Coe (1957).

The following depicts a sequence of events, following the enhancement of feeding currents through tidal channel activation, that may describe the mode of occurrence (and decline) of the James City *Crepidula* beds (see Fig. 14).
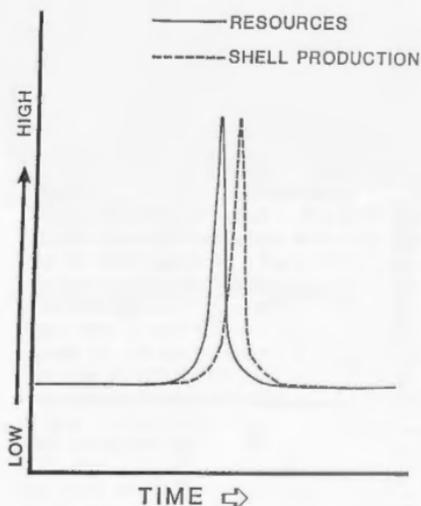
Figure 14. The Resurgent Population Mechanism.

1. The sudden availability of a previously limited resource significantly raises the carrying capacity for the environment, and induces the rapid population growth of an innately fecund species.

2. In a relatively short period of time, the resurgent species attains a population density that is commensurable with the environment's new carrying capacity.

3. A sudden or gradual reduction in the critical resource leads to either a catastrophic or stepwise decline in the resurgent population. The temporal scope of population resurgence and decline is on the order of years to tens of years, or within *ecologic* time.

The Resurgent Population Mechanism proposes that the enhancement of a critical resource in the environment, coupled with the fecundity and resource utilization abilities of a particular species were the crucial ingredients in the production of the *Crepidula* beds. The main selling points in this explanation are simplicity and feasibility. Enhanced nutrients would be a direct result of strong current activity in the ancient

environment. In addition, the likelihood of resurgence in *C. fornicata* populations seems feasible, given the ecologic and biologic background of the species, and the fact that fluctuations of this sort are known to be widespread in benthic communities. There is, however, a considerable degree of variability in capacity of groups to fluctuate, which complicates the simple idea of formation through relatively rapid hardpart input. In other words, could the increase in shell-production rate alone have been sufficient to produce the dense beds? Invoking another influence in the origin of the beds (*i.e.*, sedimentation) necessarily comes to bear on the question of temporal scope.

The *Crepidula* beds are ecological oddities in that they are composed predominantly of epifaunal suspension feeders, but occur in fine-grained sediment. The co-occurrence of these two features contradicts a well recognized concept regarding the influence of sediment on benthos, *viz.*, deposit feeders tend to be more abundant in muddy sand, and suspension feeders are more likely to predominate in shell/gravel grounds (Craig and Jones, 1966). However, Hoagland states (1989, written comm.) that in muddy sediments, the large *Crepidula* stacks are not attached to the substrate, are often in direct contact with the mud, and can roll around on the bottom in strong currents.

Reduced sedimentation rate provides an explanation for the development of dense shell beds dominated by epifaunal organisms in a mud bottom setting. The sequence of events might be as follows (see Fig. 15).

1. Initial colonization of the muddy substrate is by opportunistic species, which are most likely deposit feeders, but could also be specially adapted suspension feeders or sediment floaters.

2. Shell production exceeds the rate of sedimentation locally transforming the soft ground into firm ground, and colonization by epifaunal suspension feeders is permitted.

3. As more and more carbonate material is introduced to the substrate through death and fragmentation of the shelled community members, epifaunal

A. Pioneer Stage

Opportunists in muddy substrate, initiation of shell production.

B. Sediment Stabilization

Colonization by epifaunal suspension feeders, enhanced shell production.

C. Faunal Turnover

Proliferation of epifauna, restriction of infauna, rapid shell production.

D. Resultant Condensed Shell Bed

Epifaunal suspension feeders numerically predominate.

Ongoing Low Rate of Sedimentation

Figure 15. The Reduced Sedimentation Mechanism.

organisms become more prolific, while deposit feeders undergo spatial restriction.

4. Faunal transformation, which is already in progress, is facilitated by the fecundity of epifaunal species involved, and the situation eventually gives way to complete faunal turnover and the establishment of a complex, structured community dominated by suspension feeders.

Reduced sedimentation provides a sensible explanation for several important characteristics of the James City *Crepidula* beds, particularly the predominance of epifaunal suspension feeders in a mud bottom setting. Unfortunately, this can not be entirely proven on the basis of observed features of the shell beds. The salient features of the Reduced Sedimentation Mechanism are: reduction in sedimentation relative to shell production; local firm

ground development; and faunal turnover. Evidence of these three processes might be: high shell/matrix ratios; inhomogeneity of sediments between the dense shell beds and intervening layers, with the possible occurrence of omission surfaces; and mixed faunal assemblages, including opportunistic and soft-bottom infaunal, and firm ground (epifaunal) inhabitants.

High shell/matrix ratios in the beds only indicate that sedimentation was slow relative to shell input. If a high rate of shell production due strictly to biologic processes had occurred in conjunction with a constant rate of sedimentation, the net effect would be the same (Johnson, 1960). As in the case of population resurgence, there is a question of relative influence that comes to bear on the problem of temporal scope. Still, reduced sedimentation is consistent with the environmental interpretation. If the beds were deposited in an area of the basin that was receiving inlet circulation, then they had the lowest rate of sedimentation of any of the bay environments. The necessary sedimentologic clues of reduced sedimentation (*e.g.,* inhomogeneity and omission surfaces) are not available. All traces of bedding have been obliterated in the units through intense bioturbation, as have such features as the nature of the original stratigraphic contacts. The overprinting of time and sedimentologic processes on biologic events, (and vice versa), makes it extremely difficult to interpret original community dynamics. Faunal analysis of the *Crepidula* beds shows them to contain a mixture of epifaunal and infaunal species. This may suggest a change in substrate characteristics and faunal turnover, but could also be the result of other factors, including mixing of taxa from adjacent environments.

VII. CONCLUSIONS

The James City *Crepidula* beds are biogenic accumulations, produced primarily through episodes of resurgence by *Crepidula fornicata* populations. These events occurred in response to periodic increases in current velocity (and nutrients) in a shallow, semi-restricted basin. Tidal channel activation through natural disturbances was the likely catalyst for the production of these units. A reduced rate of sedimentation during periods of enhanced currents probably contributed significantly to the suitability of that environment for habitation by epifaunal suspension feeders in general, and *C. fornicata* in particular.

The *Crepidula* bed communities were physically controlled communities whose compositions varied under the direct influence of the physical environment. An environmental gradient along which substrate, as well as other parameters, changed in a continuous fashion is reflected in the faunal compositions of the *Crepidula* beds. Aspects of the *C. fornicata* populations (mortality, growth, recruitment, and morphologic variablity) were likewise largely controlled (directly and indirectly) by environmental factors.

VIII. ACKNOWLEDGMENTS

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