VARIATION OF RECENT AND FOSSIL *CRASSOSTREA* IN JAMAICA

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ABSTRACT. Biological studies have indicated that the oysters *Crassostrea virginica* (Gmelin) and *C. rhizophorae* (Guilding) may be a single species. This is surprising as they are morphologically dissimilar, *C. virginica* being far larger and thicker than *C. rhizophorae.* We postulate that this variation may be ecophenotypic in origin, a cause of gross variation in form in other oysters. To test our hypothesis, we have compared the palaeoecology and ecology of Plio-Pleistocene *C. virginica* and Recent *C. rhizophorae* from Jamaica. A spectacular Plio-Pleistocene deposit is dominated by *C. virginica*, other organisms being almost absent. One exceptional bed, over 3 m thick, is dominantly composed of oysters. This sequence appears to have been near-shore marine, or possibly estuarine, but, somehow, the environment was obviously highly favourable for *C. virginica.* Conversely, modern *C. rhizophorae* mainly attach to mangrove rhizophores and may compete with a very broad variety of organisms. Physical factors, such as salinity, can vary rapidly within this environment. In consequence, *C. rhizophorae* seems to grow fast, reproduce early and die early, whereas Plio-Pleistocene *C. virginica* grew to a large size which probably indicates considerable maturity. Environmental stress necessitates a rapid life cycle for *C. rhizophorae*. Therefore, ecophenotypic variation may indeed be the cause of morphological variation between *C. virginica* and *C. rhizophorae*. However, detailed studies on living populations of both species are considered essential to test this hypothesis further.

IN the fossil record of many organisms, such as oysters and scallops, we can only attempt to differentiate between evolutionary and ecophenotypic variation if we have tight stratigraphic control and large samples for statistical analysis (for example, Bayer *et al.* 1985; Johnson 1981). However, different methodologies are used to determine such variation more precisely in modern organisms. Gunter (1954, p. 134) stated that 'within certain limits, defined by the fact that the shells consist of two hinged valves, oysters are among the most plastic organisms known'. This plasticity in shell form has caused much confusion in oyster taxonomy as many morphological variants of one species are similar to those of others. Indeed, the distinction of an oyster genus upon shell morphology alone has been questioned by a number of authors (for example, Ranson 1942; Gunter 1950), as macroform is strongly influenced by substrate (Galtsoff 1964; Palmer and Carriker 1979).

The two oysters *Crassostrea virginica* (Gmelin) and *C. rhizophorae* (Guilding), which are on first sight morphologically distinct, may be two end members of a single, highly variable taxon (a review of the literature comparing *C. rhizophorae* with *C. virginica* is given in Newball and Carriker 1983).

C. virginica and *C. rhizophorae* each have a diploid number (2n) of 20, hybridize readily (Menzel 1972, 1973), have morphologically similar karyotypes (Rodriguez-Romero *et al.* 1979), and, by means of electrophoretic studies, it has been shown they share approximately 72% of the same genes (Buroker *et al.* 1979). Menzel (1972, 1973) suggested *C. rhizophorae* may be a subspecies of *C. virginica*, but although these 'species' hybridize readily in the laboratory, such a phenomenon would not necessarily occur under natural conditions (Menzel 1971). Survival of hybrids between these 'species' was 34% after one year and compares favourably with survival rates of 25% and 72% of pure bred *C. rhizophorae* and *C. virginica* over the same period (Menzel 1971). Detailed ultrastructural examinations of young individuals of each species have led Newball and Carriker (1983) to suggest that *C. rhizophorae* is an ecotype of *C. virginica.*

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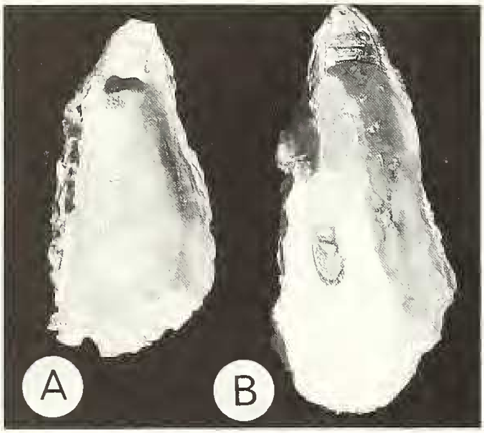
C. rhizophorae and *C. virginica* are not the only species within the genus *Crassostrea* Sacco, 1897 to show close affinities. For instance, Singarajah (1980) believed *C. rhizophorae* to be synonymous with both *Ostrea arborea* and *C.* (*Ostrea*) *brasiliana* Lamarck, and Durve (1986) has likened *C. madrasensis* (Preston) to *C. virginica*. On the other hand, physiological variation within the species *C. virginica* has also been demonstrated (Stauber 1950; Loosanoff 1958), where morphologically indistinguishable groups within this species are considered to be physiological races that are functionally different from one another. Palmer and Carriker (1979) review factors suspected to affect shell morphology in *C. virginica* and other ostreids. The list includes substrate, culture technique (bottom and off-bottom), temperature, current velocity, turbidity, salinity, and exposure to direct sunlight. However, *C. virginica* is never seen to vary so much that it appears to approach *C. rhizophorae* closely in morphology.



TEXT-FIG. 1. Small specimens of the attached valves in *Crassostrea virginica* (Gmelin). A, fossil specimen from the Plio-Pleistocene Round Hill Beds of Jamaica. B, Recent specimen from Prince Edward Island, Canada. Both ×0·45.

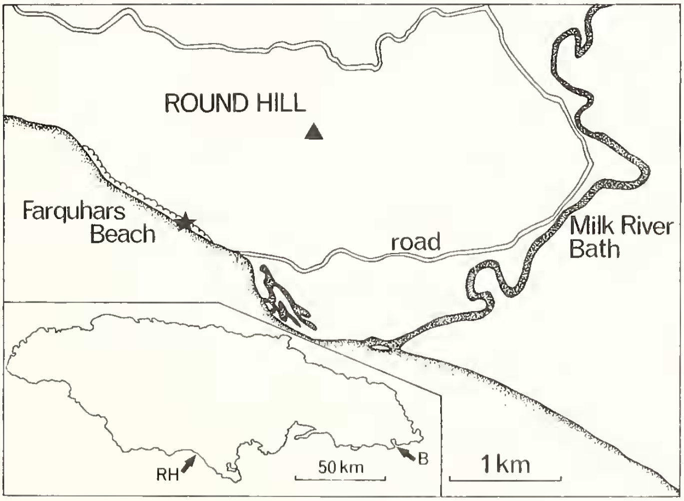
The features which differentiate the two 'species', *C. rhizophorae* and *C. virginica*, include heavier muscle scar pigmentation and greater lower left valve plication in *C. virginica* (Gunter 1951; Galtsoff 1964). Additionally, maximum height of *C. virginica* approaches 400 mm, whereas that of *C. rhizophorae* rarely exceeds 100 mm. It has already been mentioned that substrate affects macroform. Even though the habitats of *C. rhizophorae* and *C. virginica*, mangrove prop roots and soft sediment or hard, shelly substrates, respectively, may not explain the difference in plication, other factors, such as different growth rates, may be at least indicative of cause and effect. Although Mattox (1949) failed to find evidence of alternational hermaphroditism in *C. rhizophorae*, a feature common to the genus, Angell (1986) suggested protandrous hermaphroditism may occur in this species. The evidence includes the predominance of females in populations of *C. rhizophorae* (Angell 1973), the presence of hermaphroditic gonads, and the observation that males tend to be smaller than females (Angell 1986).

If, indeed, *C. virginica* and *C. rhizophorae* are members of a single, highly variable species, then nobody has yet explained why they are so different. In the case of such variation within a species of fossil oyster, difference of environment is usually cited as the probable principal reason for variation in form. Herein, we examine the environments of *C. virginica* and *C. rhizophorae* in Jamaica. *C. rhizophorae*, the mangrove oyster, is a common element of the modern fauna, but *C. virginica* is extinct in Jamaica and is only known from the Plio-Pleistocene. One exceptional fauna, dominated by the latter taxon, sheds light on the environment of *C. virginica* and enables us to make at least some comparisons with modern *C. rhizophorae*. The fossil *C. virginica* are morphologically indistinguishable from Recent members of the same 'species' (text-fig. 1).

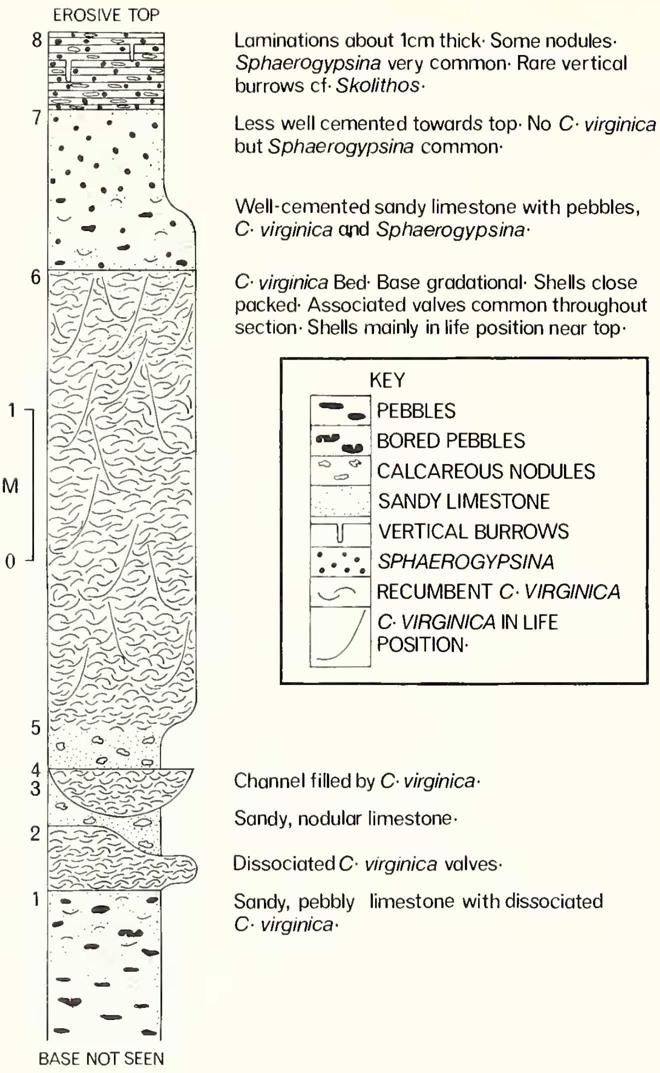
CRASSOSTREA VIRGINICA IN THE PLIO-PLEISTOCENE OF JAMAICA

The highly fossiliferous succession in the August Town Formation of the Coastal Group (late Miocene to Pleistocene) at Round Hill, Clarendon, Jamaica (text-fig. 1) is a sequence of more or less sandy limestones, with a fauna dominated by benthic molluscs, foraminiferans, and corals, with rare clypeasteroid echinoids. Dips are steep to the south or vertical, and the outcrop is cut by occasional faults. This coastal section was first described by Duncan and Wall (1865, p. 6, fig. 4), who considered the succession to be comprised of Miocene sediments overlain by a white limestone. Robinson (1968) correctly reinterpreted the structure as a possibly conformable contact between the underlying Newport Formation of the White Limestone Group and the younger Round Hill Beds which, however, are in turn unconformably overlain by cemented limestone screes of late Pleistocene age derived from Round Hill itself. Robinson (1968, p. 46) noted '. . . Several remarkable beds of oysters occur near the base of the sequence, with the oysters in an original position of growth, and with many individual shells reaching 15 inches or more in length'. Prescott and Versey (1958, p. 39) considered that these oysters resembled *O. haitiensis* Sowerby. The age of the Round Hill Beds is probably Pliocene, perhaps extending into the early Pleistocene (E. Robinson, written comm.).

The Round Hill Beds have yet to be described in detail. Herein we only wish to discuss a small part of the sequence that includes a remarkable bed, over 3 m thick and dominated by *C. virginica* (Gmelin) (Pl. 91, figs. 1 and 2; text-fig. 3), which outcrops on Farquhars Beach at Jamaica grid reference H415345 (text-fig. 2). A measured section from this locality is illustrated in text-fig. 3. Eight beds are recognized in this part of the sequence. Bed 1 (the lowest in text-fig. 3) is a sandy limestone with limestone pebbles, some of which are bored. The fauna consists solely of dissociated valves of *C. virginica*, which are only present towards the top of the bed. This is succeeded by a unit with an abrupt, planar, and apparently erosive base. The top is uneven and thickness is variable. This bed is dominated by *C. virginica*, most shells being dissociated and often apparently broken. No other faunal elements are present at this horizon. This unit may represent a channel fill or shell bank, with all valves recumbent, unlike the vertically orientated concentrations of dead, dissociated *C. virginica* valves found off the Florida coast (Grinnell 1974). The overlying bed 3 is a sandy, nodular, white to orange banded limestone. This has been cut into by bed 4, which has the geometry of a channel. As with bed 2, bed 4 is principally composed of mainly dissociated, recumbent, and possibly broken valves of *C. virginica*. Although some valves retain encrusting basal plates of *Balanus* spp., no complete barnacles are preserved and no other



TEXT-FIG. 2. Locality map showing the position of the principal outcrop of the Round Hill oyster bed, Clarendon, south-central Jamaica, WI. Fossil locality on Farquhars Beach marked by a star; summit of Round Hill by a triangle. Inset map shows position of Round Hill (RH) and Bowden (B). North towards top of page in both maps.



TEXT-FIG. 3. Graphic, annotated log of the Round Hill Beds at the fossil locality marked in text-fig. 1. Widths of units indicate how beds have weathered relative to each other at this locality.

EXPLANATION OF PLATE 91

Figs. 1–11. *Crassostrea virginica* (Gmelin) at Farquhars Beach, Clarendon, Jamaica. 1, general view of north-west end of sequence illustrated in text-fig. 3. Top and bottom of bed 6 (about 3·3 m thick) indicated. 2, detail of beds 1 (bottom) to base of 6, shown towards the left of text-fig. 1. Hammer (280 mm long) resting against bed 5. 3, bored oyster in bed 7, ×0·40. 4, curved, adult shell in upright, life position and encrusted by numerous, juvenile oysters, ×0·17. 5, large valve with single boring, ×0·46. 6, large, upright valve showing a triangular ligament area about 45 mm in length, ×0·38. 7, particularly thick shell, ×0·25. 8, very large, recumbent oyster, ×0·18. 9, paired, upright valves showing external evidence of boring, ×0·34 10, large recumbent shell encrusted by a pair of younger oysters which are almost as large, and in the same orientation, as the adult, ×0·22. 11, upright valve encrusted by *Balanus* sp., ×0·18.

Specimens in figs. 4–11 all from bed 6. All figures are of uncoated specimens taken in the field.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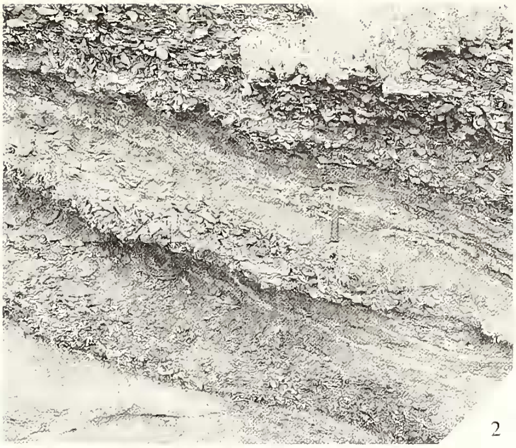
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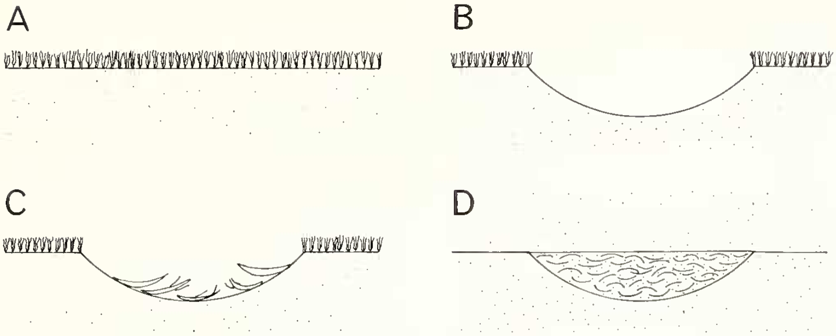
LITTLEWOOD and DONOVAN, *Crassostrea virginica* fauna noted. Both beds 2 and 4 have sharp contacts with their underlying and overlying units. Bed 5 is similar to bed 3 but occasional dissociated valves of *C. virginica* occur near the top. This unit grades into the overlying main oyster horizon, bed 6 (Pl. 91, fig. 1), which is 3·3 m thick and dominantly composed of *C. virginica*, preserved variously as broken shell fragments, dissociated valves (Pl. 91, fig. 6), recumbent, associated valves (Pl. 91, figs. 7, 8, 10), and upright, associated valves (Pl. 91, figs. 4 and 9). *Balanus* spp. (Pl. 91, fig. 11) and juvenile *C. virginica* (Pl. 91, figs. 4 and 10) encrust valves, on both the inner and outer surfaces. Young oysters are particularly prominent on some of the largest, upright, mature specimens of *C. virginica* near the top of the bed (Pl. 91, fig. 4). Additionally, some shells are encrusted on their lower valve by juvenile *C. virginica*. The only other body fossils are rare, thick-walled calcareous tubes of uncertain affinity (possibly annelids?) and a single gastropod. Some shells of *C. virginica* have been bored (Pl. 91, figs. 5 and 9), probably post-mortem, by bivalves and clionid sponges (an exposure of a further *C. virginica* horizon to the north-west includes common calcareous tubes, plus valves bored by polydorid polychaetes). The matrix is an orange limestone, with larger, sand-sized grains probably being derived from fragmented oyster shells. The matrix is more muddy towards the bottom of the bed and more gritty towards the top. Valves in life position occur throughout this unit but are concentrated at particular horizons, especially towards the top, where shells reach 400 mm in height. Such shells are amongst the largest *C. virginica* known.

Bed 7, in contrast, contains only rare, mainly disarticulated and occasionally bored, valves of *C. virginica* in its lower half (Pl. 91, fig. 3), with occasional pebbles and the spherical benthic foraminifera *Sphaerogypsina*, in a well cemented, sandy, orange limestone. *C. virginica* shows little or no encrustation at this level. In the upper half of this bed *C. virginica* is absent but *Sphaerogypsina* is very common, often being preserved as clusters of tens or hundreds of individuals. The overlying bed 8 consists of finely laminated limestone horizons, each about 10 to 40 mm thick and differentiated by being alternately more or less well cemented. Some of these horizons appear to be nodular. *Sphaerogypsina* is very common and dominates some units. Occasional moulds of bivalves and simple vertical burrows, cf. *Skolithos*, are present. The sequence is truncated by an angular unconformity with the overlying limestone screes derived from Round Hill.

The presence of common, upright, articulated shells in bed 6, many of which retain a well-preserved epifauna (Pl. 91, figs. 4, 10, 11), indicates that some, if not all, of these oysters are preserved *in situ*, with minimal or no transport. The origin of oyster beds 2 and 4 is more problematic. Bed 4 has the geometry of a channel fill; bed 2 is either a channel fill or a shell bank. It is difficult to envisage large *C. virginica* valves being transported very far, except under very high energy conditions, perhaps due to storm action, and abrasion is minimal. There are several indications that this sequence was shallow water in origin (see discussion below) and, therefore, well within the lower limits of storm wave base. Nevertheless, it is possible that these are *in situ* shell deposits which have been little altered in geometry by gross physical processes. Although Ager (1963, p. 200) concluded that '. . . epibiontic communities will almost invariably be moved and dispersed before fossilization . . .', some studies indicate that dead shells often accumulate with little or no post-mortem transport. Reineck and Singh (1973, pp. 134–136) recognized that shell concentrations are produced both by post-mortem transport and dumping or *in situ* accumulation. Warme (1969) concluded that, even within a high energy sand channel environment, transportation of shells away from their life habitat was minimal within a coastal lagoon. Holme (1961, pp. 433, 443) and, in a much more detailed study, Carthew and Bosence (1986), noted that live and dead shell-gravel assemblages on the shallow shelf off Plymouth, UK, had essentially similar molluscan faunal compositions and agreed that post-mortem transport was negligible. These are important conclusions when we recognize the great size of *C. virginica* compared with most other bivalves. Intuitively, we must conclude that only particularly high energy conditions would be capable of transporting even an uncemented *C. virginica*. Seilacher (1984, pp. 215–217) considered *Crassostrea* (possibly thinking more of the common European species *C. angulata* (Lamarck), the Portuguese oyster) to be well adapted as a 'boulder-shaped recliner' on soft sediment and noted that storm tells of this taxon sometimes reach 20 m thick, soft sediment presumably



TEXT-FIG. 4. A suggested sequence for the passive formation of a *Crassostrea virginica* channel fill. A, soft, calcareous sediment stabilized by sea grass. B, channel formed by storm action. C, invasion by *C. virginica*. D, eventual burial of channel.

being removed by winnowing. This is a potential explanation of all *Crassostrea* beds at Round Hill, particularly bed 6.

An alternative scenario for development of an *in situ C. virginica* channel fill deposit is illustrated in text-fig. 4. It is possible that the sea-floor sediment was stabilized by vegetation, possibly sea grass, at least in the lower part of the section (Brasier 1975; Eva 1980; text-fig. 4A). Modern sea grass communities of Jamaica are not favourable habitats for *C. rhizophorae* and we might speculate that they would also have been unsuitable for *C. virginica* at Round Hill; certainly, in those limestone units apart from the three shell beds (= substrates that may have been stabilized by sea grass), *C. virginica* is uncommon and almost always disarticulated. However, removal of the sea grass might have encouraged successful spatfalls of oysters. One event that would remove sea grass would be the formation of a channel (text-fig. 4B), possibly during a storm. The substrate, cleared of vegetation, would now be more suitable for colonization by *C. virginica* (text-fig. 4C), although the oyster would not be able to spread out of the channel. We could thus develop a passive channel fill, with disarticulation and abrasion being produced by relatively low energy post-mortem processes with some slight transport. It is unlikely that breakage of valves would be produced by weight of overburden (Rettger 1935). Final burial (text-fig. 4D) could result from a number of causes.

The main oyster bed, 6, is much thicker than either beds 2 or 4. It is visible over about 90 m of coastal exposure and may represent a very large channel deposit, appearing to thin to the south-east (north-west end obscured by slipped material), or is perhaps even a laterally extensive bed. Many of the oysters are in life position (Pl. 91, figs. 4–11). The only other mollusc found was a single gastropod near the top of the bed. Conditions thus appear to have been extraordinarily favourable for *C. virginica*, to the virtually complete exclusion of all potential molluscan competitors. What might those conditions have been? Certainly evidence from various parts of the Round Hill section indicate that this sequence was deposited in a shallow water environment. In the overlying bed 8 there are occasional vertical burrows, suggestive of Seilacher's (1967) *Skolithos* ichnofacies and indicative of littoral deposition. Channelling, possibly due to storm action in shallow water, is found in bed 2 and possibly 4. Elsewhere in the section molluscan assemblages appear similar to those found within snorkelling depth today. The presence of two species of clypeasteroid, *Encope* aff. *sverdrupi* Durham and *Clypeaster* cf. *rosaceus* (Linnaeus), is possibly also indicative of shallow water conditions. In particular, we have never seen the large, heavy tests of modern *Clypeaster* washed up on beaches; it is always found subtidally, even after death, forming a hard substrate for encrusting and cryptic organisms. The two species of acorn barnacle found in bed 6 suggest restricted marine to brackish conditions. *Balanus improvisus assimilis* Darwin is common in modern inshore, near-marine habits, whereas *B. eburneus* Gould is characteristically estuarine (Dr P. R. Bacon, written comm.). There is no indication that *Crassostrea virginica* was a mangrove oyster, unlike *C. rhizophorae*.

If we accept this environmental assessment, then it is apparent that *C. virginica* was living in shallow, well oxygenated and highly energetic water. Plankton would probably have been in ample supply, but the substrate would have been unsuitable for the growth of sea grass, being composed primarily of oyster valves. Other organisms were obviously largely excluded, although we cannot speculate whether this was due to the oysters influencing the environmental conditions or to a prevalent condition that encouraged *C. virginica* initially. Certainly, once established, a substrate dominated by oyster valves would have been unsuitable for burrowing molluscs to colonize. A third possibility, perhaps less probable, is that other mollusc shells have been winnowed away. Nevertheless, large valves of *Strombus* sp., found elsewhere at Round Hill, were probably as heavy as the shell of *C. virginica*, yet are absent from the measured section.

Salinity and dissolved calcium carbonate content were probably normal or possibly brackish. The above wave base, high energy conditions would have kept sediment mobile and prevented inorganic fouling of the valves. Indeed, energy conditions appear to have been so high that sediment within bed 6 was largely winnowed away. Oyster spatfalls could settle on both soft and, more probably, hard substrates. Experiments by D.T.J.L. have shown that growth in young *C. rhizophorae* is most vigorous on the underside of attachment surfaces. Well-preserved shells of young *C. virginica* seen growing on the lower valves of adult oysters are thus possibly indicative of similar settlement rather than of reworking.

CRASSOSTREA RHIZOPHORAE IN THE RECENT OF JAMAICA

C. rhizophorae lives in many of the mangrove stands found around the coast of Jamaica. The largest population of *C. rhizophorae* is found at Bowden, St Thomas (text-fig. 2; GR N788362), where the red mangrove, *Rhizophora mangle*, fringing the smaller inner bay, supports most of the population. Collection and culture of young spat for commercial purposes takes place in the larger outer bay (Wade *et al.* 1981).

The bottom of each bay is covered in thick layers of fine, muddy sand with occasional outcrops of the turtle grass, *Thalassia testudinum*. The inner bay is less than 1 m deep and is fed by two small rivers. The salinity and temperature vary between 5-35‰ and 25-28 °C, respectively, throughout the year. Although salinity in the outer bay rarely falls below 35‰ (unpublished data, D.T.J.L. and Oyster Culture Jamaica Project, Ministry of Agriculture), the oyster thrives in these marine conditions. The tidal range is approximately 350 mm (Meteorological Service, Kingston) but occasionally varies with heavy rainfall and winds.

Hubbard (unpublished data) studied the distribution of *C. rhizophorae* in the swamps at Bowden and found the greatest number to occur 6-9 m behind the mangrove fringe. Characteristically the oyster cements itself to any substrate relatively free from other organisms. Although this settlement is usually on young rhizophores, the shells of the bivalve *Isognomon alatus* Gmelin and mature *C. rhizophorae* often serve as a substrate for the oyster. Siung (1976) showed that 70·7% of mangrove oyster spat settle in the intertidal zone and that competition for food and space from other organisms prevents successful recruitment in the subtidal zone.

Table 1 is a list of fauna and flora found in association with *C. rhizophorae* in Bowden. Many of these species were collected from subtidally hung oyster substrate and are therefore not necessarily present in the intertidal zone of the mangrove swamp where *C. rhizophorae* is naturally dominant. The listing largely reflects the interests of those collectors who are responsible for identifying the species. None the less, similar fouling communities have been described for mangrove swamps in Puerto Rico (Glynn 1964; Cerame-Vivas 1974), the Bahamas (Rützler 1969), Martinique (Saint-Felix 1972), Venezuela (Sutherland 1980), and Port Royal, Jamaica (Goodbody 1961; Bruce 1968; Siung 1976). More extensive lists of fauna associated with *R. mangle*, in Cuba, may be found in Rueda and Moreno (1985) and Rueda *et al.* (1985). Although continuous breeding and settlement

TABLE 1. A list of species collected from mangrove stems and artificial substrates in the inner and outer bays at Bowden. This is not a complete list and is largely biased by the collecting specialities of those who identified the organisms. However, such a compilation is more complete than similar faunal lists presented for fossil oyster beds. Life habitat and trophic group are as follows:

EC = epifaunal cemented; B = epifaunal byssate; F = epifaunal free-living; S = suspension feeding; H = herbivorous; D = deposit feeding; C = carnivorous.

Identifications (ID): ♯ = D.T.J.L.; * = I. Goodbody (Zoology Dept., UWI, Jamaica); § = P. T. Hatfield (Biology Dept., Dalhousie University, Canada); † = K. E. Conlan and E. L. Bousfield (National Museum of Natural Sciences, Canada); ▵ = R. H. Hubbard (Institute of Marine Affairs, Trinidad); ≠ = S. Prudhoe (retired, British Museum (Natural History), UK).

Phylum	Life habitat	Trophic group	ID
FAUNA			
PORIFERA			
Various unidentified groups	EC	S	
COELENTERATA			
Hydroids	EC	S	
Aiptasia tagetes	EC	S	♯
BRYOZOA			
Bugula sp.	EC	S	▵
Caulibugula sp	EC	S	▵
Membranipora tenuis	EC	S	▵
MOLLUSCA			
GASTROPODA			
Murex recurvirostris rubidus F. C. Baker	F	C	▵
Littorina angulifera Lamarck	F	H	♯
Melongena melongena Linnaeus	F	C	♯
Caecum nebulosum (Rehder)	F		§
Cymatium pileare Linnaeus	F	C?	♯
C. muricinum Röding	F	C?	♯
Vermicularia knorri Deshayes	EC	S	♯
BIVALVIA			
Ostrea frons Linnaeus	EC	S	♯
O. equestris Say	EC	S	♯
Isognomon alatus Gmelin	B	S	♯
Anomia simplex Orbigny	B	S	♯
Brachidontes recurvus Rafinesque	B	S	♯
Modiolus americanus Lamarck	B	S	♯
PLATYHELMINTHES			
Stylochus (*Stylochus*) *frontalis* Verrill	F	C?	≠
ANNELIDA			
Sabellastarte magnifica (Shaw)	EC	S	♯
Polydora sp.	EC	S	♯
Spirorbis sp.	EC	S	♯
Serpulidae			♯
ARTHROPODA			
CRUSTACEA			
Balanus eburneus (Gould)	EC	S	▵
B. amphitrite Darwin	EC	S	▵

Table 1 continued overleaf]

TABLE 1 (*cont.*)

B. improvisus assimilis Darwin	EC	S	§
Chthalamus angustitergum (Pilsbry)	EC	S	§
C. proteus Dando & Southward	EC	S	§
AMPHIPODA			
Ericthonius brasiliensis Dana	F	D	†
Dulichiella appendiculata Say	F	D	†
Corophium bonellata Milne-Edwards	F	D	†
Ampithoe ramondi Audouin	F	D	†
Elasmopus sp.	F	D	†
Grandidierella sp.	F	D	†
Caprellids	F	D	‡
DECAPODA			
Panopeus herbstii H. Milne-Edwards	F	C	Δ
Aratus pisoni (Milne-Edwards)	F		Δ
Goniopsis cruentata	F		Δ
Mithrax mithrax spinosissimus (Lamarck)	F	H	Δ
Callinectes sapidus Rathbun	F	C	‡
Alpheids	F	C	†
CHORDATA			
Ascidians			
Botrylloides nigrum Herdman	EC	S	*
Symplegma brackenhielma Michaelsen	EC	S	*
Diplosoma listeranum Milne-Edwards	EC	S	*
D. glandulosum Minniot	EC	S	*
Lissoclinum abdominale Minniot	EC	S	*
Didemnum psammathodes Sluiter	EC	S	*
Didemnum sp.	EC	S	*
Polyclinum constellatum Savigny	EC	S	*
Perophora viridis Verrill	EC	S	*
Ecteinascidia styeloides Transtedt	EC	S	*
Ascidia nigra Savigny	EC	S	*
Styella canopus Savigny	EC	S	*
Fish			
Bathygobius soporator (Valencinnes)	F	C	Δ
Hypleurochilus aequipinnis (Günther)	F	C	Δ
FLORA			
ALGAE			
Enteromorpha sp.			‡
Ulva sp.			‡
Caulerpa racemosa (Forsk)			‡
Dictyota sp.			‡

of marine invertebrates tends to occur in the tropics (Goodbody 1962, 1965), Sutherland (1980), studying the dynamics of the epibenthic mangrove root community in Venezuela, noted that there was little recruitment of species or change in specific composition during an 18 month period. He also showed that the low rate of recruitment on mangrove prop roots could be correlated with a low rate of supply of new roots (an increase of $\simeq 8\%\ \mathrm{yr}^{-1}$ in Venezuela).

The ecological role of individual members of temperate littoral communities is better understood than that of their tropical counterparts. Organisms sharing similar biologies are most likely to compete with one another for food and space, but there appears to be little experimental evidence in the literature demonstrating this with tropical species or for those groups of organisms responsible for biofouling. For example, ascidians, of which there are twelve species at Bowden (see Table 1), are frequently referred to as possible competitors with oysters (for example, Loosanoff 1962; Arakawa 1980), but there is little evidence to confirm this. Overgrowth of one species by another is a frequent method of competition for space between sessile feeders and occurs amongst bryozoans, ascidians, sponges, bivalves, gastropods, tube-forming polychaetes, barnacles, hydroids, and corals (see reviews by Jackson 1977; Branch 1984). *Didemnum psammathodes* certainly appears to affect subtidally cultivated *C. rhizophorae* in this way, although the ascidian is not found in the intertidal zone where natural mangrove oyster populations dominate. Indeed, only bivalve species have been shown to compete with other bivalves for food and thereby reduce the growth and condition of their competitors (for example, Engle and Chapman 1952).

Growth rates of *C. rhizophorae* vary between 0·25–0·35 mm day^{-1} in the current culture system used in Jamaica (Littlewood 1987), 0·42–0·50 mm day^{-1} when cultivated on mangrove sticks in Cuba (Saenz 1965), and 0·1–0·2 mm day^{-1} on natural mangrove roots in Puerto Rico (Mattox 1949). Warmke and Abbott (1961) report that this species varies in 'length' between 50 mm and 150 mm but Nikolic and Alfonso (1971) have recorded maximum heights of approximately 100 mm after 9 months in Cuba. There is little information on the mortality of *C. rhizophorae* in its natural habitat, but some data are available on its performance in culture systems. Mortality values varying between 15–59% during the dry season and 1–20% during the rainy season have been recorded (Bosch and Nikolic 1975). Mortalities as high as 91·2% have been recorded before animals had reached 50 mm in shell height (Nikolic and Alfonso 1971; Nikolic *et al.* 1976) and 97% within 6 months of settlement (Bosch and Nikolic 1975), although little information is available on what causes these high mortalities (Nikolic 1969). Studies in progress suggest the flatworm *Stylochus* (*Stylochus*) *frontalis* Verrill, the hairy triton *Cymatium pileare* Linnaeus, the porcupine fish *Diodon hystrix* Linnaeus, and the blue crab *Callinectes sapidus* Rathbun all contribute to heavy mortality through predation, although post-spawning stress, disease, and the effects of silt load in the water column have yet to be investigated.

Although *Crassostrea rhizophorae* tends to breed and settle all year round in the Caribbean (e.g. Mattox 1950; Nascimento *et al.* 1980), there are generally two distinct spatfalls in Jamaica which coincide with the rainy seasons, beginning in May and October of each year. This contrasts with the single spatfall of extant *C. virginica* which extends from July to October depending on the locality (see, for example, Andrews 1955; Beaven 1955).

DISCUSSION

There are obvious difficulties in attempting to compare the life habits of a group of fossil animals with an extant form (see Hallam 1965). For example, we are largely unable to discuss the importance of predation or competition from associated fauna when much of this may have been either soft-bodied or too brittle to be represented in the fossil beds. None the less, certain broad comparisons and inferences are possible. First, the Round Hill *Crassostrea* species probably lived longer than the Bowden species does today. Galtsoff (1964, p. 20) noted that '. . . as a rule, oysters do not stop growing after reaching certain proportions but continue to increase in all directions and, consequently, may attain considerable size'. The fossil *C. virginica* are considerably larger than *C. rhizophorae*. Indeed, the largest specimens from Round Hill seem to be some of the largest shells of *C. virginica* ever to be found. According to Galtsoff (1964), the largest, living specimen of *C. virginica* to be documented was that found by Ingersoll (1881, pl. 30, p. 32). The shell measured 355 mm in height and 110 mm in length. We observed a fossil oyster shell from Round Hill that measured approximately 390 mm in height and 125 mm in length (Pl. 91, fig. 8).

Secondly, the Plio-Pleistocene group of *Crassostrea* appear to have been essentially shallow water or estuarine, either intertidal or subtidal, and benthic in their habitat, whereas the Recent group are predominantly intertidal, cemented directly or indirectly to narrow mangrove rhizophores. The features of these habitats may suggest how the life styles of each 'species' differed following settlement.

Mangrove swamps are typically muddy environments with high concentrations of suspended matter resulting from a continuous rain of leaf litter and detritus. Oyster spat settling on the muddy bottom would be quickly buried in an organic, and occasionally silty, downpour and would have to grow at a tremendous rate to facilitate water exchange for respiration, feeding, and excretion. Stenzel (1971, pp. N1044–N1045) noted that '. . . oyster larvae avoid settling on mud-covered substrata . . . [and due to heavy siltation] tend to colonise the undersurfaces of inclined mangrove stems rather than their top surfaces'. By attaching to a rhizophore, or to the shell of an animal already attached, the oyster ensures that it is above the detritus settling zone, although it is restricted to a vertical range limited by the position of the prop root in the mangrove swamp. Seaward fringing mangrove trunks and rhizophores are in shallow but relatively deeper water than those further landward. With the low rate of root generation (Sutherland 1980), available substrate is scarce for all epibionts settling in the subtidal and intertidal zone. Consequently, inter- and intraspecific competition for space may limit recruitment and high population densities may limit growth through competition for space and food.

The oyster's ability to withstand aerial exposure by adducting its valves predisposes it to an intertidal existence where tolerance to respiratory, thermal, and desiccation stress is required. In the intertidal zone the substrate is subject to movement relative to mean tidal levels. If oysters settle on leaf bearing stems or trunks, they may also be carried out of the tidal range and left permanently exposed as the mangrove tree grows. Given these features of the mangrove environment, one can see why the mangrove oyster may be restricted within the intertidal zone.

Hallam (1965) reviewed environmental features which may cause stunting in living and fossil marine benthonic invertebrates. Following his guidelines for determining whether or not environmental features may be responsible for a relatively smaller, 'stunted' animal (in this case *C. rhizophorae* versus *C. virginica*), we can investigate further the possibility that these two bivalves are ecophenotypes of one species and that their environments have caused the observed differences. Hallam (1965) considered the following to be principal factors: food supply, salinity, oxygen content, turbidity, agitation, and temperature of the sea water, together with population density. In view of our lack of associated fossil evidence or technical ability to describe more clearly the Round Hill Beds, we are restricted to considering only a few of these features.

Hallam (1965, p. 134) noted that '. . . the actual consumption of food is more important than its availability and is obviously the prime factor controlling size variations'. As an essentially intertidal bivalve *C. rhizophorae* may only feed during periods of tidal immersion, but the high growth rates and high organic content of the water do not suggest a food shortage. Furthermore, Littlewood (in press) has shown that aerial exposure may enhance growth in the mangrove oyster.

The inner bay at Bowden is fed by two small rivers and salinity may fall markedly and rapidly during periods of high rainfall. Although *Crassostrea* species are known for their euryhalinity, rapid drops in salinity caused by heavy rainfall are known to result in mass mortalities of tropical marine fauna (Goodbody 1961). By closing their shells the oysters can withstand limited periods of physiological stress (cf. aerial exposure). However, if exposure to fresh water is prolonged, oysters are unable to feed or respire aerobically and eventually die (see Andrews 1982). The sudden, low salinities brought on by heavy rain may therefore limit the life span of organisms in tropical environments such as mangrove swamps which, if not actually fed by rivers, would certainly experience coastal run off. The relatively calm waters in mangrove swamps may retain the fresh water for long periods. Goodbody (1961) noted that *C. rhizophorae*, and many other species in the Kingston Harbour mangrove swamps, were adversely affected by heavy rainfall during the rainy seasons. Only those species well below the less dense hyposaline waters were capable of survival. None the less, *C. rhizophorae* was one of the first organisms to recolonize the swamps following return to more marine salinites, although it was unable to re-establish as quickly as the ascidians. This may further explain the exclusion of the mangrove oyster from the subtidal zone, which is often dominated by the soft-bodied ascidians. Goodbody (1961, p. 155) suggested that '. . . the mangrove root communities of the lagoons in Kingston Harbor may seldom reach a climax condition due to repeated destruction of the developing communities'.

At Round Hill, *C. virginica* was coastal and near shore, either intertidal or shallow subtidal, thus experiencing at least moderate wave action which thereby supplied sufficient oxygen. Mangrove swamps are generally well oxygenated (see, for example, Bacon 1970). As mentioned above, the effects of heavy siltation, observed at Bowden, have not been investigated and remain a possible cause for the 'stunting' of mangrove oysters. During heavy rainfalls water agitation and the large volume of silt in the water column would result in a more turbid environment. Although no evidence of heavy siltation at Round Hill exists, and despite a proposed moderate level of water agitation, the fossil oysters cannot be considered as 'stunted'. Seilacher (1984, p. 214) noted that cemented bivalves 'eventually lift-off the substrate in order to facilitate water circulation, to widen the shell cavity, and to defend against overgrowth'. Some of the oysters from Round Hill appear to be cupping at a tremendous rate (Pl. 91, fig. 4). However, the majority of oysters are flat and lay relatively horizontal within the fossil beds, suggesting little overgrowth or silt load.

Many authors have noted that substrate topography can affect growth and shape of cemented shells and that new substrates may induce novel growth patterns (e.g. Stenzel 1971; Carreon 1973; Seilacher 1984). Although shell morphology differs little between *C. virginica* and *C. rhizophorae*, settling on mangrove roots may have induced 'ecotypic "derailment"' (Seilacher 1984, p. 214) in an ancestral *Crassostrea* stock. However, in view of the similarities between these two 'species', any genetic differences may have been strongly influenced by ecologic factors. Shell form and growth may also be affected by population density but to what extent this has played a part in the observed differences between *C. virginica* and *C. rhizophorae* cannot be investigated.

The scarcity of the substrate, the possibility of being smothered by other organisms (including other oysters), the limited amount of time available for feeding when the oyster is covered by the tide, the possibility of being killed by tropical rains, and the threat of high turbidity during such rains would suggest that the Recent *C. rhizophorae* must reproduce soon after it has settled. Gonadal development may proceed at the cost of shell and somatic growth with the result that oysters would be small when sexually mature. Indeed, Urpí *et al.* (1984) found sexually mature specimens of *C. rhizophorae* with a shell height of only 13 mm with an approximate age of between 15 and 22 days, although spawning was not observed in individuals smaller than 21 mm. Although spermatids may form when *C. virginica* is about 4 months old, it does not appear to reach sexual maturity until it is approximately 7 months old (Galtsoff 1964). The difference in sexual development between these two oysters is no doubt, in part, due to the difference in their distribution. Mangrove oysters, *C. rhizophorae*, are found in coastal regions of the West Indies from Cuba and Puerto Rico at the tip of their northern limit extending southward into regions of Brazil (Ahmed 1975) and *C. virginica* occurs along the east coast of North America from the Gulf of St Lawrence in Canada, in the north to Florida, the Gulf of Mexico, Central America, the West Indies (Stenzel 1971), and Brazil (Gunter 1951). Colder winters slow down the development of the gonads in *C. virginica* (Galtsoff 1964) and require that the oyster stores sufficient food reserves to be able to survive the winter. In contrast, less energy needs to be stored by oysters in warmer waters and the continuous breeding of *C. rhizophorae* which peaks during each of the two rainy seasons enables the 'species' to survive in a relatively unstable environment. Perhaps the rainy season spawning periods are an adaptation to maximize the chances of survival during times of environmental stress.

The Plio-Pleistocene *C. virginica* at Round Hill were obviously not living in a mangrove environment. Although the Round Hill Beds are obviously faulted, it is unlikely that their position relative to Round Hill has altered much since the Plio-Pleistocene, apart from tilting and uplift relative to present sea level. This, together with observations discussed above, suggests that these fossil *Crassostrea* may have been near shore, either intertidal or subtidal, or possibly estuarine (cf. Frey *et al.* 1987). Modern *C. virginica* is certainly known from both the intertidal and the subtidal zone (Galtsoff 1964). The advantage of living subtidally is that feeding may be continuous and the oyster may be better protected from floating layers of fresh water during and after rainfall. Furthermore, in an open coastal environment *C. virginica* would not have been subjected to severe or prolonged exposures to low salinity. Perhaps in this way *C. virginica* has been able to grow much larger and live much longer than *C. rhizophorae*, which is largely restricted to the more unstable intertidal zone when settling on mangrove. However, although the above observations and arguments all suggest ecophenotypic variation to be a plausible explanation of observed morphological differences between *C. virginica* and *C. rhizophorae*, further tests of this suggestion are desirable, particularly on extant populations of the two species living in geographic and/or ecologic close association.

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