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# Palaeoecology of corals and rudists in mixed volcanoclastic–carbonate small-scale rhythms (Upper Cretaceous, Jamaica)

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## Abstract

The Guinea Corn Formation (central Jamaica, West Indies) is represented by alternating platform carbonates and volcanoclastic sandstones and siltstones and represents the most landward shift of facies in an Upper Campanian? to Maastrichtian transgressive–regressive cycle. The succession consists of 2–30-m-thick rhythms comprising a lower volcanoclastic siltstone/sandstone division; a middle volcanoclastic siltstone/limestone with abundant corals or the rudist *Antillocaprina stellata*; and an upper division of rudist rudstones and floatstones. The lower division consists of either bioturbated sandy siltstones with lignite and abundant gastropods and infaunal bivalves (lower rhythms in the Guinea Corn Formation), or interbedded volcanoclastic siltstones and normally graded sandstones. The rudist limestones are parallel-bedded and consist of high-abundance mono- to paucispecific assemblages. The boundary between the middle and upper parts of rhythms contains a concentration of oncoids with coral nuclei and a mantle of microbial laminates, red algae and serpulids. Four coral assemblages are recognised based on diversity and coral morphology. The *Paracycloseris*-?*Dasmosmia* assemblage occurs in the lower division of the rhythms and is interpreted as a soft-substrate assemblage that was adapted to elevated nutrient levels. The *Ovalastrea-Actinacis*, *Actinacis-Multicolumnastrea* and *Actinacis-Calamophyllia-Gyrodendron* assemblages occur in the middle parts of the rhythms and consist of bedded rudstones, rudstone mounds and rarer platestones, pillarstones and mixstones. Polyparia arrangements, colony morphology and low diversity suggest the *Ovalastrea-Actinacis* and *Actinacis-Multicolumnastrea* assemblages were adapted to high sedimentation rates. The more diverse *Actinacis-Calamophyllia-Gyrodendron* assemblage is interpreted to have grown under more optimum conditions (low sedimentation rates and high light intensities). Rudists are classified on their growth orientation (elevator, clinger, recumbent) and on their communal relationships (isolated or clustered). The cluster elevator *Biradiolites mooretownensis* occurs in the lower division of rhythms and the recumbent *A. stellata* occurs in the middle part of rhythms. The upper part of rhythms contains abundant rudists including isolated elevators (*Antillocaprina occidentalis*), cluster elevators (*Bournonia* spp., *Biradiolites jamaicensis*, *Thyrastylon* spp. and *Chiapasella radiolitiformis*) and clingers (*Plagioptychus* spp.), with the topmost part contains the large recumbent *Titanosarcolithes*. © 2002 Published by Elsevier Science B.V.

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## 1. Introduction

During the late Cretaceous, rudist bivalves became the most important sediment producers on

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tropical carbonate platforms (e.g., Kauffman and Sohl, 1974; Bein, 1976; Camoin et al., 1988; Gili, 1993; Özer, 1993; Philip, 1972, 1993; Ross and Skelton, 1993; Philip et al., 1995a,b; Skelton et al., 1995; Sanders and Baron-Szabo, 1997; Sanders and Pons, 1999, 2001; Sanders and Höfling, 2000; Carannante et al., 2000). Along the boundary of the Caribbean Plate, such rudist-dominated carbonate platforms developed around island arc volcanoes, and were associated with andesitic volcanoclastic sediments (Kauffman and Sohl, 1974; Coates, 1977a,b; Kauffman and Johnson, 1988; Johnson and Kauffman, 1996). Kauffman and Sohl (1974) distinguished eight types of rudist occurrence (individual, associations, clusters, thickets, coppice, bank, biostrome and reefs) in these mixed carbonate–volcanoclastic successions. However, only the former five types of framework were observed in sedimentary successions in the Caribbean, the latter three being hypothetical. Coates (1977a,b) recognised that corals were also important, although of subordinate occurrence to rudists, in the Jamaican Upper Cretaceous limestones. In contrast, subsequent studies of rudists on circum-Mediterranean carbonate platforms have interpreted rudists as gregarious

sediment dwellers that grew in level-bottom communities (e.g., Gili, 1992; Ross and Skelton, 1993; Skelton et al., 1995; Gili et al., 1995; Sanders and Pons, 1999).

In this paper, carbonate–volcanoclastic rhythms in the Upper Cretaceous Guinea Corn Formation of Jamaica are described. The palaeoecology of the corals and rudist bivalves is considered.

## 2. Geological background

The Central Inlier of Jamaica represents an exposed fragment of a Late Cretaceous island arc system (Coates, 1968; Robinson et al., 1972; Fig. 1). The basement consists of ?Turonian–?Coniacian andesitic lava flows and associated volcanoclastic sediments (Arthur's Seat Formation), Upper Santonian–Lower Campanian marine sedimentary rocks (Peters Hill Formation) and ?Middle Campanian andesites and conglomerates (Main Ridge Formation) (Coates, 1968; Robinson et al., 1972). Subsequent to volcanic activity, and following erosion, an Upper Campanian?–Maastrichtian transgressive–regressive cycle was deposited (Jiang and Robinson, 1987; Under-

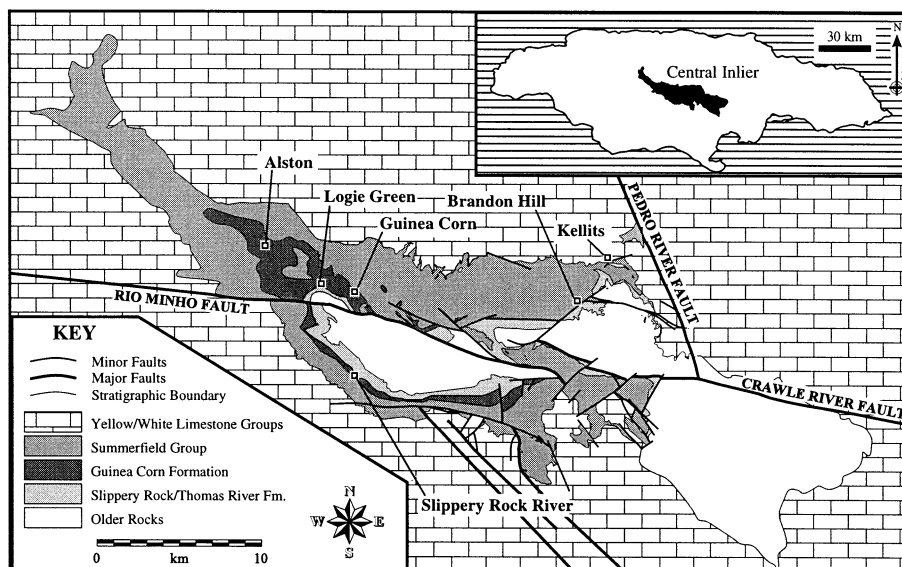


Fig. 1. Geological map of the Central Inlier, Jamaica, showing distribution of the Guinea Corn Formation. Inset: location of the Central Inlier in Jamaica.

wood and Mitchell, 2000; Mitchell and Blissett, 2001; Fig. 2). The transgressive portion of this cycle is represented by the Slippery Rock, Thomas River and Guinea Corn formations. The Slippery Rock Formation consists of fluvial conglomerates with sandstones and calcretes, whereas the overlying Thomas River Formation comprises volcanoclastic tidal flat sediments with tidal rhythmites and flaser-wavy-lenticular bedded units (Mitchell and Blissett, 2001). The Guinea Corn Formation consists of shallow-water platform carbonates, and records the most landward shift of marine facies in this cycle. The cycle was terminated by shedding of andesitic volcanoclastic debris (Sum-

merfield Group) from a newly emergent volcanic centre possibly situated to the northeast of the inlier (Coates, 1968; Roobol, 1976; Mitchell and Blissett, 1999, 2001). The Summerfield Group represents a major progradational complex and has been interpreted as a volcanoclastic braid delta because of its wide geographic extent (Mitchell, 2000).

The Guinea Corn Formation is exposed in road-cuts, and along the beds and banks of rivers. The succession can be traced across an area of 27 km E–W by 11 km N–S (Fig. 1). It consists of alternating volcanoclastic sediments and shallow-water, platform-type limestones with abundant

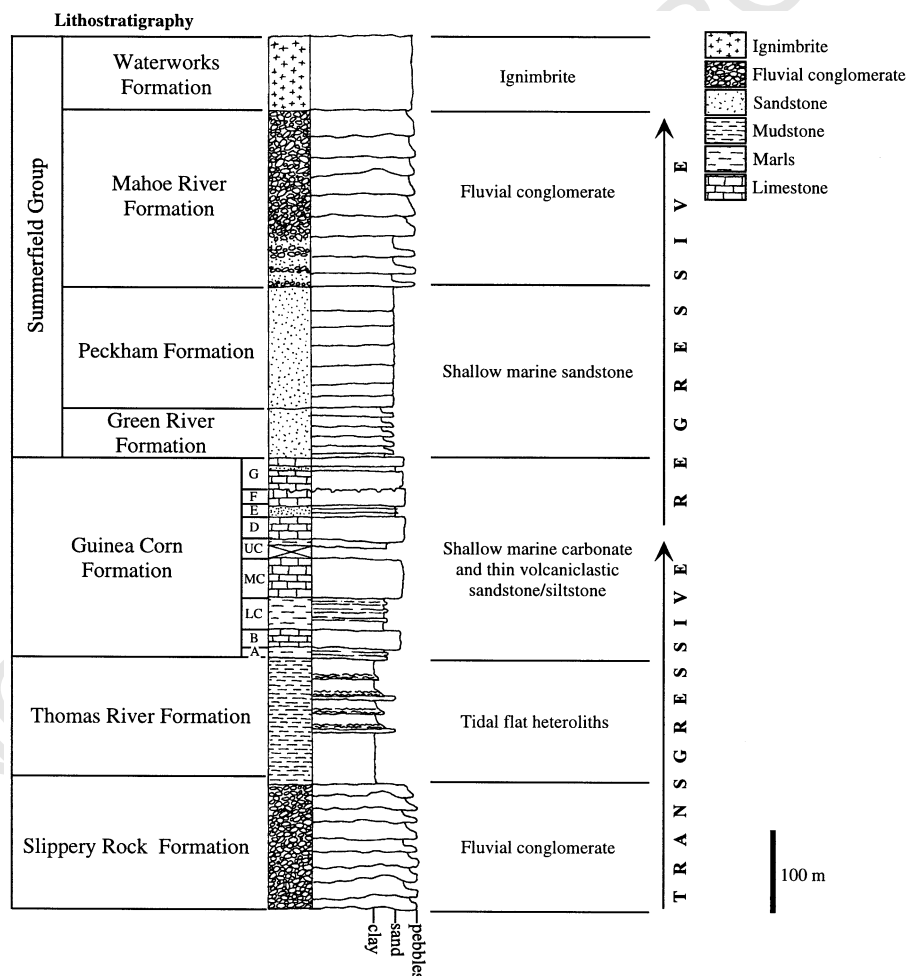


Fig. 2. Simplified stratigraphy of the Upper Campanian–Maastrichtian succession in the Central Inlier (Mitchell and Blissett, 2001).

corals and rudists. The best sections currently exposed are in the banks and bed of the Rio Minho, which repeatedly crosses the Guinea Corn Formation between Guinea Corn and Grantham (Fig. 3). In this area, the formation ranges in thickness from 165 m to 210 m (Coates, 1968; Mitchell, 1999). It was divided by Mitchell and Blissett (1999; Fig. 2) into seven units labelled A to F from the base upwards. The Guinea Corn Formation thins to the northeast and disappears near Brandon Hill where the Summerfield Group rests conformably on the Slippery Rock Formation (Coates, 1965, 1968; Robinson et al., 1972). The Guinea Corn Formation is represented by rudist- and coral-bearing limestones to the east that pass into orbitoid foraminiferan-bearing limestones to the west (e.g., around Alston: Krijnen et al., 1993). The Guinea Corn Formation lacks plank-

tonic foraminifera and is interpreted to have been deposited in an open-marine inner platform setting (Coates, 1977a; Fig. 4). The Guinea Corn Formation is characterised by asymmetrical sedimentary rhythms composed of three major lithologies: a lower volcanoclastic unit (siltstones and sandstones), a middle unit rich in corals, and an upper unit of rudist-rich bioclastic limestone (Mitchell, 1999).

Rudists are the dominant fossils in the Guinea Corn Formation (Whitfield, 1897; Trechmann, 1924; Chubb, 1971; Kauffman and Sohl, 1974), although corals are also important (Coates, 1977a,b). Other groups present include larger foraminifera (Jiang and Robinson, 1987; Krijnen et al., 1993), echinoids (Donovan, 1993), gastropods (Sohl and Kollmann, 1985; Sohl, 1987, 1998) and ostracods (Hazel and Kamiya, 1993).

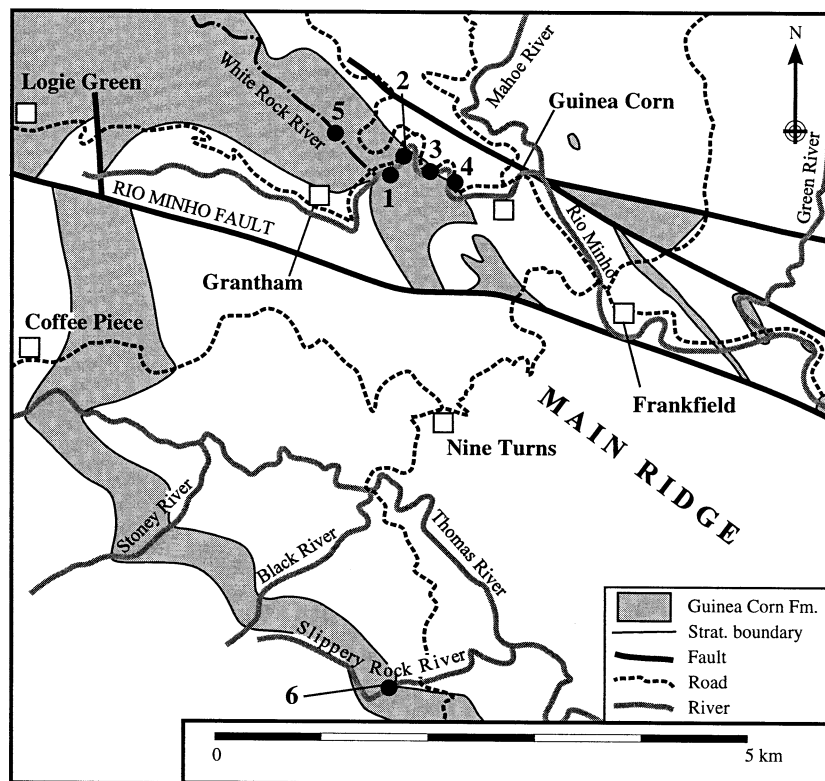


Fig. 3. Distribution of sections studied in the Central Inlier. 1, Guinea Corn type section at Grantham; 2, Coffee Piece NE; 3, Cabbage Hill section 4, Guinea Corn West section; 5, White Rock River section; 6, Slippery Rock River section.

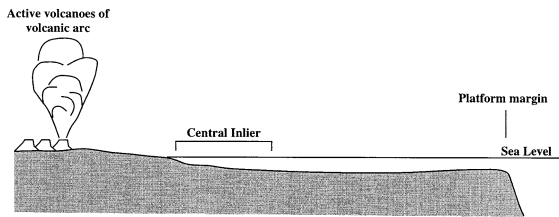


Fig. 4. General setting for the deposition of the Guinea Corn Formation.

### 3. Carbonate sediment producers in the Guinea Corn Formation

Corals and rudists were the most important sediment-producing organisms in the Guinea Corn Formation, and their skeletal fragments dominate the bioclastic component of the rocks. Descriptive schemes for growth form of both corals and rudists are discussed below. Other carbonate sediment producers included non-rudist bivalves, gastropods, regular echinoids, foraminifera and ostracods. However, most of these groups were only locally important producers of carbonate sediment. For the description of carbonate rocks, the Dunham (1962) classification as modified by Embry and Klovan (1971) and Insalaco (1998) is used here.

#### 3.1. Corals

Standard terminologies for both solitary and colonial coral morphologies are used in the present paper (e.g., James, 1983; Veron, 1986; Chappell, 1980). The range of growth forms found in the corals from the Guinea Corn Formation is shown in Fig. 5. The diversity, colony morphology and polyparia arrangement are of particular palaeoecological significance (e.g., Höfling, 1989, 1997; Sanders and Baron-Szabo, 1997; Baron-Szabo, 1997). Colony morphology and polyparia arrangement are listed in Table 1.

The term circumrotatory has been used for generally globular coral colonies belonging to genera, such as *Dichocoenia* and *Ovalastrea*, in the Upper Cretaceous limestones of Jamaica (Coates, 1977a,b). Coates (1977a) suggested that these forms may have initially been attached, and were subsequently broken off to form colonies that were rolled around in high-energy environments on the sea floor (cf. Kissling, 1973). In the Upper Cretaceous deposits of Jamaica, circumrotatory corals occur in sedimentary rocks with a volcanoclastic siltstone matrix. This suggests that they lived in low-energy environments where the fine-grained sediments could settle out. This is inconsistent with a high-energy environment where the corals were frequently rolled. Sec-

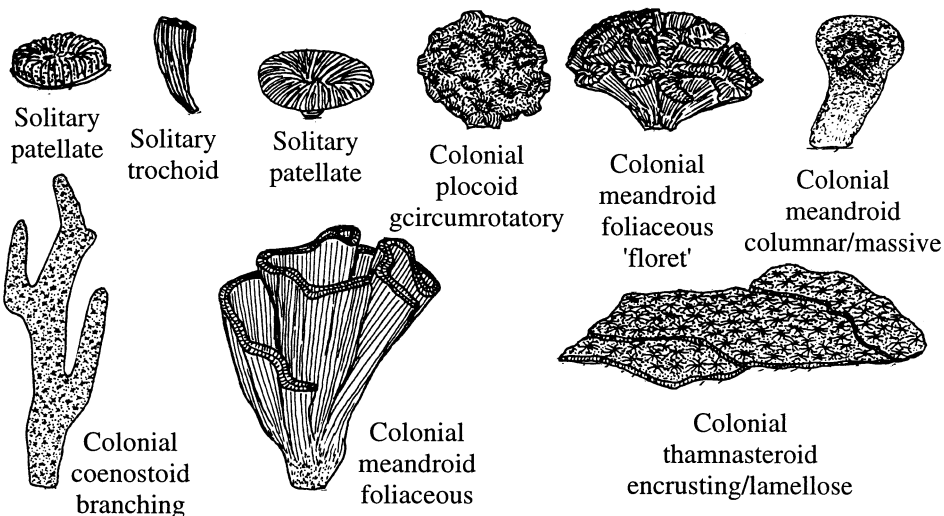


Fig. 5. Growth forms of corals in the Guinea Corn Formation (based on James, 1983; Veron, 1986; Chappell, 1980).

Table 1  
Form and polyparia arrangement in corals from the Guinea Corn Formation

Species	Solitary or compound	Form	Polyparia arrangement	Assemblage			
				1	2	3	4
<i>Paracycloseris elizabethae</i> Wells	S	Patellate/discoid	Solitary	C			
? <i>Dasmosmilia</i> sp.	S	Trochoid	Solitary	C			
? <i>Dendrophyllia</i> sp.	C	Cylindrical	Dendroid	R			
<i>Ovalastrea (Favioseris)</i> sp.	C	Circumrotatory	Plocoid	R			
<i>Goniopora</i> sp.	C	Massive	Ceroid	R			
<i>Ovalastrea trechmanni</i> (Wells)	C	Circumrotatory	Plocoid		C		R
<i>Ovalastrea (Favioseris) anomalus</i> (Wells)	C	Circumrotatory	Plocoid		C		
<i>Dichocoenia</i> sp.	C	Circumrotatory	Plocoid		C		
<i>Actinacis</i> sp. (branched)	C	Branching	Plocoid		C	C	C
<i>Multicolumnastrea cyathiformis</i> (Duncan)	C	Branching/massive	Plocoid		C	C	C
<i>Leptoria (Dictyophyllia) conferticostata</i> (Vaughan)	C	Massive	Meandroid		R		C
<i>Trochoseris catadupensis</i> Vaughan	S	Patellate	Solitary		R		C
<i>Vaughanoseris catadupensis</i> Wells	S	Patellate	Solitary		R		C
? <i>Pachygyra</i> sp.	C	Massive	Meandroid		R		C
<i>Calamophyllia quaylei</i> (Wells)	C	Branching	Phaceloid				C
<i>Gyrodendron</i> sp.	C	Branching	Meandroid				C
<i>Actinacis</i> sp. (encrusting-lamellose)	C	Encrusting/lamellose	Plocoid				C
<i>Ovalastrea</i> sp.	C	Circumrotatory	Plocoid				R
<i>Microsolenia</i> sp.	C	Lamellose	Thamnasterioid				C
<i>Synastrea adkinsi</i> Wells	C	Encrusting/lamellose	Thamnasterioid				C
<i>Actinastrea</i> sp.	C	Branching/massive	Ceroid				C

Assemblages: 1, *Paracycloseris*-?*Dasmosmilia*; 2, *Ovalastrea*-*Actinacis*; 3, *Actinacis*-*Multicolumnastrea*; 4, *Actinacis*-*Calamophyllia*-*Gyrodendron*.

tioned examples of *Ovalastrea* show that these circumrotatory colonies grew from a single attachment point indicating attached growth on the sea floor (Fig. 5).

### 3.1.1. Coral assemblages in the Guinea Corn Formation

Coates (1977a,b) recognised four coral assemblages in the Guinea Corn Formation: 1, *Paracycloseris*-*Trochoseris*-*Actinacis* assemblage; 2, *Multicolumnastrea*-*Astrocoenia*-*Actinacis* assemblage; 3, *Multicolumnastrea*-*Actinacis*-*Dictyophyllia*-*Dichocoenia* assemblage; and 4, *Dichocoenia trechmanni* assemblage. In the present paper, four assemblages, based on taxonomic composition and diversity, are recognised (Fig. 6). Only Coates' (1977a) assemblages 1 and 4 are adopted into new subdivisions of coral assemblages.

#### ***Paracycloseris*-?*Dasmosmilia* assemblage (equivalent to Coates' assemblage 1)**

*Description:* This assemblage is restricted to vol-

caniclastic siltstone lithofacies. It is a low-diversity assemblage of predominantly solitary corals that rarely exceed a few centimetres in size. The corals are scattered through the sediment. The common species include the solitary (ahermatypic) discoid-coral *Paracycloseris elizabethae* Wells and the trochoid ?*Dasmosmilia* sp. (Fig. 6, top left). Other, rare species include the dendroid ?*Dendrophyllia* sp., and colonial *Ovalastrea (Favioseris)* sp. and *Goniopora* sp. The assemblage is associated with abundant infaunal bivalves and suspension-feeding gastropods (such as *Turritella*), together with abundant lignite fragments.

*Interpretation:* This assemblage is dominated by solitary corals (Table 1), and is interpreted to represent a soft-substrate assemblage, with the trochoid solitary corals attached to skeletal debris lying on the sea floor. The dominance of ahermatypic, solitary corals suggests increased turbidity. The high abundance of lignite in the associated sediments indicates high terrestrially derived detrital input, suggestive of increased nu-

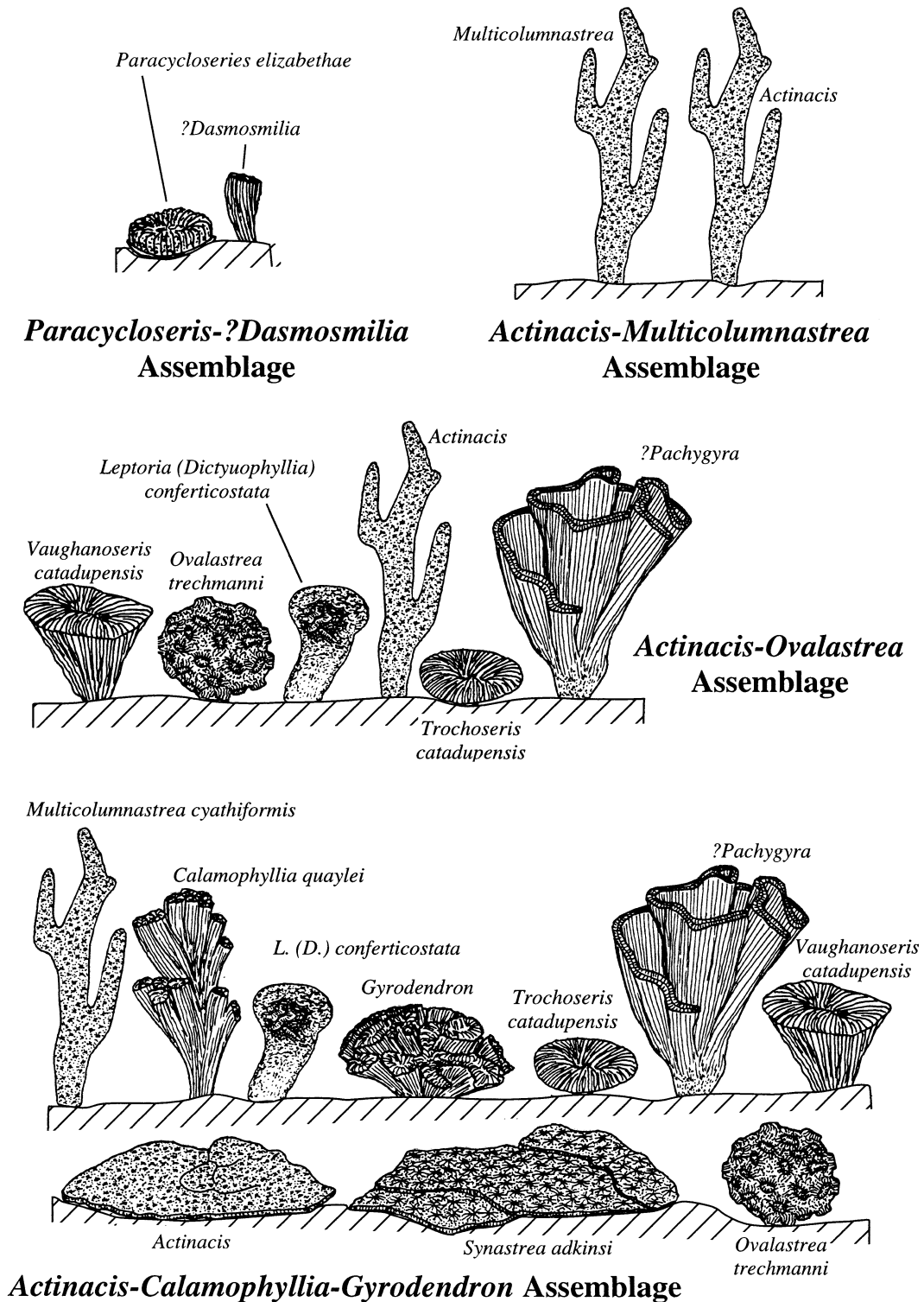


Fig. 6. Coral assemblages distinguished in the Guinea Corn Formation.

trient fluxes (Brasier, 1995). This is further supported by the abundance of suspension-feeding gastropods and infaunal bivalves indicating an abundance of suspended food sources (Brasier, 1995; Harper and Brenchley, 1997). Taken together, this suggests that the *Paracycloseris*-?*Dasmosmia* assemblage was adapted to increased nutrient levels.

#### ***Ovalastrea-Actinacis* assemblage (equivalent to Coates' assemblage 4)**

**Description:** This assemblage is also restricted to epiclastic siltstone lithologies. It is characterised by a more diverse assemblage of predominantly colonial corals that range in size from a few centimetres up to about 10 cm. The corals commonly occur in beds of coral rudstone. The assemblage is dominated by large numbers of the circumrotatory species *Ovalastrea trechmanni* (Wells), *Ovalastrea (Favioseris) anomalos* (Wells) and *Dichocoenia* sp. together with branched taxa such as *Actinacis* sp. and *Multicolumnastrea cyathiformis* (Duncan). Taxa more rarely encountered include small *Leptoria (Dictuophyllia) conferticostata* (Vaughan), *Trochoseris catadupensis* Vaughan, *Vaughanoseris catadupensis* Wells, and ?*Pachygyra* sp. (Fig. 6, top right). No corals are undoubtedly preserved in growth position. The assemblage is dominated by branched and circumrotatory morphotypes with plocoid polyparia arrangement (Table 1).

**Interpretation:** The low diversity and dominance of plocoid polyparia suggests environmental stress, such as sediment input (e.g., Baron-Szabo, 1997; Sanders and Höfling, 2000). The branched corals are present as fragmented colonies, suggesting some degree of reworking. The assemblage is interpreted as an assemblage that grew within siltstone lithologies subject to periodic high-energy events, possible storms, that fragmented the branched colonies.

#### ***Actinacis-Multicolumnastrea* assemblage**

**Description:** This is a rare assemblage of corals found only at two localities in the Guinea Corn Formation (Slippery Rock River, White Rock River: Fig. 3, localities 5 and 6). The assemblage consists of branched corals (*Actinacis* sp. and

*Multicolumnastrea cyathiformis*; Fig. 6, middle) forming dense pillarstones. Polyparia arrangements are plocoid (Table 1). The *Actinacis-Multicolumnastrea* assemblage is associated with moderately common specimens of the elevator rudist *Hippurites* sp. Secondary frame builders and encrusters are absent.

**Interpretation:** The low diversity of the coral assemblage and plocoid polyparia arrangement suggest environmental stress, such as sediment influx (e.g., Baron-Szabo, 1997; Sanders and Höfling, 2000). The dominance of the branched colony morphology, and particularly its preservation in growth orientation, could also indicate moderate sedimentation rates and constrictal growth (e.g., Insalaco, 1998). The rudist *Hippurites*, which is also associated with this assemblage, is generally modelled as an elevator morphotype showing constrictal growth (e.g., Gili et al., 1995; Skelton et al., 1995; Sanders and Pons, 1999). The corals and rudists of this assemblage are, therefore, interpreted to represent constrictal growth fabrics in areas of moderate volcanoclastic sedimentation.

#### ***Actinacis-Calamophyllia-Gyrodendron* assemblage**

**Description:** This is the most diverse coral assemblage recognised in the Guinea Corn Formation. It is embedded within a matrix of either epiclastic siltstone or lime mudstone, and is represented by rudstones, floatstones, coral rudstone mounds, and, locally, platestones and mixstones. The coral assemblage includes (in order of decreasing abundance) branched *Actinacis* sp., *Calamophyllia quaylei* (Wells), *Gyrodendron* sp., *Leptoria (Dictuophyllia) conferticostata*, ?*Pachygyra* sp., *Trochoseris catadupensis*, *Vaughanoseris catadupensis*, encrusting-lamellose *Actinacis* sp., *Ovalastrea* sp., *Microsolena* sp., *Multicolumnastrea cyathiformis*, *Synastrea adkinsi* Wells, *Ovalastrea trechmanni* and *Actinastrea* sp. (Fig. 6, bottom). The platestone- and mixstone-forming species are *Actinacis* sp. (branched), *Multicolumnastrea cyathiformis*, *Gyrodendron* sp., *Trochoseris catadupensis* and *Actinastrea* sp. Diverse colony morphologies are present (branched, encrusting/lamellose, massive: Table 1) and there is a wide range of polyparia arrangements (meandroid, plocoid, thamnasterioid, cerioid, phaceloid: Table 1). Encrusters in-

Table 2  
Growth style of rudists in the Guinea Corn Formation

Rudist	Growth mode
<i>Antillocaprina occidentalis</i> (Whitfield)	Isolated elevator
<i>Antillocaprina stellata</i> Chubb	Recumbent
<i>Antillocaprina suboccidentalis</i> Chubb	Isolated elevator
<i>Biradiolites jamaicensis</i> Trechmann	Cluster elevator (minor clinger)
<i>Biradiolites mooretownensis</i> Trechmann	Cluster elevator
<i>Biradiolites rudissimus</i> Trechmann	Isolated elevator and cluster elevator
<i>Bournonia barretti</i> Trechmann	Cluster elevator
<i>Bournonia</i> ex gr. <i>cancellata</i> (Whitfield)	Cluster elevator (minor clinger)
<i>Chiapasella radiolitiformis</i> (Trechmann)	Cluster elevator
<i>Huppurites</i> spp.	Cluster elevator
<i>Macgillavryia nicholasi</i> (Whitfield)	Isolated elevator
<i>Plagiopychus</i> spp.	Clinger
<i>Praebarrettia sparcilirata</i> (Whitfield)	Isolated elevator
' <i>Radiolites</i> ' <i>macroplicata</i> Whitfield	Cluster elevator
<i>Thyrastylon adhaerens</i> (Whitfield)	Cluster elevator
<i>Thyrastylon coryi</i> (Trechmann)	Clinger
<i>Thyrastylon semiannulusus</i> (Trechmann)	Isolated to densely associated elevator
<i>Titanosarcolithes alatus</i> Chubb	Recumbent
<i>Titanosarcolithes giganteus</i> (Whitfield)	Recumbent

clude oysters, red algae, bryozoans and thecideline brachiopods (Mitchell, in press).

**Interpretation:** This is the most diverse coral assemblage recognised in the Guinea Corn Formation. This diversity of colony form and polyparia arrangement, coupled with the large numbers of species present, suggests optimum conditions for corals growth (e.g., Baron-Szabo, 1997; Insalaco, 1998). The presence of a volcanoclastic siltstone matrix suggests episodic deposition of fine-grained sediments.

### 3.2. Rudists

Rudists are abundant in the Guinea Corn Formation, although relatively few are found in life position. In this study, rudist growth style is determined, as far as possible, from observations of rudists in life position seen in the field.

Kauffman and Sohl (1974) introduced a set of terms for the communal growth of rudists: Individual – isolated individuals; Associations – individuals not in contact, ranges from widely spaced to partially in contact; Clusters (more or less equivalent to 'bouquets' of Philip, 1972) – lenticular to pod-like frameworks comprising one or a

few generations of closely spaced rudists, individual rudists are in point contact, less commonly they are tightly packed or mutually connecting.

For rudist morphotypes, a classification scheme has been developed by Skelton and Gili (1991) and Gili et al. (1995). Three morphotypes were recognised: elevators, clingers and recumbents. Elevators grew predominantly vertically and had a subhorizontal commissure. Recumbents grew horizontally and had the commissure at an angle of 90° to the sediment–water interface. Clingers were often bun-shaped and had the commissure at an angle of between 45° and 90° to the sediment–water interface. They were represented by attached clingers and frictional clingers (Skelton and Gili, 1991, p. 274). The elevator hippuritid rudists of the circum-Mediterranean have been interpreted as constrictal growth forms (e.g., Gili et al., 1995; Skelton et al., 1995; Sanders and Pons, 1999).

The classification scheme adopted here for rudists from the Guinea Corn Formation encompasses two criteria: (i) the rudist morphotype, i.e., clinger, elevator or recumbent, and (ii) the style of their association, i.e., individual/associations or clusters/bouquets. In a few species, different specimens may belong to different morpho-

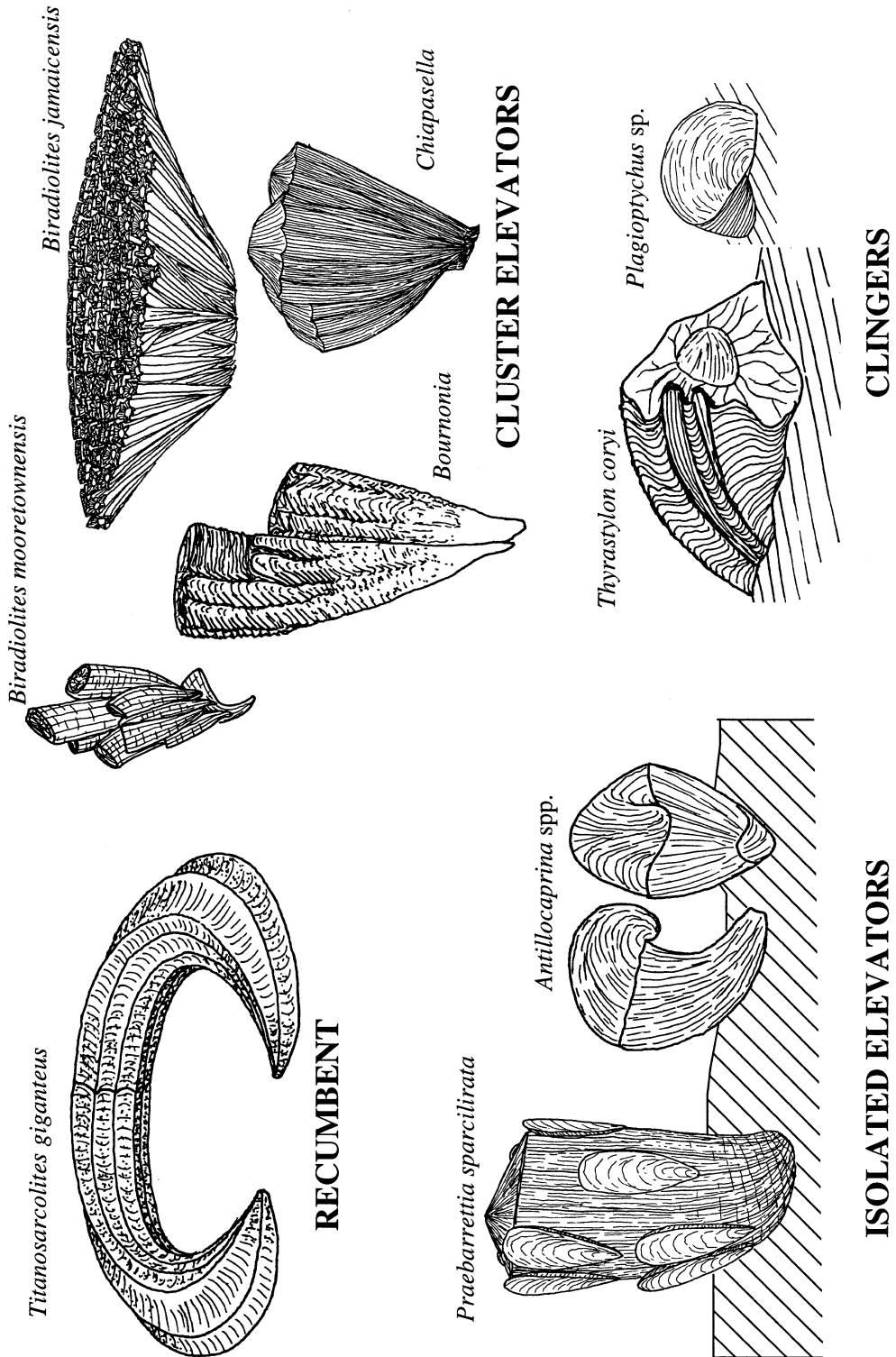
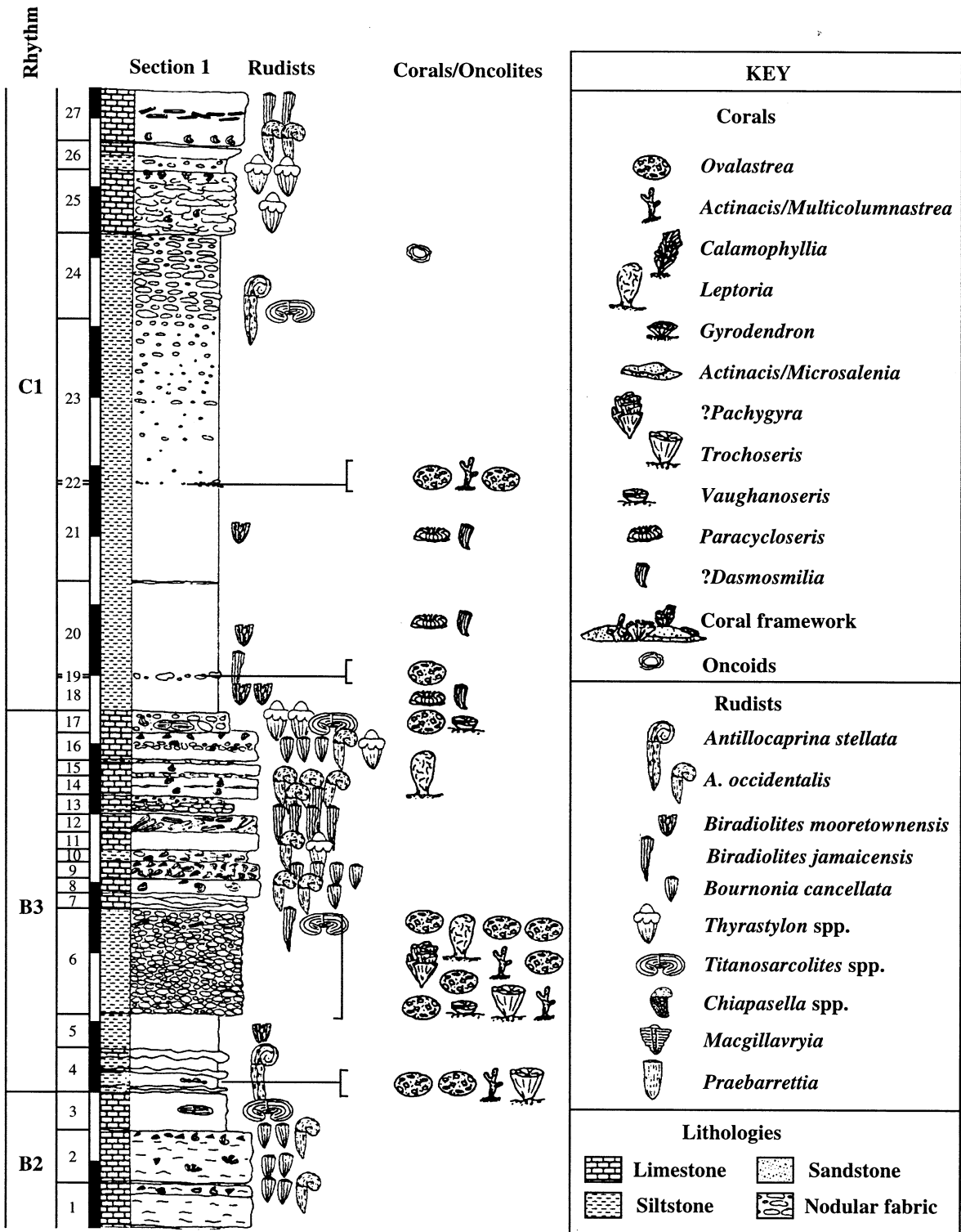


Fig. 7. Rudist morphotypes distinguished in the Guinea Corn Formation.

Table 3  
Sedimentary facies in the Guinea Corn Formation

Facies	Description	Interpretation
Facies in the lower parts of rhythms		
Poorly sorted sandy siltstone	Siltstone with scattered sand and very fine pebble-sized grains (quartz and lithic fragments). Abundant infaunal gastropods and bivalves; <i>Paracycloseris</i> -? <i>Dasmosmia</i> coral assemblage, <i>Biradiolites mooretownensis</i> .	Lagoon deposits, diverse infaunal mollusc and lignite indicating high nutrient levels.
Unbedded siltstone	Unbedded siltstone, no fossils seen.	Lagoon deposits.
Normally graded sandstone	Normally graded sandstones in beds from 10 to 110 cm thick. Grading ranges from coarse sand or granules at the base to very fine sand or silt at the top. Rare oysters and rudists at base. Top of beds may show indistinct burrow mottling.	Discrete storm beds.
Thin bedded sandstone	Medium and fine-grained sandstones in beds up to 6 cm thick. Ripple cross-lamination abundant with occasional asymmetrical and symmetrical ripple form sets. Low-angle erosion surfaces present.	Distal storm sandstone beds.
Facies in the middle parts of rhythms		
Siltstones and coral rudstone	Corals rudstones with a siltstone matrix. Corals of the <i>Ovalastrea-Actinacis</i> and <i>Actinacis-Multicolumnastrea</i> assemblage.	Coral growth in stressed environments – relatively high volcanoclastic sedimentation rates.
Coral rudstone, platestone, mixstone and pillarstone	Coral rudstones, platestones, pillarstones and mixstones with the <i>Actinacis-Calamophyllia-Gyrodendron</i> assemblage.	Coral growth under optimum conditions – low sedimentation rates and high light intensities.
Oncoid limestone	Limestones with scattered to clast-supported oncoids up to 5 cm in diameter with coral nuclei and laminae up to 1 cm thick composed of cryptmicrobial layers, red algae and ?serpulid worm tubes.	Oncoid growth during times of very low or no sedimentation.
<i>Antillocaprina stellata</i> growth fabric	Carbonate-rich mudstones with or without nodular fabric. <i>A. stellata</i> common, other rudists rare or absent.	Growth of recumbent rudists during reduced volcanoclastic sedimentation rates.
Coral rudstone	Coral rudstone mounds with relief of up to 1.5 m and lateral extent exceeding 5 m. Rudstone consists of corals of the <i>Actinacis-Calamophyllia-Gyrodendron</i> assemblage and contains scattered rudists ( <i>Chiapasella</i> ). Matrix consists of epiclastic siltstone or calcareous siltstone.	Coral rudstone mounds, formed under optimum conditions for coral growth – low sedimentation rates and high light intensities.
Facies in the upper parts of rhythms		
Elevator rudist rudstone	Limestone in beds from 10 to 80 cm thick consisting of isolated rudist shells and scattered fragments of rudist clusters in a clast-supported fabric. Rudists dominated by isolated and cluster elevators. Matrix: lime mudstone.	Toppling of rudists (low sedimentation rates) and reworking of rudists by storms.
Elevator rudist floatstone	Limestone in beds from 10 to 30 cm thick consisting of isolated rudist shells in a matrix-supported fabric. Matrix: lime mudstone.	Toppling of rudist shells and carbonate deposition.
<i>Titanosarcolites</i> growth fabric	Recumbent rudists in growth position.	Growth of recumbent rudists during intervals of reduced or no sedimentation.



types (e.g., *Biradiolites jamaicensis* Trechmann, Table 2).

**Isolated to densely associated elevators** (Fig. 7, Table 2). This morphotype grew as individuals in open or closely packed associations. Many rudists in the Guinea Corn Formation belong to this morphotype, including *Macgillavryia nicholasi* (Whitfield), *Praebarrettia sparcilirata* (Whitfield), *Biradiolites rudissimus* Trechmann, *Antillocaprina* spp. and *Thyrastylon semianulosus* (Trechmann). Most specimens of this morphotype are found in rudist rudstones and floatstones. The lack of preserved growth fabrics suggests that these forms were unlikely to have shown constrictal growth and they are shown as low superstratal forms in Fig. 7.

**Cluster elevators** (Fig. 7, Table 2). These grew in clusters or bouquets numbering from two or three up to several hundred individuals. They are distinctive when found preserved in clusters, but commonly when transported to form rudstones and floatstones the clusters became broken up and individual specimens became isolated. This is particularly the case with *Bournonia cancellata* (Whitfield). Chubb (1971) suggested that *B. cancellata* was a recumbent form because of the lack of ornamentation on the posterior side. While the posterior surface of *B. cancellata* is smooth, specimens found in life position in the field form clusters of up to eight individuals with attachment to neighbours along this unornamented surface. Typical cluster elevators of the Guinea Corn Formation are: *Bournonia cancellata* (clusters of up to eight individuals); *Bournonia barretti* Chubb (clusters of up to 10 individuals); *Biradiolites jamaicensis* (clusters of up to ~200 individuals); *Biradiolites mooretownensis* Trechmann (= *Distefanella* sp. of Kauffman and Sohl, 1974) (clusters of up to ~150 individuals); *Chiapasella radioliformis* (Trechmann) (clusters of up to five individ-

uals); *Hippurites* spp. (clusters of up to ~20 individuals). Other cluster elevators include: ‘*Radiolites*’ *macroplicata* Whitfield; *Thyrastylon adhaerens* (Whitfield); and *Biradiolites rudissimus* (rarely forms clusters).

**Recumbents** (Fig. 7, Table 2). The typical recumbent of the Guinea Corn Formation is *Titanosarcocolites* (e.g., Kauffman and Sohl, 1974; Gili et al., 1995, p. 261; Johnson and Kauffman, 1996). *Antillocaprina stellata* Chubb was also a recumbent. The presence of the commissure adjacent to the sediment–water interface indicates that recumbents must have lived in areas of low or no sedimentation.

**Clingers** (Fig. 7, Table 2). Among the clingers of the Guinea Corn Formation was *Plagioptychus*. The following species also have specimens which develop clinger morphotypes: *Biradiolites jamaicensis*, *Bournonia cancellata*, and *Thyrastylon coryi* (Trechmann). In clingers attached to the sea bottom, the presence of the commissure adjacent to the sediment–water interface indicates that these clingers must have lived in areas of low or no sedimentation.

#### 4. Sedimentary rhythms

The Guinea Corn Formation is a mixed volcanoclastic–carbonate succession with alternating units dominated by volcanoclastic material, derived from either primary or secondary volcanic sources, and bioclastic carbonates. Lithologies in the Guinea Corn Formation are typically arranged into rhythms, between 2 and 30 m thick, consisting of a lower volcanoclastic-rich unit, a middle clastic unit with corals and/or rudists and an upper rudist-rich limestone unit. The facies recognised in these rhythms are described and interpreted in Table 3.

Fig. 8. Section through rhythms upper B2 to lower C1 in the lower part of the Guinea Corn Formation (locality 1 in Fig. 3). From bottom to top, rhythms consist of three divisions: fossiliferous mudstones with lignite fragments; calcareous mudstones rich in corals or the rudist *Antillocaprina stellata*; and well-bedded rudist-rich limestones. Scale in metre intervals.

Correlation of rhythms between sections is based on the presence of biostratigraphic marker beds. The large elevator rudists *Macgillavryia nicholasi* and *Praebarrettia sparcilirata*, and the smaller cluster elevator ‘*Radiolites*’ *macroplacata* occur only at specific levels in units C, D and F (Mitchell, 1999). When these levels are correlated, changes in bundles of clastic- or carbonate-dominated rhythms correlate (i.e., upper Unit C is predominantly clastic dominated with thin limestones, while unit D consists of six carbonate-dominated rhythms with *Praebarrettia* occurring only in the uppermost rhythm).

#### 4.1. Rhythm B3 and C1 in the lower Guinea Corn Formation (Fig. 8)

Rhythms in the lower part of the Guinea Corn Formation consist of three distinct lithological units (from bottom to top): bioturbated siltstone; siltstone and calcareous siltstone with rudists and/or corals; and thin- to medium-bedded limestone (Fig. 8). Rhythms B3 and C1 in section 1 show the characteristics of lower Guinea Corn Formation rhythms, and these are described in detail here.

**Rhythm B3.** The upper part of rhythm B2 is characterised by rudist floatstones with scattered examples of *Bournonia* and *Antillocaprina occidentalis* in a lime mudstone matrix (beds 1 and 2). Rare clusters of *Bournonia cancellata* in growth position are present. Bed 3 consists of lime mudstone with scattered examples of *Titanosarcolites* in life position.

The boundary between B2 and B3 is sharp and marks the change from lime mudstones below to epiclastic siltstones with thin silty limestones above. The epiclastic siltstones of bed 4 contain rare examples of the recumbent rudist *Antillocaprina stellata* and a single rudstone layer with corals of the *Ovalastrea-Actinacis* assemblage. The succeeding siltstones (bed 5) contain rare examples of *Biradiolites mooretownensis* together with common gastropods including *Turritella* sp., *Tectus* sp., *Trochactaeon* sp., and *Actaeonella* sp.

The middle part of B3 (bed 6) consists of 1.8 m of alternating thin siltstones and thin coral rudstones with the *Ovalastrea-Actinacis* assemblage (Figs. 6, middle, and 9). Other faunal elements present in this bed include rare examples of the rudist *Plagioptychus zansi* Chubb, tests and radiolites of the regular echinoid *Goniopygus supremus* Hawkins, and carapaces and chelae of crabs.

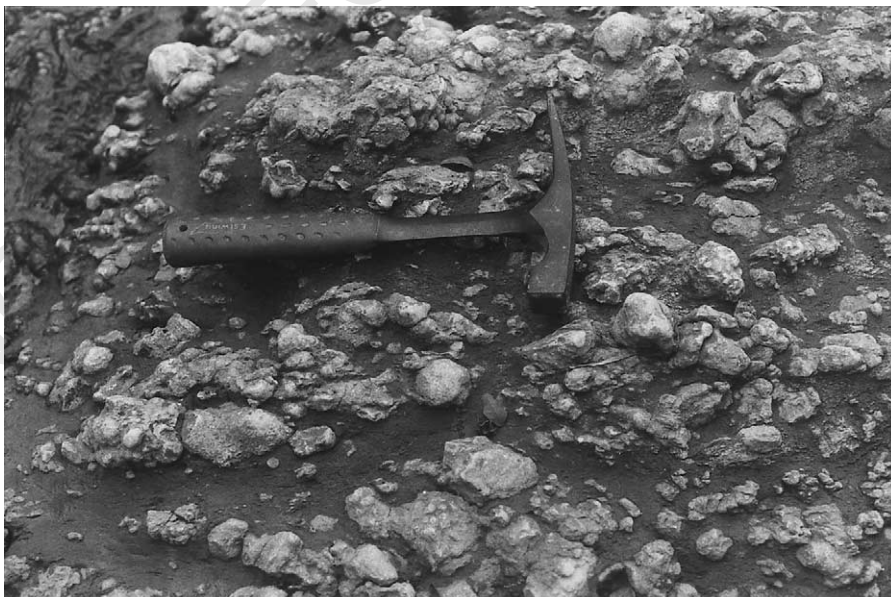


Fig. 9. Coral rudstone with epiclastic siltstone matrix, rhythm B3 middle, Guinea Corn type section (locality 1 in Fig. 3).



Fig. 10. Reworked inverted and fragmented colony of *Biradiolites jamaicensis* in the upper part of rhythm B3, Guinea Corn type section (locality 1 in Fig. 3).

Scattered examples of the rudists *Biradiolites jamaicensis*, *Antillocaprina occidentalis* and fragments of *Titanosarcolithes* occur in the upper part.

The upper part of B3 consists of bedded limestones rich in rudist shells (Fig. 8). Beds are parallel, and range in thickness from 10 to 30 cm. They are separated by distinct bedding planes or thin 1–5-cm beds of siltstone. The limestone beds consist of rudist rudstones and floatstones, with a siltstone, calcareous siltstone or lime-mudstone matrix. Each bed is characterised by a different mono- or paucispecific assemblage of rudists (Fig. 8). The rudists present include *Bournonia cancellata*, *Biradiolites jamaicensis*, *Thyrastylon* spp., *Antillocaprina occidentalis* and, more rarely, *Plagioptychus* sp. Although most of the rudists are not preserved in life position (Figs. 9–11), few show fragmentation, and many *B. cancellata* are articulated. Rare clusters of *B. cancellata* in growth position with their free valves in place occur at the base of bed 9. Other faunal elements are rare, and include corals [*Leptoria (Dictyophylia) conferticostata*], gastropods and crab chelae. Bed 17, the uppermost silty limestone of B3, has a distinctive assemblage of *Titanosarcolithes* cf. *alatus* Chubb in growth position, *B. jamaicensis*,

*Thyrastylon* spp. and common corals of the *Ovalastrea-Actinaxis* assemblage.

**Rhythm C1.** The boundary between rhythms B3 and C1 is sharp and marks the change from bedded limestones below to unbedded siltstones above. The limestones below the bounding surface show no signs of subaerial exposure and no differences in cementation to other limestones in upper B3. The lower part of C1 (bed 18) is a poorly sorted, sandy siltstone with abundant fossils. The siltstone contains scattered sand and granule-sized clastic grains (mainly quartz and lithic fragments), and abundant lignitic wood fragments up to 5 cm in length. Gastropods and bivalves are abundant and a faunal list was given by Sohl (1998, p. 31). The gastropods include: *Tectus* sp.; *Turritella* sp.; *Globularia* sp.; *Nerinea* sp.; *Actaeonella marchmontensis* Sohl and Kollmann; *Actaeonella granthamensis* Sohl and Kollmann; and *Trochactaeon granthamensis* Sohl and Kollmann. The bivalves include: *Brachidontes* sp.; *Lima* sp.; *Syncyclonema* sp.; *Neithea* sp.; *Ostrea* sp.; *Astarte* sp.; *Lucina* sp.; *Tellina* sp.; *Protodonax* sp.; *Unicardium* sp.; *Pholadomya* sp.; and large clusters of the rudist *Biradiolites mooretow-*



Fig. 11. Bedding plane view of reworked examples of *Bournonia cancellata* in the upper part of rhythm B3, Guinea Corn type section (locality 1 in Fig. 3).

*nensis*. Other faunal elements include corals of the *Paracycloseris*-? *Dasmosmilia* assemblage (Fig. 6, top left); rare scaphopods; and well-preserved radioles of the regular echinoid *Goniopygus supremus*.

Bed 19 consists of scattered carbonate concretions and rare rudists (*Biradiolites jamaicensis*) and corals (*Ovalastrea* sp.). The succeeding beds of siltstone (beds 20–24) show an upwards decrease in the proportion of sand- and granule-sized grains, an increase in the proportion of carbonate and a decrease in the abundance of fossils. The increasing carbonate content upwards is reflected by the increase in the size and number of carbonate concretions. Concretions are scattered in the lower part of bed 23, and increase in number upwards. In bed 24, the concretions have amalgamated to form a nodular limestone with siltstone flasers and lenses around the nodules. There is no evidence of a burrow origin for the concretions. The fauna of the lower part of this siltstone unit (beds 20 and 21) is similar to that of bed 18; a thin coral rudstone (bed 22) has corals of the *Ovalastrea-Actinacis* assemblage, and bed 24 contains common examples of *Antillocaprina*

*stellata*, rare *Titanosarcolites*, and at the top a few oncoids.

The upper part of C1 is composed of parallel-bedded limestones up to 80 cm thick consisting of rudist rudstones and floatstones (Fig. 8). These limestones are similar to those in the upper part of B3.

**Interpretation.** The diverse infaunal bivalves and gastropods (including suspension feeders, such as *Turritella*) together with the abundance of lignite in the siltstones in the lower parts of rhythms B3 and C1 suggest high suspended food resources and elevated nutrient supply. This suggests that the corals of the *Paracycloseris*-? *Dasmosmilia* assemblage and the small rudist *Biradiolites mooretownensis* were adapted to elevated nutrient levels.

Upwards through B3 and C1, there is a change in the coral assemblages from the *Paracycloseris*-? *Dasmosmilia* to the *Ovalastrea-Actinacis* assemblage. The low diversity, and dominance of plocooid polyparia in the latter, indicates relatively high sediment influx. The presence of oncoids and the recumbent *Antillocaprina stellata* in the middle part of C1, above the siltstones with the

*Ovalastrea-Actinacis* assemblage, indicates very low sedimentation rates.

The rudist-rich limestones in the upper part of rhythms B3 and C1 are characterised by distinct parallel beds consisting of rudist rudstones and floatstones. The presence of small clusters of *Bournonia* in life position with their free valves in place at the base of some of the rudstone beds implies that they were rapidly buried. Many rudists in the rudstone layers are randomly orientated with inverted and disintegrated clusters

(Figs. 10 and 11). This suggests high-energy reworking rather than toppling, or both. The rudist floatstone beds have a matrix of lime mudstone suggesting a low-energy environment, where the fine-grained sediment could settle out. Few of the rudists show fragmentation, again suggesting relatively low-energy conditions. The presence of lime-mudstone matrix and the rudist rudstones is interpreted to represent deposition on a low-energy carbonate platform that was affected by episodic storms.

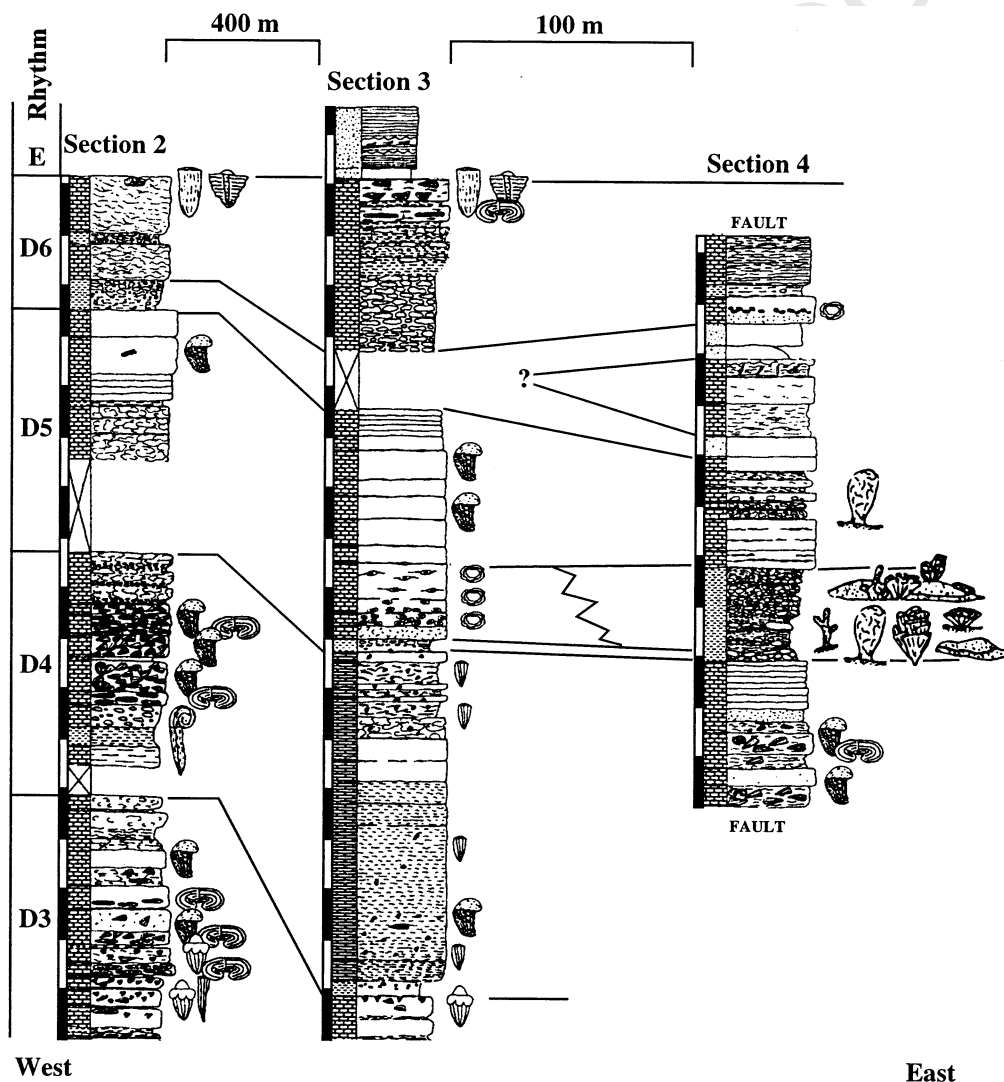


Fig. 12. Sections through rhythms D3–D6, and lower unit E, of the upper Guinea Corn Formation. Scale in metre intervals.

These limestones also show a succession of different mono- to paucispecific rudist assemblages (Fig. 8). This may have been caused by variations in environmental conditions, leading to a succession of different environmentally mediated species. Alternatively, rudist distribution on the sea floor may have been patchy, with different patches of the sea floor dominated by one or several species of rudist. Aggradation of rudist patches over time would thereby produce the alternating rudist assemblages seen. The uppermost part of rhythm B3 contains *Titanosarcolites* preserved in growth position. The presence of this recumbent morphotype indicates low sedimentation rates.

#### 4.2. Rhythms D4–5 and E in the upper of the Guinea Corn Formation

Rhythms in the upper part of the Guinea Corn Formation are well exposed in sections 2, 3 and 4 (Fig. 12). Each rhythm consists of three units: a lower volcanoclastic unit, a middle mixed volcanoclastic–carbonate unit with abundant corals and some rudists, and an upper unit of rudist-rich limestone. The rhythms are clearly recognised in

weathering profiles, where the lower volcanoclastic-rich portions weather back to form gutters in the outcrops. Rhythms D4 and D5, and E are described in detail below.

**Rhythm D4.** The basal portion of rhythm D4 is unexposed, but is soft as it weathers back to form a deep notch in the exposures. It presumably consists of siltstone. The middle part of D4 in section 2 consists of flaser limestones and rudist rudstones, calcareous siltstones and coral rudstones (Figs. 12 and 13). The lower rudist rudstone (Fig. 13) consists of shells of *Bournonia cancellata* set in a siltstone matrix. This is succeeded by an unfossiliferous flaser limestone. Above the flaser limestone, coral rudstone mounds (cf. Wilson, 1975, p. 21) are locally developed with a preserved relief of about 1.5 m (Fig. 13). They can be traced laterally only for distances of 5 m (Fig. 13), and have no internal stratification. The rudstones consist of rolled colonies of branching *Actinacis* sp. and *Multicolumnastrea* sp. together with *Leptoria* (*Dictyophyllia*) *conferticostata* and rare examples of the rudist *Chiapasella radiolitiformis*. Between the coral rudstone mounds, the preserved topography is filled by silty limestones with scattered

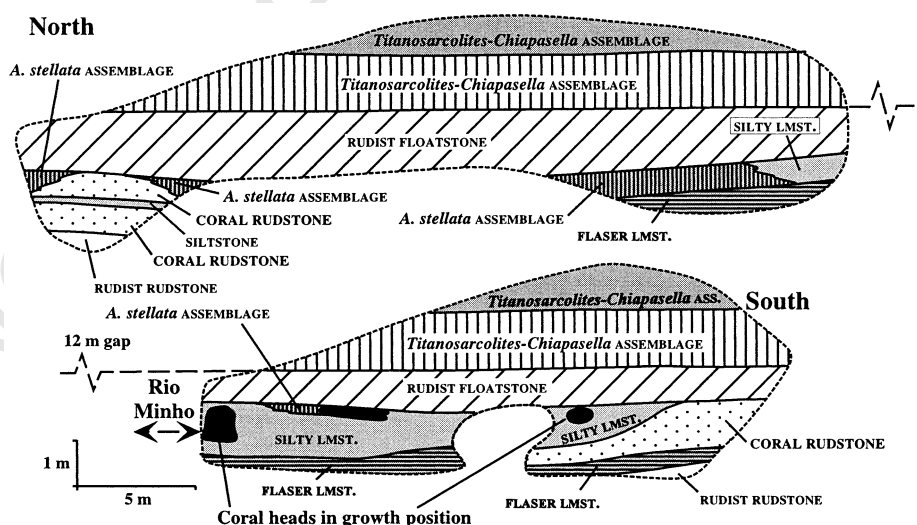


Fig. 13. Coral rudstone mounds in rhythm D4 (locality 2 in Fig. 3). The fill between the rudstone mounds consists of siltstone, siltstone with the rudist *Antillocaprina stellata* and large coral heads. The rudstone mounds are succeeded by bedded rudist floatstones and rudstones. The two sections are connected as shown by arrows.

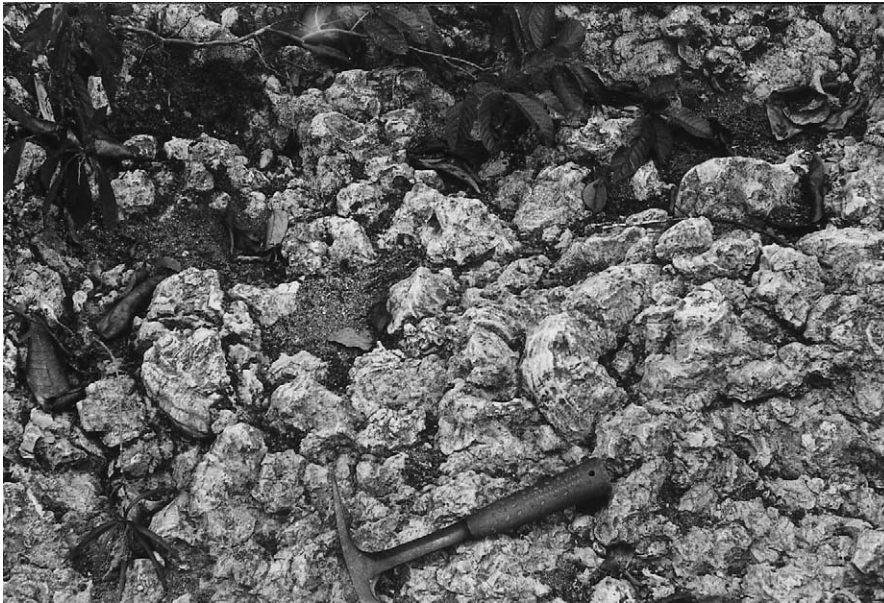


Fig. 14. Reworked clusters of *Chiapasella* in rhythm D4 (locality 2 in Fig. 3).

large coral heads (*L. (D.) conferticostata* and *Actinacis* sp.) in growth position, and local associations of recumbent *Antillocaprina stellata*. The top of the middle part of D4 in section 2 is marked by the scattered occurrence of oncoids.

The upper part of D4 in section 2 is characterised by rudist rudstones and floatstones with a lime-mudstone matrix. The rudists commonly occur in mono- to paucispecific assemblages of *Titanosarcolites giganteus*, *Chiapasella radiolitiformis* (Fig. 14) and *Thyrastylon* spp. Rarer species include *Bournonia thiadensi* Vermunt and *Plagioptychus zansi*. A single layer of *Chiapasella* in growth position, but lacking free valves, is seen at the top of a rudstone in upper D4.

In section 3, the siltstones at the base of D4 are succeeded by rudist floatstones with a lime mudstone matrix. The rudists present include scattered *Chiapasella radiolitiformis* and *Bournonia cancellata*.

**Rhythm D5.** This is well-exposed in sections 3 and 4. In section 3, the lower part consists of a 20-cm-thick siltstone with a few calcareous concretions in the upper part. The base of this siltstone sharp-

ly overlies the limestones of rhythm D4, which do not show any signs of subaerial exposure. The siltstone is succeeded by a 75–110-cm-thick limestone bed containing abundant oncoids in the lower part, and scattered oncoids in the upper part. The oncoids have a nucleus consisting of a rounded fragment of coral, some of which have lithophagid borings. The nucleus is mantled by up to 1 cm of crinkly cryptomicrobial laminae, with less frequent red algae and serpulids. Occasionally, the coral nucleus is completely mantled by red algae forming a rhodolith. The upper part of D5 is represented by bedded rudist floatstones with a lime mudstone matrix. The only rudist identified is *Chiapasella radiolitiformis*.

In section 4, rhythm D5 consists of a lower portion of coral rudstones, platestones, and mixstones, and an upper part of interbedded limestones and coral rudstone. The coral rudstones are up to 10 cm thick, have an epiclastic siltstone matrix and are interbedded with epiclastic siltstone beds up to 5 cm thick. The platestones and mixstones are also up to 10 cm thick and have observable lateral extends of up to 120 cm. The diverse corals belong to the *Actinacis-Cala-*

*mophyllia-Gyrodendron* assemblage, and are associated with diverse algae, echinoderms, brachiopods, crabs and molluscs (Mitchell, in press).

**Unit E.** This unit (which forms the lower part of a rhythm with F1) is well exposed at section 3, where it is divisible into lower and upper parts. The base of unit E is sharp. The lower part consists of interbedded laminated sandstones and siltstones up to 5 cm thick. The bases of some sandstone beds show load casts. Unidirectional ripple-cross-lamination is widely developed, and some unidirectional ripple form sets are preserved, as are rare scour-and-fill structures. No fossils are present. There is a sharp transition from the lower to upper parts of unit E. The upper part of unit E (28 m thick) consists of 6.5 m of unbedded, volcanoclastic siltstones; 13 m of thick-bedded, coarse-grained, graded sandstones; and 8.5 m of thinly bedded, finer-grained, graded sandstones. The normally graded sandstones in the middle occur in beds from 10 cm to 110 cm thick and have sharp, erosive bases, and are interbedded with siltstones. They grade from medium- or very-coarse-sandstone at the base to siltstone at the top. The tops of some sandstones grade into the overlying siltstones, while others may be indistinctly burrow-mottled (mottling with a 3–4 mm diameter). Fossils are absent. The sandstones in the upper 8.5 m of unit E become progressively finer-grained and thinner-bedded upwards. Similar graded sandstones to those in unit E occur in rhythm D6 in section 5 (Fig. 12), and have rare reworked rudists and oysters present at their bases. Unit E is succeeded by F1, which consists of rudist floatstones with a lime-mudstone matrix. The rudist fauna includes *Macgillavryia nicholasi*, *Chiapasella radiolitiformis* and *Plagioptychus jamaicensis* (Whitfield). The transition from E to F1 is gradational with an increase in carbonate content (increasing concretion development) over a thickness of 20 cm.

**Interpretation and discussion.** The lower clastic division of some of the rhythms in the upper part of the Guinea Corn Formation is similar to the Green River Formation of the Summerfield Group (Mitchell and Blissett, 2001). The sedimen-

tology of the volcanoclastic sediments in the Green River Formation was considered by Roobol (1972, 1976) and Mitchell (2000). Roobol attributed the normally graded units in these sedimentary formations to be due to discrete ash-fall events. Cas and Wright (1988) suggested that ash beds, at distance from source, typically have a thickness of a few centimetres at most. The graded sandstones in the Guinea Corn Formation (and lower Summerfield Formation) range in thickness up to 60 cm, include grain sizes up to very-fine-pebble to fine-pebble and some units in the Guinea Corn Formation contain reworked rudists and oysters in their lower parts. Furthermore, no proximal volcanic deposits have been mapped in the Upper Campanian to Maastrichtian succession of the Central Inlier (Coates, 1965, 1968; Roobol, 1976; Mitchell and Blissett, 1999). Because of the lack of proximal volcanic deposits, the thickness of the graded beds, the coarse-grained nature of the sediments and the presence of reworked fossils in the lower part of graded beds, an ash-fall origin for the normally graded sandstone units in the Guinea Corn Formation and Summerfield Group is rejected. Herein, the clastic graded units in the Guinea Corn and Green River Formations are attributed to storm deposits formed through the reworking of terrestrially derived volcanoclastic sediments.

The middle parts of the rhythms show alternations of volcanoclastic-dominated sedimentation with coral rudstone units and lenses with *Antillocaprina stellata*. The coral rudstones occur in mounds with a relief of 1.5 m and represent the largest amount of relief recognised in outcrop in the Guinea Corn Formation. This is interpreted as depositional relief, with the mounds forming positive features on the sea floor. The corals are characterised by relatively diverse colony morphology and polyparia arrangements (assemblage 4 in Table 1) indicating optimum conditions for coral growth (low sedimentation rates, low water turbidity, high light intensity). Similarly, the presence of the recumbent rudist *A. stellata* indicates low sedimentation rates. Taken together, the coral rudstone mounds and *A. stellata* lenses indicate low sedimentation rates, while the interbedded

volcaniclastic sediments suggest infrequent, episodic influxes of fine-grained sediment.

Oncoids (and rarer rhodoliths) are widely distributed at the junction between the middle and upper parts (or at the base of the upper part, where the middle part is absent) of the rhythms. Oncoids can form in a variety of environments (Tucker and Wright, 1990), and the presence of algae indicates formation in the photic zone. Although commonly regarded as growing in shallow-marine, back-reef environments (e.g., Bosellini and Ginsburg, 1971), Reid and Macintyre (1988) reported living foraminiferal–algal nodules in water depths of 30–60 m in the eastern Caribbean. Reid and Macintyre (1988) suggested accretion rates for the laminae in these nodules of between 0.01 and 0.09 mm/yr. Assuming a similar accretion rate, this would suggest that the 1-cm mantle seen in the Guinea Corn oncoids may have taken 100–1000 years to develop. These levels in the rhythms in the Guinea Corn Formation also indicate pauses in sedimentation or intervals of slow deposition.

The rudist assemblages in the upper part of the Guinea Corn Formation have a different taxonomic composition to those in the lower Guinea Corn Formation (Coates, 1965). In the upper Guinea Corn Formation, large elevators (*Chiapasella*) and recumbents (*Titanosarcolithes*) predominate, while smaller elevators (*Bournonia*, *Biradiolites* and *Thyrastylon*) are less frequent. Few elevators are preserved in life position, other than a single bed of *Chiapasella* at the top of a rudstone bed that do not have their free valves in place. This suggests that they died prior to burial, allowing the ligament to decay and the loss of their free valves. The upper part of rhythms in D5 and D6 contain alternating assemblages of the elevator *Chiapasella* and the recumbent *Titanosarcolithes*. While the former could tolerate sediment influx, the latter could not. It is, therefore, possible that variations in carbonate sedimentation rates in these limestones controlled the rudist morphotypes present.

## 5. Conclusions

(1) Two types of asymmetrical rhythm are recognised in Guinea Corn Formation. They consist of a lower volcaniclastic division, a middle volcaniclastic/carbonate division with abundant corals and an upper rudist limestone division.

(2) Four coral assemblages are recognised in the Guinea Corn Formation. They occur as coral rudstone mounds, bedded rudstones and rare pillarstones, platestones and mixstones. Diversity, colonial colony morphology and polyparia arrangement vary between assemblages and suggest that the corals lived in a wide range of environments. These include soft-substrate, high-nutrient lagoons (*Paracycloseris*-?*Dasmosmia* assemblage), areas of high to moderate sediment influx (*Ovalostrea-Actinacis* and *Actinacis-Multicolumnastrea* assemblages) and in more optimum conditions of low sedimentation and high light intensities (*Actinacis-Calamophyllia-Gyrodendron* assemblage).

(3) The small rudist *Biradiolites mooretownensis* was also associated with the *Paracycloseris*-?*Dasmosmia* assemblage coral assemblages, and was adapted to increased nutrient levels.

(4) The upper part of rhythms is represented by parallel-bedded rudist rudstones/floatstones. Rudists in growth position are notably rare. Such rudstones are usually mono- to paucispecific and alternate with rudstones containing different assemblages. The elevators are rarely preserved in growth position and probably indicate low superstratal growth, with the rudstone/floatstone fabrics being produced either by toppling after death or by storm reworking. Successions of different mono- to paucispecific rudist assemblages in successive beds suggest either environmentally driven succession, or a patchiness in rudist distribution on the sea floor and aggradation. The recumbent rudists (*Titanosarcolithes* and *Antilocaprina stellata*) lived in areas of low sedimentation rates.

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