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GROWTH-FORM-ANALYSIS AND PALEOECOLOGY OF THE CORALS OF
THE LOWER MISSISSIPPIAN LODGEPOLE FORMATION,
BEAR RIVER RANGE, NORTH-CENTRAL UTAH

by

Judith M. Miller

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Geology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1977



*Les cieux même ont varié,
et toutes les choses de l'univers
physique sont comme celles du
monde moral, dans un
mouvement continuel de variations
successifs.*

*--Buffon, Époques de la
Nature, 1778*

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I would also like to thank my parents, my family and my friends for their encouragement and moral support.

Judith M. Miller

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ABSTRACT

Growth-Form-Analysis and Paleoecology of the Corals of
the Lower Mississippian Lodgepole Formation,
Bear River Range, North-Central Utah

by

Judith M. Miller, Master of Science

Utah State University, 1977

Major Professor: Dr. Richard R. Alexander
Department: Geology

The Mississippian (Kinderhookian-Osagean) Lodgepole Formation contains a diverse fossil assemblage. Taxa present include brachiopods, crinoids, gastropods, cephalopods, trilobites and corals. Corals and associated fauna were collected from four localities within the Bear River Range. These are, from north to south, Beirdneau Hollow, Spring Hollow, Leatham Hollow and Porcupine Dam. The well-preserved tabulate and rugose (compound and solitary) corals exhibit a high degree of morphologic variability. The colonial corals of the Lodgepole Formation (particularly *Lithostrotionella*, *Syringopora*) exhibit a morphologic gradient from platy to hemispherical forms. The six morphologic categories of colonial corals discussed in this study are identified by mean corallus diameter/corallum height ratios, by the corallite growth direction, and by the shape of the base of the colony. Type I corals have an average mean diameter/height ratio of 3.4; corallites are directed laterally away from the flat base. Type I corals are

interpreted to have been adapted to offshore, quiet-water conditions. Type II corals are flattened hemispheres; they have an average mean diameter/height ratio of 4.1. Corallites are directed radially (i.e., with vertical as well as a lateral component) away from the flat colony base. Type II corals are interpreted in this study to have been adapted to shallow, moderately-turbulent environments in which vertical growth was inhibited. Type III corals have an average mean diameter/height ratio of 3.9 and are similar to Type II corals in all respects but one, namely that there is an absence of corallites on the crown of the corallum. This feature is called balding and is interpreted in this study to have been the result of desiccation and subsequent death of coral polyps. Type III corals are thus interpreted to have inhabited very shallow water wherein subaerial exposure of the crown of the corallum occurred during periods of exceptionally low tides. Type IV corals are dome-shaped or slightly-flattened hemispheres; they have an average mean diameter/height ratio of 2.3. Corallites are directed radially away from the flat base. Type IV corals are interpreted to have inhabited a depth zone intermediate between that of Type II corals (within or barely below tidal range) and Type I corals (near or below wave base). The average mean diameter/height ratio of Type V corals is 1.7. Corallites are directed almost entirely vertically away from the rounded-to-conical colony base. Type V corals are interpreted to have inhabited areas where sedimentation rates were sufficiently high to encourage vertical growth to the virtual exclusion of lateral growth. Type VI corals are composite corals, consisting of combinations of

hemispherical forms and platy forms. This morphologic type is characterized by a change in the direction of growth during the astogenetic development of the colony. The combinations of varying growth forms presumably reflect fluctuations in sedimentation rate.¹

Type I corals display a significantly higher degree of intermural budding than Types II, III, IV or V corals. A high frequency of intermural budding accompanied slow growth, according to Jones² and Philcox.³ In rather deep, quiet water environments, skeletal accretion may have been retarded.⁴ Thus the high budding frequency of Type I corals is consistent with the bathymetric assignment of this growth-form.

Among the solitary rugose corals, five morphologic types were identified. The coralla of Type 1 corals are straight. This feature is interpreted to be the result of vertical growth after an initial stable attachment (i.e., the coral exhibited a negative geotropic response). Another possibility is that the coral, although initially obliquely oriented in the substrate, inhabited an area of slow sedimentation and/or low current velocities. Type 2 rugose corals are

¹M. E. Philcox, "Growth Forms and Role of Colonial Coelenterates in Reefs of the Gower Formation (Silurian), Iowa," Journal of Paleontology 45 (1971):338-346.

²O. A. Jones, "The Controlling Effect of Environment Upon the Corallum in *Favosites*; with a Revision of Some Massive Species on This Basis," Annals and Magazine of Natural History 17 (1936):1-24.

³Philcox.

⁴R. R. Graus and I. G. Macintyre, "Light-adapted growth of Massive Reef Corals: Computer Simulation." Geological Society of America, 1975 Abstracts with Programs, Annual Meeting (1975).

geniculate and have been interpreted to have formed as a result of penecontemporaneous erosion of the surrounding matrix. Scouring caused the coral to topple to a horizontal position. Vertical growth away from the substrate would result in the geniculation. Increasing rates of sedimentation in the immediate vicinity of obliquely-attached corals would necessitate rapid vertical growth in order that the polyp maintain a position above the substrate.⁵ Repetition of these processes accounts for the Type 3 (multiply geniculate) morphology. Either sedimentation rates were variable, and/or current velocities sufficiently high to cause toppling of rugose corals. Type 4 rugose corals have prominent constrictions of their epithecae, a feature referred to as rejuvenescence. Changing environmental conditions that may have proven traumatic to the coral (i.e., storm), resulting in temporary growth-stoppage are interpreted to have caused this feature. Type 5 corals include coiled and grooved protocoralla. These features are interpreted to be adaptations which facilitated post-larval attachment of juvenile corals to objects at or above the sediment-water interface.⁶

Detailed study of internal and external calical features allowed for interpretation of the relative abilities of the Lodgepole corals in terms of their efficiency at rejecting sediment from the calice. Each coral genus was rated on the basis of calical relief, calical shape, septal density and septal length. In general, the corals

⁵J. A. E. B. Hubbard, "Coral Colonies as Micro-Environmental Indicators." *Extrait des Annales de la Societe Geologique de Belgique*, Tome 97. Fascicule I (1974):142-152.

⁶W. J. Sando, "Significance of Coiled Protocoralla in Some Mississippian Horn Corals," Palaeontology 20 (1977):47-58.

categorized as inefficient sediment rejectors, such as *Caninia*, had low calical relief, horizontal calical floors, low septal densities and short septae. The inefficient corals (i.e., those inferred to have possessed comparatively passive polyps) were most often found in mudstones and wackestones. In contrast, corals categorized as efficient sediment rejectors, such as *Zaphrentoides* and *Lithostrotionella*, had high calical relief, v-shaped calical floors, high septal densities and long septae. The more efficient corals (i.e., those inferred to have possessed active polyps) are comparatively ubiquitous in their lithologic associations and are often found in impure mudstones or wackestones, or in grainstones and packstones.

At least one insoluble residue sample was prepared for the lithologic matrix associated with each taxon. In general, the lithologic matrix associated with deposit-feeding organisms (trilobites, gastropods), trace fossils and algal structures yielded the highest weight percent insoluble residue values. Crinoids, bryozoans and corals yielded intermediate values, and the lowest values were obtained for the brachiopods.

A similarity matrix based on indices of affinity as calculated by Faber and McGowan,⁷ facilitated an analysis of faunal associations. Two assemblages, one dominated by suspension-feeders and one a mixed assemblage of suspension and deposit feeders, are apparent. Although some biological interrelationships were inferred to have operated

⁷E. W. Fager and J. A. McGowan, "Zooplankton Species Groups in the North Pacific," Science 149 (1963):453-460.

between the organisms, the physical factors (i.e., substrate, turbulence, sedimentation rate depth) are interpreted to have been the dominant controlling factors in the distribution of the Lodgepole fauna.

The construction of a hypothetical bathymetric profile showing the inferred bathymetric distribution of the fossil corals, associated faunal elements, abiotic sedimentary structures, trace fossils and algal structures was based upon a model of carbonate deposition in clear-water epeiric seas.⁸ According to the model, three marine, intergrading hydraulic zones characterized epeiric seas. Zone X is a low-energy, quiet water zone located offshore. The pelletal, fossiliferous mudstones and wackestones of the Lodgepole Formation are interpreted to have formed in this zone. Types I, IV, V colonial corals and Type 1 solitary corals probably inhabited Zone X. Zone Y is located landward of Zone X and is a high-energy zone, located above wave base and subject to both wave and strong current action. Packstones, bioclastic grainstones, boundstones and fossiliferous wackestones may have formed in this zone. Types II and III colonial corals and Types 2 and 3 solitary corals probably formed in Zone Y. Zone Z, the nearshore quiet-water zone, is the zone in which impure pelletal mudstones and wackestones, and laminated calcilutites were deposited. No colonial corals other than the *Aulopora* were found in these rocks. *Zaphrentoides*, an efficient sediment-rejector, and (rarely) *Vesiculophyllum* are the only

⁸M. L. Irwin, "General Theory of Epeiric Clear Water Sedimentation," American Association of Petroleum Geologists Bulletin 49 (1965):445-459.

solitary corals found in Zone Z. On the basis of their functional morphology and sedimentary and biological associations, the corals of the Lodgepole Formation are interpreted to have inhabited the shallow subtidal to intertidal regime.

(175 pages)

INTRODUCTION

Objective and Procedure

The objective of this study is to identify the various growth-forms of the rugose and tabulate corals of the Mississippian Lodgepole Formation and to relate the morphologic types to environmental parameters, i.e., illumination, bathymetry, current activity and sedimentation rates. The study area is located in the Bear River Range of north-central Utah (Figure 1).

Weathered-free fossils and fossiliferous slabs were collected in the field from the extensive talus slopes which form immediately below the cliffs and form in-place strata of the Lodgepole Formation. Lithologic and faunal associations were recorded for corals found in the strata or talus blocks. Corals and associated fossil organisms were collected from the following four localities: Beirdneau Hollow, Spring Hollow, Leatham Hollow and Porcupine Dam.

In the laboratory, sixty-eight insoluble residues were prepared from representative matrices of each taxon found in the Lodgepole Formation. The results were graphically represented. Numerous solitary and colonial corals were sectioned, longitudinally and transversely, in order to facilitate study of internal features. Both external and internal features of the coralla were examined in detail. Septal densities, septal lengths, corallite diameters, depths and shape were determined for each coral morphologic type. In addition, the mean

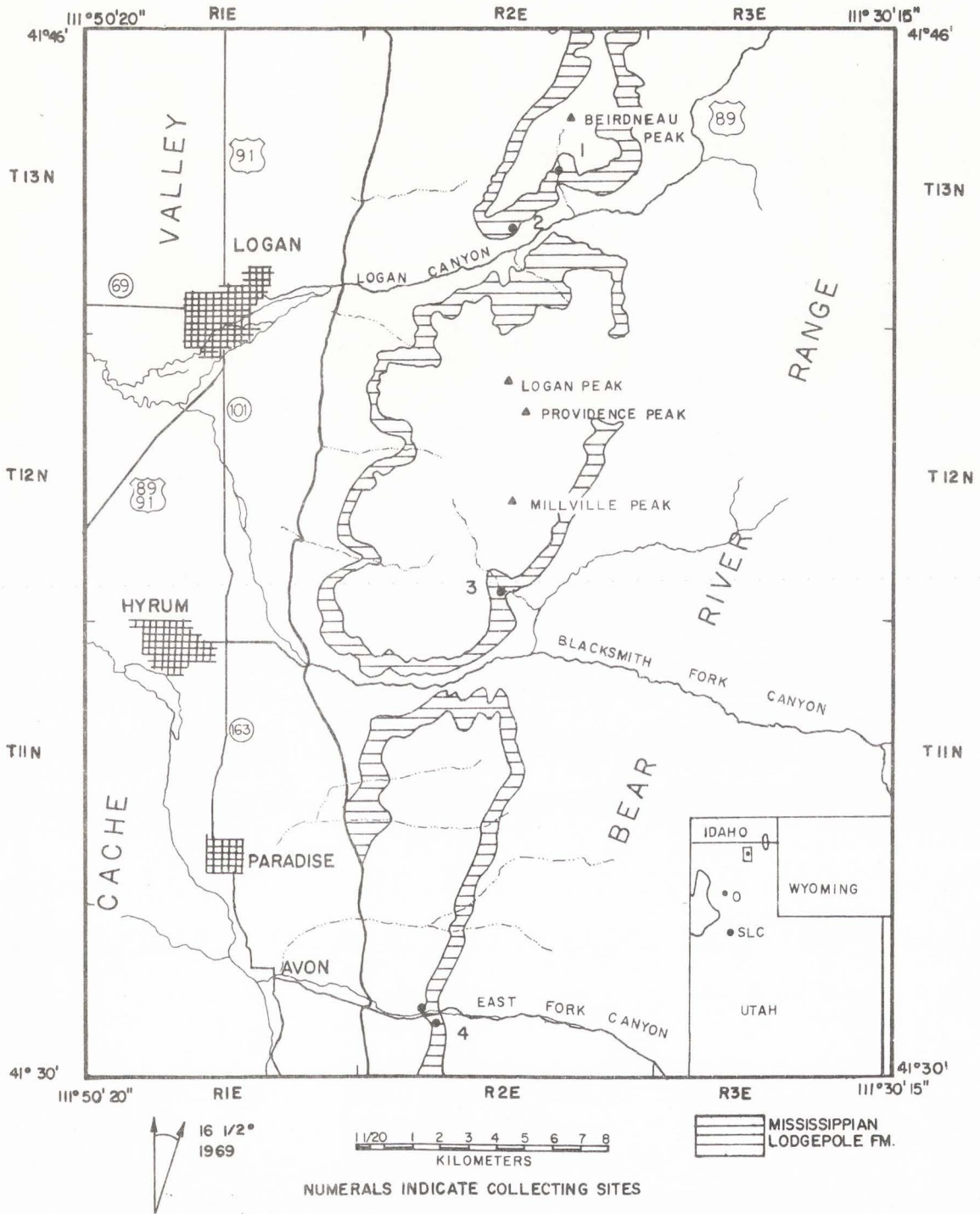


Figure 1. Index map showing the four collecting localities (solid circles) within the study area (from Williams, 1948).

diameter/height ratios of colonial corals and pregeniculation lengths of solitary corals were measured. Six colonial and five solitary coral growth-forms were identified. Comparison with growth forms of modern corals facilitated interpretations of the environmental setting of each Mississippian growth-form. On the basis of morphology and lithological associations, sediment-rejection capabilities were inferred for each coral genus, based on the model proposed by Hubbard and Pocock (1972). Delicate features of juvenile rugose corals were studied upon selective dissolution of the limestone matrix.

Cluster analysis and resulting dendrograms illustrated faunal associations. A synthesis of growth-form-analysis, lithologic evidence, insoluble-residue data and faunal associations provided the basis for the construction of a probable bathymetric distribution of the organisms of the Lodgepole Formation (Plate 1). Samples illustrated in this study have been deposited with the Department of Geology of Utah State University. Samples have been labelled in the following way: the first letter of the sample label refers to the coral type, where:

L = lithostrotionid

S = syringoporoid

R = solitary rugose coral

A = auloporoid

M = *Michelinia*

O = other miscellaneous structures

the second, a digit, refers to the actual sample number; the third, a letter, refers to the collecting site,

where:

B = Beirdneau Hollow

S = Spring Hollow

L = Leatham Hollow

P = Porcupine Dam

Location and Accessibility

Fossils were collected from the following four sites, within the Bear River Range: Beirdneau Hollow, Spring Hollow, Leatham Hollow and Porcupine Dam. All of these localities may be found in the Logan, Utah quadrangle (1:125,000, 1914).

Beirdneau Hollow (Figure 2) and Spring Hollow (Figure 3) are located in Logan Canyon, along U. S. Route 89. Beirdneau Hollow is located 8.4 km east of the mountain front. A small Forst Service sign for the Beirdneau Summer Home Site marks the turnoff on the northern side of the highway. The dirt road is about .5 km long; it ends at the base of the hollow. The Lodgepole crops out in conspicuous cliffs along the north, east and west sides of the north-trending hollow. The sites from which most samples were collected are along the western side and the northernmost point of the hollow. The outcrop on the western side is located at a distance of about 2.9 km from the end of the dirt road, at an elevation of 2043 m (6700 feet). The south-facing cliff at the northern head of the hollow is 1.9 km from the end of the dirt road; the elevation at the base of the outcrop is 2226 m (7300 feet). The fallen trees which have accumulated in the lowest part of the hollow



Figure 2. The Lodgepole Formation at Beridneau Hollow: view east.



Figure 3. The Lodgepole Formation at Spring Hollow: view north.

are best avoided by rapidly gaining elevation and approaching the cliffs from the side or top rather than from the bottom.

Spring Hollow is 5.8 km east of the mountain front. The Lodgepole crops out on both north and south sides of the highway, and is readily accessible by foot. The elevation at the highway is about 1554 m (5100 feet); the base of the Lodgepole is at an elevation of 1767 m (5800 feet). The distance from the road to the outcrop is less than .6 km.

Leatham Hollow (Figure 4) is in Blacksmith Fork Canyon (State Route 101), east of Hyrum, Utah. A turnoff on the northern side of the road is 7.7 km east of the mountain front. The turnoff is well marked (Left Fork Canyon). The road is a light-duty gravel road. Another left-hand turnoff is marked by a Forest Service sign (Leatham Hollow) about .5 km from the main highway. This unimproved dirt road leads directly to the Leatham Hollow section. The elevation at the base of the very conspicuous cliffs of the Lodgepole is approximately 1770 m (5800 feet); the elevation of the highway at the Left Hand Fork turn-off is 1570 m (5150 feet). A short hike from the dirt road is necessary to reach the talus slopes.

The Porcupine Dam section (Figure 5) is readily accessible. Porcupine Dam lies 9.9 km southeast of the town of Paradise, Utah. Paradise is located on State Route 163, south of Hyrum, Utah. The west-dipping strata of the Lodgepole Formation crops out on either side of the dam. It also crops out below the dam, .3 km to the southwest.



Figure 4. The Lodgepole Formation at Leatham Hollow: view east.



Figure 5. The Lodgepole Formation at Porcupine Dam: view east.

Talus slopes of this lower section are visible to the southwest when standing on the dam. An unimproved dirt road which branches to the south from the road to the dam leads to the slopes below the dam. Samples were collected at both of these sites.

Stratigraphic and Paleogeographic Setting

The stratigraphic and paleogeographic setting of the Lodgepole Formation will be discussed briefly to establish the temporal, latitudinal and depositional framework within which the corals lived. Holland (1952:1731) stated that "virtually all, if not all, of the Madison in Leatham Hollow is Lodgepole in age." He assigned a Kinderhookian age to the Madison of Leatham Hollow. Beus (1963:48) studied the Paleozoic stratigraphy of Samaria Mountain, 80 km to the northwest of the study area. He stated that the Early Mississippian limestone of the region under investigation, "once designated the 'Madison Limestone' is now better referred to as the 'Lodgepole Limestone'." Dutro and Sando (1963) assigned a Kinderhookian and/or earliest Osagean age to the Lodgepole Formation. Sando et al. (1976) stated that the Lodgepole is Kinderhookian and early Osagean in age. Rose (1976) placed the Lodgepole in the lower phase of the lower depositional complex of the Mississippian, which is Kinderhookian to early Meramecian in age.

The name Madison, according to Strickland (1956:51), was applied to a "tripartite series of carbonates of Carboniferous age by A. C. Peale in 1893." The three lithologies referred to by Strickland (1956) are, from older to younger, laminated limestones, massive limestones and

jaspery limestones. In 1922, Collier and Cathcart designated the laminated limestone the Lodgepole Formation and the massive limestone as the Mission Canyon. Sando and Dutro (1960:118) stated that the Lodgepole "includes both the 'laminated limestones' and the 'massive limestones of Peale'."

Holland (1952) described and measured the Madison in Leatham Hollow (Figures 13, 14, 15 and 16, pp. 1724-1728), and reported a thickness of 250 m (803 feet). A lithologic description accompanied the measured section. The following information may be found on pages 1723 through 1731 of the article (Holland, 1952). The lower 9.2 m (30 feet) of Lodgepole consists of "brownish gray to brownish-black arenaceous, carbonaceous, noncalcareous, fissile shale." The shale is calcareous in places. The first cliff, or lower "Chinese Wall" rises abruptly from the shale. The cliff is described as "275 feet of very hard, dense, resistant, thin-to-medium bedded limestone. The beds are dark gray fine-crystalline limestone rhythmically interbedded with shaly limestone beds." Above the lower "Chinese Wall" a slope-forming "dark gray, fine-crystalline to sublithographic thinly bedded limestone" is "rhythmically interbedded with one-eighth inch beds of grayish orange, soft, silty to argillaceous limestone." The second cliff, or upper "Chinese Wall" is 56 m (180 feet) thick, and is composed of "thin-bedded, dark gray limestone interbedded with grayish-orange to olive-gray calcareous siltstone." At the top of the Lodgepole about 15 feet (4.6 m) of "medium light gray to medium dark gray, hard medium crystalline dolomitic limestone" is overlain by "62 feet of cherty limestone."

Holland (1952:1731) stated

The lighter color, greater coarseness, and thicker bedding near the top of the Madison are noteworthy. The silty limestone, like that which is rhythmically interbedded with the limestones lower in the section, is absent in this part of the formation.

The Great Blue formation overlies the Lodgepole in Leatham Hollow.

The Leatham Formation (U. Devonian or L. Mississippian) is found directly below the basal shale layer of the Lodgepole.

Figure 6 is a composite stratigraphic section of the Lodgepole formation in Leatham Hollow. The lithologic information is taken from Holland (1952).

The Mississippian paleogeography of North America and the major structural features of the western United States during Mississippian time are illustrated by Sando (1977, Figure 9, p. 15 and 1976, Figure 1, p. 318 respectively) and are reproduced for convenience in Figures 7 and 8. Most of the northern Rocky Mountain region was a part of the craton during the Mississippian. The Transcontinental Arch extended southward from the Canadian Shield into Arizona and New Mexico. Sando (1976) stated that most of the arch was emergent throughout the Mississippian, although it may have been breached at times. Haun and Kent (1965:1785) stated "Mississippian rocks probably once covered the entire region but were thinnest over the transcontinental arch and the incipient ancestral Rockies." The Cordilleran platform occupied a position west of the arch, and was... a broad cratonic area of relatively thin marine sedimentation that extended from southern Canada

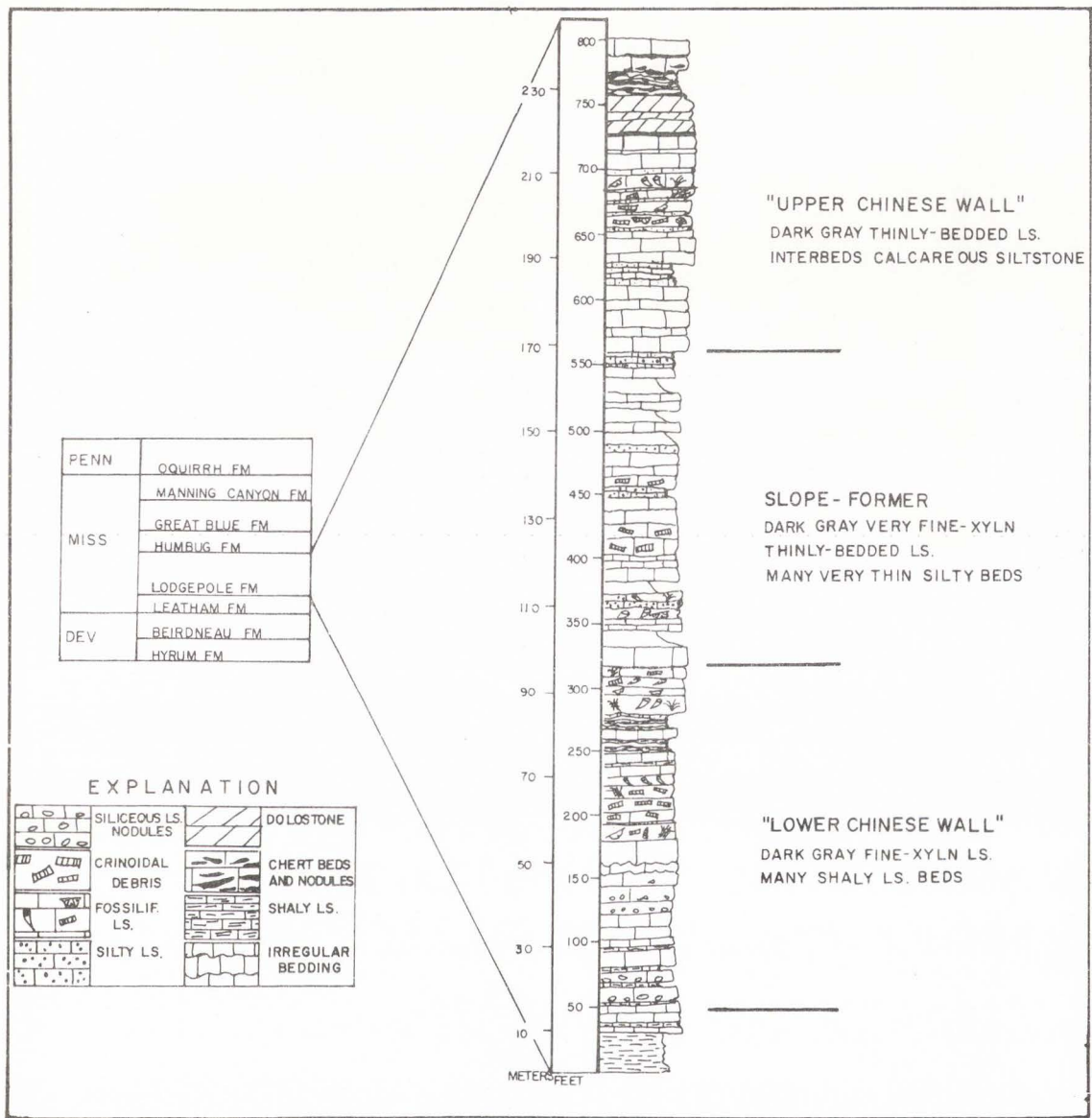


Figure 6. Composite stratigraphic column of the Lodgepole Formation in Leatham Hollow, as described by Holland (1952).

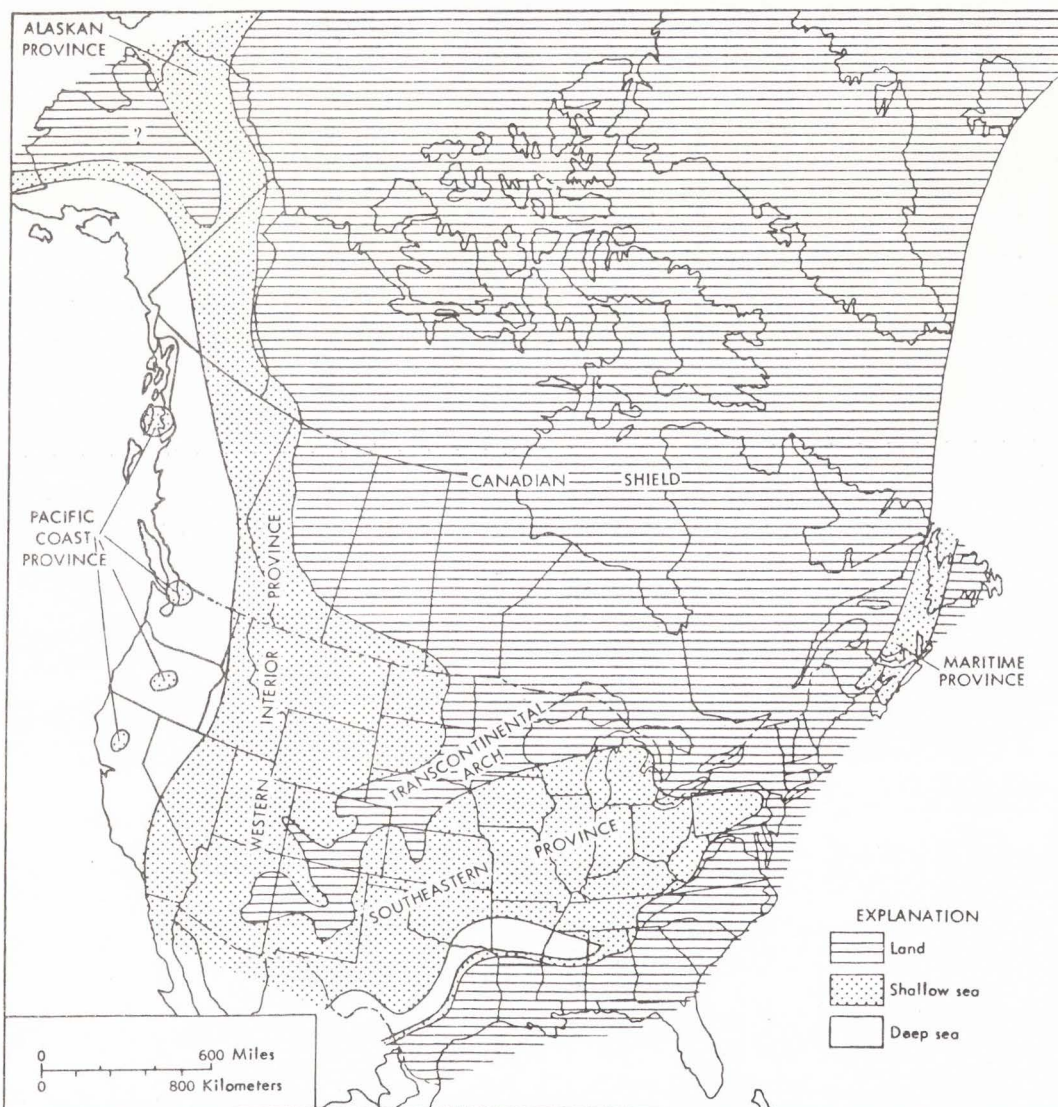


Figure 7. Nonpalinspastic map of North America showing paleogeography and coral provinces during Mississippian time (from Sando, 1977, p. 15).

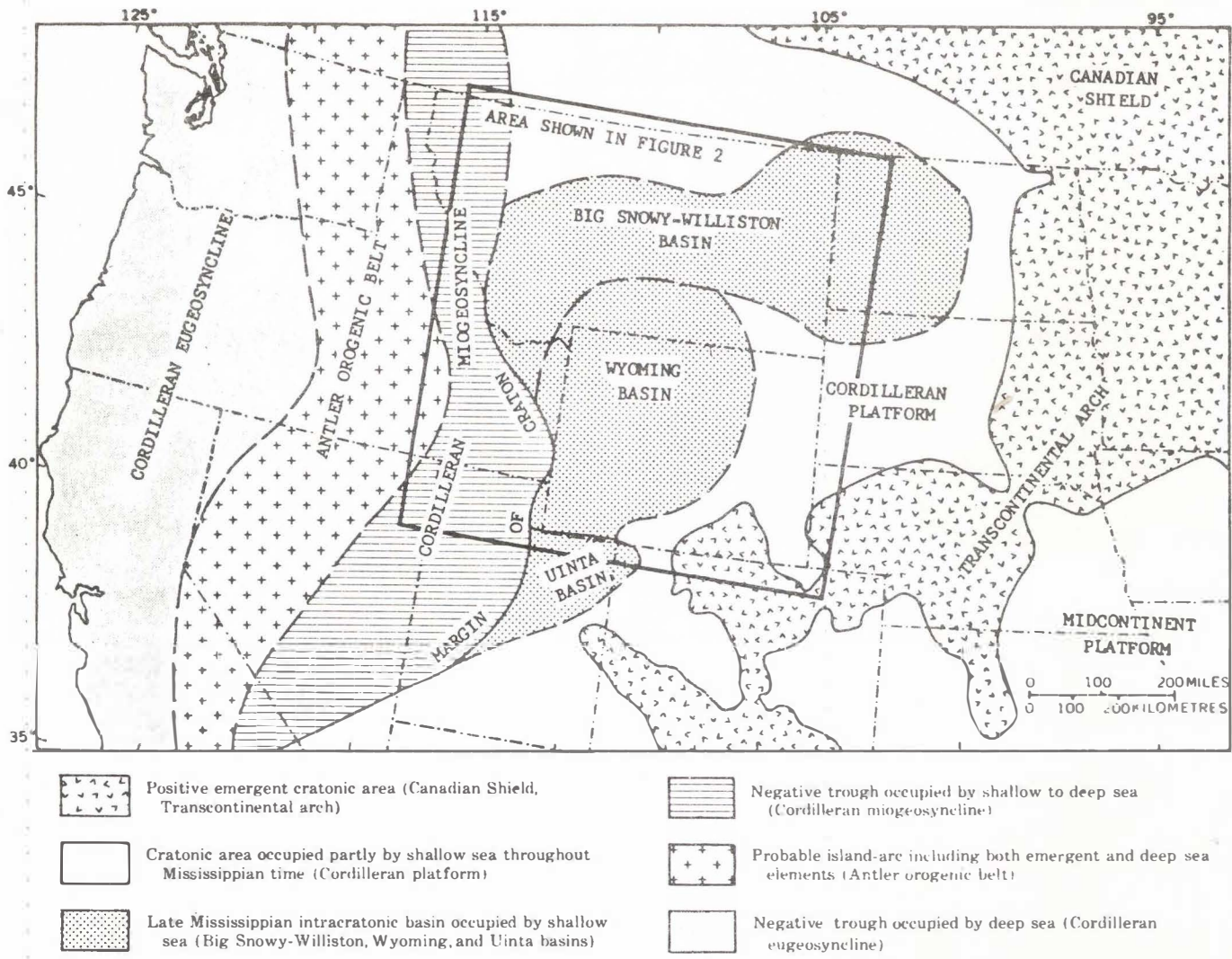


Figure 8. Major structural features of the western United States during the Mississippian.

southward into Mexico" (Sando, 1976:318). The platform constituted a depositional shelf during early Mississippian time, dominated by carbonates and evaporites. To the west of the Cordilleran platform, the Cordilleran miogeosyncline, Antler Orogenic belt and Cordilleran eugeosyncline together formed a "... linear belt of thick sedimentation ..." (Sando, 1976:318). The Antler Orogenic belt constituted an island chain during Mississippian time, "... undergoing sporadic tectonism ..." (Sando, 1976:318). The eugeosyncline to the west was occupied by a deep sea.

Sando (1976) described the Mississippian history of the northern Rocky Mountains as "two principle depositional cycles separated by a cycle of epeirogenic uplift and erosion." Cycle I sedimentation (early Kinderhookian-early Meramecian) occurred on the broad shelf. The Kinderhookian transgression of the Cordilleran sea, coupled with Osagean and early Meramecian regression, constitutes Cycle I.

Cycle I is represented by predominantly carbonate rocks included in the Madison Limestone or Group over most of the miogeosyncline and platform. ... The Madison Group is represented only by the Lodgepole Limestone in parts of southeast Idaho and northeast Utah. (Sando, 1976:320)

Cycle I is subdivided into phases; the Lodgepole Formation was deposited during Cycle I, phases 1 through 4. During phase 1, according to Sando (1976), argillaceous and carbonaceous mud, along with quartz silt, were deposited in a shallow basin in northeast Utah. Holland (1952) reported about 9 m of fissile shale at the base of the Lodgepole. During Cycle I, phase 2, subtidal carbonate sediments were deposited on an open-marine shelf. Holland (1952) noted a thick sequence of dark,

thin-to medium-bedded limestone interbedded with shaly limestone beds. In phase 3 of Cycle I, the shelf environment migrated eastward, and argillaceous and silty carbonate mud was deposited on the slope and the trough in northeastern Utah. Holland (1952) described a slope-forming thin-bedded limestone interbedded with silty, argillaceous limestone. The fourth phase of Cycle I sedimentation in northeast Utah is characterized by cyclic intertidal and subtidal shelf carbonate deposits. The upper "Chinese Wall" consists of thin-bedded, dark gray limestone interbedded with calcareous siltstone, followed by a thin unit of dolomitized limestone and 19 m of cherty limestone.

The successional lithologic similarities between the phases of Cycle I (Sando, 1976) and the lithologies represented in the Lodgepole Formation in Leatham Hollow are striking. Rose (1976) also delineated two episodes of Mississippian deposition, the lower depositional complex and the upper depositional complex, shown in Figure 5. The lower depositional complex comprises rocks of Kinderhookian-early Meramecian age. Included in it are the following formations, or units: Allan Mountain limestone, Castle Reef Dolomite, Lodgepole and Mission Canyon limestones, Madison limestone or Group, Gardison or Deseret limestones, Leadville, Redwall and Monte Cristo limestones. The succession thickens to the west toward the Cordilleran geosyncline. The lower part of the lower depositional complex (which corresponds to the Lodgepole) is described by Rose (1976:453) as "... transgressive and open marine."

"Comparison with modern carbonate sediments suggests deposition in a marine setting in water perhaps 30-100 m deep" (Rose, 1976:455).

Rose (1976:459) summarized the setting for the early portion of the lower depositional complex as follows:

... the lower depositional complex represents a complete miogeosynclinal sequence with a wide cratonic shelf thickening gradually to the west. This carbonate shelf was terminated on the west by an accretionary barrier-type shelf margin having seaward topographic relief of several hundred metres. Behind this stratigraphic reef accumulated shelf-interior evaporites and low-energy, very shallow water dolomites and limestones.

The following large, cylindrical, solitary corals were collected from the Lodgepole Formation: *Vesiculophyllum* sp. Easton (1944), *Caninia* sp. Michelin in Gervais (1840), *Rylstonia* sp. Hudson and Platt (1927), *Turbophyllum* sp. Parks (1951). Small, solitary, conical corals include *Zaphrentoides* sp. Stuckenbergl (1895), and *Amygdalophyllum* sp. Dun and Benson (1920). The massive colonial corals are *Lithostrotionella* sp. Yabe and Hayasaka (1915) and *Michelinia* sp. de Koninck (1841). The following fasciculate colonial corals were found: *Syringopora* sp. Goldfuss (1826), *Lithostrotion* sp. Fleming (1828), *Aulopora* sp. Goldfuss (1829) and *Cladochorus* sp. M'Coy (1847).

CORAL ECOLOGY

Because recent scleractinian corals are interpreted to be the modern analogues of Paleozoic corals, the ecology of scleractinians is discussed in detail. Scleractinian corals can be classified into two ecologic types, hermatypic and ahermatypic. Hermatypic, or reef corals, contain zooxanthellae (unicellular dinoflagellate algae) within their endodermal tissues (Wells, 1957). The incorporation of algae within the tissues of the coral aids in the absorption of metabolic wastes and in calcification of the corallum, thus encouraging prolific coral growth (Heckel, 1972). Ahermatypic corals lack zooxanthellae (Wells, 1957).

The overwhelming majority of hermatypic corals are stenohaline. The optimum salinity for reproduction and larval recruitment is near 34 to 36‰. Hermatypic corals will tolerate, but not reproduce in salinities ranging from 27‰ to 41‰ (Wells, 1957; Vaughan and Wells, 1943). Kinsman (1964) observed living hermatypic corals in salinities of 48‰ in the Persian Gulf. Ahermatypic corals are found in marine waters where salinities exceed 34‰ (Wells, 1957).

Hermatypic corals can tolerate a minimum temperature of 16-17°C and a maximum temperature of 36°C. Optimal growth and breeding occur between 25 and 29°C (Wells, 1957). Ahermatypic corals, on the other hand, are eurythermal. They can survive temperatures ranging from -1.1°C to 28°C. Maximum abundance of ahermatypic corals (number of

individuals/unit area) occurs in the range 8.5 to 20°C (Wells, 1957). Coates and Kauffman (1973) stated that the Cretaceous ahermatypic coral *Archohelia dartoni* preferred cool waters (6-10°C for banks, 15-16°C for thickets).

Due to the symbiotic relationship existing between hermatypic corals and algae (zooxanthellae), these corals are restricted to the photic zone. Depths at which hermatypic corals live range from 0-90 m; however, most are found in depths less than 50 m (Wells, 1957). Maximum abundance occurs at a depth of less than 20 m (Wells, 1957). Ahermatypic corals are not limited to the photic zone. Found at depths from 0-6000 m, their maximum abundance is concentrated in depths of 180-360 m (Wells, 1957). Coates and Kauffman (1973) estimated depths of 200-500 feet (61-152 m) for a Cretaceous ahermatypic coral which apparently preferred aphotic or dimly illuminated depths.

Suspended sediment is tolerated by hermatypic corals only if it does not reduce the amount of light penetration, which would greatly inhibit photosynthesis by zooxanthellae (Wells, 1957). Dodge et al. (1974) found that excessive turbidity resulted in a decrease in the growth rate of modern hermatypic corals. Ahermatypic corals also will tolerate some suspended sediment.

Corals cannot survive heavy, rapid sedimentation or shifting substrates. Firm substrates are required for the attachment of planula larvae (Wells, 1957). Larvae are easily smothered by excessive sedimentation. All modern corals are capable of rejecting very fine sediment in small amounts (Hubbard and Pocock, 1972). Heckel (1972) stated that some solitary ahermatypic corals can live on soft substrates, but

that colonial ahermatypic corals require hard substrates for attachment. By contrast, Coates and Kauffman (1973) reported the occurrence of Cretaceous ahermatypic coral thickets enclosed in a mud matrix. They concluded that these corals preferred firm clay mud substrates.

Vaughan and Wells (1943:59) stated that "Coral polyps, so far as has been definitely proved, are wholly carnivorous. Their food consists of small floating and swimming animals which they capture by their tentacles and the action of nematocysts ..." Yonge (1940:352) called scleractinians "... specialized carnivores"; he cited zooplankton as the food supply of scleractinians. Goreau (1959:66) cited the work of Boschma (1926) who indicated that hermatypic corals may be capable of digesting zooxanthellae in the absence of animal food. However, Yonge and Nicholls (1931a) found that corals when deprived of animal food and faced with starvation, were not capable of extracting enough food from zooxanthellae to prevent starvation.

Very little work has been done on the paleosalinity tolerances of Paleozoic rugose and tabulate corals. Most assume, as does Heckel (1972:234) that "... the modern marine assemblage has been 'marine' ever since the constituent organisms have appeared." A hypersaline habitat (tidal flat) has been inferred for the Silurian tabulate coral *Favosites cayugensis* (Floyd, et al., 1972), but no examples of hyposaline Paleozoic corals have been published.

The annual minimum temperature at which Paleozoic corals lived was between 16° and 21°C, according to Wells (1957). Hill (1956) stated that the profuse reef growth of the Carboniferous occurred in warm-water seas.

Wells (1957) designated 50 m as the approximate maximum water depth at which Paleozoic corals lived. Warm, shallow waters served as the habitat for Silurian and Devonian reefs (Wells, 1957). Hill (1956) discussed reef habitats, clear shallow seas and deep murky waters as probable habitats of Paleozoic rugose corals. The overwhelming majority of Paleozoic colonial corals do not appear to have been adapted to the highly agitated reef environment in which modern corals flourish (Wells, 1957; Heckel, 1972; Hubbard and Pocock, 1972). The stromatoporoids apparently filled this niche through the Ordovician-Devonian interval of the Paleozoic. Wells (1957:773) attributed the lack of Paleozoic corals in reeflike deposits to their "... insecurity of attachment." However, Wells added, "... there is no evidence that Paleozoic corals flourished in 'deep' water." The zone of wave action probably extended to a maximum depth of 30-40 m, more commonly to a depth of 5 m, according to Wells (1957), and it is the zone immediately below this one that Wells cited as the habitat of Paleozoic corals. However, Kissling (1965) reported a Silurian favositid coral which is characterized by the distribution of corallites over the entire corallum. By analogy to the modern *Siderastrea radians*, he concluded that this coral inhabited the windward side of Silurian reefs, and was well adapted to a turbulent, intertidal environment.

Paleozoic corals, by nature of their structure, were probably less efficient sediment rejectors than modern scleractinians according to Hubbard and Pocock (1972). However, all but the least efficient sediment rejectors (those with passive polyps) among Paleozoic corals probably could tolerate suspended sediment (Hill, 1948; Hubbard and

Pocock, 1972). Wells (1957) stated that most Paleozoic corals probably inhabited niches similar to those occupied by modern lagoonal reef corals.

Most Paleozoic corals appear to have been best adapted for life on relatively soft substrates, unlike modern reef corals which prefer hard substrates (Wells, 1957; Hubbard, 1970). Due to the unattached post-juvenile stage which was common to Paleozoic rugose and tabulate corals, toppling of rugose corals and overturning of colonial forms would occur on hard, wave-swept bottoms. Paleozoic rugose corals appear to have required a substrate firm enough to support the corallum in an upright position, yet fluid enough to allow the coral to subside partially into the substrate as its size and weight increased (Hubbard, 1970). The heavy skeletons and large size of some of the Paleozoic corals may have provided them with added stability.

Hubbard and Pocock (1972) studied sediment-rejection capabilities of recent scleractinian corals, and compared these corals to those of the Paleozoic. On the basis of several skeletal features they rated some Paleozoic corals in terms of their efficiency at sediment rejection. The criteria they used will be discussed in detail in a later section. They found a relationship between the morphology of the calice and the type of rock matrix in which the coral is enclosed. Very efficient corals (those whose morphology suggests a capability to reject large, foreign particles from the calice), were often found in calcarenites. This lithological association suggests that these corals were capable of inhabiting a sandy substrate and of shedding coarse-grained particles from the calice. The least efficient sediment rejectors, inferred

from morphological features, were found enclosed in micrite, which supports the suggestion that these particular corals may have been capable of rejecting only very fine sediment. Wells (1957:774) stated that Paleozoic corals were probably confined to substrates "... clear or relatively free from rapid accumulation of sediment." Excessive sedimentation smothers polyps and kills all but the most active polyps. Philcox (1971) found that fluctuations in sedimentation rate are reflected in the overall corallum morphology and preserved growth rate.

MORPHOLOGY OF MISSISSIPPIAN SOLITARY
AND COLONIAL CORALS

External Morphology of Colonial Corals

The coralla of the tabulate and rugose (solitary and compound) corals of the Lodgepole Formation exhibit much variability in size and shape. Corallum is defined as the "... exoskeleton of a coral colony of solitary coral" (Moore, 1956:247). The term corallite is defined as the "... exoskeleton formed by an individual coral polyp" (Moore, 1956: 247). A compound rugose or tabulate coral may have hundreds of corallites within one corallum; a solitary rugose coral houses only one coral polyp within the corallum.

Type I corals are flat or platy and are asymmetrically developed in the plane of the corallum parallel to the substrate. Both *Lithostrotionella* and *Syringopora* exhibit this morphologic type. Lateral increase, or growth parallel to the sediment-water interface, has greatly exceeded vertical growth, which is growth perpendicular to the sediment-water interface. The average mean diameter/height ratio of *Lithostrotionella* is 3.6 (range 2.5-5.0), and that of *Syringopora* is 3.2 (range 2.7-3.5). The basal portions of the lithostrotionid coralla clearly show the preponderance of lateral growth. The corallites extend horizontally and radially outward from the base, and bend upward at the margins of the corallum. Figures 9 and 10 are examples of Type I corals.

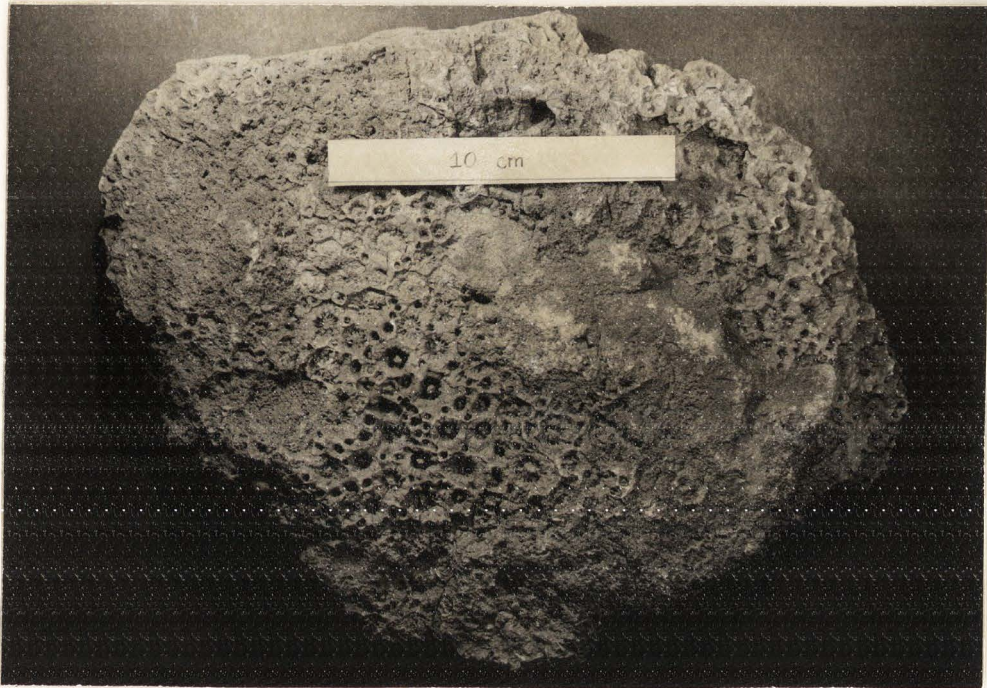


Figure 9. Top view of a Type I lithostrotionid coral (L-1-L).



Figure 10. View of the base of a Type I syringoporoid coral, showing lateral growth orientation of corallites away from the flat base (S-9-S).

The coralla of Type II corals are flat-based, lenticular in the plane perpendicular to the sediment-water interface, and they are symmetrically developed; that is, the corallites do not exhibit a preferred orientation.

Both *Lithostrotionella* and *Syringopora* exhibit Type II morphology. Mean diameter/height ratios of *Lithostrotionella* range from 3.2 to 5.5, with an average value of 4.1. For *Syringopora*, the mean diameter/height ratios range from 3.6 to 4.3, with an average value of 4.0. Growth, when observed in a cross-section of the corallum perpendicular to the sediment-water interface, is both vertical and lateral. The corallites grew directly upward from the base, rather than outward as in Type I. Although the lateral dimension of the corallum exceeds the vertical, this lenticularity of the corallum primarily reflects deceleration of vertical growth rather than an inhibition of vertical growth, as in Type I corals. Aside from the lensoidal appearance of these corals when viewed in transverse cross section (Figure 11), these corals are very similar to Type IV hemispherical forms. Figures 12 and 13 are examples of Type II corals.

Type III corals are bald, flat-based, and slightly lenticular. A bald area of a corallum is an area on the crown of the corallum, devoid of corallites. Both *Lithostrotionella* and *Syringopora* exhibit balding. The bald areas on *Lithostrotionella* and *Syringopora* are quite small, 5.5 and 2.5 cm in diameter respectively. The mean diameter/height ratios of Type III *Lithostrotionella* and *Syringopora* are 4.2 and 3.6 respectively. Corallites appear to be directed both vertically and

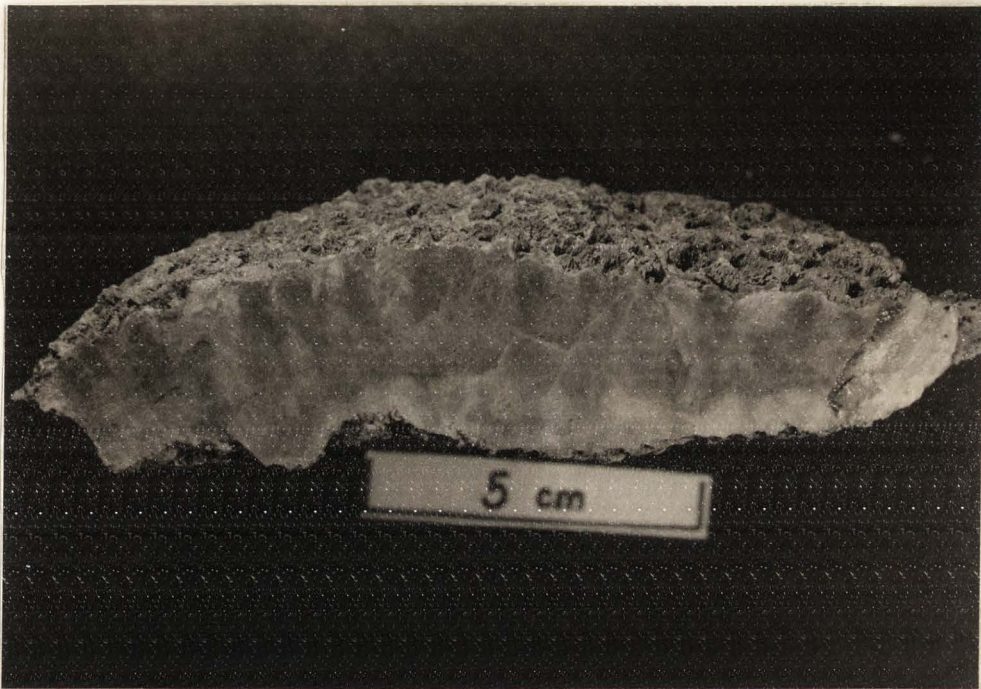


Figure 11. Cross-sectional view of a Type II lithostrotionid coral, showing vertical/radial orientation of corallites and flat base (L-24-S).



Figure 12. Top view of a Type II lithostrotionid coral (L-5-L).

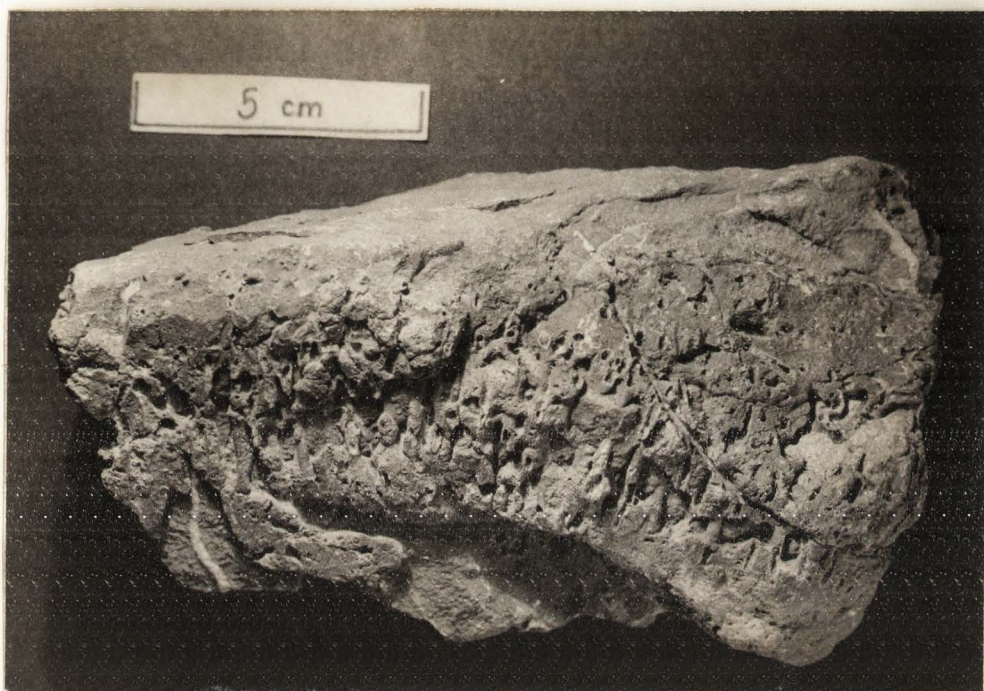


Figure 13. Side view of Type II syringoporoid coral (S-5-L).

marginally, as in Type II corals, with little or no preferred orientation. These corals are very similar to Type II corals, the only difference between the two types being the balding of Type III corals.

Figures 14 and 15 are examples of Type III corals.

Type IV corals are flat-based hemispheres. Vertical and lateral accretion rates were apparently comparable. Both *Lithostrotionella* and *Syringopora* exhibit this morphologic type. Philcox (1971) described this type of colony as radial. Mean diameter/height ratios of *Lithostrotionella* and *Syringopora* are 2.1 and 2.5 respectively, (range for each genus is 1.7-2.6 and 2.0-2.5, respectively). Corallites of Type IV corals occasionally show a preferred orientation. That is, the corallites are not evenly distributed in terms of density (number/unit area) over the corallum surface, but are more densely spaced on particular portions of the corallum. Figures 16 and 17 are examples of Type IV corals.

Type V corals have rounded to conical rather than flat bases. Vertical growth commonly exceeded lateral growth. *Syringopora* and *Lithostrotionella* Type V corals were found. In this respect, Type V corals are the opposite of Type I corals, in which lateral growth exceeded the vertical. The average mean diameter/height ratio for *Lithostrotionella* is 2.1, with a range of 1.3 to 2.6. The average mean diameter/height ratio and range for *Syringopora* 1.4 and 0.8 to 2.0 respectively. Several lithostrotionid fragments also show pronounced vertical growth. Figures 18 and 19 are examples of Type V corals.

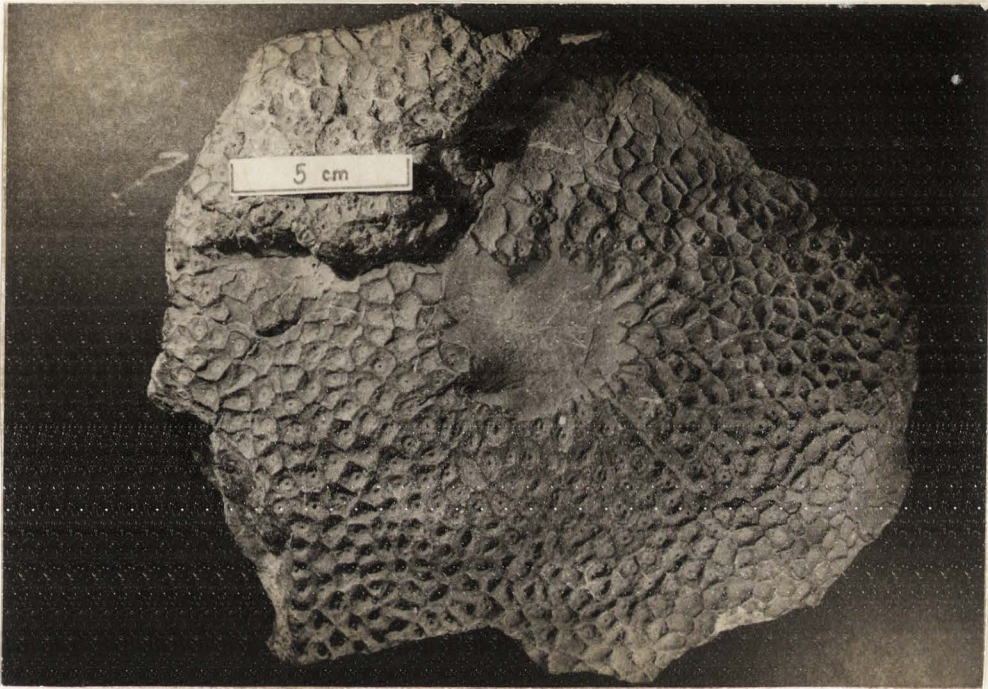


Figure 14. Top view of a Type III lithostrotionid coral, showing bald crown (L-8-L).



Figure 15. Top view of Type III syringoporoid coral, showing bald crown (S-7-L).

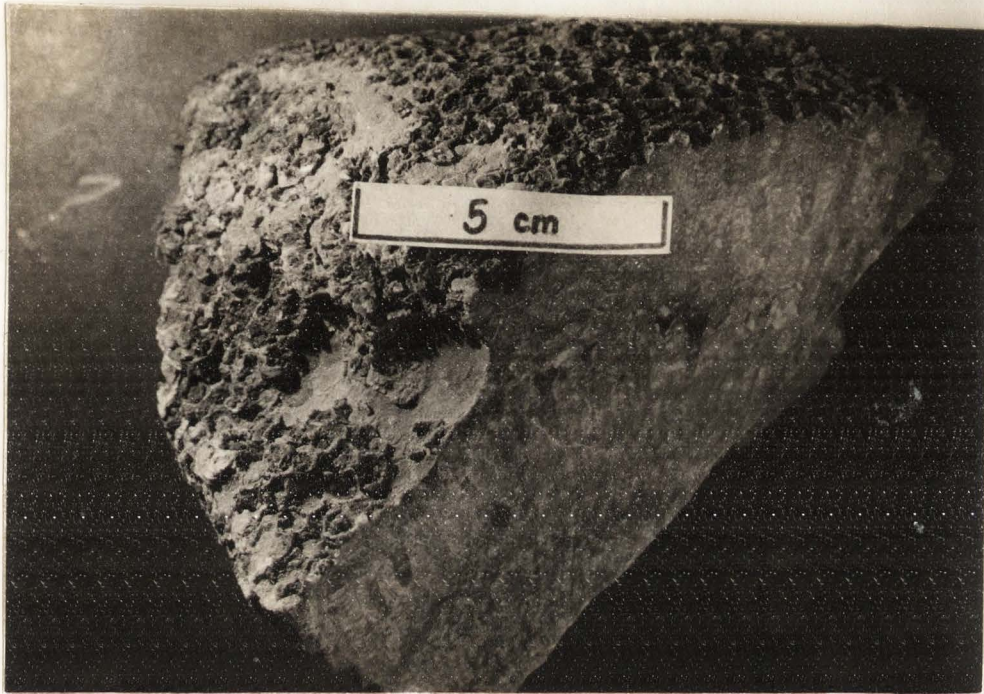


Figure 16. Oblique view of a sectioned Type IV lithostrotionid coral, showing radial orientation of corallites and hemispherical morphology (L-9-B).



Figure 17. Side view of Type IV syringoporid colony, showing hemispherical growth-form (S-8-S).

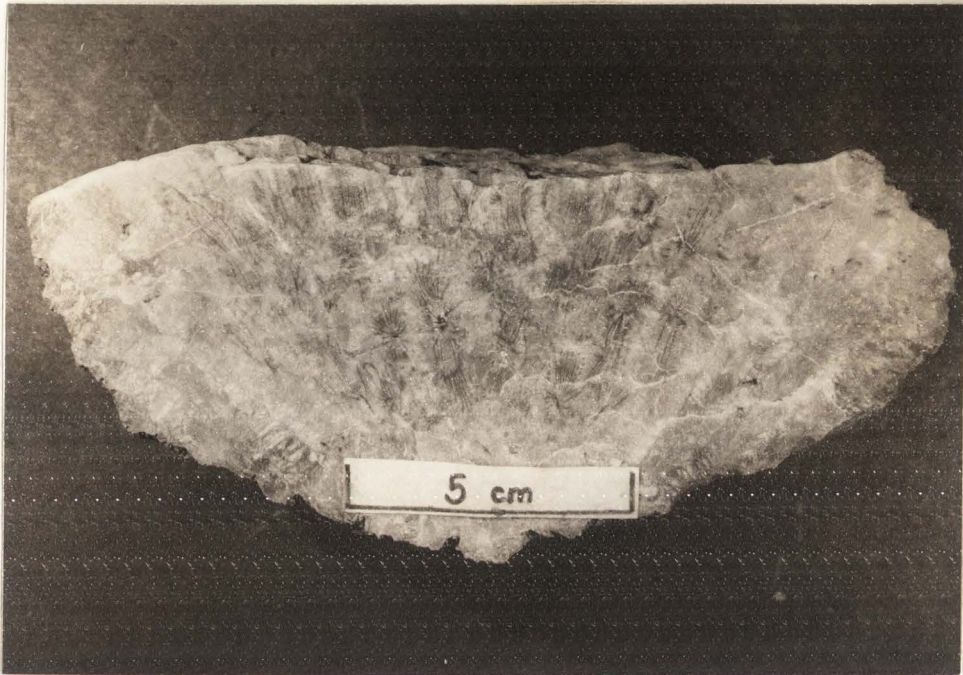


Figure 18. Cross-sectional view of a Type V lithostrotionid coral, showing vertical orientation of corallites and rounded conical base (L-12-L).



Figure 19. Side view of a Type V syringoporoid coral, showing vertical orientation of corallites and rounded conical base (S-10-S).

Type VI corals are composite corals, consisting of combinations of radial (hemispherical) forms and platy or sheet-forms. This morphological type is characterized by a change in the growth-form of the colony during its astogeny. For example, a coral which initially grew laterally, with minimal vertical increase, might exhibit pronounced vertical growth later in its development. New growth over a dead area of the coral surface, or resumption of growth after temporary stoppage would also result in the development of a composite coral. Complete specimens of composite corals are limited to *Lithostrotionella*.

Sample L-26 (Figure 20) is a small-based (4 cm diameter) coral; vertical growth at first exceeded lateral growth. During the astogeny of the coral, the corallites began to change direction from the vertical to a more radial (vertical with a lateral component) direction. At a height and diameter of about 5 cm and 8 cm, respectively, a non-growth surface is found. A non-growth surface is distinguished by a dark, sediment-filled band, usually 8-10 mm in thickness, which may be seen internally and/or externally. When viewed in longitudinal cross section (parallel to the direction of growth), the sediment-filled calices are clearly visible. Growth resumed, again strongly vertically oriented, on this surface, although it is obliquely overlapping the original corallum. One portion of the coral appears to have grown without interruption.

Sample L-20 (Figure 21) is a sheet-form lithostrotionid which initially grew asymmetrically in the plane of the corallum parallel to the sediment-water interface. Although the small original colony is a

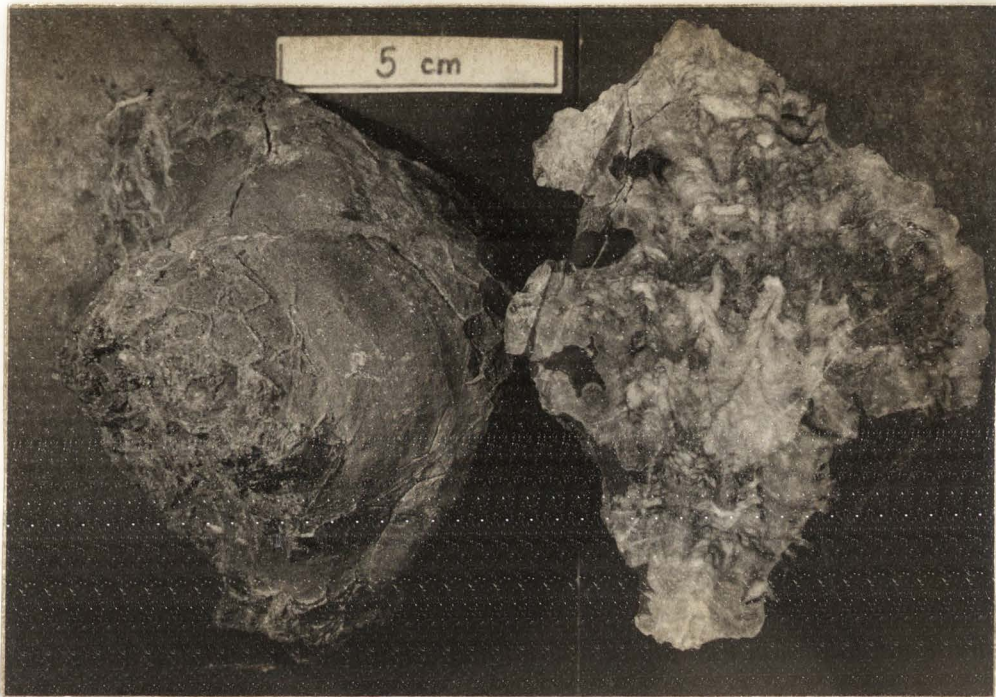


Figure 20. External (left) and internal views of a Type VI coral (L-26-L) showing interrupted growth. Corallite growth direction from bottom to top of illustration.

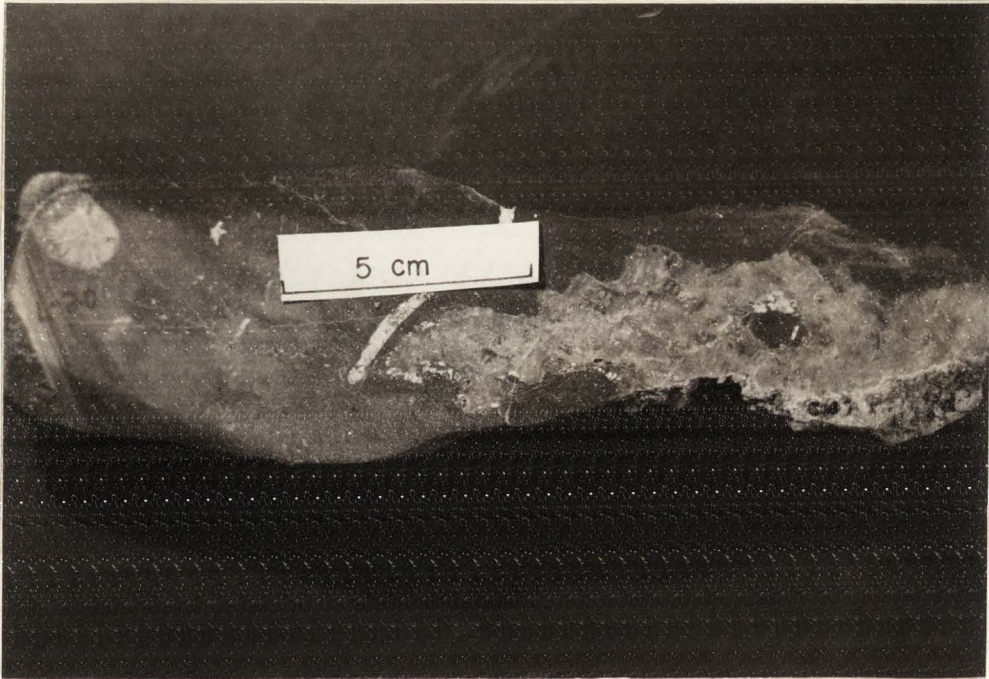


Figure 21. Cross-sectional view of a Type VI coral (L-20-B) showing irregular sheet-like growth-form.

flattened hemisphere (Type II), the corallites are directed horizontally and radially outward from the center of the base, as in Type I corals. The coral attained a diameter of approximately 7 cm. There are two small lateral satellite colonies which are connected to the original corallum by thin (2 cm diameter) "arms." These satellite colonies are small (4 cm diameter, about 2 cm height), irregular or lumpy flattened hemispheres. At a distance of about 3 cm from the original corallum, a small portion of a lithostrotionid is imbedded upside-down in the matrix. In cross-section (perpendicular to the sediment-water interface) an irregular sheetlike growth-form is evident.

Sample L-19-L (Figure 22) is a composite radial coral. At a height of about 10 cm a non-growth surface (diameter 15 cm) is clearly visible, externally and internally. A smaller (diameter 10 cm), obliquely-overlapping colony formed on top of the non-growth surface. The total height of the composite colony is 15 cm.

Sample L-21-L (Figure 23) is also a composite radial colony. It is similar to Sample L-19-L except that it is smaller (maximum diameter and height are 15 cm and 8 cm respectively), and the satellite colony is obliquely overlapping the original colony. The satellite colony attained a maximum diameter and height, respectively, of 9 cm and 5 cm. The original colony is a Type II coral.

Sample L-28-S (Figure 24) is a composite radial colony. It is similar to L-19-L and L-21-L, except that the dark, sediment-filled band which marks the non-growth surface is not as prominent. Several features (widened tabulae, abrupt change in direction of corallite growth, and in internal dark band which corresponds to an epithelial constriction)



Figure 22. Cross-sectional view of a Type VI coral (L-19-L), showing non-growth surface (dark band) and satellite colony.

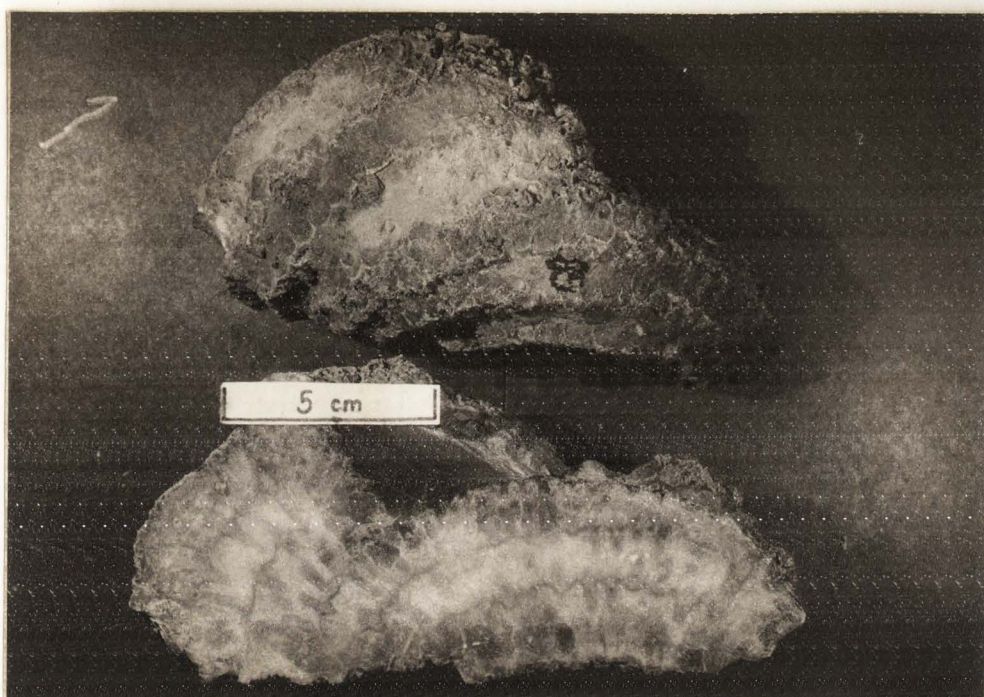


Figure 23. External (top) and internal views of Type VI coral (L-21-L) showing composite growth-form.



Figure 24. Cross-sectional view of a Type VI coral (L-28-S) showing locally widened tabulae within dark band.

suggest interrupted growth. One portion of the colony never increases in height beyond this band; however, two portions of the colony did survive to form another slightly overlapping radial colony.

Sample L-27-S (Figure 25) is an incomplete specimen of a colony in which growth was clearly interrupted. Although only a portion of the colony is visible, it appears that growth occurred in a vertical-radial fashion. A thick accumulation of sediment stopped growth on most of the colony, but growth continued in one area. Corallites of the second episode of growth grew over and partially encased the lens of sediment; the corallites of the second episode of growth diverge at an angle of 25° from the original, predominantly vertical direction of growth.

A variety of corallite packing arrangements are displayed by the colonial corals of the Lodgepole Formation. *Lithostrotionella* is a cerioid compound rugose coral. The term cerioid describes a type of compound corallum in which the "... walls of adjacent polygonal corallites are closely united" (Moore, 1956:238). *Lithostrotion* (Figure 26) is a fasciculate compound rugose coral. Fasciculate is defined as a "... corallum with cylindrical corallites which are somewhat separated from one another but may be joined by connecting tubules" (Moore, 1956:248). *Syringopora* is a fasciculate tabulate coral. The corallum is "... composed of cylindrical corallites connected by transverse stolons" (Moore, 1956:472). *Michelinia* (Figure 27) is a cerioid tabulate coral. "The corallum is hemispherical; corallites are large and thick-walled" (Moore, 1956:466). *Aulopora* and *Cladochonus* (Figure 28) are fasciculate tabulates. *Aulopora* is characterized by a "... report

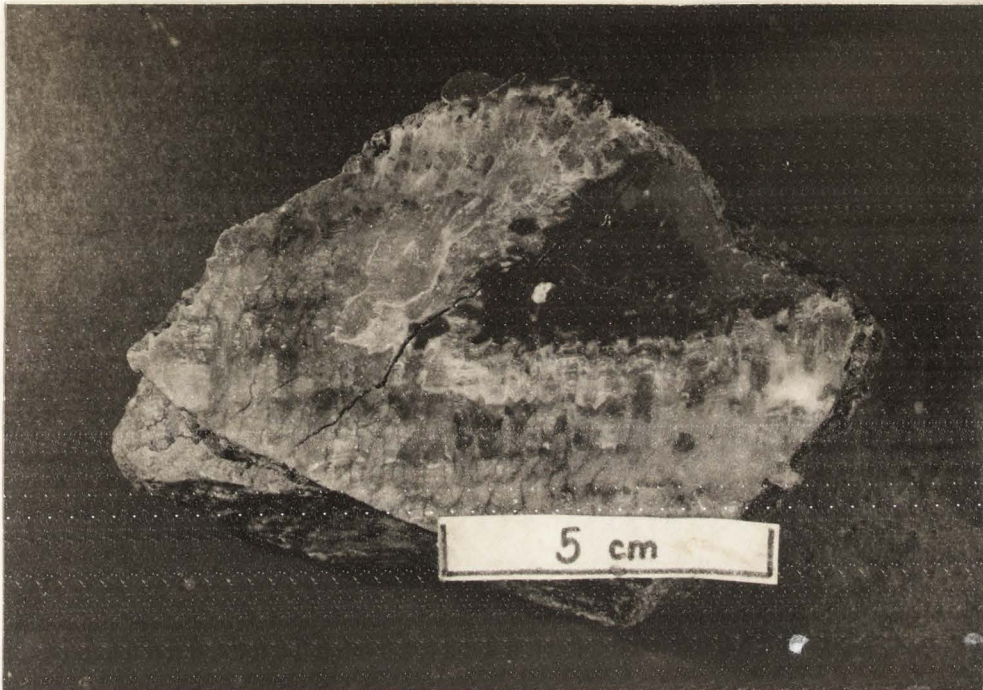


Figure 25. Cross-sectional view of a Type VI coral (L-27-S) showing pod of biomicrite within colony and corresponding change in growth direction.

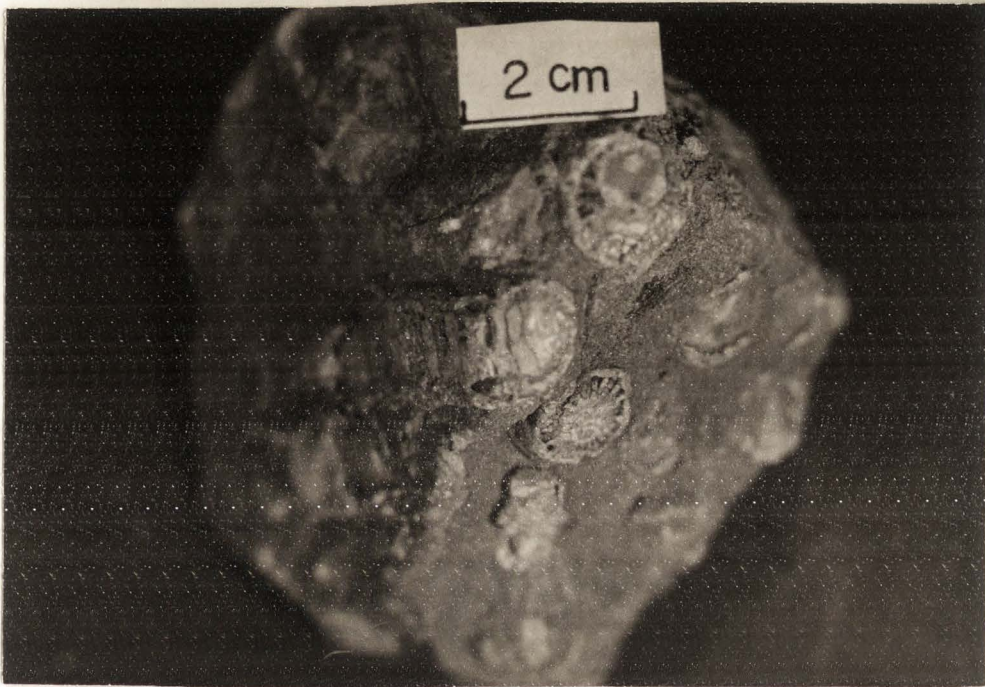


Figure 26. *Lithostrotion* showing fasciculate, circular calices (L-29-L).

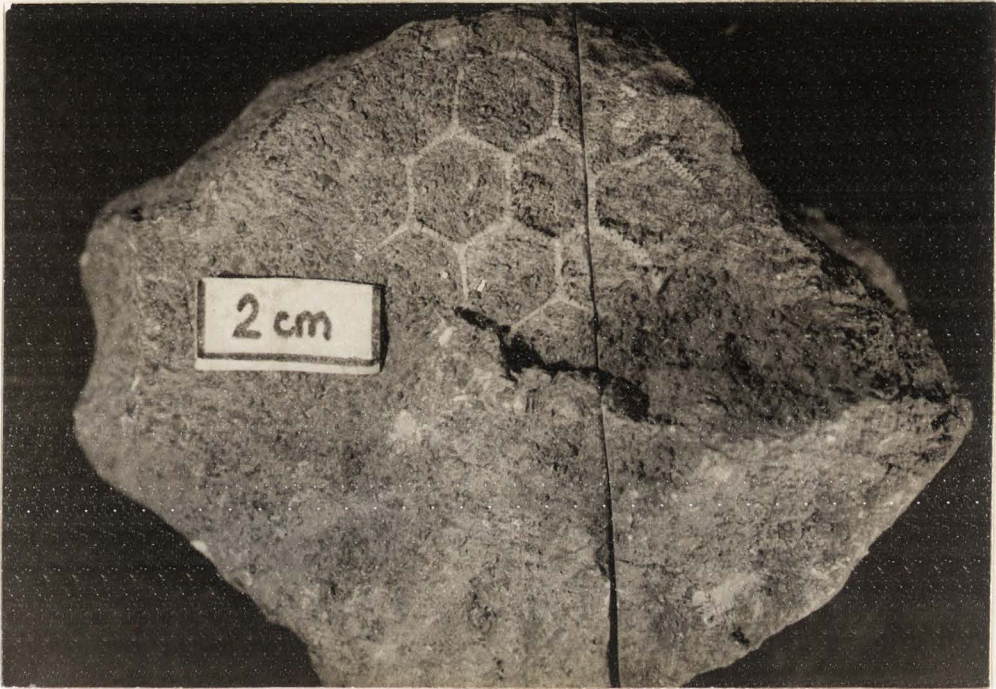


Figure 27. Top view of *Michelinia* showing cerioid polygonal corallites (M-1-L).

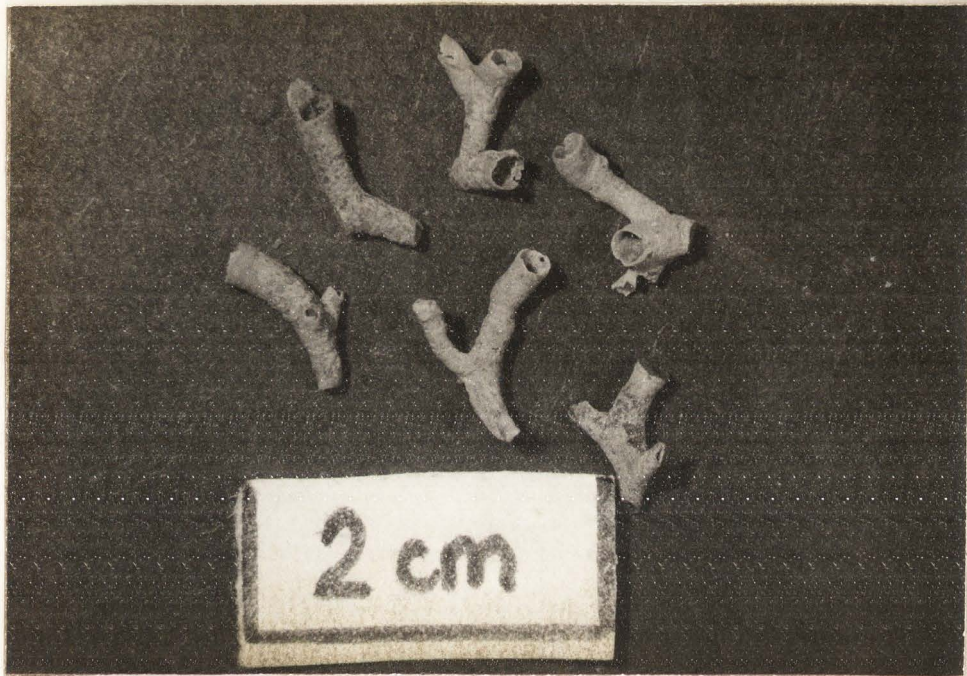


Figure 28. The tabulate corals *Aulopora* and *Cladochonus* (upper center, upper right, lower right) showing trumpet-shaped corallites (A-1-P).

network of trumpet-shaped corallites with circular, obliquely set calices" (Moore, 1946:472).

Two techniques were used to determine if corallite geometry varied across the corallum of *Lithostrotionella*. First, two mutually perpendicular transects were made across a corallum from margin to margin, perpendicular to the base. The maximum and minimum diameters of each corallite crossed by the transect were measured, in millimeters. Nine corals were examined. The ratios of maximum/minimum diameter thus obtained across the transect were then subjected to statistical analyses (t-test) which revealed that there is no statistically significant change in corallite geometry from the crown to the edge of the corallum. The second technique employed unit circles of varying radii (2, 4 or 8 cm), depending upon the size of the corallum. Again, the t-test showed no significant variation in corallite geometry from the crown to the margin.

Two mutually perpendicular transects were made across the coralla of three complete specimens of *Syringopora* to determine if corallites are evenly spaced over the corallum. Squares measuring 2 cm to a side were placed contiguously along the transects and the number of complete corallites located within each square was recorded. The t-test showed that there is no significant change in corallite density across the corallum.

Seventeen specimens of *Lithostrotionella* were examined to determine whether or not a relationship exists between the degree of budding and the overall gross morphology of the corallum (Table 1). Small corallites (those whose diameter is less than 50 percent that of mature

Table 1. Mean ratios of the number of buds to the number of mature corallites of Types I, II, III, IV and V corals

Colonial coral type and sample size		Ratio of number of intermural buds to mature corallites
Type I	n = 4	1.04
Type II	n = 4	.15
Type III	n = 2	.23
Type IV	n = 4	.19
Type V	n = 3	.16

Table 2. Mean corallite diameters of selected colonial corals

Sample number	Mean corallite diameter	s.d.	n	Morphologic type
L-1	1.04	.21	46	I
L-3	1.16	1.22	69	I
L-5	.68	.13	18	II
L-7	.77	.17	34	II
L-8	.64	.13	47	III
L-15	.60	.17	40	IV
L-21	.69	.15	66	IV

corallites) are interpreted as intermural buds. Ratios of the number of buds to large, mature corallites were determined. The t-test showed that Type I corals have significantly higher ratios of intermural buds to mature corallites than do Types II, III, IV and V corals.

Corallite diameters were measured on seven lithostrotionid coralla to determine whether or not a relationship exists between gross corallum morphology and corallite size. Mean corallite diameters were compared. The information is summarized in Table 2. Although limited by sample size, these data strongly suggest that mean corallite diameter of Type I (Figure 29) corals is significantly greater t-test than that of Types II, III and IV corals (Figure 30).

Almost always, the polygonal corallites of *Lithostrotionella* are in linear contact, forming a very thin (1-2 mm) wall. However, sample L-1-L, a platy (Type I) coral, was found to possess thickened corallite walls (Figure 9). The calicular platform of the coral is highly calcified (thickened). The net result of the thickening of corallite walls is to increase the distance between adjacent corallites. The walls of this particular coral are two to three times thicker than is "normal" for *Lithostrotionella*.

External Morphology of Solitary Corals

The coralla of Type 1 rugose corals are straight. This morphologic type is comparatively rare. Specimens of *Vesiculophyllum*, *Amygdalophyllum*, *Turbophyllum* and *Caninia* were found with straight (uncurved) coralla. Figure 31 is an example of a Type 1 coral.



Figure 29. Close-up view of a Type I lithostrotionid coral, showing extreme variability in corallite diameter; small corallites are intermural buds (L-1-L).

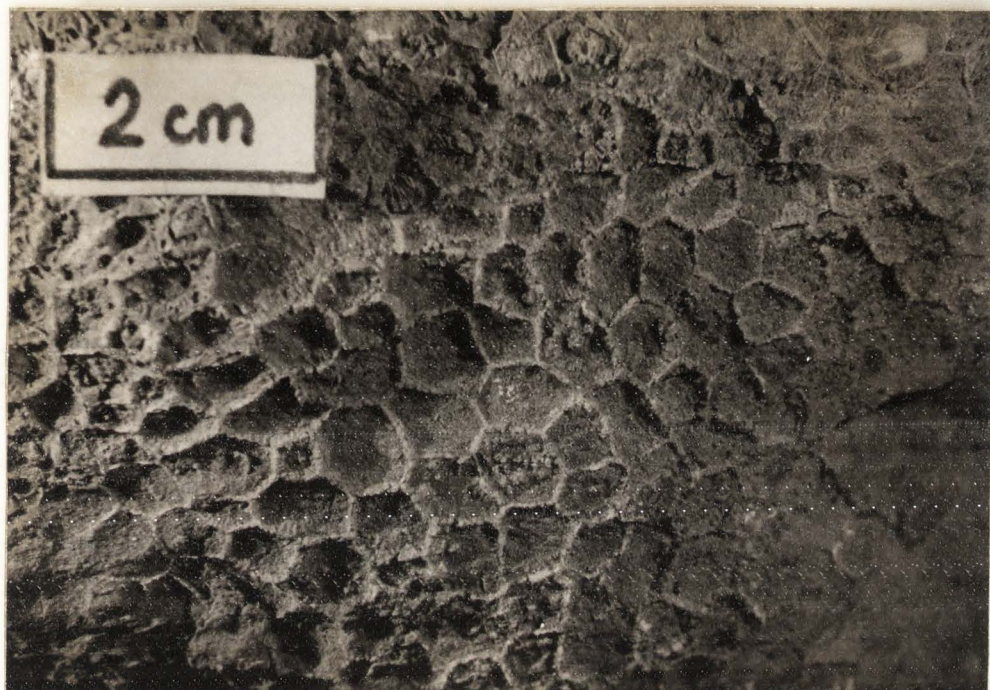


Figure 30. Close-up view of a Type IV coral, showing little variability in corallite diameter and few intermural buds (L-31-S).



Figure 31. Example of a Type 1 rugose coral, showing straight corallum of a mature specimen of *Vesiculophyllum* (R-1-S).

Type 2 rugose corals are geniculate; that is, the coralla are gently or sharply curved. Many degrees of geniculation were found, and each genus exhibited geniculation. Mean pre-geniculation length (the length of the section of the corallum between the apex and the first point of inflection of the outer edge of the corallum) of the large rugose corals *Caninia* and *Vesiculophyllum* is 1.5 cm (s.d. = 1.3; n = 45). Pre-geniculation length comprises, on the average, about 25 percent of the total adult corallum length. Consequently, it appears that these corals were most susceptible to toppling and subsequent re-directed growth in juvenile and young adult stages. Figures 32 and 33 are examples of Type 2 rugose corals.

Type 3 rugose corals have more than one geniculation per individual corallum. The geniculations (usually two, rarely three) may be in one plane or in more than one plane, in which case they are called vermiform (Hubbard, 1970). *Caninia*, *Vesiculophyllum*, and a small unidentified rugose coral were found with multiple geniculations. Figure 34 is an example of a Type 3 rugose coral. Slabs covered with numerous adult geniculate rugose corals were found (Figure 35).

Rejuvenescence characterizes Type 4 corals. Rejuvenescence is defined in the Treatise on Invertebrate Paleontology (1956:F245) in the following way:

A corallite, instead of continuing its growth with increasing or constant diameter, suddenly becomes much constricted, usually leaving a ledge of older calice round the constricted part. It then increases in diameter, and the process may be repeated. During rejuvenescence the corallite recapitulates earlier growth stages in a condensed form.

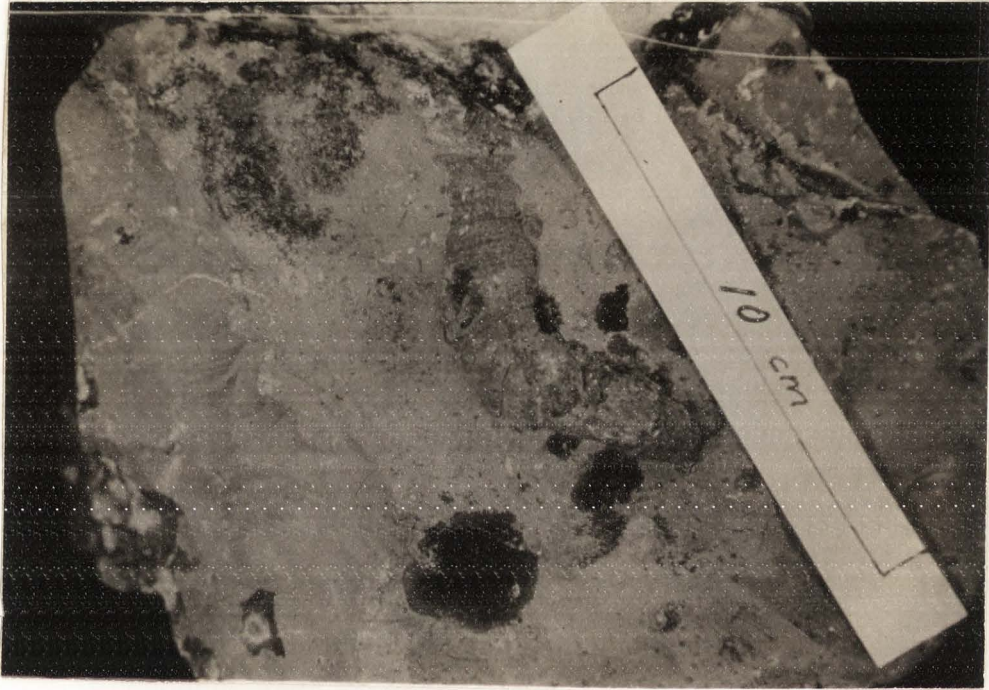


Figure 32. Sharply geniculate specimen of *Caninia* (R-2-L).



Figure 33. Typical Type 2 (geniculate) rugose corals of the genus *Vesiculophyllum* (R-3-S).

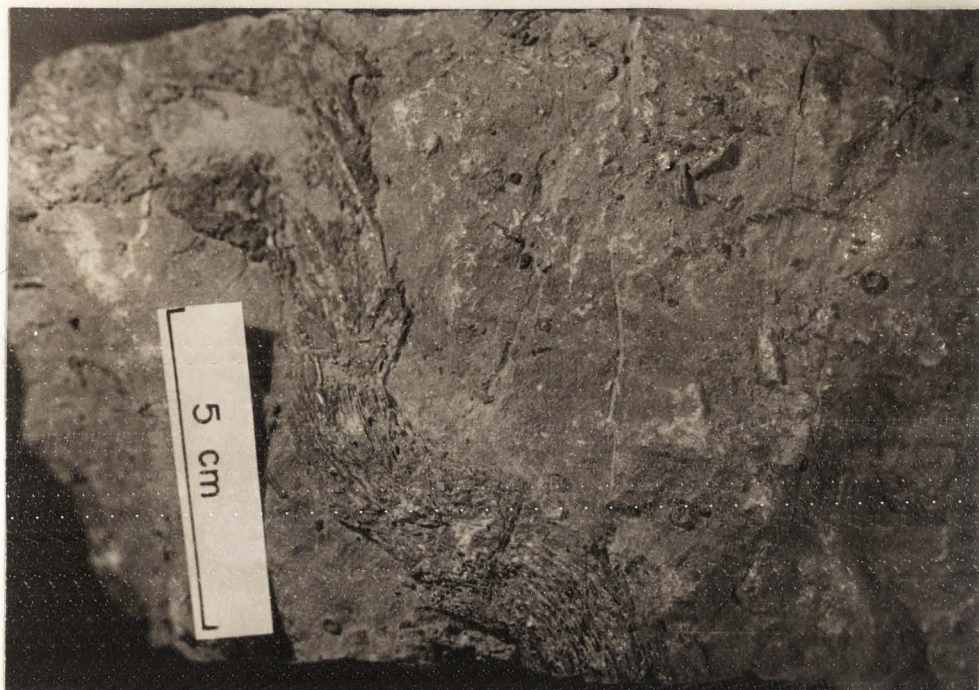


Figure 34. Type 3 (multiple geniculate) specimen of *Vesiculophyllum* (R-4-L).

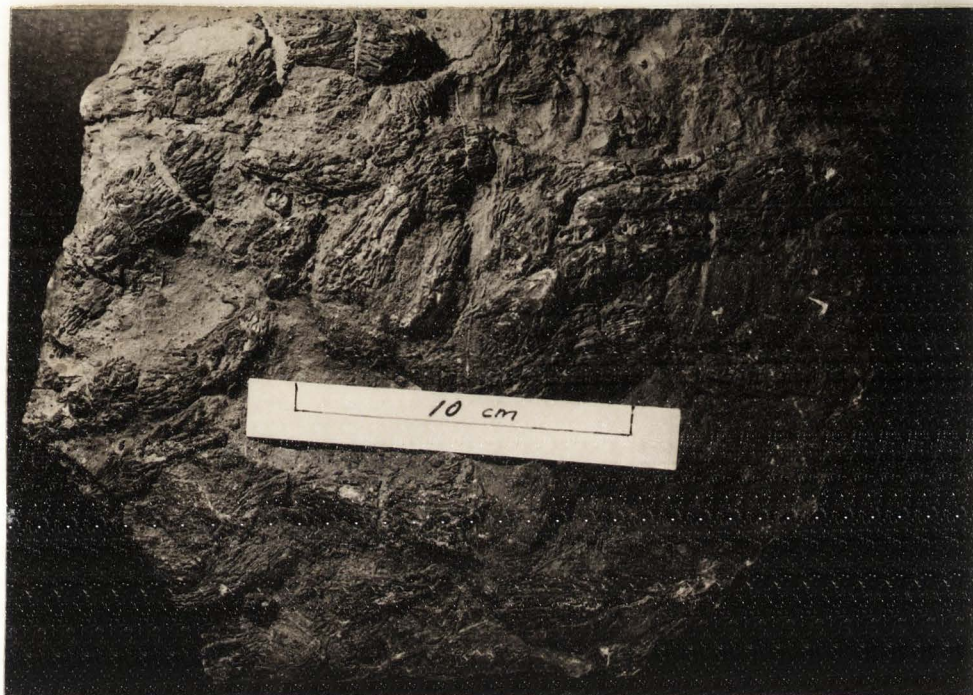


Figure 35. Bedding surface strewn with several adult, prone, geniculate corals (*Vesiculophyllum*) (R-5-B).

Rejuvenescence was observed in *Caninia* and *Vesiculophyllum*.

Figure 36 shows examples of Type 4 corals.

The various types of protocoralla of rugose corals are referred to as Type 5 corals. Several different features can be seen on the protocoralla (Figures 37 and 38). Talons, or radiciform processes, are common. A talon is defined in the Treatise on Invertebrate Paleontology (Moore, 1956:250-251) as a "buttress produced by outgrowth of corallite wall, served as an aid in fixation." Talons were found either at or within 2-3 mm of the apex. Without exception a pair of talons was found; single talons were not found. Some of the protocoralla had a flattened area at the point of the apex. This flat area is smooth, and often at an angle to the corallum; that is, it is not oriented perpendicular to the vertical plane of the corallum. These flat areas are interpreted as basal attachment scars. Smooth scars located on the sides of the epithecae are interpreted to represent lateral attachment points. A smooth, shallow groove may be seen on some of the protocoralla. Usually only 3-4 mm in length, the groove extended from the apex for, or through, a few millimeters up the epitheca. One specimen was found with a shallow, curved groove which extends from the apex of the coral through 3mm up the epitheca, at which point a talon extends outward from the epitheca on each side of the groove. Several of the corals have a curved, shallow groove which appears to be oriented conspirally; the groove can be traced through an arc of approximately 240° of the coral diameter. The width of the groove varies from about 1.5 to 2.5 mm. A few of the corals are deformed in such a way as to suggest that they may



Figure 36. Type 4 rugose corals, showing prominent constrictions of the epithecae (R-6-S, R-7-S, R-8-S, R-9-L).



Figure 37. Protocoralla of *Zaphrentoides* showing growth lines holdfasts, groove and v-shaped calice (R-10-L).

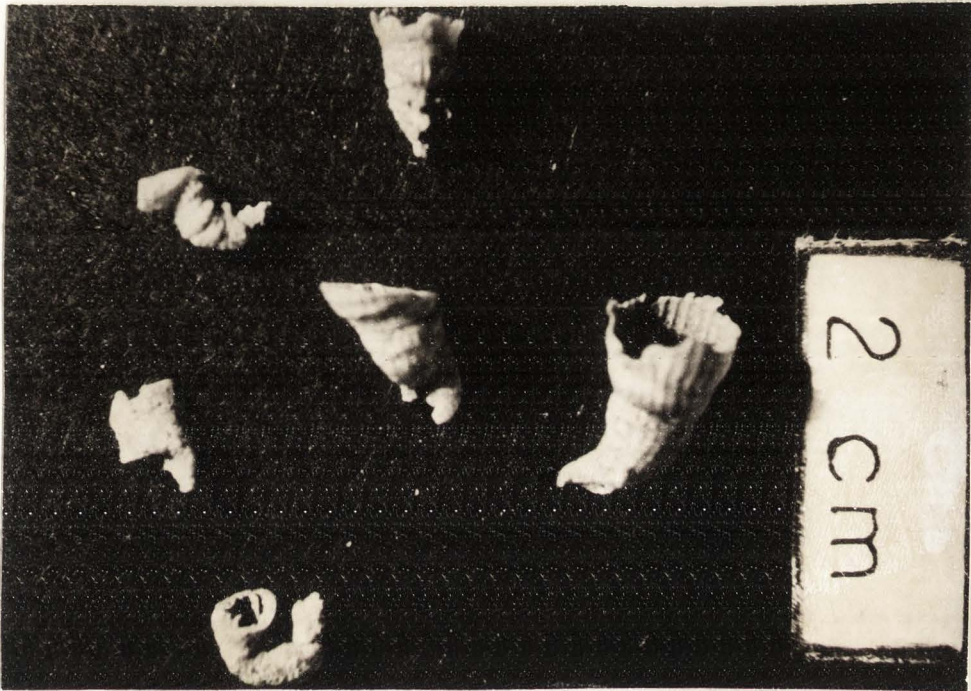


Figure 38. Protocoralla of solitary rugose corals showing holdfasts, attachment scars, and extreme phenotypic variability (R-11-L).

have been coiled around a linear object. The morphology of the coral, in these cases, apparently was determined by the size and shape of the object to which it had attached. One specimen exhibited faint ornamentation consisting of thin, parallel indentations along the length of the inner groove surface and aligned perpendicular to the groove axis. Gently to sharply geniculate protocoralla were found. A fairly persistent feature of the protocoralla is flattening and broadening of the corallum along the convex side of the curvature (Figure 39).

Internal Morphology of Colonial Corals

The calice of a coral is defined as the "... oral surface of corallite," or the "... distal surface of a corallite ... a mold of the base of the polyp" (Moore, 1956:239, 246). The calices of *Lithostrotionella* are hexagonal in cross-sectional outline and beaker-shaped in longitudinal profile. They taper from their maximum diameter at the outermost edge to a minimum diameter at the floor of the calice. The calicular platform (the gently sloping outer or upper part of the calical floor), comprises, on the average, 57 percent (s.d. = .09, n = 20) of the total diameter of the calice. The calicular pit (the central depressed part of the calice) is modified by a type of axial structure called a columella. A columella is "... formed by the vertical prolongation of the axial end of the counter septum" (Moore, 1956:242). The columella is a solid, rod-like structure; in *Lithostrotionella*, it extends from the floor of the calice to about halfway up the calicular pit. The conical tabular floors are upturned at the margins. The shape of the calice is shown in Table 3.

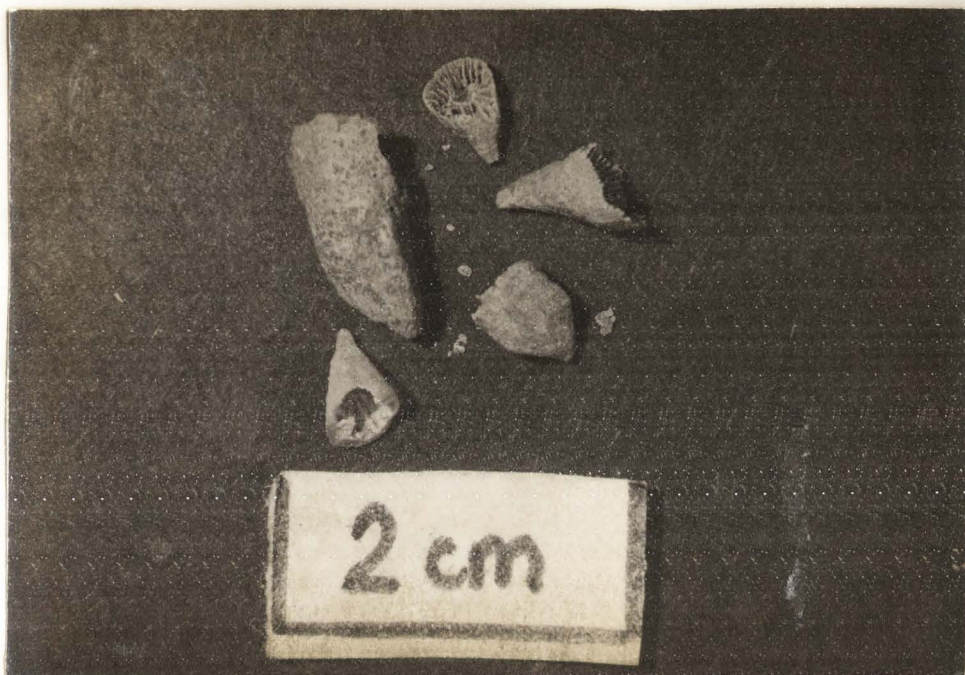


Figure 39. Protocoralla of rugose corals (Type 5), showing flattening and broadening of the corallum along the convex side of the curvature (R-12-L).

Table 3. Calical relief, calical shape, septal density and septal lengths of the fossil corals

Coral	Calical relief	Calical shape	Septal density	Septal length
<i>Lithostrotionella</i>	1.89	W	37.3	very long
<i>Lithostrotion</i>	2.00	W	35.6	very long
<i>Michelinia</i>	5.5	U	ridges	very short
<i>Syringopora</i>	1.0	U	ridges	very short
<i>Aulopora</i> and <i>Cladochonus</i>	1.0	U	ridges	very short
<i>Amygdalophyllum</i>	2.3	W	22.0	very long
<i>Turbophyllum</i>	2.3	W	20.6	long
<i>Vesiculophyllum</i>	1.9	V	11.4	intermediate
<i>Caninia</i>	2.4	U	11.6	short
<i>Rylstonia</i>	2.0	W	27.9	long
<i>Zaphrentoides</i>	1.5	V	35.2	long

Depth of the calice from the highest point (outermost edge of the calicular platform) to the lowest point (area of the calicular pit surrounding the columella) was initially calculated and then compared with corallite diameter. For *Lithostrotionella*, maximum to minimum diameter ratios were averaged for each corallite measured. The ratio of mean corallite diameter/depth of the calice will henceforth be referred to as calical relief is 1.89 (s.d. = .71, n = 20).

The calice of *Lithostrotion* (Figure 26) is circular in transverse cross-section. Precise measurements were difficult to obtain from the available samples. The tabulae are flat, and there is a weak axial structure. Depth of the calice is approximately .06 cm; calical relief is approximately 2.0.

The cerioid calices of *Michelinia* (Figure 27) are large (average diameter is about 1 cm) and hexagonal in outline. Calices are flat-floored. Numerous incomplete tabulae form the floor of the calice (Moore, 1956:466). The corallites have "irregularly distributed tunnel-like mural pores and septal spines (Moore, 1956:466). Mural pores are small holes found in the walls between adjacent corallites. The calice is very shallow, with a depth of about 0.2-0.3 cm. Calical relief is approximately 5.5.

The calices of *Syringopora* are cylindrical. The calice is flat-floored and is lined with horizontal tabulae which are "closely set, deeply depressed axially" (Moore, 1956:F472). Calical relief is difficult to determine because of infilling

of the calices by sediment and silicification of many specimens. However, those specimens which appear to be unaltered yield values of calical relief of about 1.0 which suggests that the calices are approximately as deep (0.4 cm) as they are wide. The circular calices of *Syringopora* may be seen in Figure 13.

The trumpet-shaped calices of *Aulopora* are small (diameters range from 1.5-4.0 mm) and cylindrical in transverse cross-section. Tabulae are either absent or not preserved. The calices appear to be quite deep relative to diameter. However, it is impossible to determine at what point within the corallite the polyp lives. *Cladochonus* is morphologically very similar to *Aulopora* (Figure 29).

Septal density is defined as the number of septa per corallite per mean diameter. The number of septa is size dependent to a certain extent; that is, young corals will have fewer septa than mature corals. The large ranges in septal densities are interpreted to be a result of the age/size dependency.

Septal densities of corallites of *Lithostrotionella* range from 32.0 to 80.0 cm^{-1} with a mean septal density of 37.3 cm^{-1} . The septa of *Lithostrotionella* are very long. They extend from the outermost edge of the calicular platform to the tip of the columella. A corallite with a calical diameter of 1.0 cm may have a total septal length of about 1.3 cm. Septal densities in *Lithostrotion* range from 19.0 to 50.0 cm^{-1} with a mean value of 35.6 cm^{-1} . The samples of *Lithostrotion* are poorly preserved; however, the septa appear to extend to the columella as in *Lithostrotionella*. The four tabulate corals,

Michelinia, *Aulopora*, *Cladochonus* and *Syringopora*, do not have actual septa, although faint septal ridges occasionally may be preserved. In tabulate corals, these ridges often number twelve (Moore, 1956). The septal spines of *Michelinia* are oriented parallel to the direction of growth, and they are very short "... extending but a little toward the axis from the periphery" (Moore, 1956:F446). The septal spines of these three tabulates are very short, barely extending inward toward the axis from the epitheca.

Tabulae spacing in *Lithostrotionella* ranges from .06 to .08 mm (s.d. = .03-.04). Alternating light and dark growth bands can be seen in *Lithostrotionella* when the corallum is sectioned parallel to the direction of growth (Figure 40). The mean width of light bands is 0.92 cm and of dark bands is 0.69 cm. In the one sectioned specimen eight pairs of bands are visible. A pair consists of one light plus one dark band. Cumulative thickness of light bands is 7.4 cm; cumulative thickness of dark bands equals 5.5 cm.

Internal Morphology of Solitary Corals

The calice of *Zaphrentoides* (Figure 38) is circular in cross-sectional outline. A deep cardinal fossula extends from the periphery of the corallum inward to about five-eighths of the diameter of the calice. The calice is essentially v-shaped in longitudinal section because of the high numbers of long septa. The tabulae are "... incomplete, conical, with highest point at inner edge of the fossula"



Figure 40. Longitudinally-sectioned view of *Lithostrotionella*, showing alternately light and dark growth bands (L-23-L).

(Treatise on Invertebrate Paleontology, 1956:F267). Mean calical relief is 1.52 (s.d. = .07). The actual mean depth of the calice is .9 cm.

The calice of *Rylstonia* (Figure 41) is circular in cross-sectional outline. In longitudinal section, an axial structure is evident. Tabulae are arched and incomplete (Treatise on Invertebrate Paleontology, 1956:F296). The pronounced axial structure and moderately high septal densities modify the calical shape; the calice is essentially w-shaped in longitudinal section. Calical relief averages 2.0; mean calical depth is 1.2 cm. The calice of *Amygdalophyllum* (Figure 42) is circular in transverse section. The coral is characterized by a large columella which extends above the floor of the calice. The columella and numerous septa together combine to yield a calice which is w-shaped in longitudinal section. Calical relief averages 2.3 cm; actual calical depth averages 1.2 cm.

The calice of *Turbophyllum* (Figure 43) is modified by tent-shaped tabulae and numerous septa in a manner similar to *Amygdalophyllum*. Calical relief was measured in only one specimen, because of the small number of samples and lack of preservation of epithecal walls above the calical floor; the value of calical relief is 2.3. Actual calical depth is 1.2 cm. The calice of *Vesiculophyllum* (Figure 44) is v-shaped in longitudinal section. Tabulae are rarely seen for two reasons: they are incomplete and they are masked by the high numbers of septa. Calical relief averaged 1.9, with a mean calical depth of 2.0 cm.

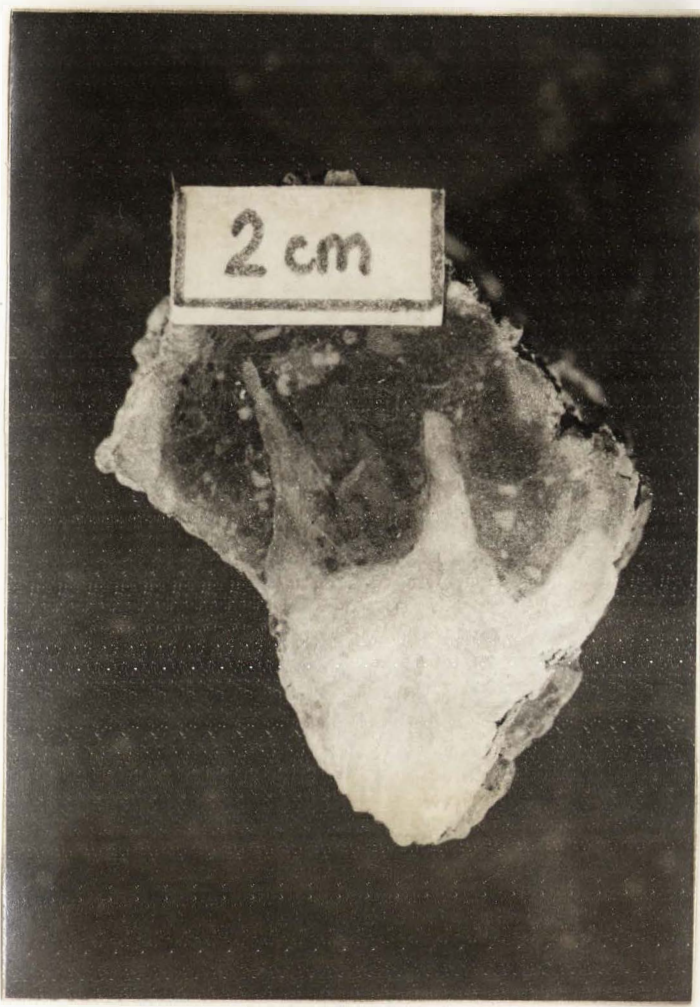


Figure 41. Longitudinally sectioned view of *Rylstonia* (R-13-L).



Figure 42. Weathered specimens of *Amygdalophyllum*, showing long major septae and axial structure (R-14-S).

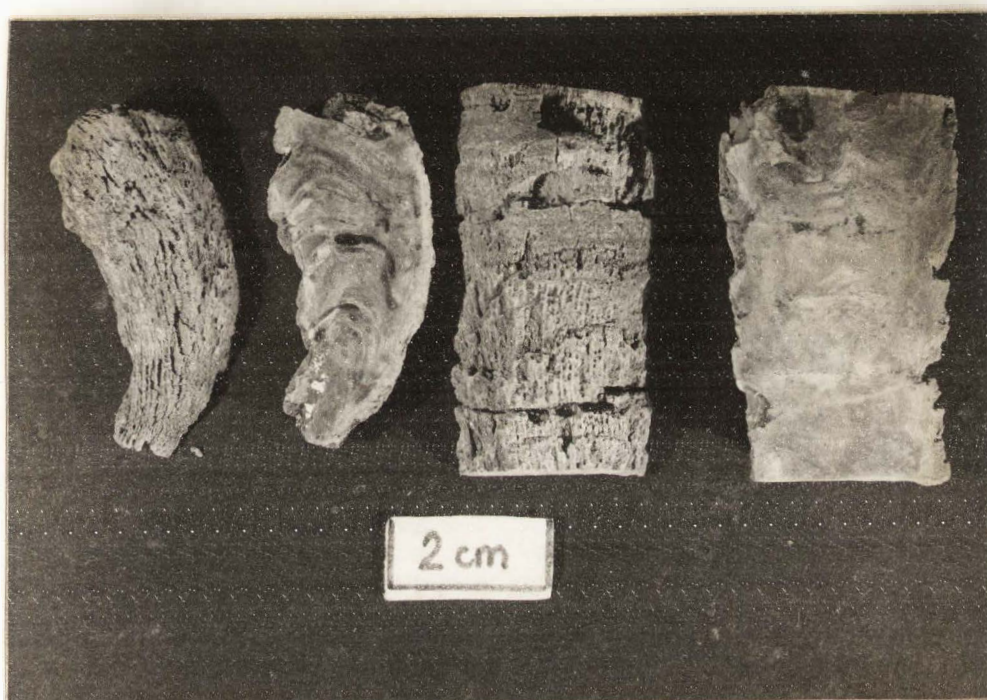


Figure 43. Internal and external longitudinal views of *Turbophyllum*, showing axially-tented tabulae (R-15-S).



Figure 44. Internal and external longitudinal views of *Vesiculophyllum*, showing V-shaped calice (R-16-L).

Caninia (Figure 45) has a "... broad, flat-floored calice" (Hubbard and Pocock, 1972:622). Dixon (1970:55) described it as a "... deep, beaker-shaped calice." The septa do not extend inward to the apex of the corallum. The tabulae (flat, with down-turned edges) thus form the floor of the calice. Calical relief averages 2.4, with a mean calical depth of 1.3 cm. *Caninia*, like *Vesiculophyllum*, has relatively few septa. Septal densities range from 11.1 to 12.2 cm⁻¹. Adult caninoids have amplexoid, slightly dilated septa (Moore, 1956:F292). The beaker-shaped calice of *Caninia* is a consequence of the absence of septa in the tabularium. The septa extend inward from the epitheca slightly less than halfway to the axis of the corallum. Average spacing of tabulae in one specimen of *Caninia* is .82 mm (s.d. = .04).

Most of the major septa of *Zaphrentoides* reach the axis of the corallum. Short minor septa occupy the spaces between major septa (Easton, 1975). Septal densities of *Zaphrentoides* range from 30.0 to 43.3 cm⁻¹ with a mean value of 35.2 cm⁻¹.

Most of the major septa of *Rylstonia* do not extend to the axis of the corallum. The axial structure appears to be discontinuous from the septa. The septa appear to extend inward toward the axis to about two-thirds of the radius. Septal densities of *Rylstonia* range from 23.6 to 33.6 cm⁻¹ with a mean value of 27.9 cm⁻¹. *Amygdalophyllum* yielded a septal density value of 22.0 cm⁻¹. Parks (1951) reported septal densities of 20.8 to 23.3 cm⁻¹ for *Ekrasophyllum* [actually *Amygdalophyllum*, according to Moore (1956:290)].



Figure 45. Longitudinally sectioned view of *Caninia*, showing beaker-shaped calice (R-17-L).

The long major septa of *Amygdalophyllum* extend to the axis of the corallum, where they are welded together in an axial structure. Septal density of *Turbophyllum* is approximately 20 cm^{-1} . Parks (1951) reported a range of septal density of 21 to 26. The long major septa of *Turbophyllum* extend from the epitheca to the axis of the corallum, where they meet the sharply tented axial tabellae (Moore, 1956:290). *Turbophyllum* also has long minor septa. The septa of *Vesiculophyllum* are "... typically ... amplexoid in the wide tabularium" (Moore, 1956: F247). Amplexoid septa are axially shortened and longitudinally discontinuous (Moore et al., 1952:139). The septa do not extend to the axis of the corallum. They extend inward toward the axis from the epitheca to a distance averaging about 40% of the total corallum diameter. Minor septa are very short. *Vesiculophyllum* displayed a mean septal density of 11.4 cm^{-1} .

ENVIRONMENTAL INTERPRETATION OF MORPHOLOGY

External Variability of Colonial Corals

Type I corals (Figures 9 and 10) are platy, that is, there is very little variation in thickness (or height) of the corallum in the plane perpendicular to the substrate. Type I corals also exhibit some asymmetry in development; this feature suggests that the corallites had a preferred orientation. Type I corals are interpreted in this study to have been adapted to life in relatively deep, quiet waters.

The flattened coralla of Type I corals may be interpreted in various ways. Philcox (1971) studied sheet-form favositids in which vertical growth had been inhibited (Figure 46). He suggested that these corals inhabited deeper waters than did the "normal" hemispherical corals. Sedimentation rates must have been very low, according to Philcox (1971), in order for this type of coral to survive. His assumption is that a flat coral is relatively easily smothered and killed by an influx of sediment. Conversely, Hubbard (1974) concluded that a low, encrusting asymmetric growth-form resulted from life in areas of intense current or wave action. However, she also mentioned a flattened fasciculate form which is characteristically found in wackestone lithologies. Wackestones usually are interpreted as normal lagoonal or offshore, shelf deposits formed in moderately quiet waters. Graus and Macintyre (1975:1090) reported that modern unbranched reef corals

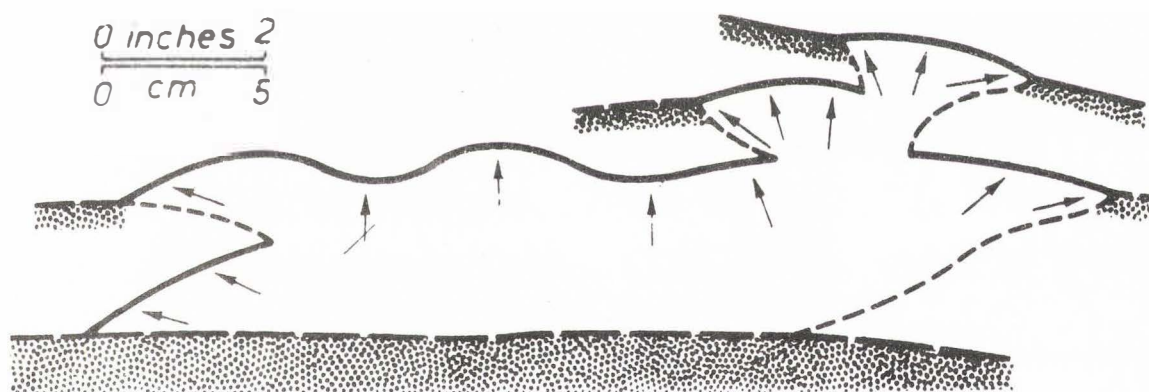
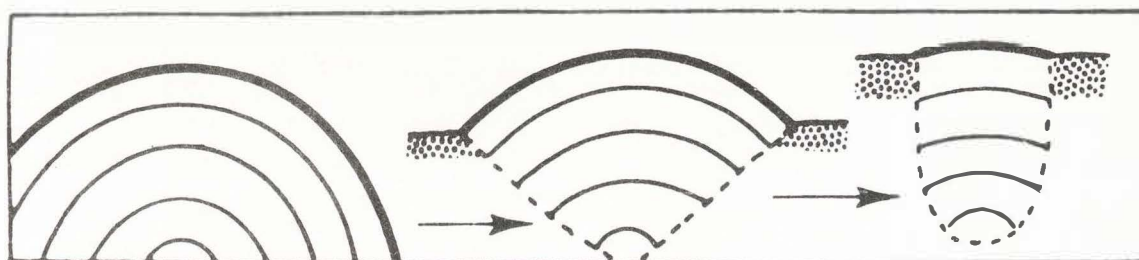


Figure 46. Upper diagram summarizes the effect of increasing sedimentation rate on growth-form of radial favositids. Lower diagram is a schematic representation of a sheet-form colony which was forced by accumulating sediment to migrate back and forth during growth (from Philcox, 1971:342 and 344, respectively).

... exhibit the following growth trends with increasing water depth: (1) a gradient in corallum morphology from hemispherical to columnar to platy, and (2) a decrease in the mean skeletal accretion rate.

They stated that the predominant factor controlling these trends is the "... systematically varying underwater light field." That is, skeletal growth rate decreases as the amount of available light decreases. Goreau (1959) found that calcification rates in modern scleractinian corals were significantly reduced by the exclusion of light. Goreau and Goreau (1959:250) studied growth rates of scleractinians in the open reef, as opposed to in the laboratory. They found that "... light intensity had a profound influence on the growth rate under the conditions of our experiments. All corals tested deposited calcium fastest in sunlight, less during cloudy weather and least in darkness." Zooxanthellae are believed to be in part responsible for the decreased calcification rate in darkness (Goreau, 1959). Goreau (1963) reported that flat, mushroom-shaped growth forms of modern hermatypic corals are an adaptation to deeper water conditions (decreased light intensity). However, Goreau (1959, 1963) cited the effects of zooxanthellae on calcification as a major determining factor in growth-form. Because we do not know whether or not Paleozoic corals contained zooxanthellae within their endodermal tissues, analogies based on decreased illumination must be extrapolated cautiously.

Anstey and Delmont (1972) stated that the gross morphology of bryozoan colonies may be in part under nutritional control. According to their model, a flat colony is an adaptation to deep, quiet waters

where food for filter feeders is less abundant than in shallow waters. In quiet water, a smaller volume of water passes over each individual per unit time than in agitated waters. If the individual zooids are more widely spaced, as they are on a flat colony as opposed to a hemispherical colony, there is a greater volume of water available for each individual to filter. Although the more widely spaced individuals of a flat colony filter a greater volume of water than those of a hemispherical colony, the former packing arrangement requires the deposition of additional calcium carbonate between zooecia. Thickened corallite walls were found on one Type I coral. This will be discussed under the section entitled "corallite variability."

Perkins (1963) suggested that broad, flat-based colonies may have been an adaptation to soft substrates; that is, the increased surface area of the bottom of the colony would prevent sinking. The corallites of Type I corals grew initially in a horizontal manner, directed outward from the base of the colony; however, at the margins of the colony these corallites bent upward, away from the sediment-water interface. Philcox (1971:342) noted this feature in favositids and concluded that the corallite shape was "... probably controlled by some factor in the growth environment" If indeed illumination is a controlling factor as Goreau (1963) and Graus and Macintyre (1975) supposed, the upward bending of the corallites may be an adaptation to deeper water conditions, where the incidence of light penetration is much reduced. That is, maximum incidence of light would be achieved if the corallites faced upward after or during their initial horizontal expansion.

The asymmetry of development which is found in some of the Type I corals may be interpreted in several ways. Philcox (1971) suggested that asymmetrical growth, which he found to be very common, may be the result of growth on sloping substrates. Broadhurst (1966) interpreted asymmetry in stromatoporooids as current-induced (positive rheotropic response). Positive rheotropism seems a plausible explanation for the asymmetry of the Type I corals. If indeed they represent deeper water forms, food may have been sufficiently scarce to encourage growth toward food-bearing currents. Another possible explanation for the asymmetrical development is that the corals grew toward the direction from which solar incidence was greatest (positive phototropism); this interpretation requires the assumption that Paleozoic corals were in some way linked to light for survival (e.g., that they incorporated algae within their tissues).

On the basis of corallum morphology, Type I corals are interpreted to have inhabited offshore, subtidal environments perhaps below effective wave base. This interpretation is further supported by corallite size, packing and variability, which will be discussed in a later section.

The flat-based, lenticular coralla of Type II corals are interpreted to have inhabited shallow waters. The factor responsible for the inhibition of vertical growth may have been excessive turbulence and/or the tidal effects associated with very shallow water. These corals are, without exception, flat-based. Philcox (1971) reported that flat-based colonial corals form when sedimentation is slow; unrestricted radial

growth is necessary to establish a flat base (Figure 47). These coralla differ from Type I platy corals in two ways: they are thickest directly above the central base of the colony, and taper to their thinnest points at the margins of the colony. Type I corals are of uniform thickness regardless of the portion of the corallum that is measured. The second difference is in the orientation and growth direction of the corallites. Growth in Type II corals is radial; that is, the corallites are "... nearly straight and radiate outwards away from the original growth center" (Philcox, 1972:339). A view of the base of a Type II coral clearly shows that corallites are directed obliquely, rather than horizontally as in Type I corals.

Hubbard and Pocock (1972) noted that flattened cerioid lithostrotonids are characteristically found in grainstones. Grainstones contain little or no micrite and are entirely grain-supported (Dunham, 1963). The absence of micrite suggests a moderately high-energy environment. Hubbard and Pocock (1972) also suggested that corals with low cross-sectional profiles are typical of areas of intense wave or current action. Perkins (1963:1340) stated that "... somewhat flattened hemispherical forms ... attained stability with their broad, flat, commonly wrinkled bases." He suggested that the large, flat-based colonies may have been sufficiently stable to resist overtuning during storms.

Radial growth appears to have been unrestricted in these corals; however, vertical growth was strongly inhibited. Environmental factors (excessive turbulence, exposure to air) are interpreted to have been

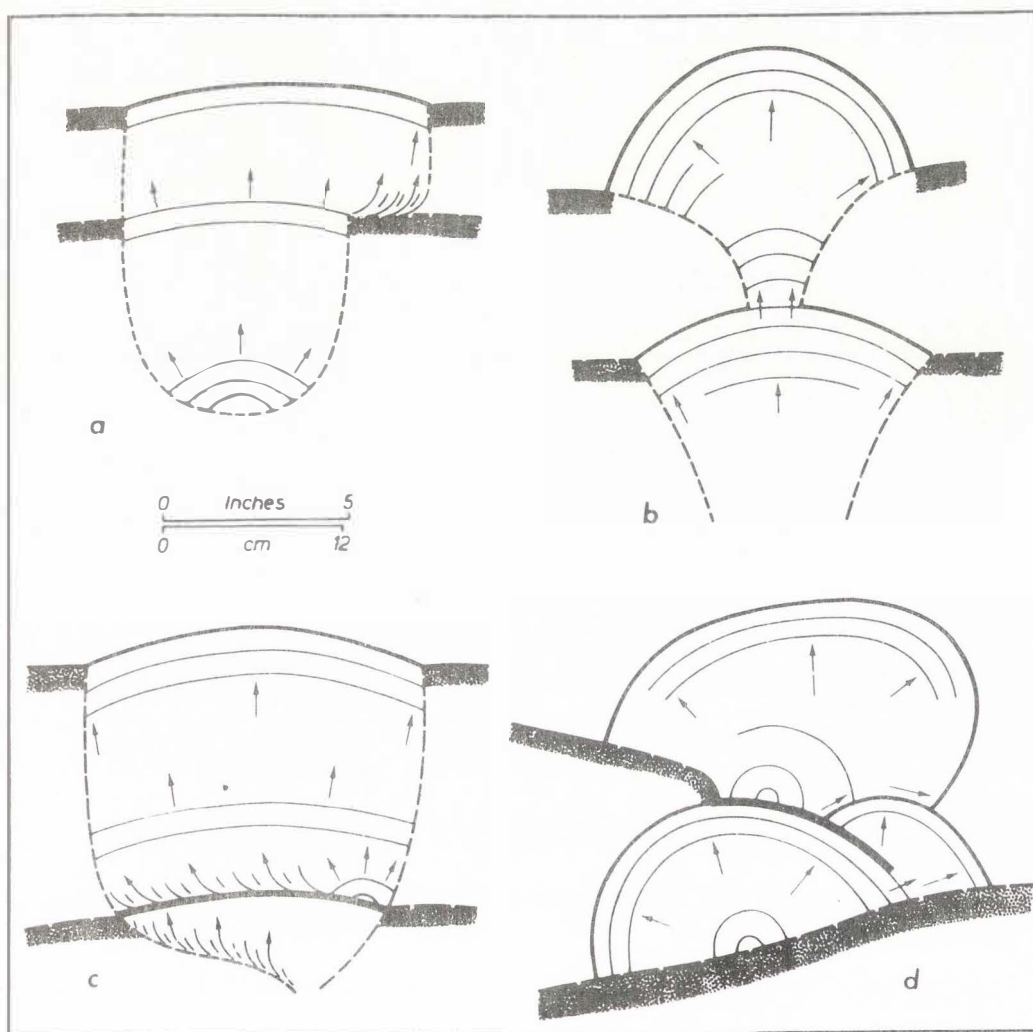


Figure 47. Simplified diagrams of favositid colonies, showing how fluctuations in sedimentation rate are reflected in the corallum. Corallite growth directions shown by arrows. Sediment surfaces shown at time of changes in coral growth form. a) Colony expanded during brief interval in otherwise rapid sedimentation. b) Colony nearly killed by excess of sediment, but recovered to live some years during moderate sedimentation. c) Colony nearly killed at early stage by unknown event, followed by non-radial expansion across crust on own former surface, and subsequent growth during rapid sedimentation. d) Sedimentation remained slow, but colony nearly killed by unknown event. Two satellite colonies are visibly continuous with earlier corallum (from Philcox, 1971:343).

responsible for the discouragement of vertical increase. These corals are interpreted to have inhabited shallow water. A coral which grew in shallow water may not have been able to survive the effects of desiccation and/or excessive turbulence if it were to grow upward into the tidal zone where it might be exposed briefly to the atmosphere during periods of exceptionally low tides.

The hypothesis that Type II corals formed in shallow water (high subtidal/low intertidal) is supported by data concerning corallite variability, which will be discussed in a later section.

Type III corals (Figures 14 and 15) are characterized by their lenticularity and by the absence of corallites on restricted areas of the crown of the corallum (balding). Balding, or destruction of corals, has been studied by Multer (1969), who found that modern corals in patch reefs undergo destruction due to both organic and inorganic causes. Organic processes include the boring action of worms, algae, mollusks, echinoids, chitons and fish (Multer, 1969:87). Inorganic factors responsible for balding include the effect of subaerial exposure and resultant desiccation of polyps, and silting on the flat tops and within depressions of coral heads.

Depth inferences based upon balding must be made with caution. Excessive sedimentation was found to smother and kill corallites of hemispherical corals as well as flattened forms, a phenomenon which will be discussed in detail in the section on composite corals. However, the two good specimens of bald corals are similar in all other respects to Type II corals, which probably were adapted to the shallow subtidal regime. Also, no evidence of organic destruction (bore holes)

was found in the Lodgepole corals. Therefore, the lenticular, bald corals of the Type III category are interpreted as subjected to periodic subaerial exposure during periods of exceptionally low tides. They probably inhabited slightly shallower water than Type II corals.

Type IV corals (Figures 16 and 17) are dome-shaped or slightly flattened hemispheres. In longitudinal section the straight, radially-arranged corallites are visible. These corals have flat or nearly flat bases. Neither lateral nor vertical growth appears to have been impeded. Some of these corals are asymmetrically developed. Philcox (1971:341) stated that "... few colonies have perfect growth forms. Even simple radial forms are usually to some extent misshapen or asymmetrical." Although there are several possible explanations for the preferred orientation or imbrication of corallites (positive rheotropism, negative geotropism, positive phototropism), it seems most likely that the imbrication is current-induced in these massive corals. Hubbard and Pocock (1971:616) found that conical mounds of coarse sediment dominate the marginal reef corona, and interpreted their asymmetry to be the result of unequal forces, such as "... heavy surge from a constant direction." Type IV corals are interpreted to have inhabited slightly deeper water than Type II corals (as evidenced by the preponderance of vertical growth as well as lateral growth), although they still may have been within the zone of moderate wave energy. Graus and Macintyre (1975) found that among modern unbranched reef corals, hemispherical forms dominated in shallow water. Because there is a positive relationship between light intensity and the rates of processes associated with calcification, they reason that

hemispherical forms (which require greater calcification than platy forms), are predominantly found in shallow water. Goreau (1963) also related growth-form to light intensity, and concluded that hemispherical corals are shallow-water forms. Anstey and Delmont (1972) stated that hemispherical bryozoan colonies form in shallow waters-where food is abundant and a large volume of water reaches each individual per unit time. According to Philcox (1971), the flat bases of Type IV corals indicate that sedimentation rates were low.

On a bathymetric profile, Hubbard (1974:150) placed "... the optimal hemispherical growth form resulting from constant radial increase ..." just below the tidal range. On the basis of gross corallum morphology, Type IV corals are interpreted to have inhabited a depth zone intermediate between that of Type II corals (within tidal range or barely below) and Type I corals (near, or below wave base).

Type V corals (Figures 18 and 19) are characterized by a strong vertical orientation of the corallites and by rounded to conical bases. According to Philcox (1971:340), "... when sediment accumulated around a colony ... only those corallites above the sediment could maintain outward growth." If sediment accumulated rapidly enough to prevent lateral growth, upward growth exceeded lateral growth, and the base of the colony became conical or rounded rather than flat (Figure 46). Hubbard (1974) described a similar growth form; she interpreted it to be the result of overcrowding, high sedimentation rates and reduced illumination. The work of Graus and Macintyre (1975) and Goreau (1963) suggested that flattened forms predominate in deep water, where

illumination is reduced. In contrast, many of the Type V corals exhibit considerable relief. Therefore, it does not seem likely that reduced illumination was the predominant factor controlling Type V corals. Since the crowded, constructional reefal environment (ecologic reef of Dunham, 1970) was not established during the Mississippian, overcrowding may be discounted as the main factor responsible for vertical growth. Therefore, the Type V corals are interpreted to have inhabited areas where sedimentation rates were sufficiently high to encourage vertical growth to the virtual exclusion of lateral growth.

Composite corals are fairly common in the Lodgepole Formation, and they exhibit a wide variety of forms. Philcox (1971:341) stated that composite growth forms "... reflect a variety of changes in the immediate environment, particularly fluctuations in the sedimentation rate ..." (Figure 48).

Sample L-26-L is a composite coral. Early growth is dominantly vertical, suggesting that sedimentation rates may have been high (Philcox, 1971; Hubbard, 1974). A gradual change in the direction of growth, from vertical to radial, is seen in a cross-section of the coral, as shown in Figure 20. The change in corallite direction may reflect a decrease in the rate of sedimentation, although lateral growth still appears to have been somewhat impeded. An abrupt change in the color of the corallites internally, from light to dark, corresponds to a growth stoppage, and is thus interpreted to mark a catastrophic event in the life of the coral. The darker color may be attributable to inclusion of sediment, subsequently lithified, within

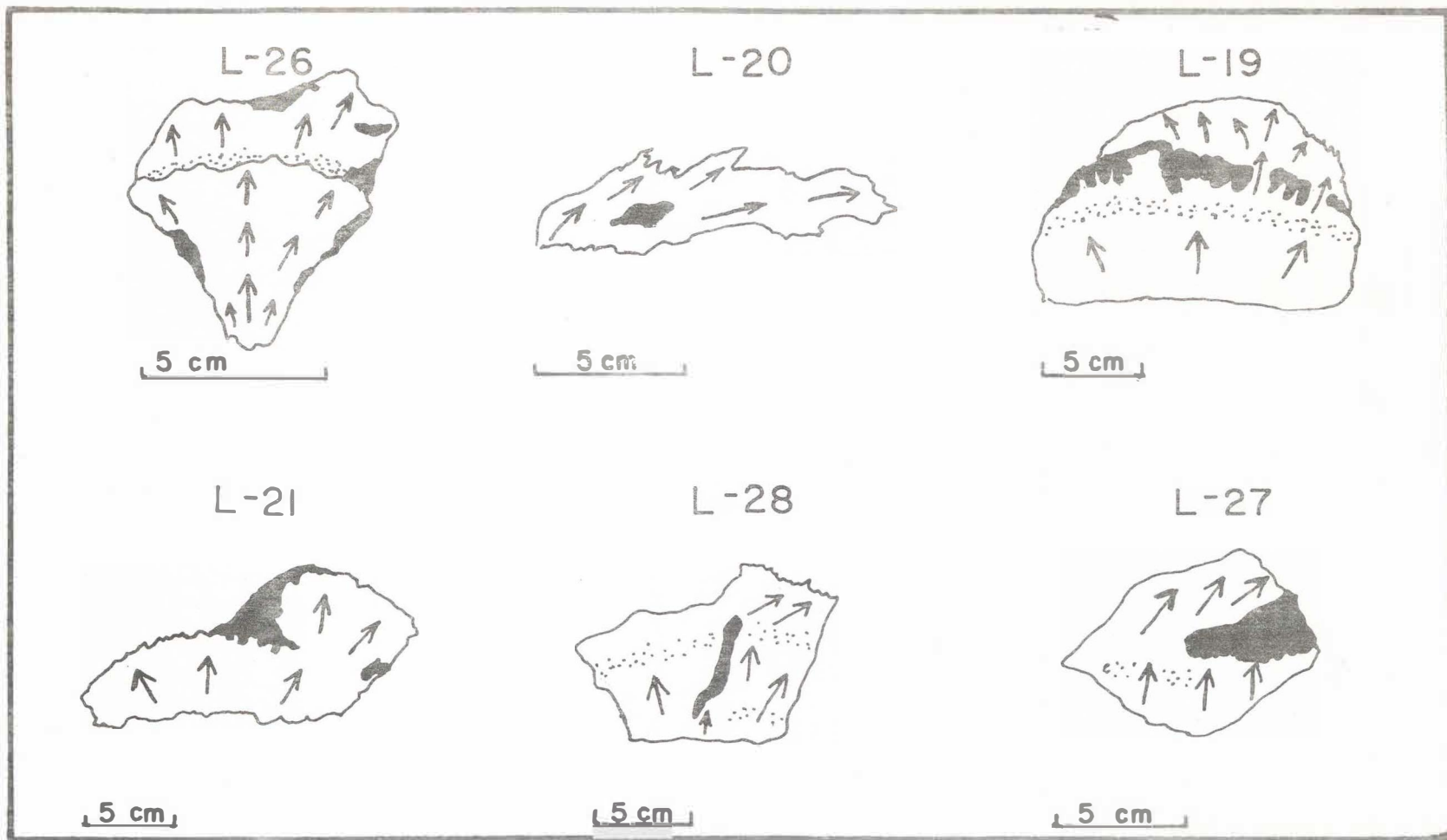


Figure 48. Schematic representation of some of the composite (Type VI) corals, showing areas of retarded growth due to excessive sedimentation (stippled areas), rock matrix interpreted to indicate excessive sedimentation (shaded areas), and direction of growth (arrows).

the calices of the coral. One-third of the coral was killed by the event. However, most of the corallites survived, and a lightening of the color of the corallites (due to absence of sediment within calices as well as to widened tabulae) suggests that growth resumed in a "normal" manner, again with a vertical/slightly radial corallite orientation. Both below and above the dark band there are areas of exceptionally widened tabulae. This is interpreted to be due to the necessity for rapid upward growth in order to maintain a position above the sediment-water interface.

The main corallum of sample L-20-B (Figure 21) is a Type II flattened hemisphere. Lateral growth exceeded vertical growth, and the corallites are directed outward at the margins of the colony, much in the way of Type I corals. The coral appears to have at first directed growth both upward and outward. Subsequently, lateral growth was greatly accentuated while vertical growth was impeded. The main corallum was then smothered by sediment; two projections (satellite colonies) off the main corallum are interpreted to have formed from surviving corallites. These extensions of the original colony are spatially removed from it, and appear to have formed at a higher elevation in the sediment than the original colony. This coral is best described as a sheet-form coral. The coral, when seen in longitudinal section is very flat, with a lumpy, irregular surface. Philcox (1971:342) found encrusting sheet-form favositids which had been "... partially buried by sediment and then their margins have subsequently re-advanced at a higher level." Accumulating sediment, according to Philcox (1971),

forced the colony to "migrate." The irregular composite Type I/Type II sheet-form coral is interpreted as subjected to varying rates of sedimentation.

Sample L-19-L (Figure 22) is a composite lithostrotionid radial coral. Two episodes of radial growth are present. Throughout most of the ontogeny of the colony, the coral is a typical Type IV (flat-based hemisphere), a growth-form affected when sedimentation rates were probably quite low (Philcox, 1971). At a height of about 8.5 cm, the coral was nearly killed by an influx of sediment which can be seen infilling calices; however, all of the corallites survived to grow vertically for about 2 more centimeters, at which point most of the coral was killed by an additional influx of sediment. The dark, micritic sediment can be seen internally and on the outside of the corallum, completely fillint the calices. The sediment layer averaged 0.9 cm thick. Three small (2 cm average width) areas of the colony survived; these corallites can be traced vertically through the micritic layer. It is interesting that the surviving areas are not on the crown of the corallum, but are near the margins. Hubbard (1973:38) reported that sediment is more easily rejected from calices which are oriented at an angle to the sediment-water interface than from those which are vertically oriented. "This results from the fact that the angle of rest of the individual particles is more rapidly increased to a level of instability by distension of an already inclined surface than a horizontal one." This will be discussed in more detail in a later section.

The surviving corallites recolonized the dead surface of the original corallum, and ultimately formed another radial, flat-based colony. The morphology of the satellite colony suggests that conditions similar to those that existed during the early life of the first colony had resumed. The satellite colony attained a height of 3.8 cm.

Sample L-21-L (Figure 23) is a composite radial coral and is very similar to sample L-19-L, although it is much smaller, and is somewhat flattened (like a Type II coral). A normal hemispherical coral early in its ontogeny, it was smothered by an influx of sediment at a height of 4.6 cm. The corallites at one margin of the corallum survived, and are vertically continuous with those of a satellite colony which grew on the old surface. Again, fluctuations in sedimentation rate are inferred to have caused the near death of the colony.

Sample L-28-S (Figure 24) is a composite radial coral. A sharp growth stoppage is not visible, although there are several features which suggest that some environmental factor changed during the ontogeny of the coral. The epitheca is very lumpy, with large sections (usually lower sections) covered with sediment. Internally, a narrow dark band of calices partly or wholly filled with micrite suggests growth stoppage. Within and immediately above this band, tabulae are very widely spaced (mean width = 1.9 mm), compared with other parts of the corallum, where mean spacing of tabulae is 1.1 mm. Hubbard (1970:201) discussed variability in the intertabular distance of caninoid rugose corals. She attributed locally widened tabulae to two types of adverse conditions: (1) lack of carbonate for skeletal growth, and (2) need of rapid upward

extension of the skeleton to avoid choking by mobile sediment. Although there is no evidence to discount the first of these possibilities (other than the obvious presence of calcium carbonate-secreting organisms), what evidence is observed favors the second explanation. Constriction of the epitheca coincides with the internal sediment-filled calices. There is also an abrupt change in corallite growth direction, although very few of the corallites appear to have been killed. This feature may be analagous to the redirection of growth in solitary rugose corals called geniculation; that is, the corallites may be bent away from the direction from which the sediment was derived. Another possibility is that the current direction changed, and that the corallites are exhibiting positive rheotropism.

Figure 48 is a schematic representation of some of the composite lithostrotionid corals which were found in the Lodgepole Formation. The original colony of L-27-S (Figure 25) was partially killed by an influx of sediment which may be seen externally (on the surface of the corallum) and internally (in a cross-section parallel to the direction of growth). The corallites of one side of the colony survived and continued to grow in a dominantly vertical direction, although there is a slight change in growth direction. The corallites bent further away from their original orientation and ultimately grew over much of the pod of sediment. This corallum geometry probably formed as the result of excessive sedimentation.

Jones (1936) related the variability in the diameter of corallites on a single corallum to the type of growth. Lithostrotionids increase

(reproduce asexually) by intermural budding. A high degree of variability is indicative of rapid budding and slow growth. On the other hand, "if ... gemmation is not excessive and the upward growth of the corallites keeps pace with the intercalation of buds, the result is a corallum with corallites of almost equal size" (Jones, 1936:4).

Budding frequencies (measured as ratios of intermural buds/mature corallites) were determined for each lithostrotionid coral type (Table 1). The budding frequencies of Type I corals are significantly higher than those of the other coral types. On the basis of overall corallum morphology, the Type I corals are interpreted to have inhabited relatively quiet and deep water. This hypothesis is supported by the degree of corallite variability.

The Type I corals apparently had energy available to expend in the process of producing new buds. This implies that the coral inhabited an environment where rapid growth was not essential in order to keep pace with sedimentation. If sedimentation rates were high, the coral would expend much of its energy budget in the process of sediment-rejection, and skeletal accretion, thereby diverting energy from asexual reproduction. Growth and reproduction require considerable energy expenditures among invertebrates with calcareous skeletons. This may preclude the simultaneous occurrence of both processes. Philcox (1971:342) stated that the sheet-form favositids may have expanded horizontally faster than radial forms. He attributed the faster expansion to "... frequent budding rather than a higher growth rate of individual polyps."

If a high frequency of intermural budding accompanied a slow growth rate as stated by Jones (1936:4), then the association of Type I corals with inferred deeper water substrates is reasonable. Graus and Macintyre (1975) cited biological studies on recent corals strongly suggest a decrease in mean growth rate among modern corals as depth increases. The flattened coralla of Type I corals is interpreted as an adaptation to deep, quiet water environments, where skeletal accretion may have retarded. In lieu of radial accretionary growth of corallites, frequent budding developed the sheet-like growth form. Thus the high budding frequency of Type I corals is consistent with the bathymetric assignment of this growth-form. In contrast, the Type II through V corals all had quite low ratios of bud/mature corallites; this pattern suggests that growth was more rapid and that budding frequencies were lower. The rigors of the environment (i.e., rapid or variable sedimentation rates, wave and current activity) encouraged skeletal accretion, which diverted energy away from intermural increase.

The limited data suggest that mean corallite diameter of Type I corals exceeds that of Types II, III and IV corals. Corallite size may be under nutritional control. Type I corals have been interpreted as deep, quiet-water forms. Zooplankton abundance in general decreases with depth (Suchanek and Levinton, 1974), and as suspension feeders, corals are dependent upon currents to provide their food and to remove their metabolic products (Vaughan and Wells, 1943). Large corallites would enable each individual polyp to filter from a greater volume of water. The large corallites of Type I corals are thus interpreted as

an adaptation to an environment where food was less abundant and current velocities low, a situation common to deeper water habitats.

The relatively smaller, corallites of the hemispherical (Type IV) and flattened hemispherical (Types II and III) corals suggest that current velocities were high enough, and food sufficiently abundant that resident polyps of small corallites were able to extract enough nutrients to live.

The exceptionally thick walls of Sample L-1-L (Figure 9) (Type I) may be a means by which the colony partitioned food resources in a quiet-water habitat. Since *Lithostrotionella* is a cerioid massive coral, the only way corallites can be separated spatially from one another is through thickening of the intercorallite walls. Anstey and Delmont (1972) found that widely spaced bryozoan zooids separated by thickened zooecial walls, are more efficient at meeting nutritional requirements and in removing wastes in quiet waters. Only one specimen of *Lithostrotionella* was found with thickened walls, which suggests that this morphological strategy for adaptation to quiet water was infrequently elicited by environmental stimuli. Figure 49 is a schematic representation of the colonial coral morphologic types and their inferred bathymetric position.

External Variability of Solitary Corals

Much variability in shape is exhibited by the rugose corals of the Lodgepole Formation. Wells (1937) attributed shape variability to the following causes: (1) reproductive precocity, (2) gerontism,

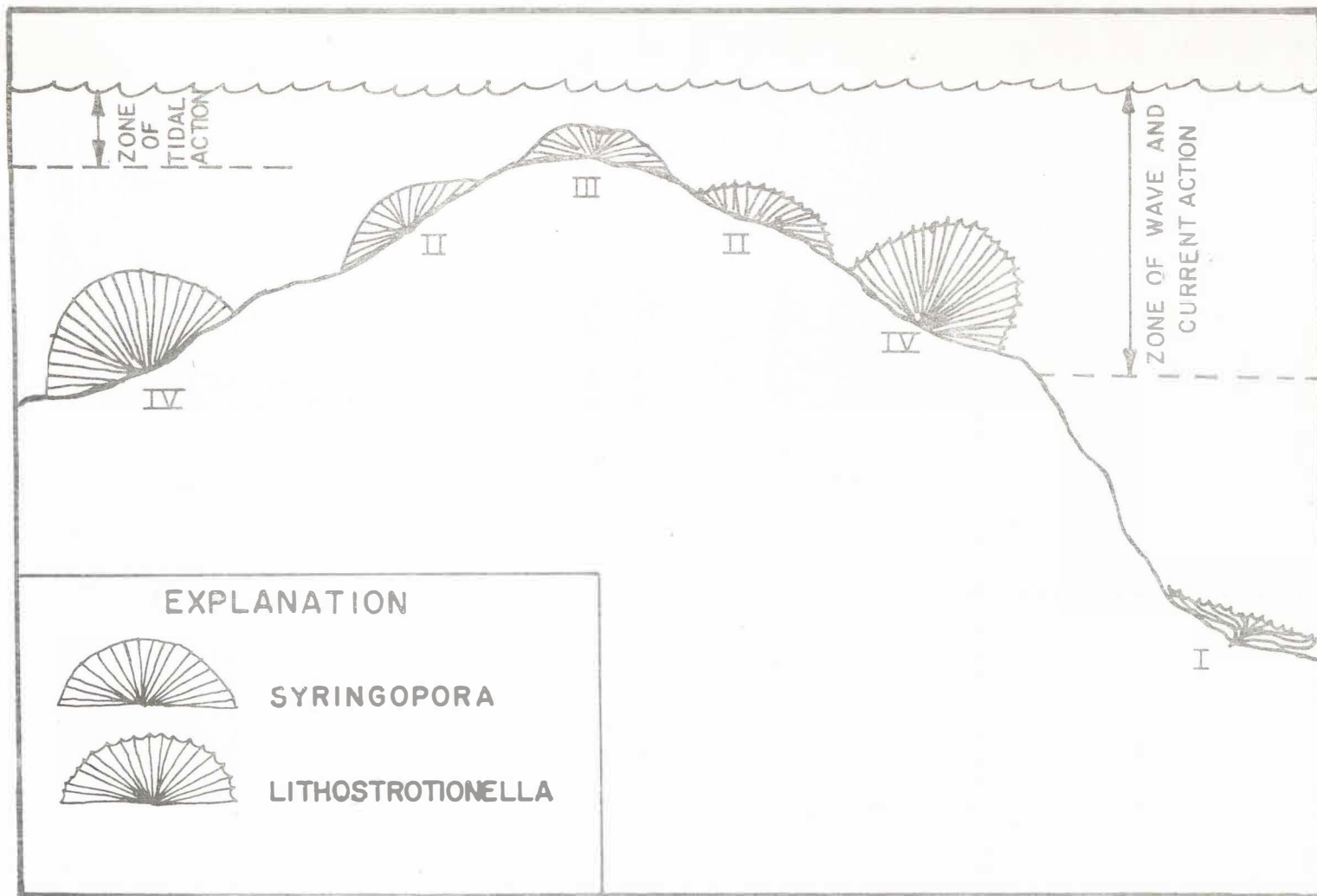


Figure 49. Schematic representation of colonial coral morphologic types and inferred bathymetric life position. Roman numerals refer to coral morphologic types discussed in text.

(3) irregular rejuvenescence, (4) differential growth rate, (5) genetic variables, (6) crowding and food shortage. Oliver (1958:836) emphasized differential growth rate attributable to ecological variation in extrinsic factors (food and oxygen supply, depth of water and water movement) in his study of variation among Devonian rugose corals. Hubbard (1970) studied the morphologic features which resulted under the influence of mobile sediment. Genetic causes of variation were discussed by Sandy (1961).

The various common rugose growth-forms have been assigned to types. The straight coralla of Type 1 corals (Figure 31) may form in two ways, according to Hubbard (1974). Vertical growth after an original stable attachment will result in a straight adult corallum, if the coral is never toppled (Figure 50). A straight corallum may form even if the coral is obliquely oriented on the substrate, provided that sedimentation rates are never high enough to threaten smothering; i.e., if the growth rate of the coral exceeds the sedimentation rate, the coral will be able to reach maturity without changing its direction of growth.

Type 2 corals (Figures 32, 33, 34) are characterized by geniculation. Sando (1977:49) defined geniculation as a change in the direction of the corallum axis in one plane. Geniculation is an environmentally-induced variation. A change in the direction of growth might be the consequence of a negative geotropic response, a positive rheotropic response, or a positive phototropic response. Unstable original attachment, instability on the substrate and directional growth away

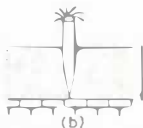
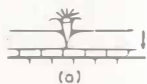
1 CANINOID SPAT BECOMES ATTACHED TO A SOLID PARTICLE ON THE VISÉAN LIME-MUD SEA BED



2 JUVENILE CORNUTE CANINOID DEVELOPS

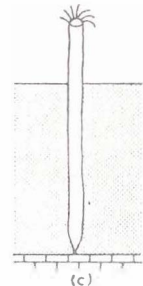


3i VERTICAL GROWTH RESULTING FROM STABLE ATTACHMENT IN VERTICAL ALTITUDE

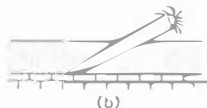
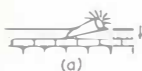


Starting from the optimum growth position negative geotropic growth continues faster than the rate of deposition of the matrix

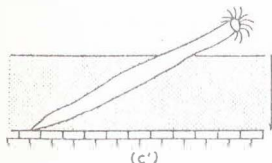
Eventually continuous sedimentation and regular growth result in a straight cylindrical adult caninoid



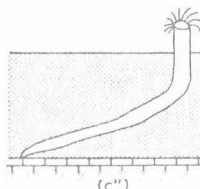
3ii OBLIQUE GROWTH RESULTING FROM INSTABILITY OR OBLIQUE ATTACHMENT



Negative geotropic growth continues faster than the rate of deposition. The depositional rate is slower than in case history 3i



Finally after uniform conditions of slow deposition an adult caninoid seemingly indistinguishable from 3i(c) results



A comparative increase in the depositional rate causes the corallum to grow vertically in order to avoid suffocation by settling mud. Thus a geniculation develops

LEGEND

Live polyp

Caninoid corallum

Matrix 1—generally biomicrite

Matrix 2—generally shaly micrite

Matrix 3—generally shale

Matrix 4—generally biomicrite

Substrate—generally calcarenite

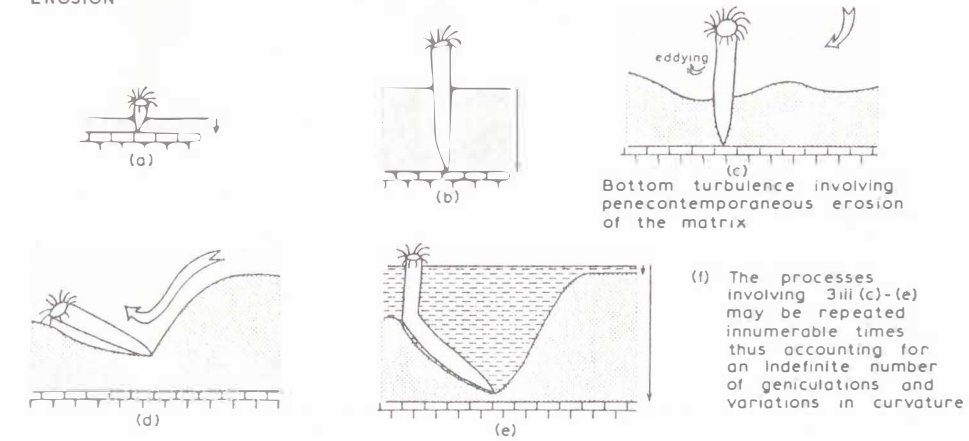
Bottom turbulence inducing erosion

The intensity of the arrow indicates the comparative strength of the process of deposition:—

↓ Minimum ↓ Standard ↓ Maximum

Figure 50. Flow diagram showing possible origins of the various caninoid growth-forms (from Hubbard, 1970:206)

3iii VARIATION IN GENICULAR STYLE RESULTING FROM MOBILITY OF THE SUBSTRATE COMBINED WITH THE ALTERNATION OF DEPOSITION AND PENECONTEMPORANEOUS EROSION



Bottom turbulence involving penecontemporaneous erosion of the matrix

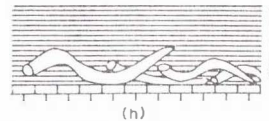
(f) The processes involving 3iii(c)-(e) may be repeated innumerable times thus accounting for an indefinite number of geniculations and variations in curvature

Penecontemporaneous erosion and current activity over-balance the corallum

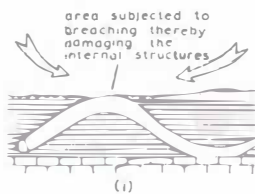
Renewed influx of sedimentation with the caninoid resuming its negative geotropic tendencies



Renewed winnowing. Bottom turbulence removes all the original matrix tumbling and rolling the coralla

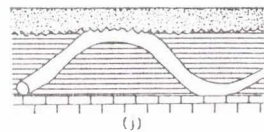


Influx of extraneous mud with rapid deposition causes final suffocation of any but the most recalcitrant caninoid



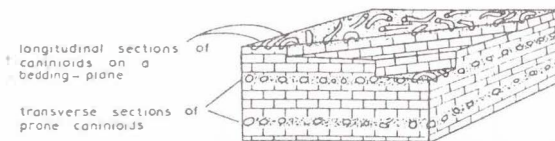
Partial burial and/or subsequent erosion may cause the upstanding geniculate area to be breached

THECAL BREACHING



Subsequent deposition infills the buried topography of the eroded caninoid

4 RESULT



Segregations of "prone" adult caninoid-dominated bedding-planes alternate with almost "barren" units

Figure 50. Continued.

from the sediment are possible causes of geniculation (Hubbard, 1970: 201). The environmental causes of geniculation include rapid sedimentation (which would force the coral to grow vertically), bottom turbulence (could result in toppling of the coral and subsequent redirected growth), and shifting current directions. Dixon (1970:55) stated that certain biocharacters, including curves and geniculations of the coralla, were affected by environmental conditions such as instability of bottom sediments.

The stability of a coral depends upon the following factors, according to Hubbard (1970): (1) length of the buried portion of the corallum, (2) the fluidity of the matrix, (3) current velocities. Presumably, the greater the length of the buried portion of the corallum, the more stable the coral becomes. However, Hubbard (1970:196) found that "geniculations show no constant relation to the situation of the cardinal quadrant, apex, or calice." The mean pregeniculation length of large rugose corals in the Lodgepole Formation comprised only about 25 percent of the total adult corallum length. Consequently, these rugose corals were more susceptible to factors causing geniculation during their juvenile and young adult stages.

While some of the geniculations of corals are very sharp, suggesting a sudden redirection of growth, others are very gentle curves and comprise most of the length of the corallum. Hubbard (1970:196) described a gently arcuate geniculation which suggested that "... this coral's life was periodically fraught with the dangers of silting up during adverse conditions."

The gentle geniculations (those with large radius of curvature) are interpreted to have been caused by gradually increasing sedimentation rates, or possibly by a gradual increase in water depth and corresponding decrease in illumination (positive phototropic response). Another possible explanation of gently arcuate geniculation is that the coral progressively sank into the soft muds as it increased in size and weight. Sharp geniculations, on the other hand, may have resulted from toppling, particularly if the matrix in the immediate vicinity of the coral were sufficiently fluid to threaten smothering the polyp. Precipitous vertical growth would result in a sharp geniculation.

Both abrupt and gradual geniculation is very common among corals of the Lodgepole Formation. Either sedimentation rates were variable, and/or current velocities sufficiently high to cause scouring and toppling among rugose corals. Previously discussed evidence of rapid changes in sedimentation rates was found among compound rugose and tabulate corals.

Doubly geniculate and vermiform corals (Type III) are found locally in the Lodgepole Formation. Presumably, the cause of multiple geniculations is repetition of those of single geniculations.

Slabs covered with recumbent, similar-sized adult corals are interpreted as winnowed death assemblages. Figure 51 is a graph of the relative percentages of straight, geniculate, prone (recumbent) and upright coralla on one large slab. The high proportion of geniculate corals, including several with multiple geniculations, suggests that currents may have repeatedly buffeted these corals during their lives

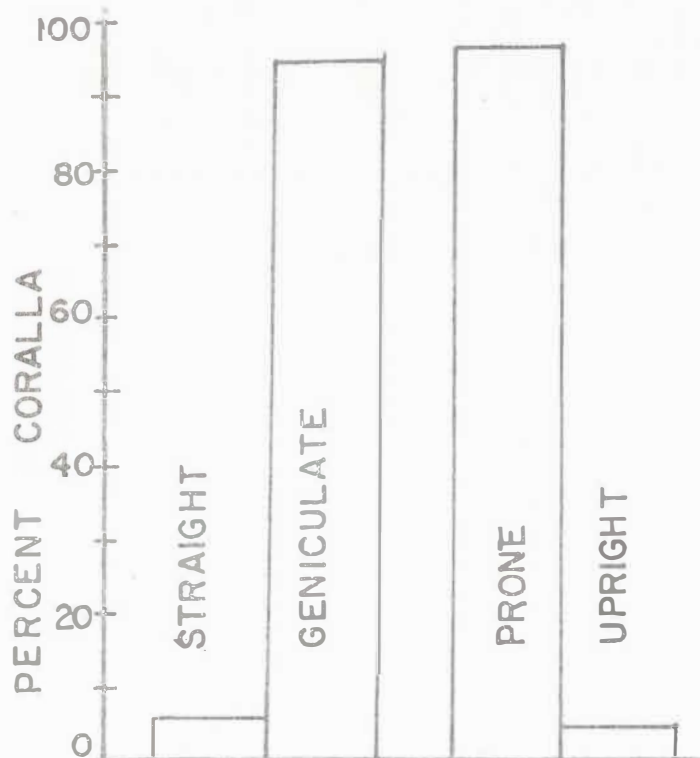


Figure 51. Graph of the relative percentage of straight coralla, geniculate coralla, prone coralla and upright coralla on a single bedding surface ($n = 38$).

and scoured sediment from around the coralla. Exposure of the apical region by scouring resulted in instability, toppling and subsequent redirected growth of the corallum. The paucity of juveniles suggests that these slabs represent composite, winnowed death assemblages.

Type 4 corals display rejuvenescence. Rejuvenescence is interpreted to result from changing environmental conditions that proved traumatic to the coral, such as an influx of sediment, a storm or changes in salinity.

Type 5 solitary corals include coiled or grooved protocoralla, the first skeletal stage secreted by the polyp. The 'normal' ontogeny of a rugose coral proceeds as follows: The polyp, after a short planktonic (or longer epiplanktonic) stage, attaches itself to a solid substrate of some kind. The polyp becomes increasingly unstable in this position as it increases in size and weight. The coral topples and breaks loose from the substrate. The coral may then reattach to the same object, and direct its growth vertically, or it may remain free on the substrate.

Sando (1977) reported planispirally-coiled protocoralla. He interpreted the coiled tip of the corallum, which is rarely preserved, as an adaptation which facilitated attachment to objects above the sediment-water interface. The specimens with coiled apices lacked attachment scars, which suggested to Sando (1977) that the corals may have been coiled around some flexible, possibly organic, object near the sea floor. Sando (1977) rejected productid brachiopod spines and the meshwork of fenestellid zooaria as possible attachment sites for

these corals because of the extremely small size of the umbilicus of the protocoralla. This umbilicus, and the absence of preserved corals actually coiled around a solid object, led Sando (1977) to the conclusion that the protocorals may have been coiled around planktonic algae.

Talons present on the protocoralla are interpreted as a means of fixation for the coral to the substrate following the larval planktonic stage. Another possibility is that the talons served a clasping function for the juvenile in an epiplanktonic situation. Lateral and basal attachment scars mark the points at which the coral attached by cementation to a solid substrate. The grooves observed on the protocoralla, particularly the coiled grooves, suggest that the corals may have been attached to or coiled around a solid linear object. Possible attachment sites include crinoid pinnules or stems, fenestellid zoaria and productid spines. On the insides of some of these grooves, faint lines resembling impressions of crinoid columnals are visible. Thus, crinoid stalks or stems may have served as attachment sites for juvenile corals. The geniculate protocoralla probably formed when the coral toppled from its attachment position. Negative geotropism would account for the sharp change in growth direction; that is, the coral grew away from the sediment-water interface after toppling to a prone position. The flattening of the protocoralla also was noted by Sando (1961:78). He described and interpreted the flattening as follows: "... curvature and flattening and broadening of the convex side of the corallum are regarded as genetic instruments for maintaining negative geotropic growth and stability after toppling from an erect, apically attached position."

Variability in the Structures of Colonial
and Solitary Corals

Recent studies of the calical features and sediment rejection capabilities of scleractinian corals have provided valuable insights for interpreting Paleozoic corals by analogy. However, there are several important ecological differences between the two groups. According to Wells (1957) the main difference is mode of life. Paleozoic corals lived freely on muddy substrates, whereas modern corals often attach to rock surfaces and are constructional reef-formers. Other ways in which modern corals differ from those of the Paleozoic are structural. Paleozoic corals have tabulae and rather smooth septa, whereas modern corals do not have tabulae, and often have highly ornamented septa. The presence of tabulae in Paleozoic corals "... unless modified by a number of steep septa, renders the calice flat-floored and thereby comparatively inefficient" (Hubbard and Pocock, 1972:618). Thus, Paleozoic corals did not occupy exactly the same niches as recent corals. For this reason caution must be exercised in the use of adaptive morphology of modern corals to interpret the inferred functional morphology of ancient genera.

Modern coral polyps exhibit varying degrees of activity. When currents are strong, all corals will retract their polyps from the distended position (Hubbard, 1974). Some recent corals utilize their polyp tissue in active interspecific aggression (Lang, 1971). Other coral polyps are very active and are capable of moving the entire corallum. *Diaseris*, for example, can move at speeds of 0.3 mm/minute.

It also can crawl, uncover itself from sediment, overturn and climb (Hubbard and Pocock, 1972; Goreau and Yonge, 1968). These activities are accomplished by tentacular action, mucus manipulation, and polypal distension of the stomodeal uptake of water.

Corals are capable of rejecting sediment from the corallites by four methods (Hubbard and Pocock, 1972): (1) distension by the stomodeal uptake of water, (2) tentacular action, (3) ciliary beat, (4) mucus entanglement. Goreau and Yonge (1968) found that some corals use a combination of two or three of these methods. The most common mechanism found by Hubbard and Pocock (1972) for sediment rejection is through the stomodeal uptake of water. This means that a coral can take water through the stomodeum (an esophagus-like connection between the mouth and the gastrovascular cavity (Vaughan and Wells, 1943:13), which causes the polyp to swell, thus reducing its effective density to the point where it actually "floats" to the surface of the sediment (Goreau and Yonge, 1968). The swelling of the inundated area displaces the sediment particles by changing their angle of rest. The corals then use tentacles to pass the large particles from one polyp to the next, "... thus systematically moving the particles away from the center of irritation ..." (Hubbard, 1973:34). Hubbard and Pocock (1972:608) found the *Diaseris* also can "... manipulate its tissue in such a way that this water is then forcefully ejected in a chosen direction." Ciliary action may be used most often for the removal of fine sand and silt, according to Hubbard (1974), whereas polypal distension is more useful for the removal of coarser sediment.

Passive polyps are inefficient at rejecting coarse sediment or at removing themselves from sediment. Active polyps, on the other hand, are capable of rejecting sediment quite efficiently. Most corals, according to Hubbard and Pocock (1972:617) are "... size-specific sediment rejectors." They also found that the distension potential of a polyp is directly related to the surface area of the calice. The shape of the calice is an important factor in the distension potential of a polyp. Figure 52 is a representation of calical symmetry and function. The shape of the calice determines the "angle of intersection between the calical elements and the direction of tension which may be exerted by the three sheets of polypal muscle tissue" (Hubbard, 1973:37). The fact that sediment is more easily rejected by calices which are at an angle than by those which are oriented horizontal to the sediment-water interface may explain why balding was found to occur only on the crowns of colonial corals in the Lodgepole Formation. That is, the corallites on the crown of the coral, whose floors are oriented parallel to the sediment-water interface, might be less efficient than those which are located on other parts of the corallum. "This results from the fact that the angle of rest of the individual particles is more rapidly increased to a level of instability by distension of an already inclined surface than from a horizontal one" (Hubbard, 1973:38). The fact that composite radial lithostrotionid usually survived at the margins of the colony may reflect the greater efficiency in sediment-rejection of corallites located on the sloping side of a colony.

CALICAL ANGLES

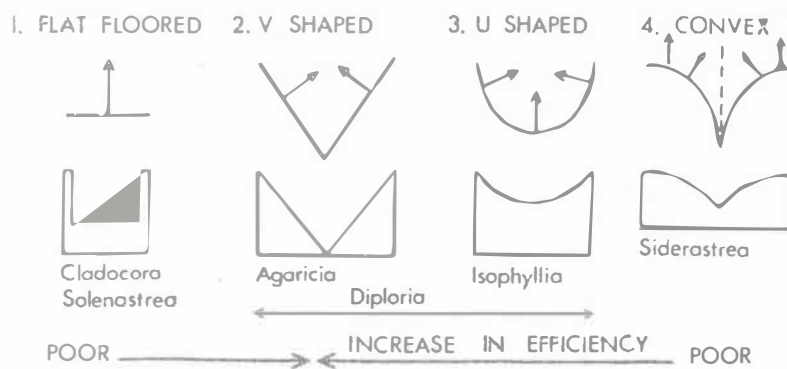


Figure 52. Schematic longitudinal sections through some calical geometries which appear to have functional significance with respect to capability for sediment rejection (from Hubbard, 1973:37).

Skeletal features reflect polypal features. Hubbard and Pocock (1972:617) composed a list of skeletal features which may be used as "... guides to function" (Table 4).

Calical relief, geometry, septal density and length were determined for the Lodgepole corals and discussed in a preceding section. The information is summarized in Table 3. Each of these features was then rated, in terms of inferred efficiency at sediment rejection, on a scale from 1 to 4, with 1 = poor, 2 = medium, 3 = good, 4 = very good. The results are summarized in Table 5.

The most efficient corals, on the basis of skeletal features, are *Lithostrotionella*, *Lithostrontion*, *Zaphrentoides* and *Rylstonia* and *Amygdalophyllum*. Intermediate corals include *Turbophyllum*, *Vesiculophyllum*, *Aulopora* and *Cladochomus*. The least efficient are *Michelinia*, *Syringopora* and *Caninia*. Cerioid lithostrotionids are more efficient sediment rejectors than fasciculate lithostrotionids (Hubbard and Pocock, 1972). One would infer, therefore, that *Lithostrotionella* was a more efficient sediment rejector than *Lithostrontion*, and that *Michelinia* was more efficient than *Syringopora*. Cerioid coralla are less efficient sediment rejectors than plocoid or meandroid, according to Hubbard (1973), because the particles of sediment must be moved up and down (over corallite walls) except when the polyps are fully distended. By analogy, it seems obvious that fasciculate forms would pose difficulties in removing sediment because of the separation of corallites.

Table 4. Skeletal features of active and passive polyps†

Active polyps	Passive polyps
1. Larger number of septa	Fewer septa
2. Complex septal ornament	Comparatively smooth septa
3. Fenestrate septa	Solid septa
4. Higher calical relief	Lower calical relief
5. V-shaped calica- floors	Horizontal skeletal floors
6. Lighter skeleton	Heavier skeleton

†From Hubbard and Pocock, 1972:617.

Table 5. Summary of the relative sediment-rejection-efficiency of the fossil corals based upon calical features (4-6 = poor, 7-10 = medium, 11-14 = good, 14-16 = very good)

Coral	Calical relief	Calical shape	Septal density	Septal length	Total (sum)
<i>Lithostrotionella</i>	2	4	4	4	14
<i>Lithostrotion</i>	2	4	4	4	14
<i>Michelinia</i>	1	1	1	1	4
<i>Syringopora</i>	3	1	1	1	6
<i>Aulopora</i> <i>Cladocchorus</i>	3	2	1	1	7
<i>Amygdalophyllum</i>	1	4	2	4	11
<i>Turbophyllum</i>	1	3	2	3	9
<i>Vesiculophyllum</i>	2	3	1	2	8
<i>Caninia</i>	1	1	1	1	4
<i>Rylstonia</i>	2	4	3	3	12
<i>Zaphrentoides</i>	3	3	4	3	13

Axial structures are interpreted to have increased the coral's efficiency by increasing the surface area of the calice for tentacular muscle attachment as well as by increasing sepal lengths.

Sedimentological evidence from the associated coral matrix can be used to support the above morphologic inferences. However, two problems exist in the reconstruction of the former substrate and sedimentation regime of the corals of the Lodgepole Formation. The first is that recrystallization and diagenesis have altered original depositional textures. In this section, much of the spar of hand specimens appears to be diagenetic in origin. The other problem is that the corals have a pronounced tendency to weather free of their matrix; this is particularly true of the *Rugosa* (colonial and solitary). One can use the sediment found within the calices of the coral, however. A more severe problem arises where the corals are concentrated on bedding surfaces which may have undergone winnowing.

Despite these problems, a few generalizations concerning corals and rock type can be made. *Caninia* is very often either enclosed in micrite or with micrite infilling the calice. *Vesiculophyllum* is in various lithologies, including micrite, but is most common in wackestones. *Zaphrentoides* is common in very impure mudstones and wackestones, although it is not limited to these types. *Zaphrentoides* is common at the Porcupine Dam collecting locality. Shaly and silty interbeds are common in this exposure and the insoluble residue analysis yielded, without exception, high values of "impurities." *Lithostrotionella* is commonly enclosed in a packstone or grainstone matrix, as is *Lithostrotion*. However, *Lithostrotionella* was smothered by

large amounts of biomicrite. The other corals did not show a preferential association with a particular rock type, although most are in wackestone.

Total (average) insoluble residues (calculated as weight percent of the original sample) were highest for *Aulopora*, *Caninia*, *Lithostrotion* and *Zaphrentoides* (Figure 53). At first it seems anomalous that the matrix of *Caninia* yielded a relatively high insoluble-residue value, considering that it has been interpreted as an inefficient sediment rejector and is associated with micritic rocks. However, although the mean value obtained (19.4) is high for the corals, it is not high compared to the other Lodgepole organisms, and is comparable to the mean values obtained for trilobites and gastropods. If indeed *Caninia* inhabited an offshore, subtidal zone as here interpreted, then it seems reasonable that the insoluble-residue values would be similar to those of other offshore organisms. The fact that the insoluble residues are higher in the offshore zone than in the higher energy deposits may be a function of hydraulics. Perhaps the comparatively high energy zone which has been postulated to lie between the nearshore and offshore zones (Irwin, 1965) inhibited deposition of fine-grained detritus. The caninoid coral insoluble-residue values are low compared to values obtained from the lower Lodgepole (i.e., at the Porcupine Dam) section. However, two of these corals (*Aulopora* and *Zaphrentoides*) had very large ranges in terms of insoluble residue of associated lithologic matrix and samples of *Lithostrotion* are sufficiently rare that this comparison must be treated with caution. Smaller mean insoluble-residue values were obtained for the other corals considered to have

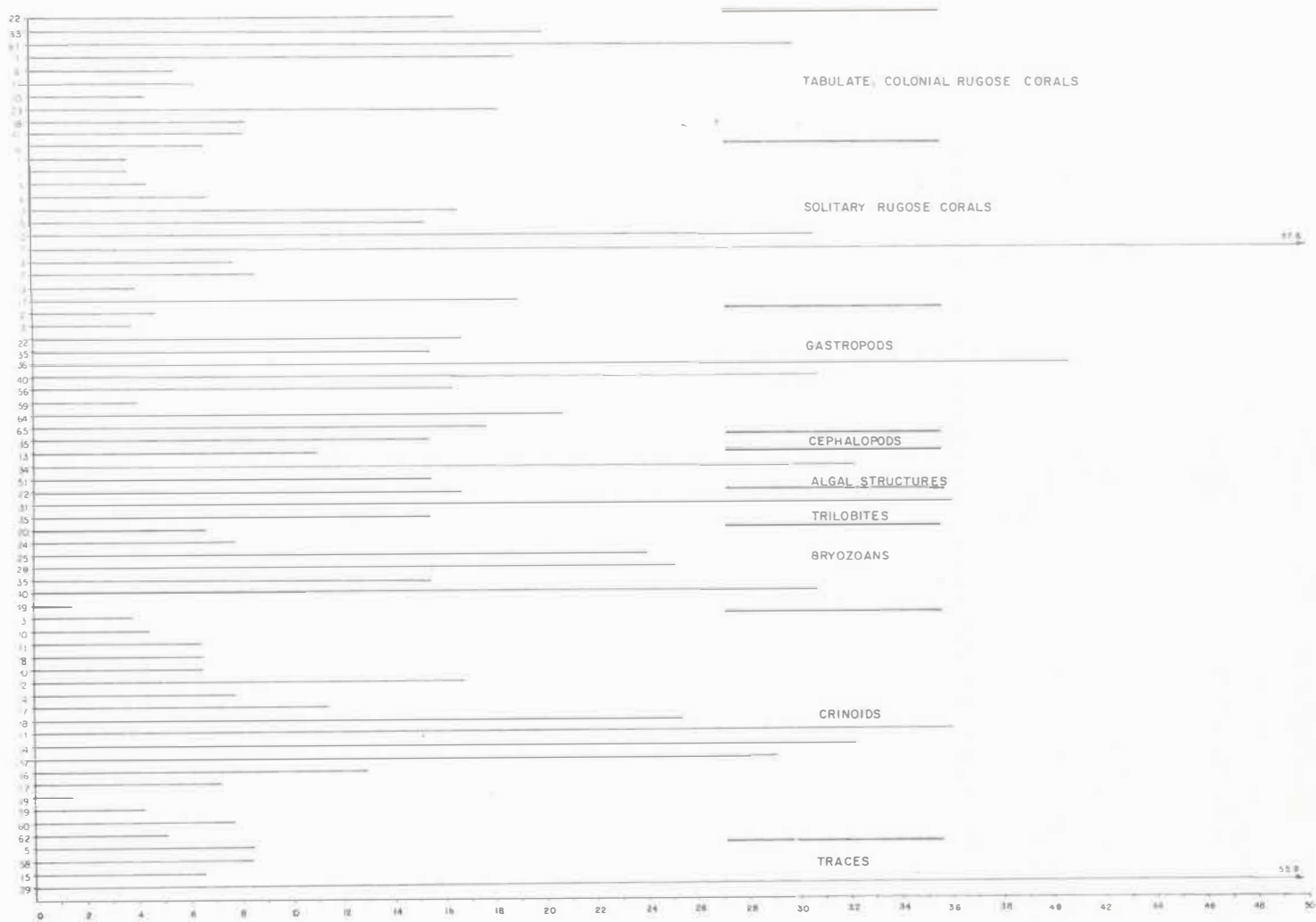


Figure 53. Graphic representation of the results of the insoluble-residue survey. Weight percent of insoluble-residue is on the abscissa, sample numbers are on the ordinate.

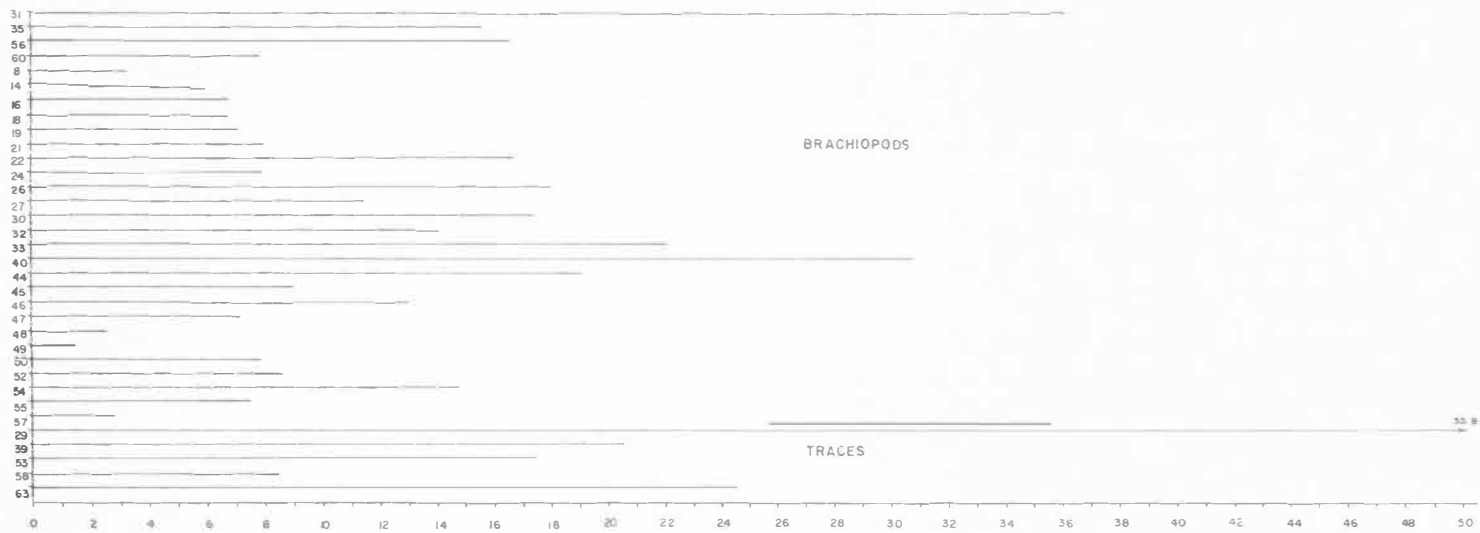


Figure 53. Continued.

been inefficient sediment rejectors, *Rylstonia* (7.2%), tabulate (*Syringopora*, *Michelinia*, *Aulopora* and *Cladochonus*) corals (12.5%) and colonial rugose (*Lithostrotion*, *Lithostrotionella*) corals (15.6%).

Hubbard (1966) found the following relationships between lithology and coral type in the carboniferous limestone sequences of northwest Ireland: (1) cerioid lithostrotionids: calcarenites, (2) fasciculate lithostrotionids: finer-grained intervals than cerioid forms, (3) *Caninia*: fine sediments, (4) *Zaphrentoides*: impure carbonate silts, fine sands and shales.

These associations and derivative conclusions are similar to those reached concerning the corals of the Lodgepole Formation.

Lack of appreciable variability in spacing of tabulae of *Lithostrotionella* and *Caninia* suggests a constant growth rate under equable conditions, and/or constant sedimentation rates. If seasonal differences were pronounced a higher degree of variability in intertabular distance would be expected (Ma, 1962).

Wells (1963) discussed the use of coral growth bands as geochronometers, i.e., as indicators of the passage of time. Organisms which have an accretionary or an additive mode of skeletal increase may record seasonal change, variation in nutrient supply, tidal effects and diurnal variation. A few growth lines were seen on solitary rugose corals in the Lodgepole Formation which may be monthly or seasonal. These lines are bracketed between two annual growth bands; however, no specimens had a complete set of monthly increments preserved. Monthly growth lines are probably linked to the tidal cycle. Environmental

factors such as depth and illumination vary with the tides. These changes would affect most strongly those organisms inhabiting the intertidal zone. Subtidal organisms might be buffered from the tidal effects by the greater depth of water and/or distance from shore. The shell microstructure of recent bivalves which Panella and MacClintock (1968) studied had poorly developed tidal increments in subtidal environments in contrast to specimens of the same species which lived in tidal environments. Another explanation which might explain these growth increments found between annuals was suggested by Scrutton (1970). Breeding cycles in modern corals are interpreted to be under lunar control. Breeding results in a temporary decrease in skeletal accretion, which might cause a constriction to form on the epithecae of the corals.

On the basis of their similarity to the growth bands of modern corals (Figures 2 and 3, Weber et al., 1973), the couplets of alternating light and dark growth bands of corals in the Lodgepole Formation (Figure 40) are interpreted as annual. A pair of bands, one light and one dark, is interpreted to represent a year (Buddemeier, 1974; Weber et al., 1975). The dark bands are interpreted to represent high-density calcification, while the light bands represent low-density calcification.

There has been considerable discussion in recent years on the subject of the causes of annual density bands. Buddemeier (1974) suggested that environmental stimuli trigger the type of skeletal deposition. He stated that light is the controlling factor in the formation of density bands. Periods of high rainfall (increased cloud cover,

therefore decreased incidence of solar radiation) were correlated with high-density, dark bands. These bands form, according to Buddemeier (1974) during the winter months, and reflect a decreased growth rate. Low-density light bands, on the other hand, form during the summer, when the growth rate was found to be greatest. However, if the annual cycle which the bands represent is controlled by the availability of light, the question as to the role of zooxanthellae must be raised. If fossil corals (Rugose and Tabulata) did not have a symbiotic relationship with algae as modern corals do, photoperiodicity alone may not explain the banding of the Lodgepole corals. Gorgonians and sclerospoges lack zooxanthellae but exhibit annual skeletal banding, so it appears that light intensity alone is not sufficient to explain these features.

Weber et al. (1975:138) suggested that seasonal temperature changes are responsible for the formation of "... alternating phases of high-density and low-density calcification." According to this interpretation, high-density, dark bands form when the surface-water temperature is above average. In the tropics, the temperature of the surface water is greatest during periods marked by high rainfall.

Although Weber et al. (1975:147) stated that "... there is no connection of the band-width ratio with characteristics of the environment," it is interesting to compare the patterns of modern corals with those observed in the Lodgepole Formation. By band-width ratio, Weber et al. (1975) referred to the ratio of low- to high-density band widths. High skeletal density (dark bands) has been correlated with high water

temperature (Weber et al., 1975:146). The high-density, dark bands of the Lodgepole specimens are quite thick compared with many of the modern corals. If Weber's correlation is correct, seasonal variability in illumination and/or temperature may have been significant during Mississippian time on the marine shelf in what is now north-central Utah.

Baker and Weber (1975) measured variability in growth rate among scleractinians with depth. They found that *Montastrea annularis* has a higher growth rate at intermediate depths (9 m) than in very shallow water or deep water. It would be interesting to compare the values of mean light-band and dark-band thicknesses of the *Lithostrotionella* from the Lodgepole Formation to the data concerning recent corals. However, the dark-band thickness of the coral measured from the Lodgepole Formation is thicker than all values of their chart; also, such extrapolations among different orders of corals is not justified.

Annual growth lines are well-preserved on silicified specimens of *Zaphrentoides* (Figure 37). The number of growth lines, width of each increment between annuals, and total length were measured in ten corals. Shown in Figure 54 (top) is a graph of the average width of each successive growth increment. The average widths of growth intervals one through six, respectively, are (in mm) 5.8, 3.7, 3.6, 2.9, 1.7, 1.8. The graph shows that most of the growth occurred early in the life of the corals; in other words, the growth rate decreased during the ontogeny of the coral. Figure 54 (bottom) is a graph of the number of annual growth lines on specimens versus frequency. This curve suggests a constantly increasing death rate (Hallam, 1972). However, since

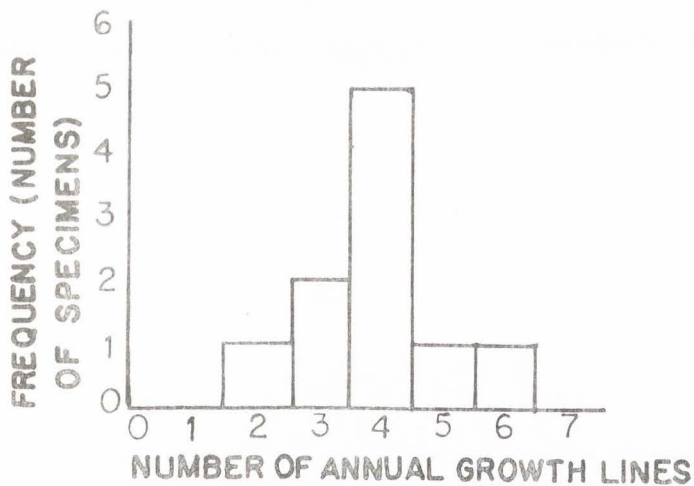
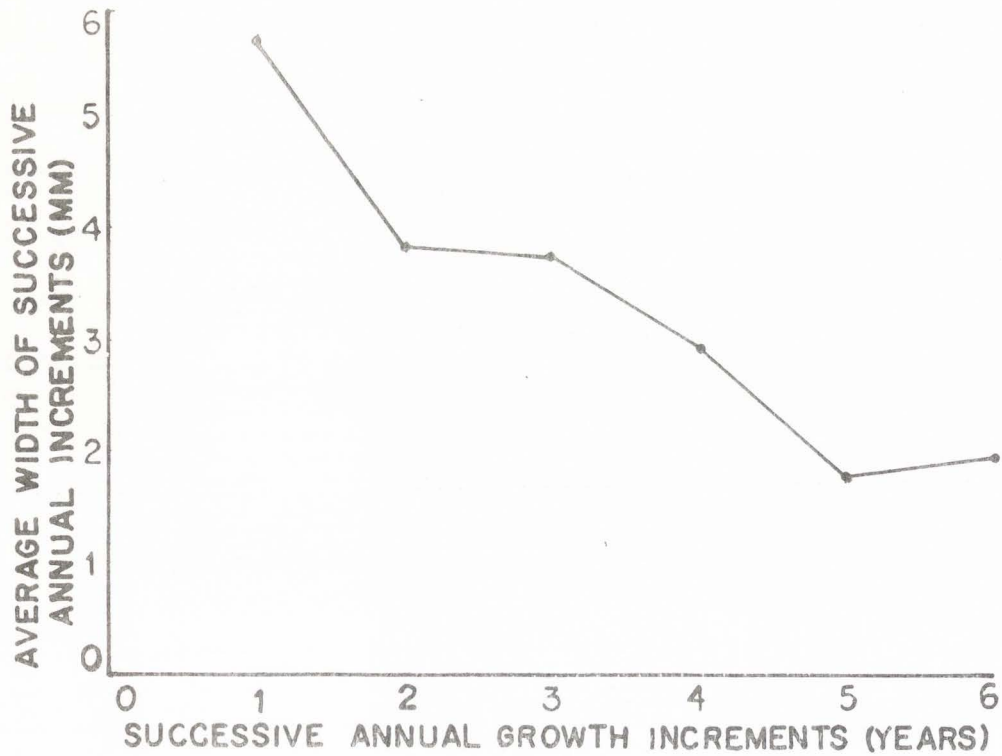


Figure 54. Average width of growth increments versus successive growth increments (upper graph), and frequency versus number of growth lines (lower graph).

this is a post-larval fossil assemblage, the high infant mortality which occurs in the planktonic larval stages of many marine benthic invertebrates is not reflected in the curve. The third graph (Figure 55) is of frequency versus total length, in class intervals. The moderately positive skew of this graph suggests a decreasing growth rate and an increasing death rate (Hallam, 1972). Although these results are highly suggestive, they must be interpreted with caution due to the small sample size.

CLASS INTERVALS

1. .5-1.0
2. 1.1-1.5
3. 1.6-2.0
4. 2.1-2.5
5. 2.6-3.0

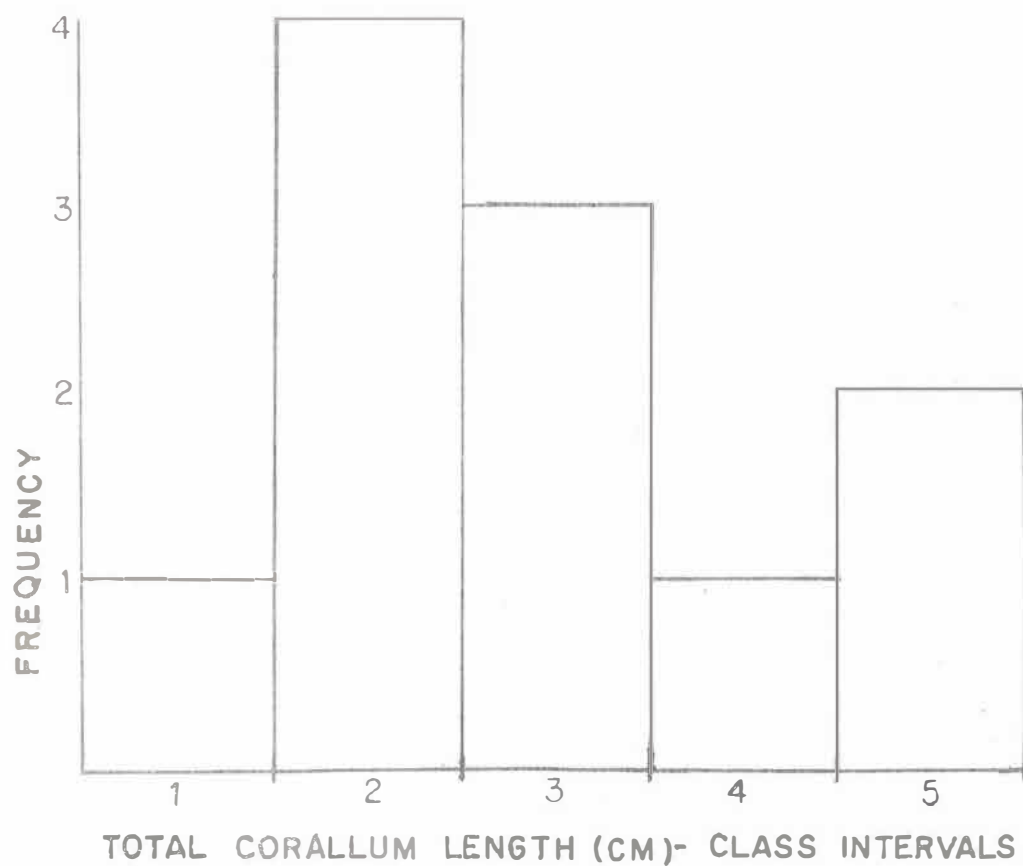


Figure 55. Graph of frequency of corals versus total corallum length (cm).

ANALYSIS OF INSOLUBLE RESIDUES

Procedure

Sixty-six insoluble residues were prepared from samples of the Lodgepole strata. At least one was prepared for the lithologic matrix associated with each taxon found in the sampled sections of the Lodgepole Formation. When a taxon was found in varying lithologies, an insoluble residue was obtained from each lithology. If a taxon was most often found in one particular matrix, only that matrix was dissolved.

After noting location and fossil type, and briefly describing each hand specimen, the specimen was cleaned and weighed. About 40 grams of the sample was ground to pea-sized chunks by the use of a rock hammer and a steel mortar and pestle. The sample then was placed in a glass beaker under a hood. A solution of 10 percent hydrochloric acid was slowly added to the beaker. When the effervescence had stopped (usually after several hours), about 200 ml of the solution was carefully decanted from the top. The solution then was agitated with a glass rod, after which the procedure was repeated until no visible reaction occurred upon addition of acid. The sample was rinsed with distilled water, which was later decanted. After air-drying for several hours, the sample was placed in an oven at 80°C for several hours. The insoluble-residue sample, when thoroughly dry, was weighed and

calculated as a percent of the original undissolved sample. A graph of the results is shown in Figure 53.

Insoluble-residues aid interpretation of paleo-environment in the following ways:

1. The insoluble mineral grains in limestone generally were derived from a terrigenous source. Determination of mineralogy is useful to inferences of provenance.
2. High amounts (weight percent) of insoluble residue may indicate proximity to source, hence, perhaps to shore.
3. High amounts (weight percent) of insoluble residue suggest quiet-water conditions, i.e., quiet water such as lagoons or offshore, beyond the zone of intense wave or current action.

Results

Some general observations about substrate associations of each phylum/class may be gleaned from Figure 53.

1. Solitary rugose corals were found in matrices with insoluble-residue weight percents ranging from 4.3 percent to 57.6 percent, with a mean value of approximately 14.0. The mean insoluble residue of rocks containing colonial rugose corals is 15.6 (range 5.9 to 30.5 percent), and that of tabulate corals is 12.5 percent (range 8.4 to 18.5 percent).
2. By comparison, associated faunal elements inferentially contemporaneous with corals display the following insoluble-residue contents in their respective associated lithologies.

Brachiopods yielded a mean value of 11.8, and a range of 1.6 to 30.8. Much variability was found within and between genera. The t-test showed that there is no significant difference in weight-percent insoluble residue among the orders of Brachiopoda. The weight-percent insoluble residue of rocks containing bryozoans ranges from 1.6 to 30.8, with a mean value of 15.0. This suggests that Lodgepole fenestellids were able to tolerate some influx of terrigenous detritus. The crinoids exhibit a very wide range of tolerance of terrigenous detritus as indexed by insoluble residue. Weight-percent insoluble residues range from 1.6 to 36.1, with a mean of 14.2.

Three values of insoluble residues (weight percent) were obtained from rocks containing trilobites. Two *Cruziana* samples were also prepared. The overall mean is 26.2; however, the mean value for the trilobites alone is 22.9. This value is the highest of any in the Lodgepole Formation, and indicates that the trilobites could tolerate considerable influx of terrigenous detritus, and in fact, as deposit feeders, may have preferred an environment where detritus accumulated.

The range of values (weight percent) of insoluble residues for gastropods is from 3.9 to 40.6, with a mean of 17.4. This is quite high in comparison with the other organisms except trilobites (mean = 22.9) and the algal structures (m = 19.8). This suggests that the gastropods could tolerate environments in which appreciable terrigenous detritus accumulated, and that they may have inhabited zones of sediment accumulation (i.e., quiet water) wherein they occupied a deposit-feeding niche.

The rock sample from which an insoluble residue was obtained for cephalopods contained trilobites and gastropods as well as the nautiloid. A weight-percent insoluble-residue value of 15.6 percent was obtained. The micritic nature of the rock, and presence of deposit feeders, suggest that the nautiloid came to rest in relatively quiet water.

The overall mean, insoluble-residue weight percent for trace fossils is 20.8. However, the traces collected from Porcupine Dam have much higher values than those from the other localities. The *Zoophycos* trace fossils, for example, averaged 8.6%. This is considerably lower than the traces of the *Cruziana* facies, which includes *Cruziana*, *Rhizocorallium* and vertical burrows. The fact that the insoluble-residue weight percent related to *Zoophycos* is lower than that of the other trace fossils may indicate that the creator of this trace lived farther offshore (i.e., at a greater distance from the source of terrigenous detritus) than the others. The average weight-percent of rocks containing algal structures is 19.8. These observations will be further discussed in the section on the bathymetric distribution of the corals and their associated fauna.

FAUNAL ASSOCIATIONS

General Statement

Slabs were collected from each of the collecting localities. Each slab was washed and the taxa found on each slab were noted. The objective of the analysis was to determine faunal associations with corals, i.e., to determine which organisms had a tendency to be found with, and which organisms tended to be mutually exclusive of, corals. The associations then will be discussed in terms of inferred environmental preferences and trophic structure.

A similarity matrix was constructed from the index of affinity, which was calculated from Fager's similarity coefficient, s_f (Fager and McGowan, 1963):

$$s_f = \frac{c}{\sqrt{N_1 N_2}} - \frac{1}{\sqrt{N_2}}$$

where

c = the number of occurrences of taxa N_1 and N_2 together

N_1 = the total number of occurrences of taxon N_1

N_2 = the number of occurrences of taxa N_2

$N_1 > N_2$

The index of affinity thus obtained may be either positive or negative. In order to obtain an index-of-affinity matrix composed only of positive numbers, the additive inverse of the smallest negative number

of the index of affinity was added to each of the numbers. These values were then inverted so that the smallest numbers represented closely associated taxa.

The two clustering methods that were used are the single linkage method (Sneath's method) and the average linkage method (Sokal and Michner method). A discussion of both of these methods may be found in Sokal and Sneath (1963:180-185). Figures 56 and 57 are the resulting dendrograms.

Table 6 is a breakdown of the faunal associates of the solitary rugose corals of the Lodgepole Formation. Three categories are shown: associated taxa, weakly associated taxa and unassociated taxa. These categories were based upon the indices of affinity levels at which the associations were formed. The upper half of the table refers to the single-linkage method, whereas the lower half of the table summarizes the results of the average-linkage method.

The following organisms were found to be closely associated with solitary rugose corals: the encrusting tabulate coral *Aulopora*, spiriferid brachiopods and crinoids. Bryozoans linked with corals at a low index of affinity with the single-linkage method, but not with the average-linkage method, which suggests that the bryozoans may not be as strongly associated with solitary rugose corals as are the spirifers or crinoids. The weakly associated fauna include the deposit feeders (trilobites and gastropods) and the strophomenid and productid brachiopods, many of which have been interpreted as adapted to soft substrates (Fursich and Hurst, 1974). The organisms/structures which are not

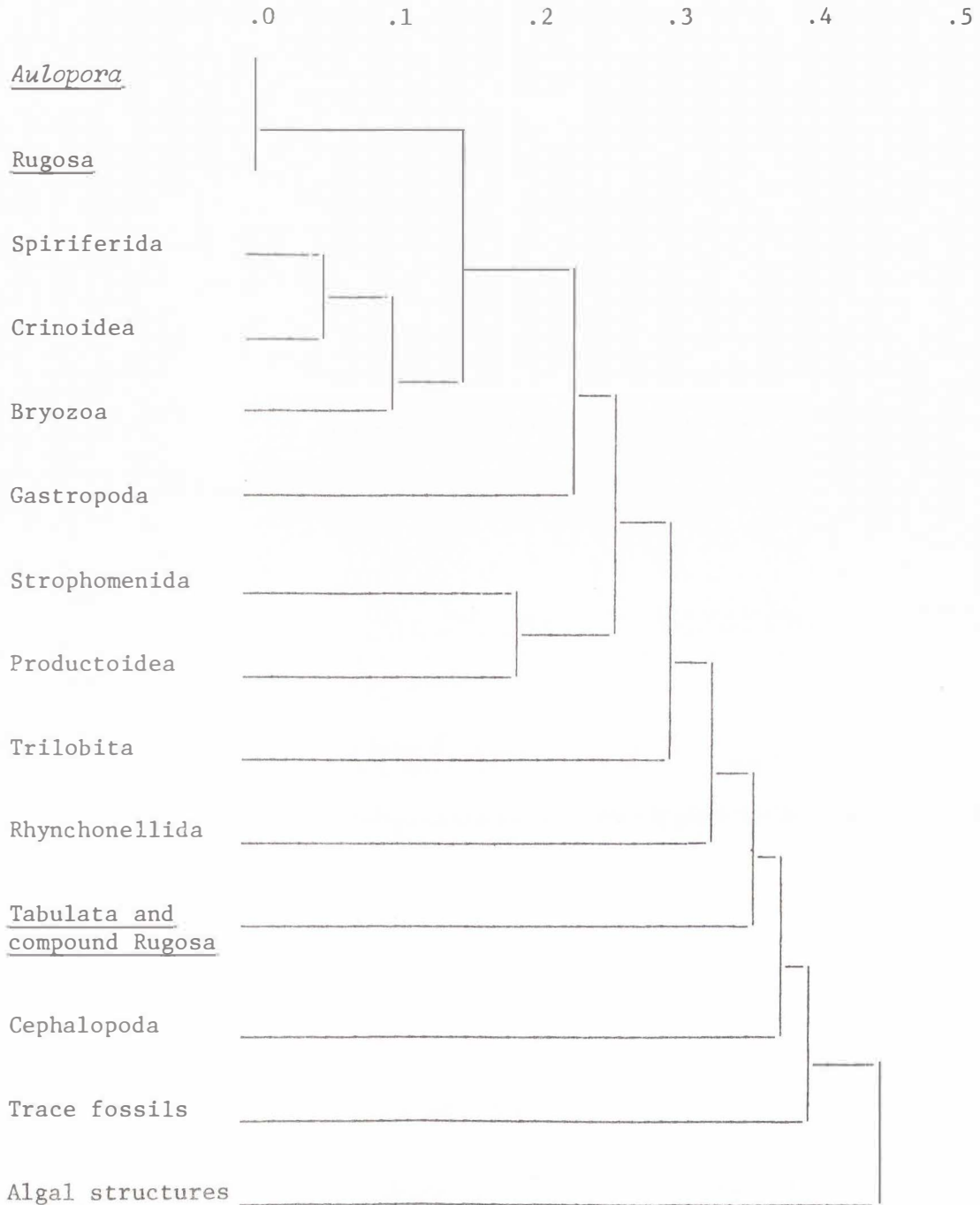


Figure 56. Dendrogram of faunal associations of the Lodgepole Formation, by single-linkage method. Clusters considered to be significant appear to the left of the .20 value of index of affinity.

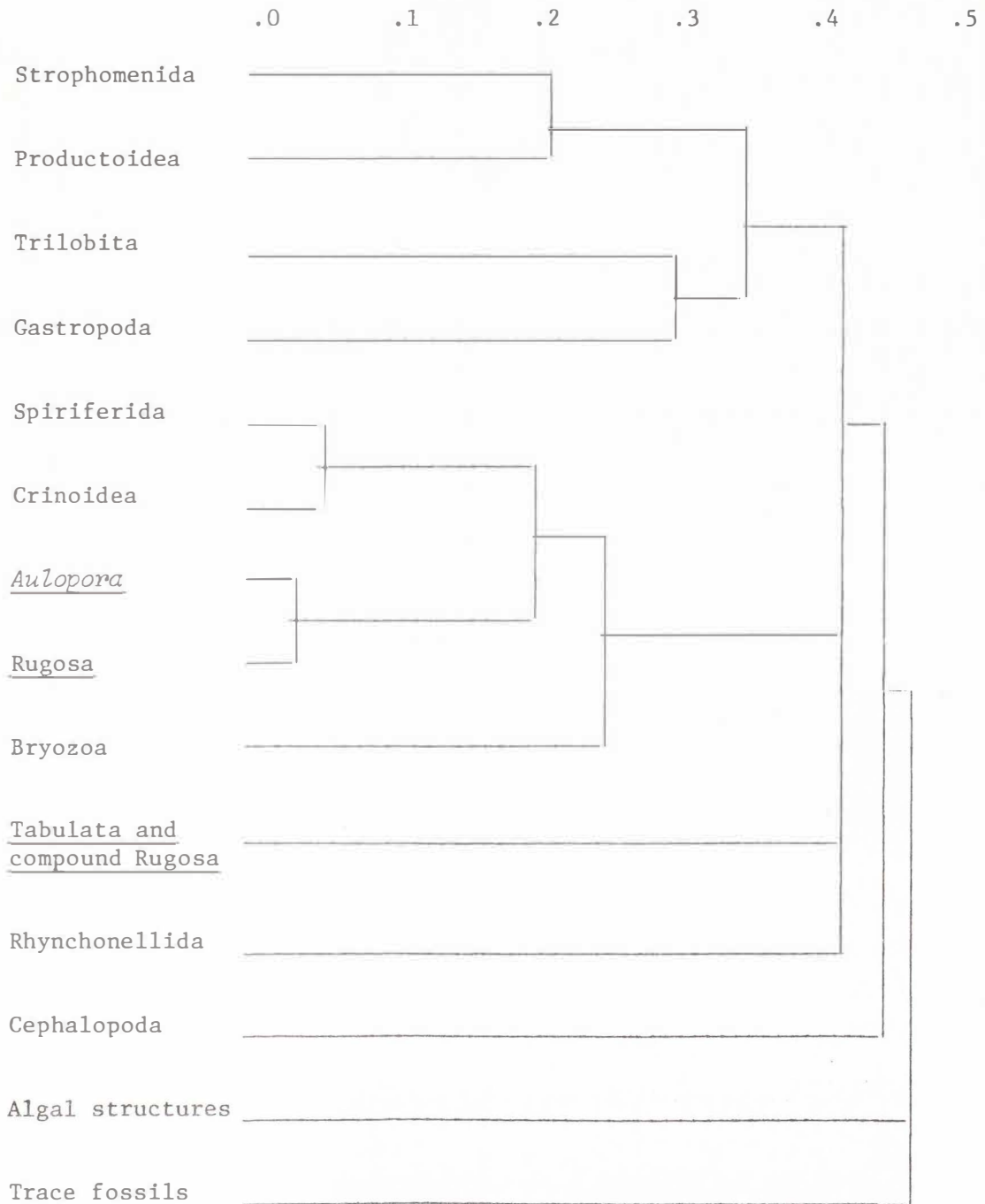


Figure 57. Dendrogram of faunal associations of the Lodgepole Formation, by average-linkage method. Clusters considered to be significant appear to the left of the .35 value of index of affinity.

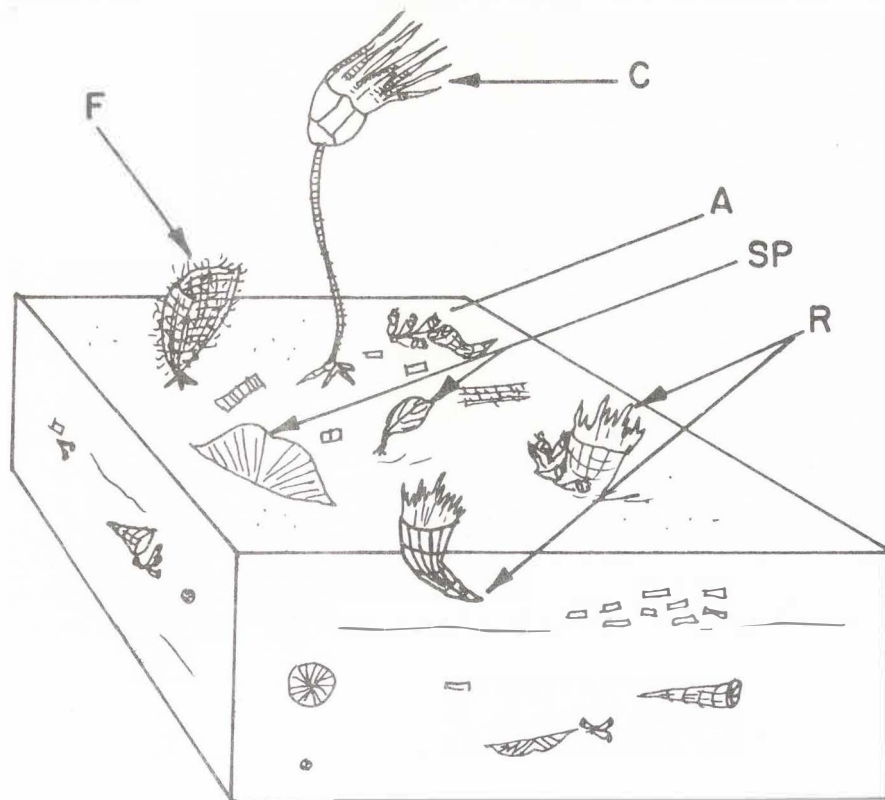
Table 6. Faunal associates of solitary rugose corals of the Lodgepole Formation

Solitary rugose corals	Associated with (i.a. < .20)	Weakly associated (i.a. > .20 < .25)	Not associated (i.a. > .25)
Single-linkage method	<i>Aulopora</i> spirifers crinoids bryozoans Rugosa	strophomenids productids gastropods	trilobites rhynchonellids Tabulate and compound rugose corals cephalopods trace fossils algal structures
	(i.a. < .20)	(i.a. > .20 < .35)	(i.a. > .35)
Average-linkage method	<i>Aulopora</i> spirifers crinoids Rugosa	strophomenids productids trilobites gastropods bryozoans	Tabulate and compound rugose corals rhynchonellids cephalopods algal structures trace fossils

associated with solitary rugose corals are the nautiloid cephalopods, tabulate and compound rugose corals, rhynchonellid brachiopods, trace fossils and algal structures. At least two of these 'nonassociations' are artifact of the sampling procedure. The compound rugose and tabulate corals, considered as one category, were often completely weathered free of the surrounding rock matrix and thereby also of the associated fauna. Cephalopods are sufficiently rare in the collection under consideration that their associates do not show up in this analysis. However, in the outcrop nautiloid cephalopods were found closely associated with trilobites, gastropods, bryozoans, brachiopods and small, solitary rugose corals. The fact that the algal structures and trace fossils were not associated with solitary rugose corals is more readily interpreted as the result of mutual exclusion. No organisms were found associated with algal structures; similarly, most of the trace fossils which were collected were not found with body fossils.

Two different assemblages of organisms appeared in the dendrograms. The first, here designated Association 1, includes *Aulopora*, solitary rugose corals, spiriferid brachiopods, crinoids and bryozoans. Association 2 consists of strophomenid brachiopods, productid brachiopods, trilobites and gastropods. These associations are depicted in Figures 58 and 59.

The problem of interpretation of the two closely associated assemblages of organisms will be approached in two ways. First biological interactions among the organisms will be considered. Secondly environmental or physical parameters which may have affected the distribution of organisms will be discussed.



- F FENESTELLID BRYOZOANS
 C CRINOID
 SP SPIRIFERID BRACHIOPODS
 R RUGOSE CORALS (SOLITARY)
 A AULOPORA

Figure 58. Block diagram depicting Association I.

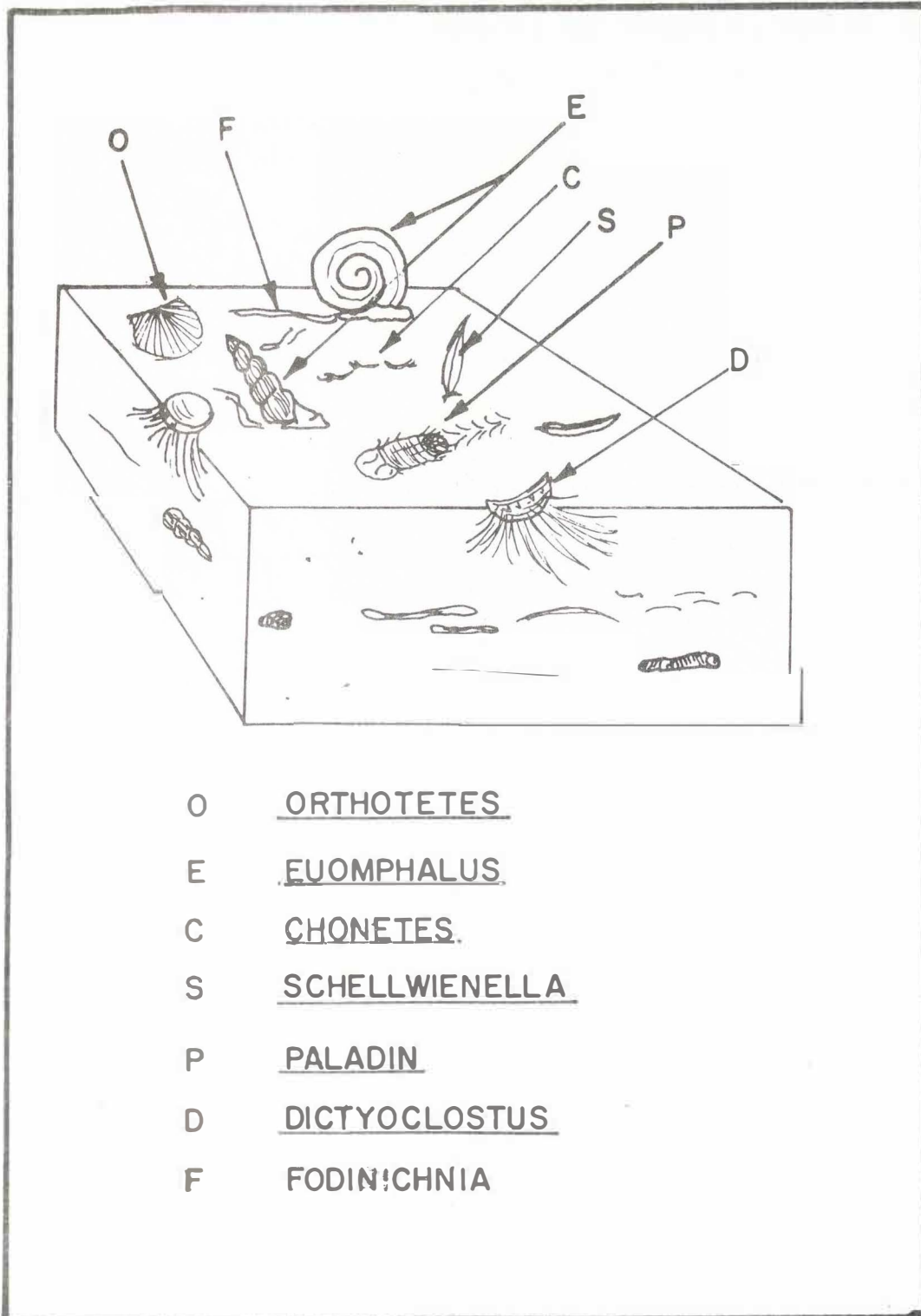


Figure 59. Block diagram depicting Association 2.

Biological Interactions Involving Corals

The corals of the Lodgepole Formation probably interacted with the other taxa in numerous ways, most of which were not recorded. The symbiotic relationship existing between modern hermatypic corals and zooxanthellae may have existed during the Mississippian, but there is no proof that Paleozoic corals incorporated algae within their tissues. Yakovlev (1926) stated that a symbiotic relationship existed between *Aulopora*, an encrusting tabulate coral, and various Carboniferous brachiopods. Presumably, the coral's nematocysts (stinging cells) protected brachiopods from predators, and the coral benefitted from the feeding currents set up by the brachiopod. *Aulopora* was found in the Lodgepole encrusting a strophomenid brachiopod valve. Hubbard (1970) found *Aulopora* encrusting both rugose corals and brachiopods. *Aulopora* and rugose corals are very closely associated in the Lodgepole. This association is interpreted to be a representation of the commensal or symbiotic relationship between the tabulate coral and rugose corals. Parasitism is common in the modern coral ecosystem, but no evidence of boring or encrustation of corals by other organisms was found in the Lodgepole.

Hubbard (1970) found juvenile rugose corals attached to adult corals. Sando (1977) found coiled protocoralla and proposed that some juvenile Mississippian corals were epiplanktonic (i.e., coiled around algae). In the Lodgepole, evidence that juvenile corals attached to narrow linear objects was found. An upright rugose coral found

"growing in close proximity to fasciculate lithostrotionid corallum" was interpreted by Hubbard (1970:202) to have derived shelter from the large lithostrotionid.

It seems likely that the corals of the Lodgepole shared similar biological relationships with the associated organisms.

The biotic components of any ecosystem may be separated into the following categories: primary producer (autotroph), primary consumer (heterotroph), herbivore, carnivore and decomposer. Of these only the primary producer and decomposer are essential to the operation of the system. A basic feature of the ecosystem is loss of energy at each successive step of the chain.

At each step or transfer of energy in the food chain, a considerable amount of potential energy is lost as heat, until ultimately the amount of available energy is so small that few organisms can be supported on that source alone. (Smith, 1974:71).

This loss of energy results in a decreasing amount of biomass at higher levels, and limits the number of levels which are supported.

Because the preserved fauna of the Lodgepole Formation are predominantly benthic organisms, and predators and primary producers are rarely preserved, a breakdown into the ecologic types mentioned above is difficult. An approach which is much more easily applied to fossil organisms was developed in 1948 (published in the United States in 1957) by a Russian scientist, E. P. Turpaeva. She proposed five feeding groups which describe benthic feeding types. The groups include suspension feeders, deposit feeders, scavengers and browsing herbivores. By using abundance data, Turpaeva (1957) analyzed communities in terms of trophic relationships, and reached the following conclusions.

1. A community is usually dominated by one trophic group.
2. If the most dominant species (in terms of biomass) in the community belongs to one particular trophic group, the next most dominant species belongs to a different group. Thus, to quote Turpaeva (1957:144), "the dominant group of species in a biocoenosis consists of representatives of different food groups."
3. Among the various species of a community which belongs to a given trophic group, a single species commonly dominates the group in terms of biomass.
4. Thus, the several most dominant species in the benthic community use the available food resources more fully than if they fed at a single level, and feeding competition is minimized. (Walker, 1972:83).

All of the organisms of the *Aulopora*/rugose coral/spirifer/crinoid/bryozoan association, here designated Association 1, are suspension feeders. Food resources were probably subdivided by vertical stratification, as these organisms feed at varying heights in the water mass (Figure 58). "This spatial subdivision permits a diversity of feeding relationships even though the variety of food may be restricted" (Walker and Bambach, 1974:69). A general definition of suspension feeders is that they are animals that "remove food from the suspension in the water mass without need to subdue or dismember particles" (Walker and Bambach, 1974:74).

Food resources vary in quantity and type depending upon height above the sediment-water interface. Swimming and floating organisms and dissolved and colloidal organic particles are found both high and low in the water mass; resuspended organic detritus is quantitatively important only low in the water mass (Walker and Bambach, 1974). Differences in feeding height, feeding mechanisms and mode of life probably aided in the minimization of competition within Association 1.

Association 2 (strophomenid/productid/trilobite/gastropod) is composed of suspension feeders (or filter feeders, which are somewhat specialized suspension feeders) and deposit feeders. Gastropods are vagile epifaunal herbivorous browsers; trilobites are also vagile deposit feeders. Deposit feeders "remove food from sediment either selectively or nonselectively, without need to subdue or dismember particles" (Walker and Bambach, 1974:74). Particulate organic detritus, living and dead members of benthic flora and fauna, and organic-rich grains comprise the food of deposit feeders, according to Walker and Bambach (1974). Walker and Laporte (1970) cited evidence that loxone-matid gastropods had adaptations for strong gill currents, which suggests that the mantle cavity may have required clearing of mud.

Biological interactions among the organisms of the Lodgepole are not interpreted to have been the controlling factor in their distribution and association. The analysis of assemblages, or communities, is beset by the problem of uncertainty as to the fundamental cause of associations. Johnson (1972:109) defined community as an "assemblage of organisms inhabiting a specified space." Other workers (Hedgpeth, 1957) have emphasized biological interactions, and considered communities as ecological units. Thorson (1957:471) cited the ideas of Lindroth (1935) who stated that "... the animal species of marine level bottoms are, as to their distribution, in broad outline governed by the 'external milieu,' by the direct physical-chemical factors. The biotic factors are of subordinate significance."

It is simply a matter of opinion as to what "force" caused associations of organisms. In the Lodgepole Formation, the associations are interpreted to have formed as a consequence of environmental preferences of the constituent organisms: Biological interaction almost certainly existed, but is not interpreted to have been the controlling factor.

Physical Factors Which May Have Controlled
or Influenced Distribution

The suspension-feeding association (Association 1) is interpreted to have inhabited a higher energy (in terms of water turbulence) environment than Association 2. Suspended food particles "... will settle out of the water onto the sea floor under very quiet conditions, whereas under more turbulent conditions, food particles will remain in suspension and those on the sea floor will be swept up into suspension ..." (Stanton and Dodd, 1976:328). Water energy also affects substrate texture. Finer-grained sediments reflect quiet-water conditions, whereas coarser sediments are produced and deposited under higher energy conditions. The suspension-feeding association is interpreted to have formed under shallow, subtidal conditions. The deposit- and suspension-feeding association is interpreted to have formed under quiet-water conditions; the silty, fine-grained impure sediments which characterize the lower Lodgepole (Porcupine Dam site) are interpreted to have formed in nearshore, protected lagoons, on the basis of sedimentologic evidence (cryptalgalaminites, high amounts of terrigenous

detritus as indicated by insoluble residues, intraclasts, ripple marks), paleontologic evidence (fauna dominated by organisms well-adapted to soft, muddy bottoms such as gastropods, trilobites and resupinate brachiopods) and trace fossils (both shallow simple vertical burrows and, more commonly, grazing traces such as *Cruziana*).

The suspension-feeding association formed in well-agitated waters, and is characteristically preserved in wackestones, packstones or even crinoidal grainstones. Trace fossils are not as common, and, where observed, are usually of the *Zoophycos* type.

BATHYMETRIC RECONSTRUCTION

Inferences regarding the bathymetric distribution of the fossil organisms of the Lodgepole are limited because the sampling had little stratigraphic control. However, a bathymetric reconstruction (Plate 1) was attempted on the basis of the functional morphology of the organism, the rock type with which each is most often associated, the insoluble-residue results, and the trace fossils and sedimentary structures which characterize the rock in which the organisms are enclosed.

The Lodgepole Formation, according to Rose (1976) and Sando (1976), was deposited during a widespread Kinderhookian transgression over the Cordilleran Platform. Rose (1976:458) stated that an ancient carbonate shelf margin formed a "... curvilinear, presumably constructional ridge trending northeast across Utah from southern Nevada, then curving north and northwest across eastern Idaho, and finally crossing into westernmost Montana." This stratigraphic reef (Dunham, 1970) formed a barrier of sorts, behind which accumulated "shelf interior evaporites and low-energy, very shallow water dolomites and limestones" (Rose, 1976:459). Sando (1976:322) described the earliest portion of the Kinderhookian transgression in the following way: "As the Mississippian sea advanced rapidly onto the Cordilleran platform over a terrane composed of Cambrian, Ordovician and Devonian rocks, terrigenous and carbonate sediments were deposited in several shallow marine basins separated by

low-lying land." A later phase of the transgression initiated "shelf carbonate deposition." According to the interpretations of Rose (1976) and Sando (1976), the Lodgepole was deposited under intertidal and subtidal conditions. Three intergrading depth zones were identified in the Lodgepole based on a model of carbonate deposition in epeiric seas proposed by Irwin (1965). The three marine hydraulic zones which Irwin (1965) discussed are depicted in Figure 60, and the corresponding sedimentation zones are depicted in Figure 61. Zone X is described as "A hundreds-of-miles wide, low-energy zone occurring in the open sea beneath wave depth where marine currents are the only form of hydraulic energy acting upon the bottom." Zone X is interpreted to have been the environment in which the pelletal, fossiliferous mudstones and wackestones of the Lodgepole formed. X-ray diffraction of a representative wackestone indicated the presence of the mineral calcite. Secondary dolomite (Sabins, 1962) was found in a stained thin section of a wackestone. Influx of terrigenous detritus (as indexed by amount of insoluble residue) is rather low, although it is higher than in Zone Y. X-ray diffraction of insoluble residues indicated the mineral quartz, although in small amounts. Primary abiotic sedimentary structures are rare, and bedding is horizontal. The biotic sedimentary structures, or trace fossils, include *Zoophycos*, *Planolites*, *Cruziana*, *Rhizocorallum* and irregular surface grazing patterns. *Zoophycos* represents the fodichnia of deposit feeders and is found from the sublittoral to the bathyal (below wave base), according to Seilacher (1964). *Cruziana* (Figure 62)

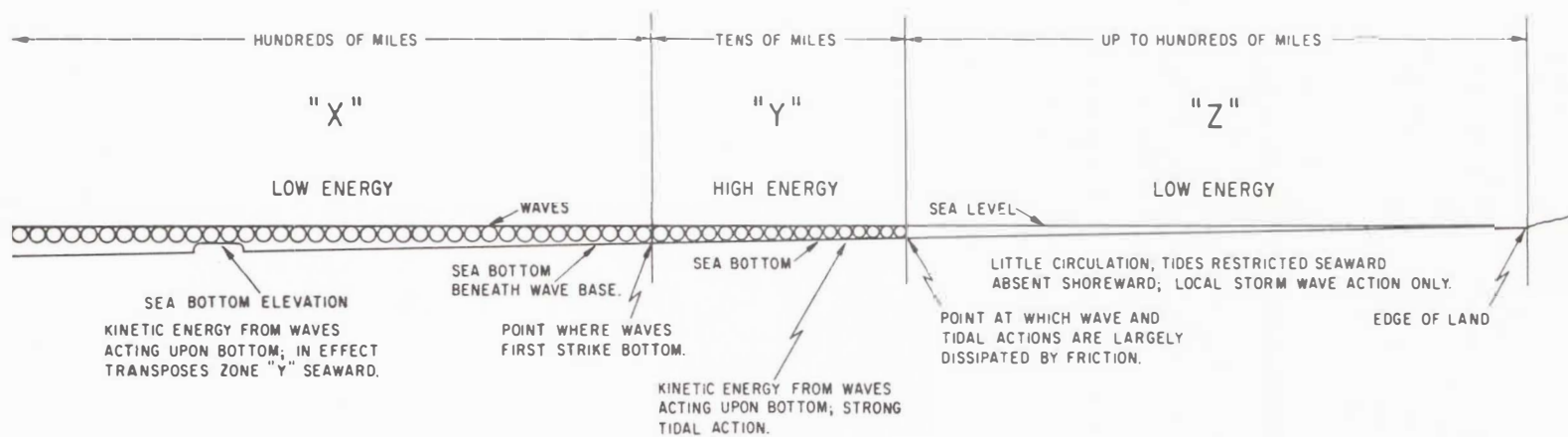


Figure 60. Diagram of the three energy zones in epeiric seas (from Irwin, 1965:450).

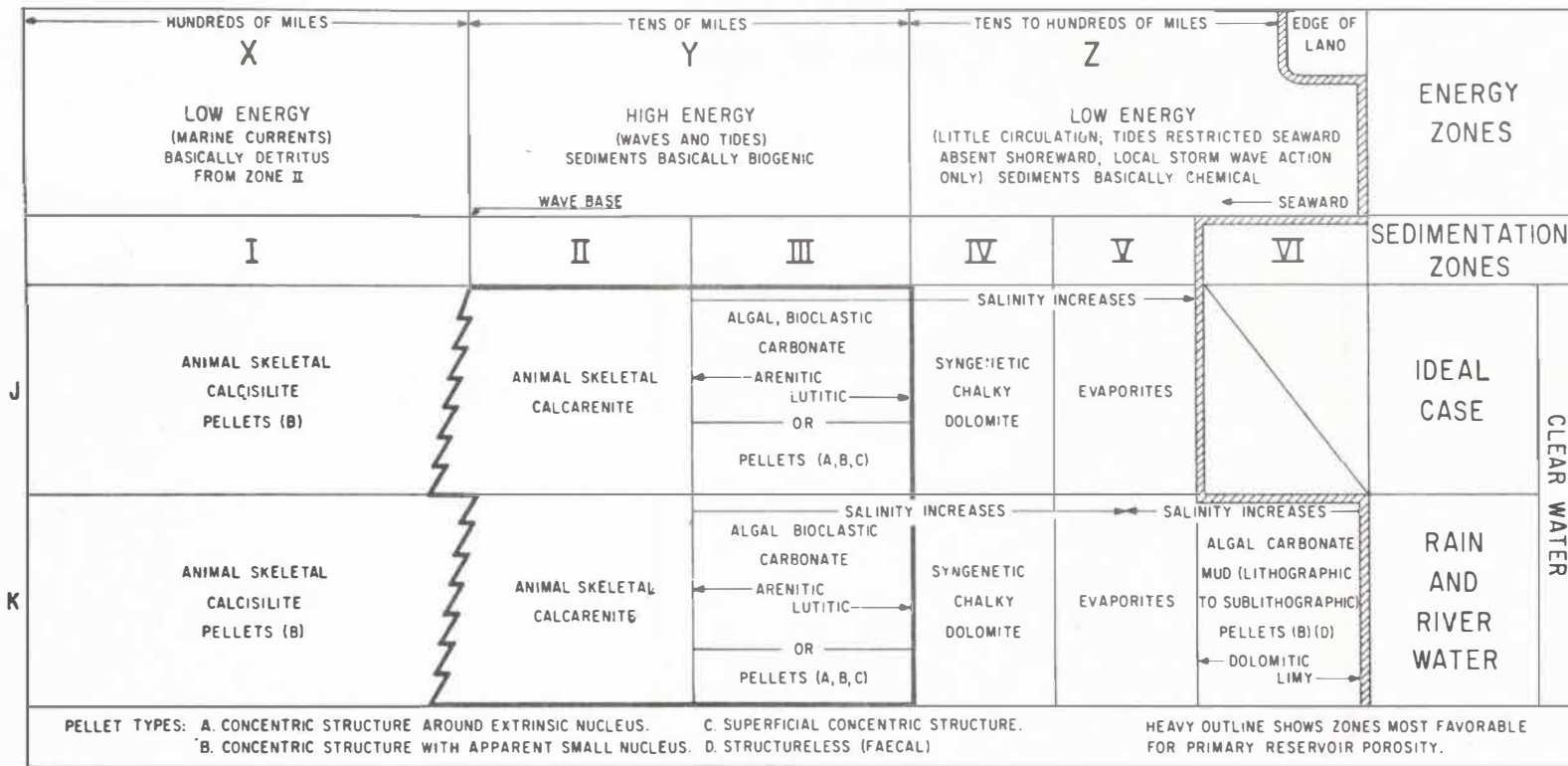


Figure 61. Clear water energy and sedimentation zones (from Irwin, 1965:452).

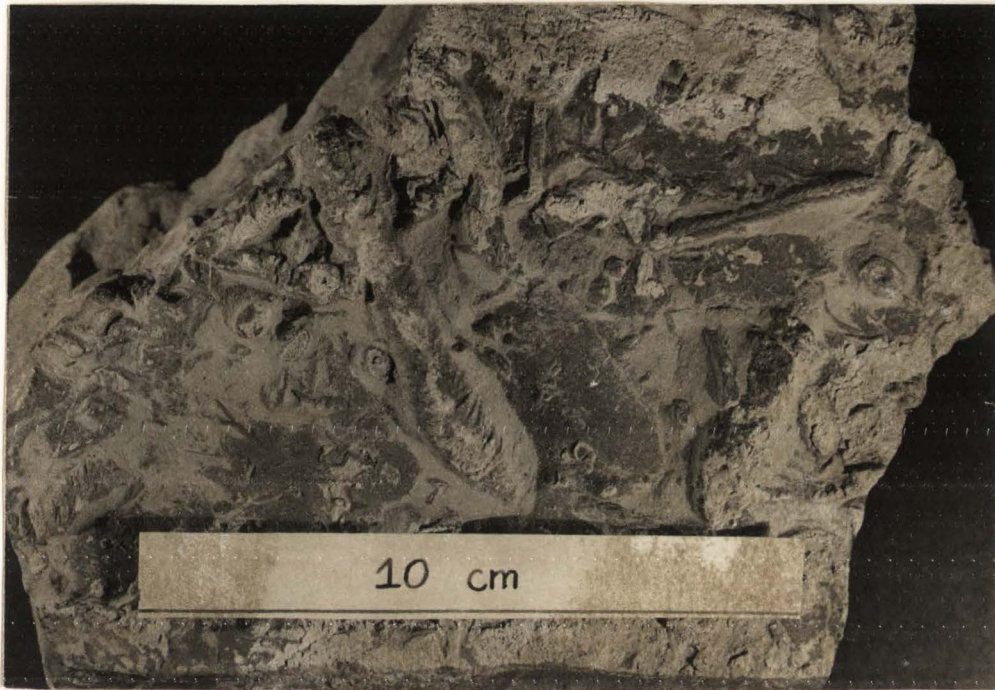


Figure 62. The trace fossils *Cruziana* and *Planolites* (M-1-P).

is also a fodichnia type of trace and is found at depths ranging from the littoral to the sublittoral, both above and below wave base (Seilacher, 1964). *Planolites* has been interpreted by Fursich (1975) as an intertidal to deep subtidal trace fossil. *Rhizocorallum irregulare* is found in rocks which formed at shallow to intermediate subtidal depths (Fursich, 1975; Seilacher, 1964). In the field (Beirdneau Hollow) *Rhizocorallum irregulare* was found in a veneer of sediment directly on top of a hemispherical lithostrotionid, which supports the hypothesis that Type IV colonial corals inhabited Zone X. In terms of the clustered organisms, both Association 1 and 2 organisms were found in medium-to-dark gray wackestones, with little or no evidence of current or wave activity. Deposit feeders as well as suspension feeders are present in Zone X rocks. The following organisms, on the basis of associated lithology, insoluble-residue amounts and mode of life, are interpreted to have inhabited an offshore, subtidal environment: gastropods (*Loxonema*, *Platyceras*, *Straparolus*, bellerophontids); brachiopods (*Dictyoclostus*, *Orthotetes*, *Schellwienella*, *Chonetes*, *Cleiothyridina*, *Spirifer*); crinoids (*Platycrinites*); bryozoans (*Fenestella*, *Ptilopora*); corals (*Caninia*, *Vesiculophyllum*, *Syringopora*, *Lithostrotionella*, *Rylstonia*, *Turbophyllum*, *Aulopora*). The fact that articulated crinoid columnals, rare complete crinoid specimens and complete fenestellid bryozoans remained in death position suggests that quiet-water conditions prevailed. Straight (Type 1) solitary rugose corals are commonly preserved in Zone X rocks. Type I corals are inferred to have inhabited the seaward edge of this zone, whereas Type IV corals may have inhabited

the landward edge. Type V corals have been interpreted to have formed as a result of high rates of sedimentation. The fine-grained detritus shed from Zone Y into Zone X (Irwin, 1965) may have been sufficient to encourage vertical growth among some of the colonial corals, particularly at the landward edge of Zone X. Type VI corals may also have inhabited the landward edge of Zone X; the rounded bases and sediment-rich areas of some of the Type VI coralla indicate that sedimentation was at times sufficient to modify the colony morphology. If Zone X is the site of accumulation of fine-grained detritus derived from Zone Y, and that influx of terrigenous detritus in the offshore subtidal environment is quite low, then even the corals which had a poor sediment-rejection capability could have inhabited Zone X. Most of the corals commonly found in micritic rocks were inferred on the basis of calical features to have been poor-to-intermediate in efficiency as sediment-rejectors.

Heckel (1972:252), in a discussion of the Irwin model, stated that

In deeper water below effective wave base, the bottom is sufficiently undisturbed to allow fine sediment to settle out. If the bottom is kept well-oxygenated by currents, the biota will be diverse and supply coarser material in the form of shells.

The diverse fauna of Zone X rocks suggests stable, offshore habitats under continual marine submergence.

Zone Y is located landward of Zone X, and was described as "An intermediate, high-energy belt, tens of miles wide, beginning where waves first impinge upon the sea floor and thus expend their kinetic energy upon the bottom, extending landward to the limit of tidal action." In the Lodgepole Formation packstones, bioclastic grainstones,

boundstones and fossiliferous wackestones were formed in this zone. X-ray diffraction indicated the mineral calcite. Insoluble residues (quartz, by X-ray diffraction) obtained from rocks interpreted to have formed in Zone Y are low, which suggests that water turbulence may have prevented deposition of fine-grained detritus. The primary abiotic structures which are interpreted to have formed in Zone Y include erosion surfaces, cross-bedding, current-oriented deposits of fossils, intraclasts and small cut-and-fill structures. An oncolite (SS-C/LLH-C) which was collected at Spring Hollow originally formed in an agitated, shallow-water environment (Logan et al., 1964; Aitken, 1967). Conspicuously absent from this zone are the deposit-feeding organisms and the trace fossils with which they are commonly associated, which suggests that there may not have been sufficient accumulated detritus in this zone to accommodate deposit feeders. Association 1 organisms, or suspension feeders, dominated Zone Y. The fossil organisms which were found in Zone Y rocks include brachiopods (*Spirifer*, *Cyrtospirifer*, *Chonetes*), corals (*Vesiculophyllum*, *Amygdalophyllum*, *Zaphrentoides*, *Lithostrotion*, *Lithostrotionella*, *Syringopora*, *Michelinia*, *Aulopora*), and disarticulated crinoidal and bryozoan debris. Algal structures (LL-H and SS-C of Logan et al., 1964) may have formed in Zone Y (Figure 63). Types II and II colonial corals may have inhabited this zone, as their morphologies were interpreted to have been the result of excessive turbulence and/or extreme shallowness of the water. Types 2 and 3 (geniculate) solitary corals probably formed most often in this zone because corals would be susceptible to scouring, toppling and subsequent redirected growth in an agitated

Figure 63. Laterally-linked hemispheroidal stromatolites (M-2-L).

environment. The corals which were found in Zone Y rocks include very efficient sediment rejectors (*Lithostrotionella*, *Lithostrotion*, *Zaphrentoides*), moderately efficient sediment rejectors (*Vesiculophyllum*, *Amygdalophyllum*, *Aulopora*, *Syringopora*) and one poor sediment rejector (*Michelinia*). The preponderance of efficient corals suggests that larger sediment grain sizes could be rejected by the polyps. Corals with imbricated corallites may have inhabited the zone of wave and current action; the preferred growth orientation is thus interpreted as a positive rheotropic response (i.e., the coral grew with polyps facing the current).

Zone Z is described as

An extremely shallow, low-energy zone, which may be hundreds of miles wide, occurring landward of Zone Y in which there is little circulation of water, where tides are essentially wanting and in which the only wave action is that produced by local storms. (Irwin, 1965:450)

Micritic rocks formed in this zone, mainly impure pelletal mudstones and wackestones and laminated calcilutites. Interbedded with these rocks are skeletal packstones. X-ray diffraction of rock samples indicated the minerals calcite, quartz and an unidentified clay mineral. Rocks collected from Zone Z contain considerably greater amounts of insoluble detritus, as indexed by the amounts of insoluble residue. X-ray diffraction of insoluble residues indicated the mineral quartz. The following abiotic sedimentary structures were found: lithiclasts, oscillation ripple marks, desiccation cracks (Figure 64), limestone-pebble conglomerates, small-scale cross-lamination, and scour-and-fill structures. Storms might have resulted in the formation of rip-up clasts. The cross-laminae and ripple marks suggest a moderate rate

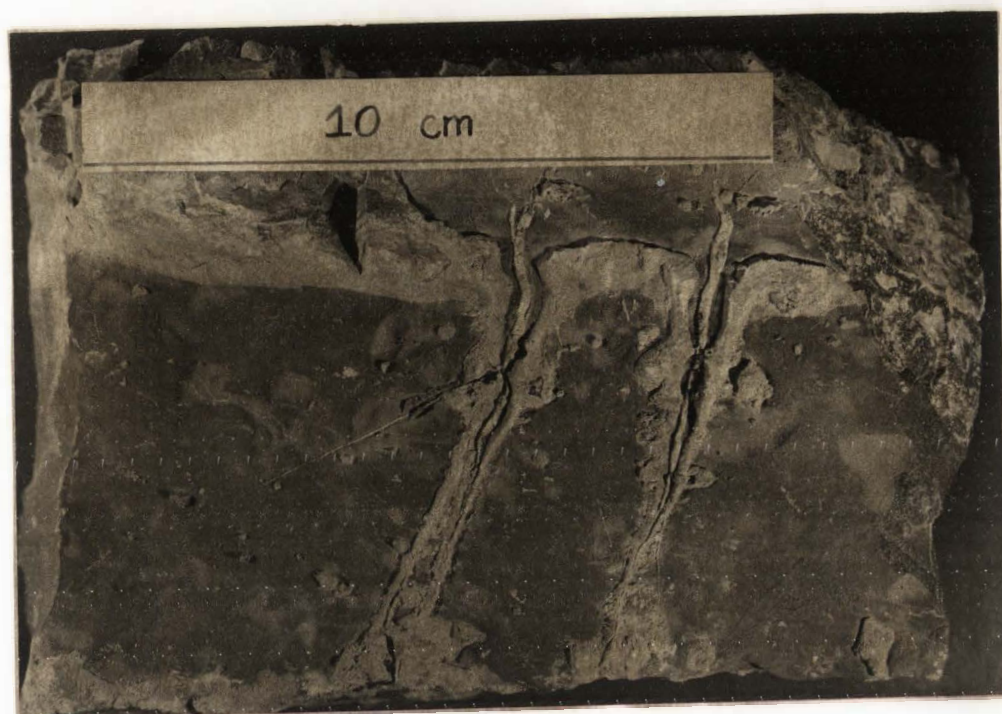


Figure 64. Spar-filled mudcracks (M-3-L).

of deposition. Scour-and-fill structures and erosional surfaces with minor relief suggest, respectively, relatively high current or wave action and intermittent subaerial exposure. Heckel (1972:247) discussed laminated calcilutites as indicators of "low-lying shorelines from extremely shallow subtidal to supratidal environments." The lamination of these "sea-margin transitional deposits" resulted from "intermittent deposition of sediment of slightly differing texture and composition," the deposition of which might be controlled by algal mats.

Trace fossils are abundant in Zone Z rocks, and include both surface types (*Cruziana*, *Planolites*, irregular surface burrows), and shallow (3-5 cm) oblique and vertical burrows. The fauna in Zone Z is dominated by deposit feeders (gastropods and trilobites), although some suspension feeders also were present (the brachiopods *Orthotetes*, *Dictyoclostus*, *Composita*, *Cleithyridina*, *Cyrtospirifer*, *Chonetes*; bellerophonid gastropods; the corals *Zaphrentoides*, *Aulopora*, *Cladochonus*, *Vesiculophyllum*). Crinoidal debris is also present in Zone Z rocks. Conspicuously absent from this facies are the colonial rugose corals; other than the encrusting tabulates, no colonial corals were found. Types 1, 2, and 5 rugose corals inhabited Zone Z. *Zaphrentoides* is fairly abundant; *Zaphrentoides* was interpreted as a very efficient sediment rejector. The lower faunal diversity of the Zone Z rocks is interpreted to reflect the greater degree of variability of the tidal-flat lagoon environment.

Table 7 is a summary of the information presented in this section. The lithologic, mineralogic, sedimentologic, paleontologic and environmental aspects of each zone (X, Y, Z) are presented.

Table 7. Summary of the bathymetric reconstruction

Hydraulic zones (Irwin, 1965)		X	Y	Z
Lithology	pelletal, fossiliferous mudstones and wacke stones	fossiliferous packstones bioclastic grainstones, boundstones	impure, laminated peletal mudstones and wackestones; skeletal calcarenites	
Mineralogy	calcite, secondary dolomite	calcite	calcite, quartz, clay	
Relative amount of insoluble residue	intermediate	low	high	
Sedimentary structures				
a. biotic	<i>Zoophycos</i> <i>Rhizocorallum</i> <i>Planolites</i> <i>Cruziana</i> horizontal burrows	oncolites algal stromatolites	algal stromatolites <i>Cruziana</i> <i>Planolites</i> algal laminae vertical and oblique burrows	
b. Abiotic	horizontal bedding	cross-stratification mudcracks	mudcracks erosion surfaces oscillation ripple marks scour-and-fill structures small scale cross-stratification limestone-pebble conglomerates	

Table 7. Continued

Hydraulic zones (Irwin, 1965)	X	Y	Z
Paleontology			
a. Feeding types (relative abundance)	suspension feeders > deposit feeders	suspension feeders > deposit feeders	deposit feeders > suspension feeders
b. Coral morphologic types	I, IV, V, VI; 1, 2, 4, 5	II, III, IV, VI; 2, 3, 5	1, 2, 5
c. Coral genera	<i>Caninia</i> <i>Vesicolophyllum</i> <i>Syringopora</i> <i>Aulopora</i> <i>Turbophyllum</i> <i>Lithostrotionella</i> <i>Lithostrotion</i>	<i>Vesiculophyllum</i> <i>Zaphrentoides</i> <i>Lithostrotion</i> <i>Lithostrotionella</i> <i>Michelinia</i> <i>Amygdalophyllum</i> <i>Aulopora</i>	<i>Zaphrentoides</i> <i>Vesiculophyllum</i> <i>Aulopora</i> <i>Cladochonus</i>
d. Associated taxa	gastropods trilobites brachiopods crinoids bryozoans cephalopods	brachiopods disarticulated crinoids and bryozoan	gastropods trilobites brachiopods disarticulated crinoids

Table 7. Continued

Hydraulic zones (Irwin, 1965)	X	Y	Z
Environment	open, shallow shelf; low energy; marine cur- rents; good circulation; stable environment; di- verse biota; low-to- moderate terrigenous influx	shallow, high energy; waves, marine currents and tidal action; shoal- type deposit, possibly with topographic relief	shallow, low energy; poor circulation; local storm action; tidal flat-lagoon; highly variable environ- ment; biota less diverse than Zone X

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