

PALEOAUTECOLOGY OF *CANINIA TORQUIA* (OWEN)  
FROM THE BEIL LIMESTONE MEMBER  
(PENNSYLVANIAN, VIRGILIAN), KANSAS<sup>1</sup>

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ABSTRACT

Nine facies are described within the Beil Limestone Member in the Forest City and Cherokee basins in eastern Kansas. The lower Beil is characterized by carbonate rocks indicative of deposition in a transgressing, shallow sea where conditions were unfavorable for abundant organic growth. As the transgression continued, a diverse fauna developed. The middle Beil records a shift from transgression to regression, and the fauna began to decline. The upper Beil was deposited in very shallow water that supported only sediment-binding algae and other organisms tolerant of a restricted environment.

The coral fauna of the Beil Member is dominated by one species of rugose coral, *Caninia torquia* (Owen), which is abundant in rocks representing maximum transgression of the unit, and where phylloid algae formed incipient mounds. Other organisms, particularly bryozoans, commonly encrust the corals; but none displays a preferred position. Corals occur in poorly defined clusters, possibly as the result of concentration of asexually budded juveniles near parents. Associated with specimens of *C. torquia* are tabulate corals, bryozoans, brachiopods, and crinoids, all of which have been interpreted as "normal marine" organisms.

Four growth forms, probably related to substrate stability, are recognized in *Caninia torquia*. Although data are sparse, small trochoid forms occur in calcareous shales; geniculated trochoid and geniculated ceratoid to cylindrical corallites occur in argillaceous carbonates; and very large, robust corallites are restricted to phylloid algae facies. Populations of *C. torquia* were characterized by high juvenile mortality. Most budded juveniles died on contact with the substrate after detachment from the parent; those surviving remained free-living. Damage during life, evidenced by disruption of growth lines and internal deformation, was repaired as growth continued.

Principal components analysis partly supports hypotheses that corals in argillaceous facies are smaller than those in phylloid algae facies. Correlation coefficients indicate that maximum diameter is highly correlated with many other characters and is sufficient to characterize the size of the coral.

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## INTRODUCTION

The paleoautecology of the most abundant rugose coral of the Beil Limestone Member, *Caninia torquia* (Owen), was investigated to determine its variation in relation to the depositional environment of the unit. Fifteen outcrops of the Beil (Fig. 1), primarily road-cut and stream-bank exposures, were measured and described (Maerz, 1975). Orientation and spatial distribution of coral specimens were noted before their removal. Samples chosen for thin-section analysis were stained following procedures outlined by Friedman (1971), and limestones were classified according to the scheme proposed by Folk (1962).

External characters of 614 coral specimens were examined, including maximum diameter, area of floor and depth of calice, morphology of attached juveniles, epifauna, number and planes of geniculations, spacing and deformation of growth lines, attachment structures, morphology of the apex, budding scar morphology, diameter at the first budding scar, and diameter at the disattachment constriction. Approximately 300 specimens were thin sectioned; the characters measured

and described included: septal pattern; length and thickness of cardinal and counter septa; number of major septa; number, length, and thickness of dilated septa; dissepiment pattern; damage; relationship between epifauna and epitheca; morphology of tabulae; zones of crowded tabulae; and growth lines. Selected corals were serially ground and acetate peels made to study ontogeny, septal insertion, and modification of internal structure associated with budding.

Data obtained from measurement of characters in transverse and longitudinal sections were subjected to principal components analysis to determine whether or not corals from different facies are morphologically different. Details of the analysis are available elsewhere (Maerz, 1975). It was found that size may be a useful environmental indicator. Furthermore, because of high correlation with many other characters, size differences are accurately reflected by differences in maximum diameter.

*Acknowledgments.*—This work constitutes a part of the author's doctoral dissertation, which was directed by Professor Curt Tei-

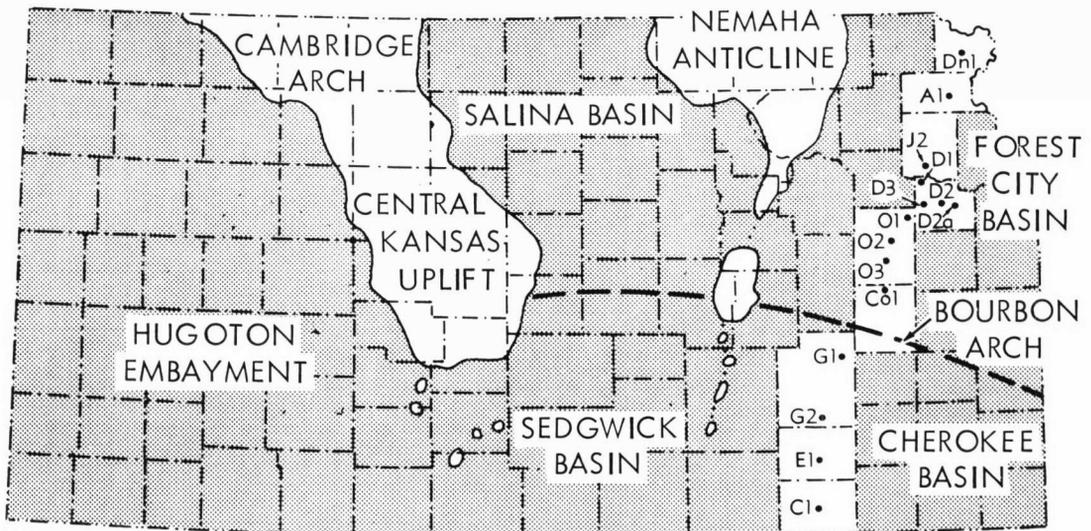


FIG. 1. Location of measured sections of the Beil Limestone Member in eastern Kansas (A, Atchison Co.; C, Chautauqua Co.; Co, Coffey Co.; Dn, Doniphan Co.; D, Douglas Co.; E, Elk Co.; G, Greenwood Co.; J, Jefferson Co.; O, Osage Co.).

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### PREVIOUS INVESTIGATIONS

*Beil Limestone Member.*—The stratigraphy and paleontology of the Beil Limestone Member of the Lecompton Limestone have been extensively studied. Brown (1958), working in eastern Kansas, and Schrott (1966) and Baird (1971), in eastern Kansas, Nebraska, and Iowa, concluded that the lower portion of the Beil represents a transgressive phase of deposition, and the middle and upper portions represent a regressive phase. Brown (1958) recognized corals as the most distinctive element of the Beil fauna, and concluded that they are most abundant in those parts of the unit representing the regressive phase of deposition. Schrott (1966) noted that corallites vary from short and stubby to elongate and narrow, and show signs of having reoriented themselves after tipping over on a soft mud sub-

strate. Baird (1971) recognized two coral assemblages, a "Coral-Algal Community Wackestone" on the Nebraska shelf and a "Fusulinid-Coral Assemblage Wackestone" on the Nebraska shelf and in the Forest City basin. In the former, *Pseudozaphrentoides* (= *Caninia torquia* of this report) is most abundant, and the phylloid alga *Archaeolithophyllum lamellosum* commonly welds the corals to the substrate. In the latter, rugose corals are smaller and their association with algae is less marked. Baird (1971) concluded that this assemblage lived in slightly deeper waters than the coral-algal community.

*Paleoecology of midcontinent Pennsylvanian rugose corals.*—Most pre-1950 work on Pennsylvanian rugose corals was taxonomic, and later studies included corals only as part of an entire fauna. Authors who addressed the problem agree that the rugose corals occur in limestones and shales deposited in shallow-water environments (Jeffords, 1948; Rowett and Sutherland, 1964; Moore, 1966; Cocke, 1969, 1970), but comprehensive work on paleoecology of midcontinent Virgilian rugose corals is lacking.

### STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENTS

The Shawnee Group (Pennsylvanian, Virgilian) consists of four limestone and three shale formations. One of these, the Lecompton Limestone, contains four limestone and three shale members, of which the Beil is the third limestone member from the base (Fig. 2). The depositional environment of the Beil Limestone Member is interpreted from facies (Fig. 3) defined and named on the basis of primary lithologic and paleontologic characters (Teichert, 1958).

#### QUEEN HILL SHALE MEMBER

The Queen Hill Shale Member underlying the Beil Limestone is divisible into two parts: 1) a lower, black, fissile, carbonaceous shale; and 2) an upper, gray to yellowish-gray, calcareous shale. The thickness of the entire unit ranges from 1.0 to 1.5 m.

The Queen Hill Shale Member has been extensively studied by Schrott (1966) and Baird (1971), who found the lower black

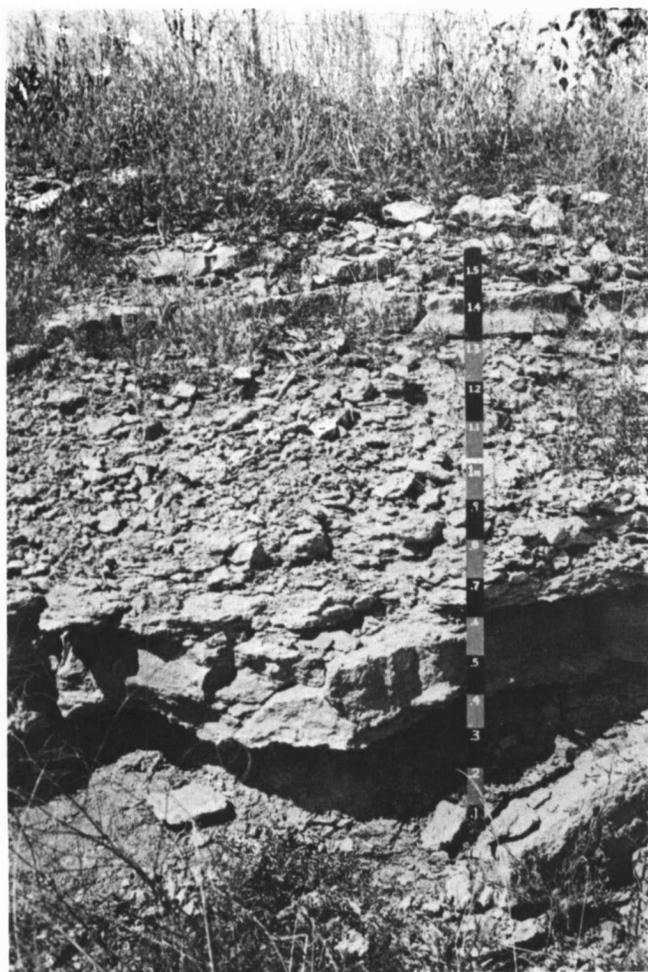
Avoca Limestone Mbr.	Lecompton Limestone	SHAWNEE GROUP	VIRGILIAN STAGE	UPPER PENNSYLVANIAN SERIES	PENNSYLVANIAN SYSTEM
King Hill Shale Mbr.					
<b>BEIL LIMESTONE MBR.</b>					
Queen Hill Shale Mbr.					
Big Springs Ls. Mbr.					
Doniphan Shale Mbr.					
Spring Branch Ls. Mbr.					

FIG. 2. Stratigraphic position of the Beil Limestone Member (after Zeller, 1968).



ments are abundant. Phylloid algae and *Osagia*-coated grains are abundant in northern localities, but typically the grains are not completely coated. Fragmented ramose and fenestrate bryozoans and echinoid fragments are common. In the upper part of this facies at locality J2, one specimen each of *Lophophyllidium proliferum* and *Caninia torquia* were observed.

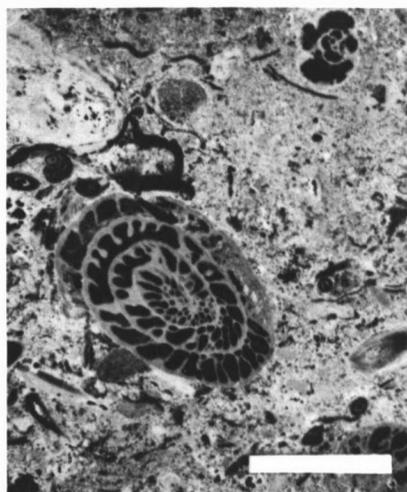
The transgression that began during Queen Hill time (Brown, 1958; Schrott, 1966; Baird, 1971) continued during early Beil time. Indications that the fusulinid-crinoid biomicrosparite was deposited in a shallow marine environment are numerous. The poorly developed graded bedding and alignment of fossils parallel to bedding planes resemble those described by Roehl (1967)



1a



2



1b

FIG. 4. 1a. Lowermost units of the Beil Limestone Member in the Forest City basin. Note sharp contact with the underlying Queen Hill Shale Member (level of 0.4 on scale). Fusulinid-crinoid biomicrosparite (0.4 to 0.7 on scale), shale-argillaceous limestone (0.7 to top of 1.4), lower part of high-diversity argillaceous limestone (above 1.4). Locality D2, Douglas County. 1b. Thin-section print of fusulinid-crinoid biomicrosparite, scale = 2 mm. Locality J2, Jefferson County. 2. Thin-section print of limestone from shale-argillaceous limestone, scale = 2 mm. Locality D1, Douglas County.

from the supratidal zone of the Bahamas, where tidal currents moving toward shore deposit bioclastic debris, which in turn is covered by muds derived from the supratidal mudflat as shore waters return seaward. The irregular layering of different-textured carbonates and burrow mottling are analogous to features observed by Moore and Scruton (1957) in shallow-water sediments of the Gulf of Mexico. The encrusting algae (biolithite) is morphologically similar to that described by Monty (1967) from shallow-water settings near Andros Island, Bahamas. The high incidence of fossil fragments and presence of occasional intraclasts, *Osagia*-coated grains, and scattered biosparite all indicate periods of increased currents. The fusulinid-crinoid biomicrosparite, then, represents deposition in a shallow-water, near-shore, marine environment with periodic current activity of sufficient strength to produce intraclasts, to fragment and align fossils, and to partially coat grains with algae.

*Shale-argillaceous limestone facies.*—A unit of argillaceous limestone consisting of thin carbonate beds 1 to 5 cm thick enclosed in calcareous shale overlies the lowest limestone unit of the Beil in both the Forest City and Cherokee basins. The shale partings thicken slightly toward the top, where the interval is capped with a thin limestone bed (Fig. 4,1a). The facies ranges in thickness from 0.23 to 1.10 m.

Biomicrosparite is the dominant carbonate rock type, but biosparite, pelsparite, and algal biolithite (Fig. 4,2) occur locally. Generally, fossil fragments are randomly oriented but may be aligned parallel to bedding where biosparite occurs. Fossils are better preserved than in the underlying facies, with fenestrate bryozoans and productoid brachiopods retaining delicate features. Two generations of carbonate cement are present, a primary drusy cement followed by a blocky spar. The shale in this facies is calcareous and often fissile. At some localities where shale predominates, it appears burrow-mottled. At all localities it is abundantly fossiliferous.

Diversity of the fauna continues to increase in this facies: fusulinids, whole and fragmental, are everywhere abundant, as are

brachiopods. Tabulate corals (*Syringopora*, *Aulopora*) make their first appearance, as do encrusting bryozoans, bivalves, gastropods, and ostracodes. Echinoid fragments and crinoids remain abundant. *Caninia torquua* is common and increases in abundance toward the top of this facies. In its upper part, encrusting algae occur in the form of small "biscuits" 0.3 to 1.0 cm in diameter.

Transgression that began at the time of Queen Hill deposition approached a maximum during deposition near the top of this facies. Characteristics indicating a shallow-water environment are essentially identical to those in underlying facies, with some exceptions. For example, fossils such as large fenestrate bryozoans are well preserved. Usually, fossils are not aligned parallel to bedding, which suggests lower energy conditions and a deeper environment or one protected from currents. The fauna of this facies: rugose and tabulate corals, ostracodes, mollusks, and phylloid algae, has been interpreted as representing "normal marine" conditions (Moore, 1966; Heckel, 1972). Finally, algal biscuits in the upper part of this facies resemble those reported by Ginsburg and Lowenstam (1958) from moderate depths (6 m) in the Bahamas.

*Wavy-bedded biomicrosparite facies.*—This facies is present at only three localities in the southern Forest City basin (O2, O3, Co1). It occupies the same stratigraphic position as the shale-argillaceous limestone facies at more northern localities. Individual limestone beds range in thickness from 5 to 15 cm and are laterally discontinuous over distances greater than a meter. Each limestone bed is separated by a zone of shale or argillaceous limestone from 1 to 3 cm in thickness. The contact with the underlying and overlying facies is gradational.

Biomicrosparite is the dominant rock type, but biosparite occurs locally (Fig. 5,2). Samples commonly contain quartz silt, which is concentrated in burrows with poorly defined walls. Fossils are fragmented and usually randomly oriented with respect to bedding. At one locality, fusulinids are concentrated in elongated ridges 5 cm wide and 15 to 20 cm long.

The fauna of this facies is more diverse

than that of the underlying facies. Fusulinids and brachiopod fragments are abundant. *Osagia*-coated grains, phylloid algae, and crinoid fragments are common. Rare elements include tabulate corals, mollusks, and echinoid spines and fragments.

This facies has characteristics almost identical to its northern equivalent, the shale-

argillaceous limestone facies, except that carbonate units predominate instead of argillaceous limestone. The corresponding environments of deposition were analogous except for a smaller influx of clay in the southern part of the Forest City basin.

*High-diversity argillaceous limestone facies.*—This facies occurs from southern Doug-

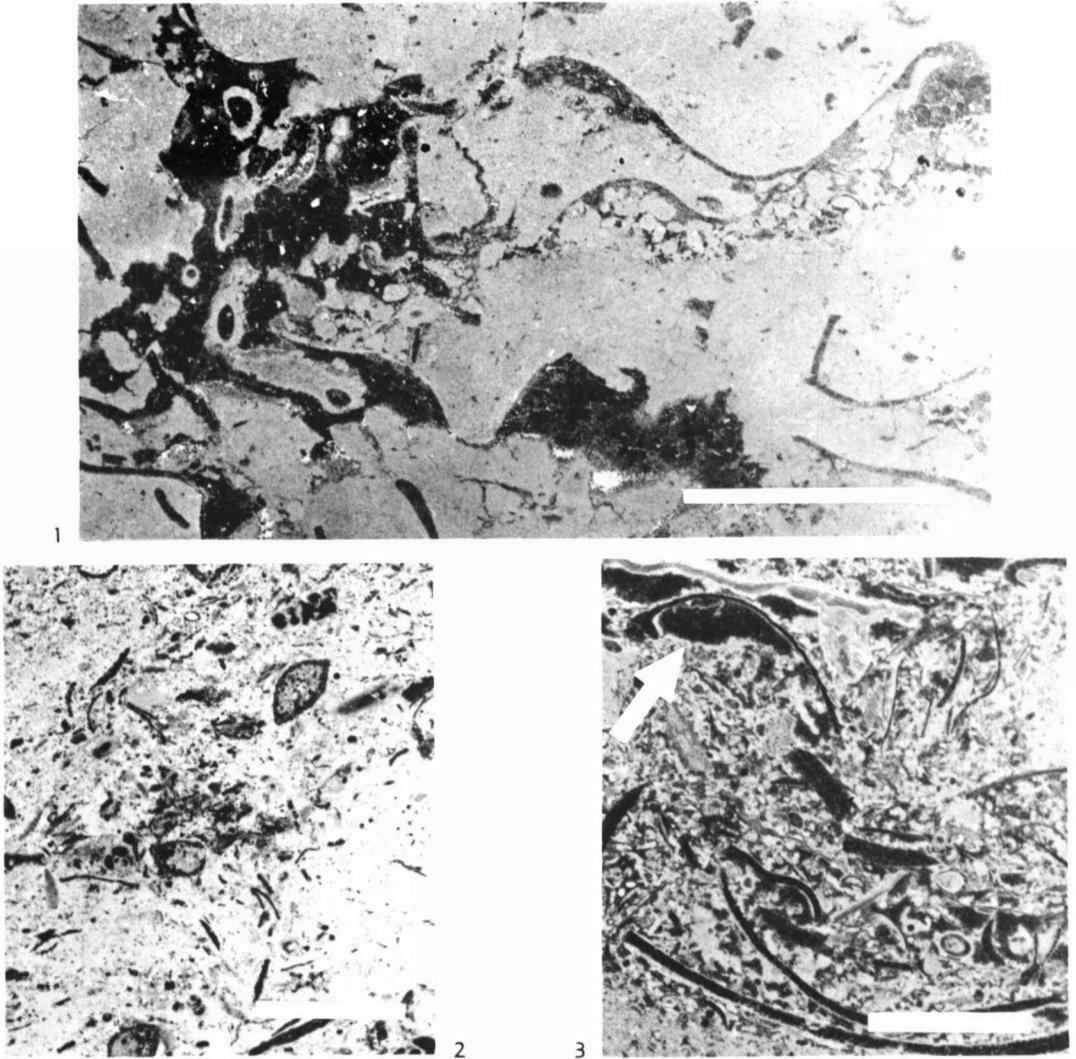


FIG. 5. 1. Peel print of phylloid algae-*Caninia* biomicrosparite, scale = 10 mm. Note sheltering by phylloid algae. Locality O3, Osage County. 2. Thin-section print of wavy-bedded biomicrosparite, scale = 2 mm. Note random arrangement of fossil fragments. Locality O3, Osage County. 3. Thin-section print of high-diversity argillaceous limestone biosparite, scale = 2 mm. Note sheltering by brachiopod (arrow) and *Osagia*-coated grains. Locality D2, Douglas County.

las County northward to Doniphan County in the Forest City basin. The lower two-thirds is similar lithologically to the underlying shale-argillaceous limestone of the Forest City basin, consisting of thin argillaceous limestone beds with enclosing calcareous shales (Fig. 4,1a). In the upper third, shale increases in thickness at the expense of limestone. This facies ranges in thickness from 1.1 m in Douglas County to 0.5 m in Doniphan County. Contacts with overlying and underlying facies are gradational.

The dominant carbonate rock type in this facies is biomicrosparite, but locally *Osagia*-biosparite and biopelsparite may be common (Fig. 5,3). Burrows with poorly defined walls commonly concentrate fossil fragments, especially fusulinids. *Osagia*-coated grains observed in thin sections are unevenly coated. Fossils are exceptionally well preserved, with delicate structures such as spines on productoid brachiopods and large fenestrate bryozoans remaining intact. Carbonate cement appears to be of two generations, the first drusy and the second blocky spar.

The lower two-thirds of this facies contains the most diverse of all Beil faunas. Fusulinids and other foraminifers; *Caninia torquia*; ramose, fenestrate, and encrusting bryozoans; brachiopods; and crinoid fragments are all abundant. *Osagia*-coated grains, phylloid algae, gastropods, bivalves, trilobite fragments, ostracodes, and echinoid spines and fragments are common. Fossils are well preserved and algal-coated grains are unevenly coated, indicating a low-energy environment; however, some poorly washed biosparite indicates occasional currents of sufficient strength to remove some mud.

The upper third of this facies consists of yellowish-gray calcareous shale. Sedimentary structures were not observed and the fauna is much less diverse than in the underlying argillaceous limestone. Only algally coated grains, fusulinids, *Lophophyllidium proliferum*, productoid brachiopods, ostracodes (much less diverse than below; Brondos, 1974), and scattered crinoid fragments were found. Fossils are fragmented, biosparite increases, evenly *Osagia*-coated grains become more abundant, and diversity drops

noticeably. The percentage of shale increases. All characters indicate a shallowing of water and a more restricted environment.

The high-diversity argillaceous limestone, then, records a change in the depositional environment of the member. The lower part of the facies represents the maximum period of transgression; the upper, the beginning of the Beil regression.

*Phylloid algae-Caninia biomicrosparite facies.*—This unique facies was found at only locality O3 in southern Osage County in the Forest City basin. It is represented by two massive beds, each about 0.5 m thick, separated by a thin shale parting. Thickness of the beds is constant along 50 m of outcrop. This facies occupies the same stratigraphic position as the lower part of the high-diversity argillaceous limestone of northern localities.

The dominant rock type is dolomitic, algal biomicrosparite, and, locally, algal biosparite (Fig. 5,1). Phylloid algal fragments often enclose microsparite, whereas the area between algae contains biosparite and local biomicrosparite. Encrusting algae form undulating matlike structures 10 to 15 cm long and 2 to 4 mm high in the upper part of this interval. In thin sections, phylloid algae represent 80 to 95 percent of the biota.

The fauna of the lower part of this facies consists primarily of whole and fragmented brachiopods. The upper part is dominated by phylloid algae, both encrusting (*Archaeolithophyllum lamellosum*) and erect (*A. missouriensis*), unusually large and robust *Caninia torquia*, and occasional specimens of *Composita ovata* and some gastropods.

The phylloid algae-*Caninia* biomicrosparite of the Beil has certain similarities to algal mound complexes described elsewhere (Heckel and Cocke, 1969). Phylloid algae act to baffle sediment and, locally, biosparite occurs. Laterally equivalent facies contain much less algae, and the fauna is generally more diverse than in the phylloid algae-*Caninia* biomicrosparite. Overlying facies are indicative of higher energy conditions. Corals and other "framework" organisms are typically not present in algal mound complexes (Heckel and Cocke, 1969).

The phylloid algae-*Caninia* biomicro-

sparite may represent a very low-relief algal mound. Currents permitted algae to trap carbonate mud and also selectively to remove some mud to produce biosparite. The setting is interpreted as shallow-water marine.

*Osagia-fusulinid biosparite facies*.—This unit lies near the top of the Beil Limestone and is present at all localities from Dn1 in Doniphan County in the Forest City basin south to G1 in northern Greenwood County in the Cherokee basin. The thickness ranges from 0.2 m in Doniphan County to 0.5 m in Douglas County, to a maximum of 1.1 m in Greenwood County. A primary characteristic of this facies, which is usually represented by one or more massive limestone beds, is its variability. In some places it is decidedly sparry, whereas in others microsparite predominates. In all places, *Osagia*-coated grains are abundant.

Biosparite is the dominant rock type, but locally biopelsparite and biomicrosparite may occur (Fig. 6,2). In all thin sections, grains are algal-coated with the coatings evenly distributed over rounded and abraded nuclei. Two generations of cement are indicated, a primary generation of small scalenohedral crystals followed by a coarse spar. Low-angle cross-bedding was observed at one locality (G1).

The fauna of this facies is markedly less diverse than that of the underlying facies. Fusulinids, *Globivalvulina*, and *Osagia*-coated grains are abundant. Brachiopod fragments; ramose, fenestrate, and fragmented encrusting bryozoans; gastropods; bivalve fragments; echinoid fragments and spines; and crinoid fragments serve as nuclei for the *Osagia*-coated grains. Only occasional fusulinids and some brachiopod fragments are not algal coated.

The formation of ooids and of *Osagia*-coated grains require similar energy conditions. Ooids form on the Bahama Banks on or near shoals where high velocity tidal currents keep grains in motion. The substrate contains no vegetation and a sparse indigenous fauna (Bathurst, 1971). The depositional environment of the *Osagia*-fusulinid biosparite was also a high-energy, very shallow marine environment, with possible shoals at some localities and some accumulation of

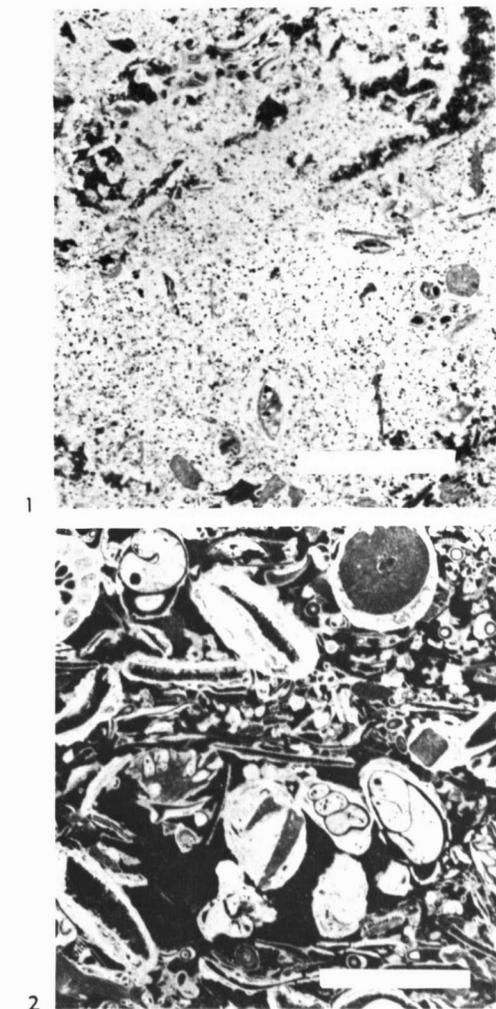


FIG. 6. 1. Thin-section print of sandy biomicrosparite, scale = 2 mm. Locality G2, Greenwood County. 2. Peel print of *Osagia*-fusulinid biosparite, scale = 2 mm. Locality G1, Greenwood County.

carbonate mud at others.

*Sandy biomicrosparite facies*.—This unit comprises the uppermost beds of the Beil Member at two localities in the Cherokee basin (E1, G2). The lowermost part of this facies is a sandy fusulinid coquina that grades upward into a sequence of sandy wavy-bedded limestone (Fig. 6,1). Thickness of the facies varies from 0.7 to 1.0 m.

The fauna of this facies is less diverse than in the underlying facies. In the lower microfacies, fusulinids, tabulate corals, bryo-

zoans, brachiopod fragments, and crinoids are common to rare, whereas in the upper microfacies only grains evenly coated with *Osagia*, fusulinids, brachiopod spines, and crinoid fragments are present. As silt content increases upward, faunal diversity decreases, and fossils are not present in the topmost interval.

As the Beil regression continued, shallow-water carbonates were deposited. The lowest part of this facies represents deposition in a very shallow sea where fusulinids were concentrated on the substrate and intermixed mud was partly removed. As deposition continued, clastic influx increased and the environment became unfavorable for organic growth. Crudely laminated carbonate mud was deposited along with quartz silt. The sea must have been very shallow but the sea floor was not emergent to permit formation of desiccation features.

*Chautauqua coral-algal biomicrosparite facies.*—This unit is developed only at Locality C1 in central Chautauqua County in the Cherokee basin. Two beds are present, a lower massive limestone 1.1 m thick and an upper wavy-bedded sequence 1.0 m thick (Fig. 7,1). The contact with the underlying Queen Hill Shale Member is not clearly exposed, although the characteristic black fissile shale was observed in a nearby drainage ditch. The King Hill Shale and the top part of the Beil members are not present and may have been removed by recent erosion.

Two microfacies are present, an underlying algal biomicrosparite and an upper coral-algal biomicrosparite to biosparite (Fig. 8,2). In the lower microfacies, fossils are fragmented and aligned parallel to bedding. Some scattered encrusting algae resembling *Archaeolithophyllum* are present. In the upper microfacies, both encrusting and erect phylloid algae are abundant as well as burrows, which generally are perpendicular to bedding.

Faunas of the two microfacies are essentially identical and consist of fusulinids, unusually large and robust *Caninia torquia*, *Lophophyllidium proliferum*, *Dibunophyllum parvum*, *Syringopora* that commonly encrust *C. torquia* lying parallel to bedding, bryozoans, gastropods, and crinoid fragments.

*Osagia*-coated grains are present in both microfacies but are most abundant in the upper one. Phylloid algae are common throughout the facies, which is similar to the phylloid algae-*Caninia* biomicrosparite of the Forest City basin, but phylloid algae are less abundant and the fauna as a whole is much more diverse.

The Chautauqua coral-algal biomicrosparite may represent algal mound development that was halted as the Beil regression caused shallowing and other unfavorable conditions. This interpretation is tentative as the upper part of this section may have been removed by recent erosion, thus destroying later facies clearly indicative of regression.

*Laminated dolomitic biolithite facies.*—This unit occurs in the uppermost Beil Limestone Member (Fig. 7,2). It is restricted to the northernmost localities in the Forest City basin and is characteristically thin, ranging in thickness from 0.03 to 0.10 m. In some places the beds of this facies thin and thicken along the length of an outcrop. At all localities, contacts with underlying facies are gradational, but the upper contact with the King Hill Shale Member is always sharp.

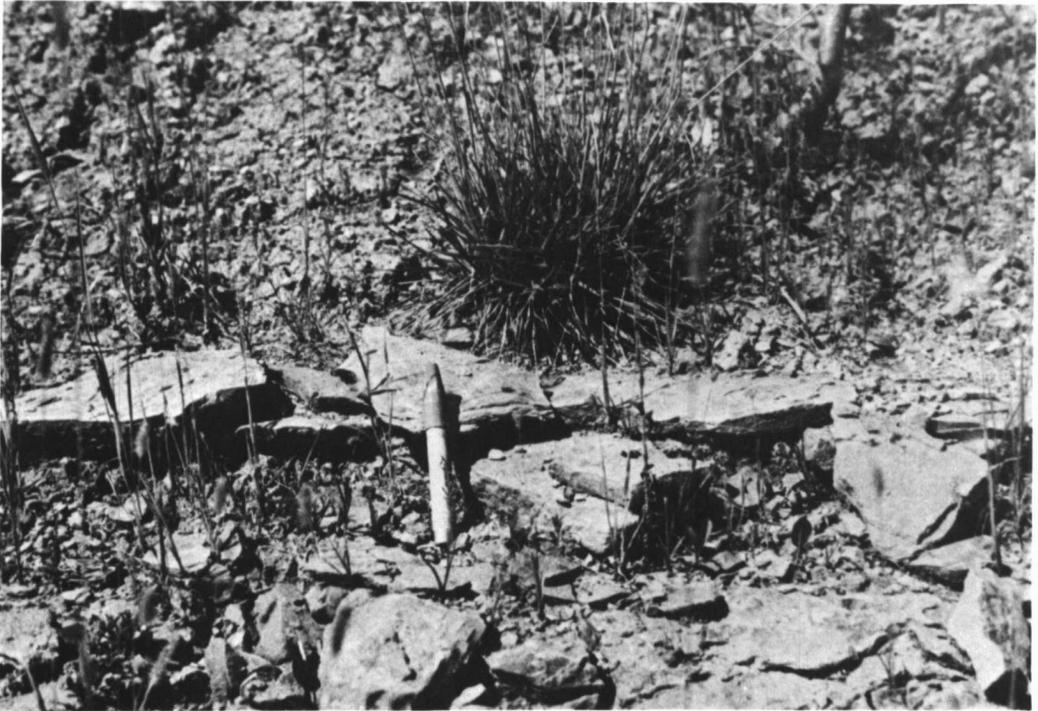
Two microfacies are present: the first and most extensive is a dolomitic, algal biolithite with encrusting algae binding all sediment (Fig. 8,1); the other is a biomicrosparite with rare intraclasts. In the latter, poorly developed graded bedding is present, with coarse bioclastic debris interlayered with biomicrosparite. Fossil fragments are all aligned parallel to bedding and, rarely, fenestral fabric is developed.

The fauna of this facies is the least diverse of all Beil faunas. *Osagia*-coated grains, fusulinids, and brachiopods are abundant, with encrusting algae and echinoid spines and fragments being common.

The uppermost Beil Limestone contains numerous indications of deposition in a very shallow-water, possibly supratidal environment. Laminated algal sediment, poorly graded bedding, rare intraclasts, and presence of dolomite are features closely resembling those of recent supratidal or intertidal carbonate environments (Roehl, 1967; Bathurst, 1971). Of importance, however, is



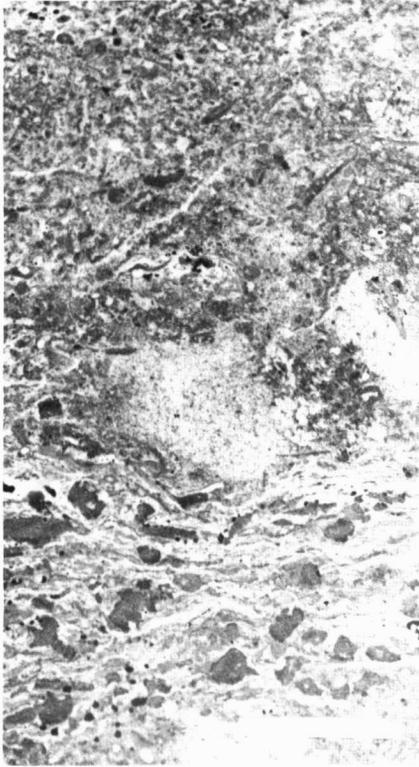
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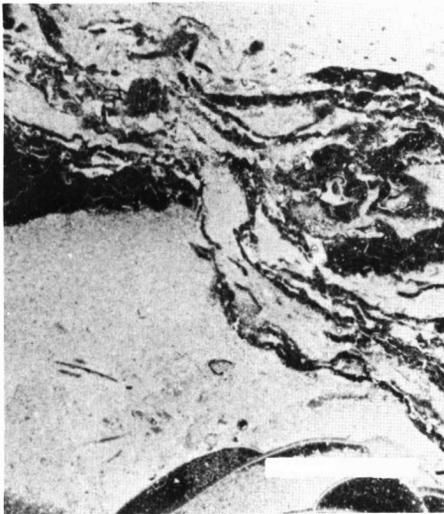
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FIG. 7. 1. Chautauqua coral-algal biomicrosparite, scale in 10-cm divisions. Locality C1, Chautauqua County. 2. Laminated dolomitic biolithite, marker 15 cm long. Locality D2, Douglas County.

the lack of rip-up clasts, mudcracks, and other desiccation features.



1



2

FIG. 8. 1. Thin-section print of laminated dolomitic biolithite, scale = 3 mm. Note algal biolithite and intraclasts. 2. Thin-section print of Chautauqua coral-algal biomicrosparite, scale = 2 mm. Note sheltering by phylloid algae.

## KING HILL SHALE MEMBER

The King Hill Shale Member of the Lecompton Limestone overlies the Beil Limestone Member with a sharp contact (Brown, 1958; Schrott, 1966; Baird, 1971) and is generally poorly exposed in the study area, especially south of Douglas County. It consists of greenish- to olive-gray, unfossiliferous shale with one or more unfossiliferous calcareous zones. A thin, yellowish limestone is present in the middle of the unit. Thickness of the member ranges from 2 to 8 m.

The depositional environment of the King Hill Member is little understood due to lack of fossils and diagnostic sedimentary features, except in the middle limestone. Schrott (1966) concluded that the member was deposited in an intertidal environment; however, P. P. Enos (1973, oral commun.), who has examined the unit throughout the entire midcontinent, believed that it was deposited in a supratidal environment, a conclusion consistent with the presence of mudcracks and other desiccation features in the middle limestone.

## SUMMARY OF DEPOSITIONAL ENVIRONMENT

The initial phase of Beil deposition in both the Forest City and Cherokee basins was characterized by carbonate deposition in a shallow marine environment in which currents aligned fossil fragments and produced intraclasts and poorly graded bedding. Conditions were evidently not favorable for abundant organic growth. The transgression that began during deposition of the underlying Queen Hill Member continued during early Beil time. As the transgression continued, current strength declined and clastic influx increased, especially in the Cherokee basin. In a shallow-water environment, conditions for organic growth improved and a diverse fauna developed. Locally, a low relief algal mound developed in Osage County.

The middle Beil records a shift from transgression to regression. In both the Forest City and Cherokee basins, diversity of the fauna began to decline as conditions for organic activity deteriorated. Energy

conditions increased as seen by increased fragmentation of fossils.

The final phase of Beil deposition was characterized by very shallow water, at times approaching shoaling and possibly supratidal conditions. Increased activity in the Forest City basin again produced graded bedding, intraclasts, and aligned fossils parallel to bedding planes. In the Cherokee basin, deposition was influenced by close proximity to the source of clastic sediments, and quartz silt and sand was deposited in the shallowing water. Organic activity was restricted to sediment-binding algae and to other organisms tolerant of a restricted environment. Beil deposition ended in very shallow water prior to the supratidal deposition of the lower King Hill Shale Member.

#### PALEOAUTECOLOGY OF SOLITARY RUGOSE CORALS

Paleoautecology considers the interrelationships of fossils either as individuals or as single taxonomic groups. These interrelationships are determined by analysis of the rocks in which the fossils are preserved, orientation of fossils in the matrix, functional morphology, growth and reproduction, and association with other organisms (Ager, 1963).

The solitary rugose coral fauna of the Beil Member consists primarily of one species, *Caninia torquia* (Owen), which I have identified by detailed comparison with the holotype. Other rugose corals collected, *Lophophyllidium proliferum*, *Dibunophyllum parvum*, and *Stereostylus lensis*, represent less than three percent of the total; consequently, this study is restricted to *C. torquia*.

Most Beil rugose corals are not well preserved. Usually the epitheca is only partly preserved or is missing, and epifauna encrusting eroded surfaces of the corallite indicates that the epitheca was easily and rapidly removed. The apex is usually broken, and the calice is damaged or filled with sediment. Some corallites have broken and crushed tabulae, and intertabular voids are sometimes filled with sediment that may display geopetal fabric. As noted by Hubbard (1970), all of these features are the

result of post-mortem effects.

*Distribution of corals in relation to facies.*—Corals occur in five facies of the Beil Member in eastern Kansas: fusulinid-crinoid biomicrosparite, shale-argillaceous limestone, high-diversity argillaceous limestone, phylloid algae-*Caninia* biomicrosparite, and Chautauqua coral-algal biomicrosparite. In the Forest City basin, corals are most abundant in the upper part of the shale-argillaceous limestone, in the lower third of the high-diversity argillaceous limestone, and in the upper part of the phylloid algae-*Caninia* biomicrosparite. Only two corals were collected in the fusulinid-crinoid biomicrosparite. In the Cherokee basin, corals occur only in the Chautauqua coral-algal biomicrosparite.

As previously mentioned, the upper part of the shale-argillaceous limestone represents deposition in a shallow-water environment of moderate to low current strength that was favorable for organic growth. The lower part of the high-diversity argillaceous limestone was deposited under similar conditions, with perhaps a lower current strength as indicated by excellent fossil preservation. The phylloid algae-*Caninia* biomicrosparite and Chautauqua coral-algal biomicrosparite are interpreted as representing deposition in environments similar to those of algal mound complexes. *Caninia torquia* is abundant in those facies deposited during maximum transgression, which are also the facies with the most diverse Beil fauna, and where phylloid algae occur in sufficient profusion to form incipient algal mounds. *C. torquia* does not occur in those facies deposited in environments representing the initial stages of transgression, the last stages of regression, or high-energy shoaling conditions.

*Associations.*—Little study has been done on organisms attached to rugose corals. Authors of monographic studies on the Rugosa have tended to select for illustration specimens that are not "spoiled" by encrusting epifauna (Edwards and Haime, 1850; Minato, 1955; Sutherland, 1958). This is particularly distressing, as recent scleractinians commonly have a rich epifauna. Clarke (1921), in one of the earliest works dealing with this topic, described several

types of worm tubes in "*Zaphrentis*" and "*Cyathophyllum*" (*Caninia*). Some were either straight or at a slight angle in transverse section with one end opening to the outside, some wound through the coral paralleling the epitheca in longitudinal section with one or both ends opening in the calice, and some were totally enclosed in the coral. Flower (1961), dealing specifically with encrusting fauna of fossil corals, described various organisms of doubtful affinity that were randomly distributed on the corallum of colonial corals from the Montoya Group (Ordovician) of New Mexico.

Many specimens of *Caninia torquia* from the Beil Member are encrusted with other organisms (Pl. 1, figs. 2-6). Bryozoans occur on most corals, and many specimens show encrusting foraminifers (*Tetrataxis*) and the serpulid *Spirorbis*. The epifauna displays no preferred positions on the corals, which may indicate absence of a symbiotic relationship and use of the coral only as a substrate. In thin sections, all encrusting organisms show a sharp boundary with the epitheca. One specimen of *C. torquia* contains a small boring (Pl. 1, fig. 7), which in size and configuration closely resembles a boring produced by a small bivalve infesting some modern Red Sea corals (Soliman, 1969).

As previously mentioned, scleractinian corals have a rich epifauna. In forms inhabiting a soft-mud substrate, the coral commonly sinks at least partly into the substrate and most encrusting organisms occur on that portion of the coral above the substrate. When the specimen is removed, a distinct line is visible below which there are no or far fewer encrusting elements (G. D. Stanley, 1975, oral commun.). No such line was observed on any rugose corals collected from the Beil Limestone.

Because the Beil coral fauna is so thoroughly dominated by *Caninia torquia*, the relationships among species of rugose corals is difficult to determine; however, field observations show that lophophyllids do not usually occur in great numbers when *C. torquia* is abundant; instead they are more abundant in intervals above and below. Of the tabulate corals in the Beil, the encrusting *Syringopora* usually occurs with *C. torquia*;

however, when *Syringopora* is in large hemispherical colonies, *C. torquia* is either rare or absent.

Although bedding-plane exposures are not common in the Beil, data available from four localities indicate an average density of 47 corals per square meter. Where bedding planes of sufficient size are exposed to permit observation, *Caninia torquia* appeared to have a clumped distribution. At locality D2a, clumps contain from 5 to 10 corallites, the distance between corals in a clump ranging from 5 to 10 cm. Clumps themselves appear to be randomly distributed, although this was not tested.

Information on distribution and density of other rugose corals as well as recent scleractinians shows densities of between 10 and 20 corals per square meter, depending on size of individuals (Young and Rush, 1956; Hubbard, 1966, 1970). In examining distribution of Atlantic reef corals, Lewis (1974) found that *Favia fragum* and *Porites asteroides* occurred in clumped distribution with colonies decreasing in size with increased distance from the largest colony in an aggregation. He concluded that the clumped distributions resulted where larvae settled on or near an established colony or from the physical splitting of large colonies as observed in *Porites asteroides*. The clumped distributions of *Caninia torquia* may have been produced by a similar splitting mechanism, especially in light of the dominance of asexual budding in this species; however, further observation is needed to determine whether adult corallites were surrounded by juveniles.

Locality D2a, where a series of bedding planes are exposed in a calcareous shale, provided quantitative data on the association of corals and other faunal elements (see Maerz, 1975, for procedure and data). A stratigraphic interval of 30 cm separates quadrat 1 and quadrat 16. Thus the data are not time-specific and permit examination of associations through a short interval of time.

Trends in faunal association for a portion of the high-diversity argillaceous limestone are shown in Figure 9, a-f. The following are apparent. 1) Tabulate (e.g., *Syringopora*) and rugose corals are equally abundant, except that where more than 10 rugose

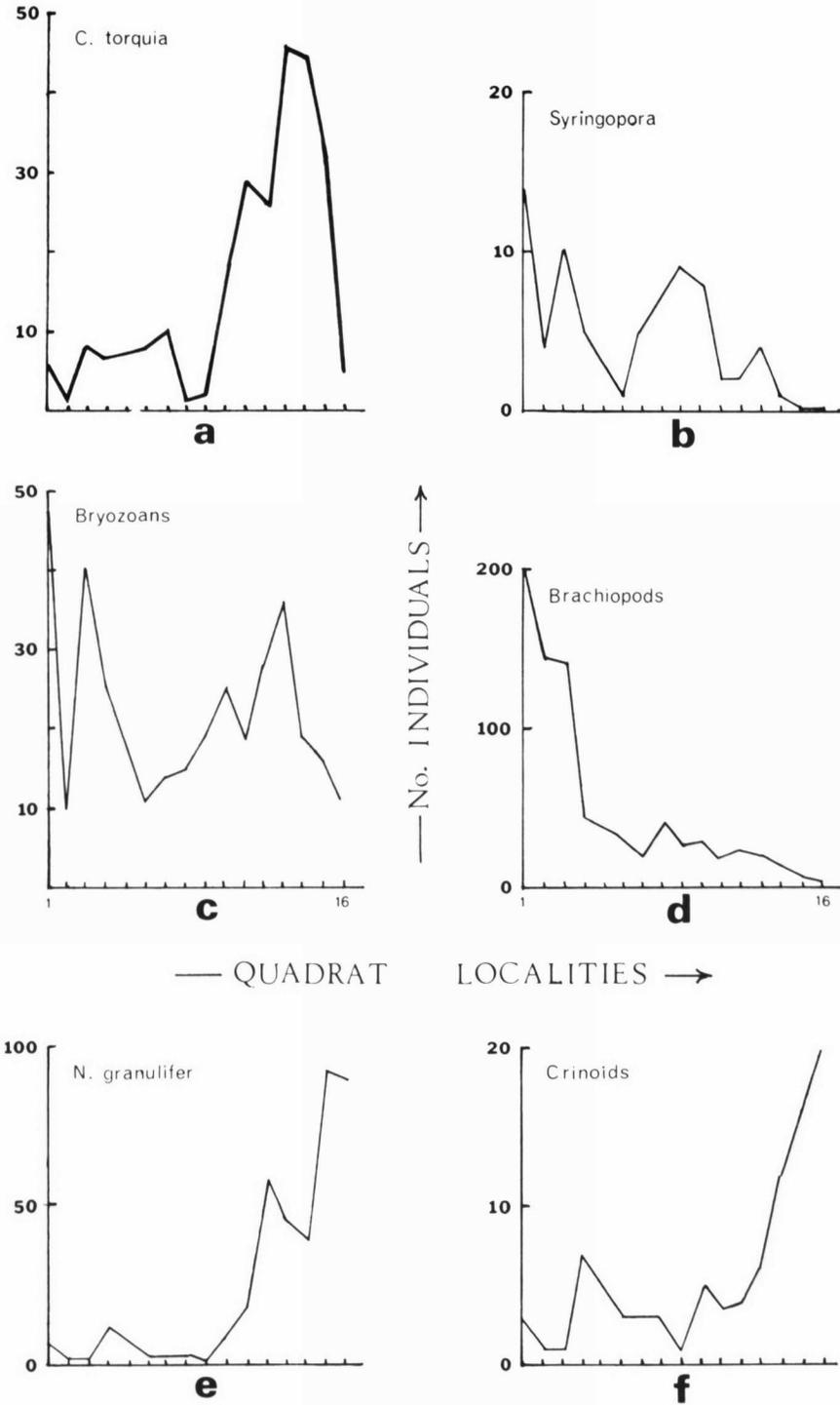


FIG. 9. Plots of number of individuals (ordinate axes) of various taxa from quadrats (abscissa axes) at locality D2a. Quadrat 1 is stratigraphically lower than quadrat 16.

corals occur per quadrat, the proportion of tabulates decreases. 2) The abundance of bryozoans (ramose, fenestrate, and encrusting) is comparable to that of rugose corals. 3) Brachiopods decrease in abundance as Rugosa increase, except for *Neochonetes granulifer*, which increases with *Caninia torquia*. 4) Crinoids increase in abundance as rugose corals decrease in the stratigraphically higher quadrats.

These data also provide information concerning changes in composition of the fauna through time. Stratigraphically lower quadrats (1-4) in general contain many taxa with many individuals, whereas stratigraphically higher quadrats (8-16) in general contain few taxa with many individuals. Furthermore, in the stratigraphically highest quadrats (13-16), the abundance of all taxa except *Neochonetes granulifer* and crinoids is reduced. Trends in other parts of the high-diversity argillaceous limestone are roughly analogous to these.

The organisms most commonly associated with *Caninia torquia* closely resembled those of Johnson's (1962) *Chonetina* association, which was interpreted as having lived offshore on a firm substrate. Few corals were present in Johnson's collections however, and the resemblance is based primarily on similar species of brachiopods. Moore (1966) described organisms associated with corals in his Beil-type and Plattsmouth-type assemblages. Both assemblages are dominated by brachiopods and mollusks, both contain corals, and both are generally similar to Johnson's *Chonetina* association. Moore concluded that these assemblages occurred in clear, sunlit, shallow water far from shore.

Occurrences of chonetid brachiopods in great abundance where other faunal elements are rare have been interpreted as representing shallow water, possibly euryhaline environments (Elias, 1966; Moore, 1966). If this interpretation is accepted, then the rapid decline in abundance of *Caninia torquia* may indicate that the restricted environment favorable for *Neochonetes* was not favorable for the rugose coral.

*Caninia torquia* associations appear controlled by the environment of deposition at a particular horizon. In the phylloid algae-

*Caninia* biomicrosparite, interpreted as representing an incipient algal mound, *Caninia* is associated only with phylloid algae and a few gastropods. In the lower part of the high-diversity argillaceous limestone, the data from the stratigraphically lower bedding planes at Locality D2a indicate associations with organisms that have been interpreted as inhabiting a normal marine, shallow-water environment. As the Beil regression began, environments became more restricted in the upper part of the high-diversity argillaceous limestone, and *C. torquia* declined in abundance as the overall diversity decreased.

*Growth*.—The problem of individual variation in solitary rugose corals has received little attention in the literature. Wells (1937), examining variation in *Heliophyllum halli* from the Devonian of New York, concluded that variation was the result of mode of reproduction, stability on the substratum, age, rejuvenescence, and differential growth rate. Oliver (1958) concluded that individual variation in the Devonian coral *Ameulophyllum exiguum* (Billings) was influenced by rate of growth, genetic differences, and density of the corals. Recently, Dixon (1970) examined variation in *Caninia benburbensis* from northwestern Ireland. He recognized four forms, primarily on the basis of such internal characters as dissepimentarium and septa; however, transitional specimens comprised 65 percent of the total collection. Dixon concluded that maximum diameter, geniculations, spacing of tabulae, and intrathecal thickening were characters dependent on the environment. This conclusion was also reached by Hubbard (1970).

Internal and external characters of *Caninia torquia* from the Beil Member show four growth forms (Fig. 10).

Form A has a simple ceratoid to trochoid corallite with a gentle curvature in one plane (Fig. 10, *1a, b*). Rugae are poorly developed or absent. The calice is bowl-shaped and, internally, tabulae are usually complete and the dissepimentarium increases in width at a constant rate. Corallites are small, with calice diameters usually not exceeding 25 mm and total length not exceeding 60 to 70 mm. Approximately 10 percent of all corals

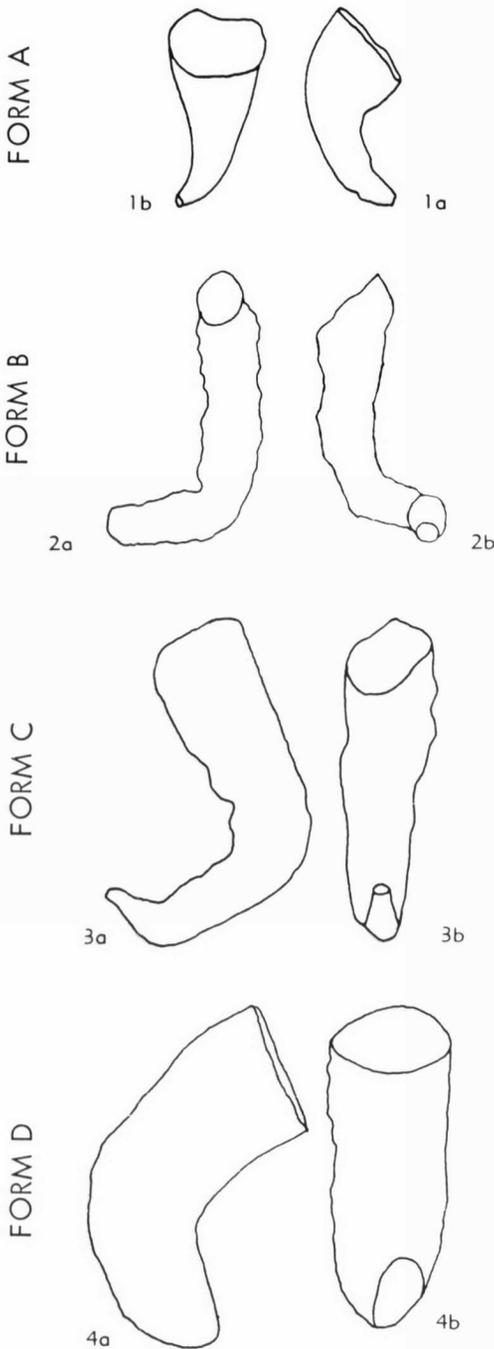


FIG. 10. Growth forms of *Caninia torquia* (Owen), views perpendicular (a) and parallel (b) to plane of geniculation; Form A,  $\times 0.77$ , KUMIP 106021; Form B,  $\times 0.77$ , KUMIP 107003; Form C,  $\times 0.46$ , KUMIP 106936; Form D,  $\times 0.46$ , KUMIP 106739.

collected were of this form.

Form B has primarily cylindrical corallites with one or more geniculations in different planes (Fig. 10,2a,b). Rugae are prominent. Diameter is small, generally not exceeding 25 mm. Corallites are extremely long; a maximum length of 270 mm was observed in a specimen from Locality C1. Internally, the dissepimentarium in longitudinal section is extremely variable in width. Specimens with this form comprise only about 5 percent of all corals collected.

Form C has ceratoid to cylindrical corallites with one or more geniculations that remain in one plane (Fig. 10,3a,b). Specimens may be U-, S-, or W-shaped. Calice diameter is smaller than in Form A and corallites are generally longer. Internal characters are similar to those of Form A. Approximately 70 percent of all corals collected were of this form.

Form D is the largest and most "robust" (Fig. 10,4a,b). Individuals are trochoid to cylindrical in form and have subtle rugae. Diameter of the calice is generally between 40 and 50 mm and length ranges from 150 to 200 mm. Specimens with this form comprise 5 percent or less of the corals collected.

About 10 percent of all *C. torquia* specimens could not be placed in one of these forms. Forms transitional between A, B, and C are most common; forms transitional between D and others are relatively rare.

Forms A, B, and C are most common in the shale-argillaceous limestone and high-diversity biomicrosparite. Although data are sparse, specimens belonging to Form A appear to be more common in calcareous shale, whereas specimens of forms B and C are more common in carbonate with abundant bioclasts. Form D is restricted to the phylloid algae-*Caninia* biomicrosparite and Chautauqua coral-algal biomicrosparite. Principal components analysis shows that corals from these facies are significantly larger than those occurring in the high-diversity argillaceous limestone.

The external gross morphology of the corallite of *Caninia torquia* appears to be much influenced by its stability on the substrate. The less stable the coral, the more often it tipped over, necessitating reorienta-

tion by production of geniculations.

Growth lines average 15 per millimeter on well-preserved specimens of *Caninia torquia*. Growth lines have been interpreted by Scrutton (1964) as representing the result of daily secretion by the coral polyp; however, the regularly spaced constrictions or "bands" described by Scrutton could not be recognized on *C. torquia*. Individual lines are more widely spaced near the apex and more closely spaced in the middle and near the calice of a corallite. Also, an individual growth line on one side of a coral may disappear on the other within a fold where the coral changed growth direction. Clearly, if each growth line was formed during a given period of time, growth of the coral was more rapid during juvenile stages, and certain parts of the coral grew more rapidly than others during a change in growth direction.

**Mortality.**—Recognition of a former population and age groups within it as opposed to recognition of a mixed assemblage is difficult (Raup and Stanley, 1971). To distinguish between altered (infants not preserved or removed) and unaltered assemblages, size-frequency plots assuming total preservation of all members of the population have been used (Boucot, 1953). High infant mortality would result in a right-skewed curve. However, Craig and Hallam (1963) argued that for most marine organisms, mortality was highest in nonpreservable larval stages. A variety of curves would then be possible depending upon growth and mortality rates of the species.

Mortality rates in a population can be determined if: 1) samples are from a single horizon, thus approximating a time-specific analysis; 2) samples are from rock deposited in a low-energy environment in which most individuals are preserved; 3) type of reproduction of the species is known; and 4) age of individuals can be determined. These requirements are nearly fulfilled in the Beil Limestone for specimens of *Caninia torquia* from locality D2a, where 16 quadrat samples were collected on bedding plane exposures (Maerz, 1975). The bedding planes are in the lowest part of the high-diversity argillaceous limestone, which was deposited in

a low-energy environment.

Asexual reproduction by budding is common in *Caninia torquia* (Pl. 1, fig. 1). Furthermore, a few well-preserved specimens still retain their apical region and the detachment constriction formed in released juveniles soon after they contacted the substrate. This constriction almost always has a diameter of approximately 7.2 mm. Thus, specimens whose maximum diameter is near this figure can be considered juveniles. The diameter at which the first budding scar occurs can be used to define an adult individual. The size-frequency diagram plotted for all thin-sectioned corals from the 16 quadrats at locality D2a (Fig. 11) shows a bimodal distribution, indicating a mixture of ages in the population. The diameter of the detachment constriction falls into the modal class of the small-size distribution, whereas the mean and ranges of the diameter at which the first budding scar occurs encompass many of the classes in the large-size distribution. Thus, *Caninia torquia* probably had a high juvenile mortality rate, with the critical time being when the juvenile became detached from the adult and fell to the substrate. If the juvenile survived this event, it most likely survived to adulthood.

**Deformation and repair.**—Little work has been done on deformation and subsequent repair in the Rugosa. Deformation has been noted in studies of growth lines (Scrutton, 1964), and Oliver (1975a) described a Devonian coral in which an empty gastropod shell and associated sediment apparently passed between the polyp and the calical wall and was "roofed" over by subsequent growth. The sediment enclosed within the gastropod indicates, as Oliver pointed out, that not all intratabular sediment commonly observed in Rugosa is the result of thecal breaching and infilling. Oliver (1975b) also described a diseased or injured specimen that reversed its growth to produce an inverted cone-shaped calice.

External and internal structures of well-preserved specimens of *Caninia torquia* provide evidence of repair of minor to severe damage during the life of individual corals. Many corallites have small areas on the

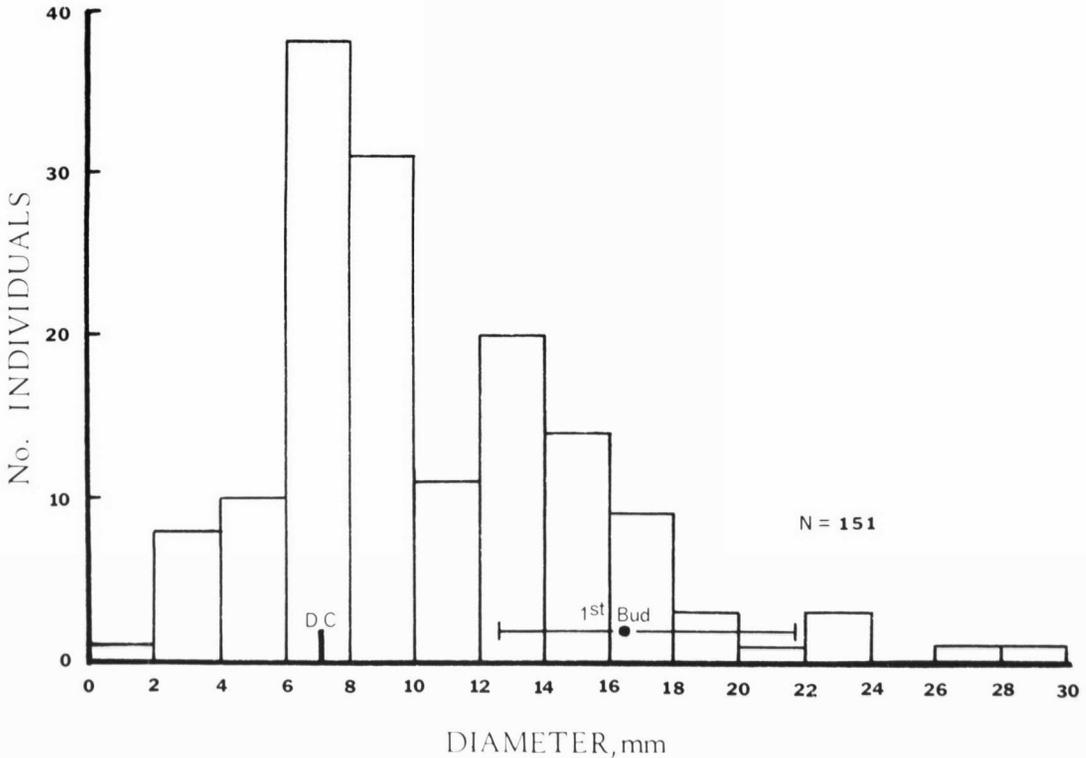


FIG. 11. Size frequency plot of diameter for specimens from the 16 quadrats at locality D2a (DC, diameter of detachment constriction; 1st bud, mean diameter and 95 percent confidence limits of diameter at which first budding scar appears).

epitheca where a few uneven growth lines indicate minor disturbance to the polyp. Subsequent growth lines return to normal spacing. More severe damage is indicated where the lip of a calice is broken, resulting in a ragged, chipped appearance. Repair by the polyp followed one of two courses: either the polyp constricted slightly and deposited new epitheca on the inside of the damaged area, or it overlapped the damaged area and deposited new epitheca on top (Pl. 2, fig. 1).

Severe damage of a large portion of the corallite over a long period affects many growth lines. Such deformation may have resulted from growth of the corallite against some type of an obstruction, possibly a shell fragment or lithoclast (Pl. 2, fig. 6).

Internal deformation in *Caninia torquia* has been observed in both transverse and longitudinal sections. In transverse sections, the median septum may show a deflection repeated in adjoining septa, or a portion of

a single septum may start to grow back upon itself before resuming a more normal growth direction (Pl. 2, fig. 5). The cause of this type of deformation is unknown.

In longitudinal sections, two types of deformation of tabulae were noted. An individual tabula may not be continuous across the tabularium and one end is left "unattached." Overlying tabulae begin their growth on the incomplete tabula. In another type, an oblong to circular open area is enclosed by tabulae (Pl. 2, fig. 3a, b). The causes of these types of deformation are unknown.

One individual from locality D3 is aberrant. Its septa are crowded into the tabularium and are highly deformed, many abutting against one another.

*Attachment.*—Some rugose corals were attached to the substrate; others were free-living. In attached forms, various modifications of the corallite were necessary for

support, including talons or rootlets (Hill, 1956). Free-living forms may have been attached as juveniles and thus retain attachment structures, or they may lack signs of support structures.

Attachment structures on *Caninia torquia* are extremely rare. Of the 614 specimens studied only three have structures that resemble talons but may represent deformation (Pl. 2, figs. 2, 4). In combination, the lack of attachment structures, the growth forms present, and dominance of asexual reproduction indicate that *Caninia torquia* was free-living.

*Relation to substrate.*—All corals observed in place in shale and argillaceous limestone lay with the plane of geniculation parallel to bedding and are judged not to be in life

position.

To examine the orientation of corals in limestone, one large block from locality C1 was slabbed at close intervals and outlines of the enclosed corals traced on glass sheets. The glass sheets were then assembled with the same spacing as the cuts, permitting a view of the orientation of the corals within the block (Fig. 12). More than half of the corallites were oriented with the plane of geniculation perpendicular to the bedding, concave side upward, and were judged to be in life position. Field observations of corallites in limestones revealed a similar mode of orientation.

As previously mentioned, the most common form of *Caninia torquia* is a ceratoid cylindrical corallite with one or more genic-

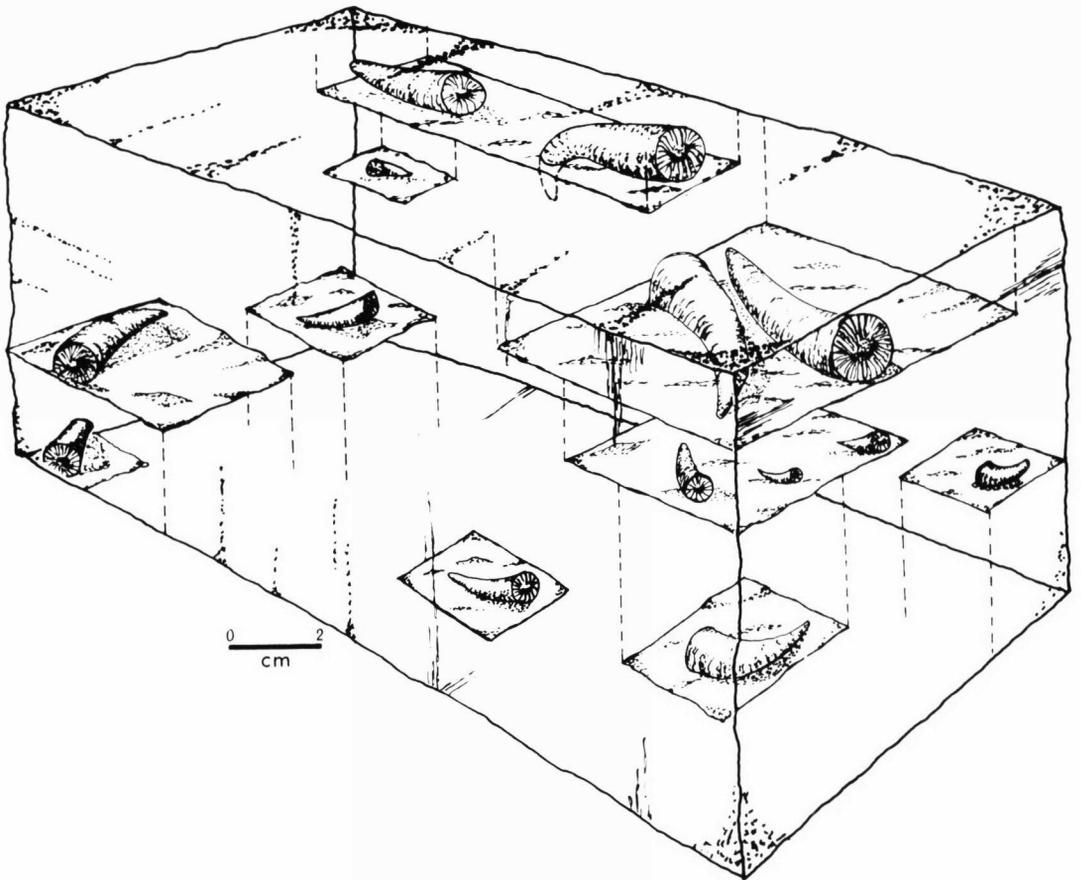


FIG. 12. Orientation of corallites within a serially sectioned block from locality C1, Chautauqua County. Corals with plane of geniculation perpendicular to bedding are judged to be in life position. Dashed lines indicate position of planes within the block.

ulations that remain in one plane. Such a form implies relative stability throughout the life of the coral and that those corallites were maintained with the concave side upward, thus raising the calice slightly above the substrate. The corallite may have been maintained in this position by partial burial in

the substrate, by algal binding as suggested by Baird (1971), or by a small mound built by currents on the lee side of the corallite. The latter possibility has been demonstrated in flume experiments on models of recent free-living scleractinians (Abbott, 1974).

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## EXPLANATION OF PLATES

### Plate 1

#### *Caninia torquua* (Owen)

##### FIGURE

1. Individual with attached juveniles, (a) lateral and (b) convex views;  $\times 1.5$ , KUMIP 107002.
2. Encrusting *Spirorbis* on convex side of large corallite;  $\times 3$ , KUMIP 106934.
3. Encrusting bryozoan on apical region of partially eroded corallite;  $\times 1.5$ , KUMIP 106749.
4. Attachment base of ramose bryozoan on concave side of small corallite;  $\times 2.5$ , KUMIP 106739.
5. Encrusting foraminiferan *Tetrataxis* on epitheca; photomicrograph,  $\times 40$ , KUMIP 110635.
6. Encrusting bryozoan partly overlapping calice;  $\times 1.5$ , KUMIP 107028.
7. Boring in corallite passing through epitheca into septum, longitudinal section, photomicrograph,  $\times 40$ , KUMIP 106911.

### Plate 2

#### *Caninia torquua* (Owen)

##### FIGURE

1. Severe damage to epitheca;  $\times 4$ , KUMIP 106679.
2. Views of possible attachment structures and crinoid fragment used as substrate; (a) top and (b) lateral views;  $\times 3$ , KUMIP 106662.
3. Internal deformation, cause unknown; (a) transverse and (b) longitudinal section;  $\times 10$ , KUMIP 106986.
4. Possible attachment structure; (a) lateral view and (b) base;  $\times 2$ , KUMIP 106894.
5. Transverse section showing deformation in septa, epitheca toward top; photomicrograph,  $\times 40$ , KUMIP 106941.
6. Severe damage to epitheca;  $\times 1.5$ , KUMIP 106816.



1a



1b



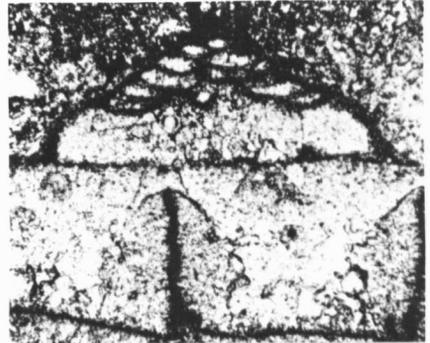
2



3



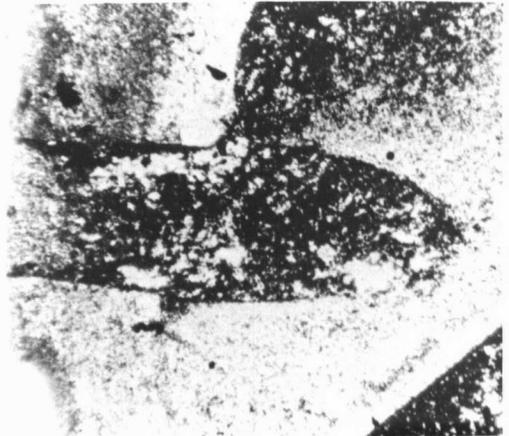
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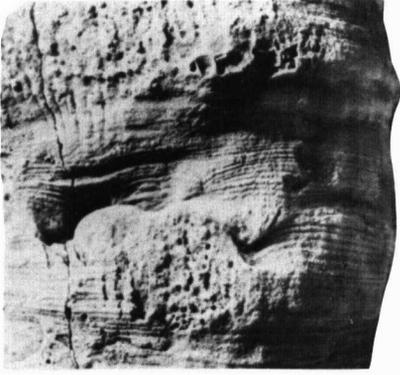
5



6



7



1



2a



2b



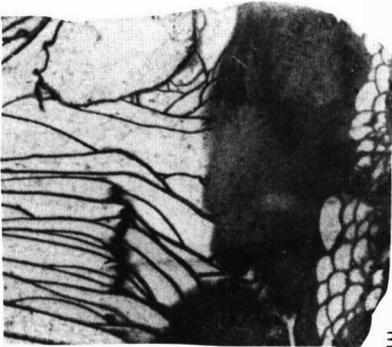
3a



4a



4b



3b



5



6