Paleoenvironmental History of the Middle Ordovician Rugosa of Eastern North America

by Gretchen Hampt

Advisor: Mary L. Droser

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Introduction

Our understanding of the structure and function of biological systems can be increased when viewed in the context of their evolutionary history on a geological time scale. Generally, both paleoecology and ecology have focused on the interrelationships of organisms and their environments in short time frames. For instance, a paleoecologist might study the fossil communities of the Columbus Limestone reefal environment at Marblehead, Ohio, or an ecologist might attempt to characterize the interrelationship of glacier lilies and their pollinators. Both workers may realize that the organisms they study evolved in response to ecological pressures, yet neither, most likely, considers that the ecological contexts in which those organisms evolved may have changed through geologic time. Because biological systems evolve through geologic time, organisms show adaptations to conditions that may or may not exist at the time they live but that must have directed the evolution of the organisms which gave rise to them. It is always the case that the ecology of extant organisms is, in part, a relict of their evolutionary histories. By considering organisms in the context of their evolutionary paleoecology, we can gain a powerful tool for understanding why they have evolved the way they have.

One means to access evolutionary paleoecology is to examine the physical paleoenvironments that organisms inhabited through geologic time. Analyses of the paleoenvironments of the first occurrences of major evolutionary novelties (Jablonski, et al., 1983) and the paleoenvironmental histories of Phanerozoic benthic marine communities (i.e. Sepkoski and

Sheehan, 1983; Jablonski, et al., 1983; and Sepkoski and Miller, 1985) have demonstrated that major communities (fossil assemblages consisting of members of groups of organisms found together in the rock record) appear to occur first in nearshore (onshore) settings. These communities appear then to spread offshore into deeper water environments with evolutionary time. Meanwhile, offshore assemblages tend to be more archaic than contemporaneous onshore assemblages (Jablonski, et al., 1983). This pattern, while demonstrated for certain community types and higher level taxa, has not been rigorously tested.

It is surprising that the first occurrences of fossil communities and major evolutionary novelties should be preferentially associated with a particular environment. Differential speciation rates cannot account for the preferential first occurrences of evolutionary novelties onshore because speciation rates are higher for offshore clades (Jablonski, et al., 1983). Statistically, it follows that major innovations are more likely to occur <u>offshore</u>. In a microevolutionary time scale, onshore origination and offshore migration are similarly unexpected. Genetic variation (mutation) within individuals appears to occur randomly. Also, at first evaluation, the short term responsiveness of evolving populations to selective pressures does not seem to vary on microevolutionary time scales. In this context, the observed patterns of onshore origination and offshore migration are not explained, and, in fact seem unlikely (Bottjer and Jablonski, 1989). Hypotheses for onshore origination consider ways that nearshore environments are distinctive and may promote the appearance of new communities. The presence of contemporaneous, but distinct, communities in different environments suggests that environmental factors play a role in the observed patterns. That there is no known progressive change or episodic fluctuation in physical environments through the Phanerozoic suggests that the observed patterns depend on changes in the global physical environment (Sepkoski and Sheehan, 1983; Jablonski and Bottjer, 1983; Jablonski et al., 1983; Sepkoski and Miller, 1985; Bottjer and Jablonski, 1989).

In order to evaluate intelligently the mechanisms underlying onshore origination and onshore-offshore migration, it is necessary to document rigorously the paleoenvironmental history of faunal groups (Bottjer and Jablonski, 1989). Patterns documented at the community-level may simply reflect individual clade histories that appear to act in concert in a broad time frame. In order to determine whether the onshore - offshore process functions at the community level or merely reflects individual clades' histories, the paleoenvironmental histories of higher order taxa (clades) must be documented. Bottjer and Jablonski (1989) and Droser, et al. (1988) have shown that the onshore - offshore pattern varies among clades in times and rates of expansion and retreat. This suggests that the mechanisms promoting onshore origination and offshore migration do not function at the community level. By first establishing and then comparing paleoenvironmental histories on a clade-by-clade basis, hypotheses which account for the community level trends can be tested. Comparing the differences in patterns and rates of paleoenvironmental changes, and the existence, or lack thereof, of onshore - offshore migration for various higher level taxa will help identify the mechanisms underlying shifts in paleoenvironments through the Phanerozoic.

The existence of paleoenvironmental shifts through time has implications for the work of many geologists. Commonly, a sedimentary environment is identified based on the modern environments of organisms related to the fossils that are present. Documenting shifts in paleoenvironments demonstrates the fallacy of assuming that the presence of particular higher level taxa can definitively identify an environment through the Phanerozoic. Thus paleoenvironmental reconstructions must not be carelessly based on the presence of representatives of higher level taxa. For example, through their evolutionary history isocrinid crinoids have been more or less restricted to different parts of the continental shelf and deep sea. Detailed study of their environmental history has shown that they originated in the Early Triassic and were deposited solely in nearshore and inner shelf environments at that time. In the Late Triassic they first appear in middle shelf sediments. Isocrinids continue to occupy a broader and broader range of environments across the shelf and into the deep sea until the Late Cretaceous. Starting in the Late Cretaceous, isocrinids become restricted to deeper and deeper environments until, in the Recent, they occur only in outer shelf and deep sea environments. It is clear that isocrinids did not randomly inhabit the seas, but their environmental history is too complex to permit generalized statements of their environments without the rigorous documentation that has been carried out (Bottjer and Jablonski, 1989).

Studies such as the isocrinid crinoid study provide a new approach to paleoecology. Historically, paleoecoloical studies have relied upon comparison of fossil taxa and communities with comparable modern analogues. The recent work documenting changes in paleoenvironments inhabited by organisms through time has delegitimated simple applications of transferred ecology. Yet, the development of evolutionary scale paleoenvironmental histories on the clade level can provide a new methodology for using fossils as paleoenvironmental indicators. Once the paleoenvironmental histories are established for various clades within well-defined time periods, the presence of representatives of one or more clades will provide clues to identify a given paleoenvironment.

The present work is a preliminary documentation of the paleoenvironments of the earliest Rugosa in a time-environment-geographical context. The focus is on the Middle Ordovician Rugosa of eastern North America. The purpose of this research is to establish the paleoenvironments of the oldest rugose corals and the environments of the early diversification of the Rugosa of eastern North America in order test the hypotheses of onshore origination and subsequent offshore migration at the level of a Paleozoic clade. This work will point the way for further documentation of the paleoenvironmental history of the Rugosa as well as contribute to a growing data base of paleoenvironmental histories on the clade level. Once we have a well-documented picture of the physical conditions under which organisms lived through time, we will be able to evaluate more knowledgeably the mechanisms that drive large scale evolutionary processes. Work such as this and future comparative analysis of patterns elucidated by such work are essential prerequisites to a discussion of the mechanisms that drive the evolution of ecological communities and their constituent clades.

Previous Work

Onshore-Offshore Patterns

The present work proceeds from earlier investigations of large scale paleoenvironmental trends in the history of Phanerozoic organisms. Jablonski, et al. (1983) documented the onshore origination of new community types and the onshore - offshore trend of faunal change that results in contemporaneous "onshore-innovation, offshore-archaic" faunas. They identified these communities based on a cluster analysis of 102 fossil assemblages that inhabited environments ranging from the nearshore to the continental slope and deep basin. The cluster analysis identified four major community types whose environmental contexts through time were tracked in the literature. A pattern was recognized in which established onshore communities move offshore as more modern communities originate in the onshore environments with the result that distinct contemporaneous evolutionary communities inhabit different parts of the ocean floor. Jablonski and Bottjer (1983), Sepkoski and Sheehan (1983; see figure 1), and Sepkoski and Miller (1985; see figure 2) further documented the community-level phenomena of onshore origination and subsequent movement into offshore environments. Each of these works includes significant discussion of the macroevolutionary and microevolutionary mechanisms that might underlie these patterns.

Analysis on the clade level is in progress by Sepkoski on targeted Paleozoic clades; in press by Bottjer and Jablonski (1989) on targeted post-Paleozoic clades (isocrinid crinoids, cheilostome bryozoans, and tellincid bivalves); and published in abstract form by Droser, et al. (1988) on deep-water scleractinia. Paleoenvironmental trends in the history of trace fossils have been examined by Droser and Bottjer (1988) and Bottjer, et al.

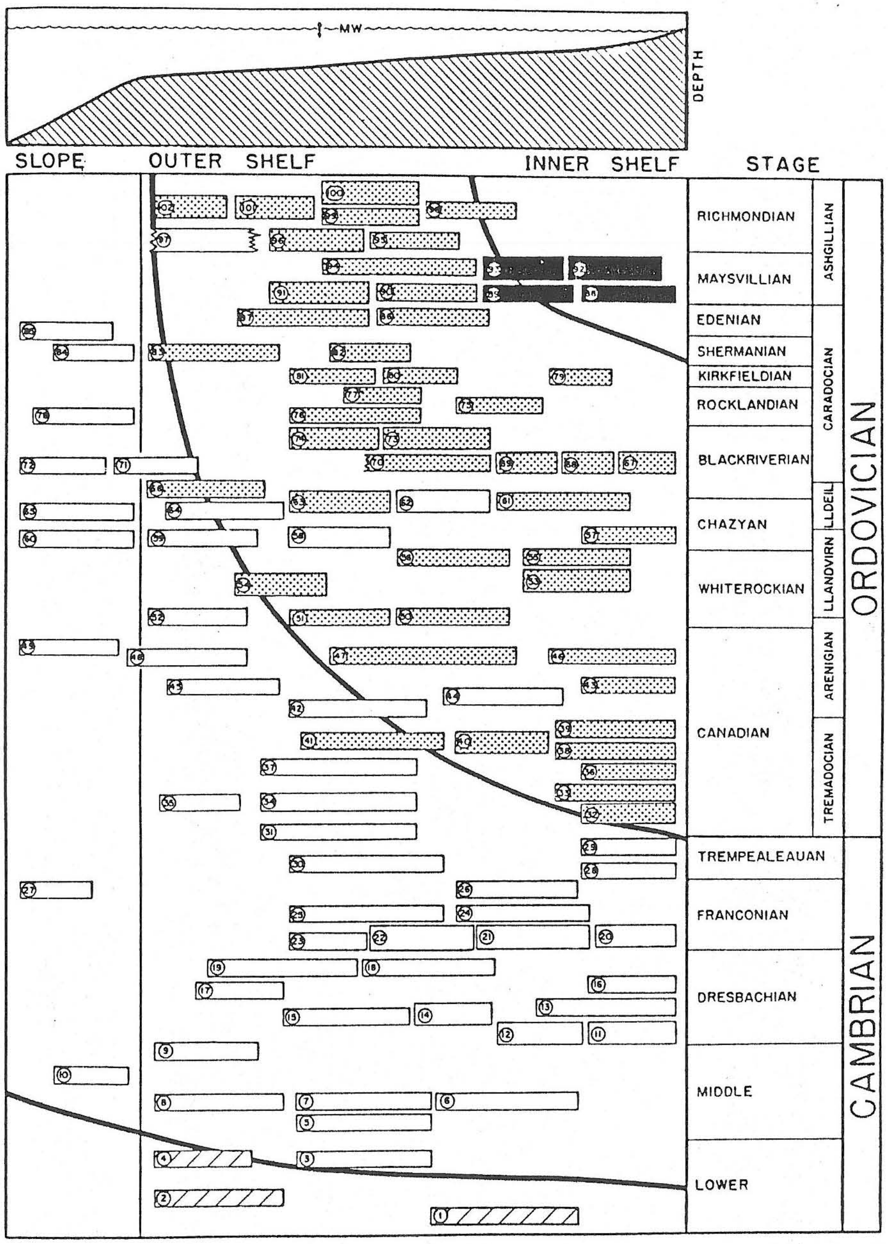


Figure 1

Time-Environment Diagram (Sepkoski and Sheehan, 1983)

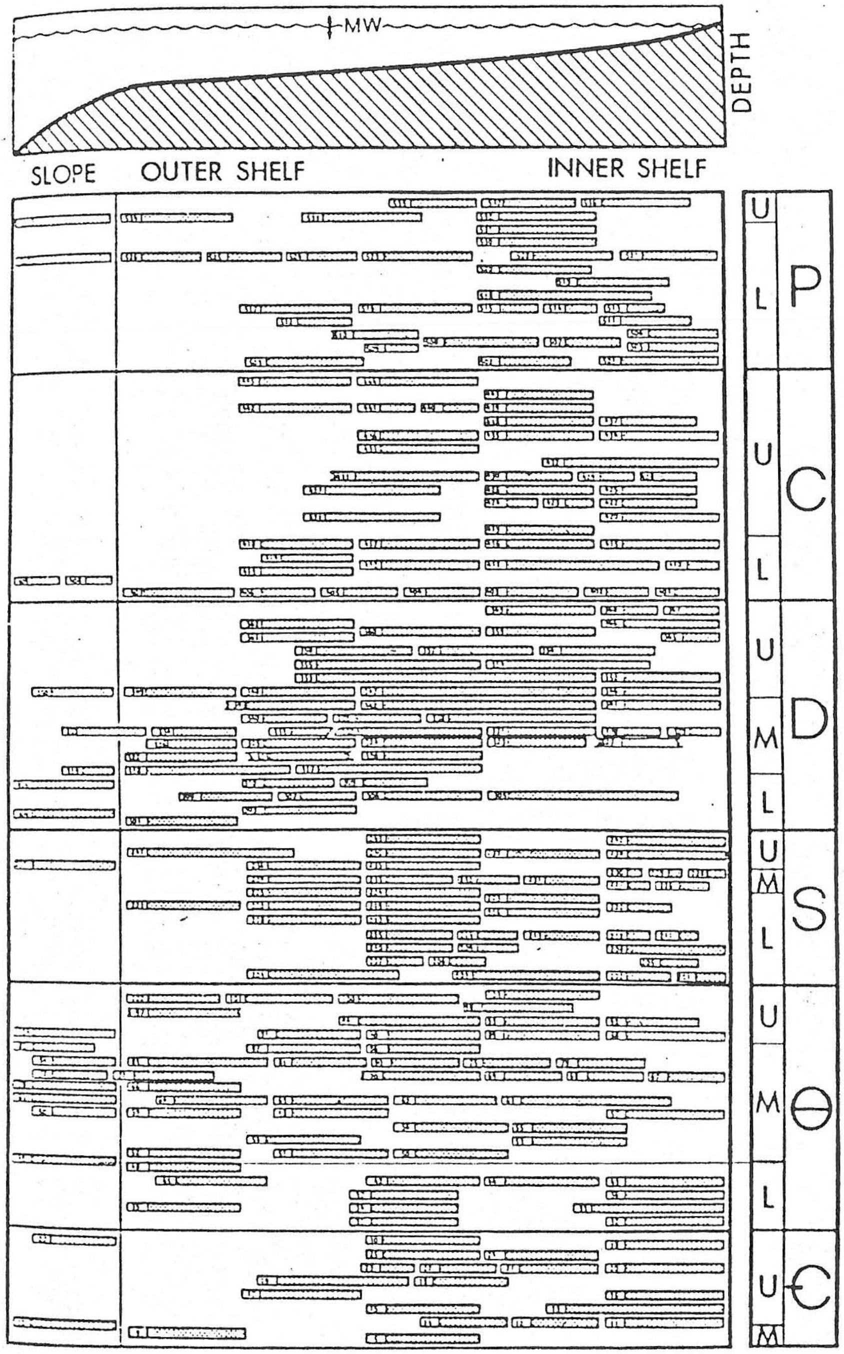


Figure 2
Time-Environment Diagram (Sepkoski and Miller, 1985)

(1988) in a similar context, and like benthic macroinvertebrates, some common trace fossils "show an environmentally linked directional pattern through time" (Bottjer, et al., 1988). Each of these papers is similar in conception and methodology to the present work in that they use the published literature, more or less supplemented by field work, to identify the depositional environments of members of the targeted clades through their histories. Onshore origination is a consistent pattern for the clades that have been studied. These works have also identified two distinct patterns of onshore-offshore migration (both of which are seen in the isocrinid crinoids). Expansion occurs as members of a clade which originated onshore begin to extend their environments across the shelf. Retreat is the pattern in which movement by some members of a clade into offshore environments is accompanied by extinction of onshore taxa. Different rates, as well as patterns, of offshore migration have been documented for these groups. This knowledge has permitteed the assertion that offshore migration is not a community-level phenomenon. In addition, demonstrating a common pattern of environmental migration on the clade level has generated discussion of the idea that higher-level taxa can legitimately be considered as units upon which evolutionary pressures can act. It must be noted that these studies have only considered a very few of the clades whose paleoenvironmental histories might be determined.

Paleoenvironments of the Rugosa

Nelson (1981), working on solitary rugose faunas of the north American Ordovician, showed that the solitary rugose faunas that he studied may be be of Middle Ordovician age but most likely belong to the Upper Ordovician. The corals he studied are not included in this analysis because the strata in which they are found are not conclusively Middle Ordovician in age.

Elias has published many detailed paleoenvironmental studies of eastern North American Ordovician solitary rugose coral faunas (e.g. Elias, 1980, 1981, 1982; Elias and Buttler, 1986; Elias, et al., 1987; Elias, et al., 1988), but these have primarily considered Late Ordovician corals and provide very detailed local paleoenvironmental analyses. In the Middle Ordovician the Rugosa were neither so common nor abundant as they became in the Upper Ordovician, so perhaps the enthusiasm to study them has not existed. Several early to middle twentieth century paleontologists (Stumm (1963), Bassler (1950), Okulitch (1938, 1939), and Rominger (1876-whoops,even earlier) concerned themselves with the identification and stratigraphic context of the earliest rugose corals. Their work was helpful in identifying areas of rugose occurrences, but rarely provided environmental information useful in the present work. Corals of western North America were not included in this project primarily because, although present (Ross, 1966), they have not been documented in detail. No recent work contains a comprehensive or complete discussion of the North American Rugosa.

Due probably to the dearth of coral workers in recent years, as well as to the need for a comprehensive revision of the classification of <u>Lambeophyllum</u>, one of the two major genera of Middle Ordovician rugose corals in North America, many of the Rugosa whose occurrences are cited in this paper are classified only to the genus level. This deficiency in classification serves to underscore the scarcity of recent work on these corals.

Through their history, worldwide, rugose corals are generally associated with reefal and perireefal environments. Actually, three major assemblages of rugose corals are recognized and each is associated with a different rock type: dark calcareous shales with or without thin-bedded limestones; argillaceous limestones; and perireefal limestones (Hill, 1981). These lithologies represent several different environments of different water depths and energy levels. In addition, in the middle and late Paleozoic strata, a sparse fauna of limited diversity is found in abyssal deposits. It is clear that rugose corals could inhabit a range of environments. But, within the Rugosa, corals of different morphologies and fauna of different degrees of diversity are associated with each of the environments. Small, solitary rugosa tend to occur in the deeper shelf and deep sea. It must also be noted that early rugosa were small and solitary (Hill, 1981).

Methods

Introduction

I used two approaches to document the paleoenvironment of the first rugose coral and the early paleoenvironmental history of the clade: 1) field observation, and 2) examination and synthesis of paleontological and sedimentological literature. The field work focused on the environments of oldest and other early North American rugosans. The paleogeographical extent and history of the Middle Ordovician Rugosa whose environments were not examined in the field for this work were assembled using the available, relevant literature. Data gathered through both the field studies and the literature was incorporated into a diagram showing eastern North American rugosan paleoenvironments through the Middle Ordovician.

Time-Environment Diagram

The time-environment diagram provides a pictoral synthesis of the rugosan paleoenvironmental history. Time is shown on the vertical axis and environments are shown on the horizontal axis for various occurences of rugose corals. It serves as a simple means to identify any trends or patterns which may exist in rugosan paleoenvironments. Sepkoski and Sheehan (1983), Sepkoski and Miller (1985), and Bottjer and Jablonski (1989) have used similar diagrams to the same purpose (remember "Previous Work").

Chronostratigraphy

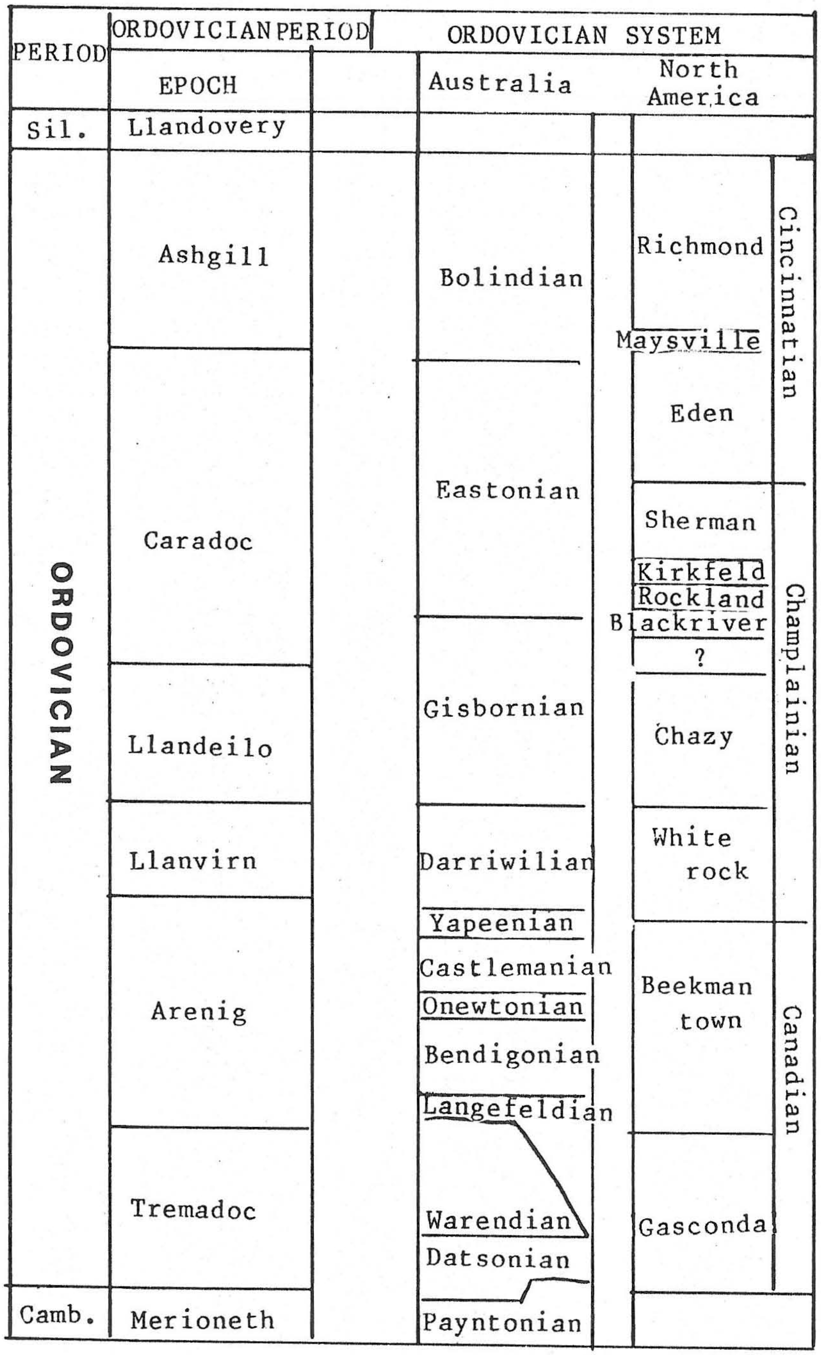
The Middle Ordovician is defined for the purpose of this paper by the boundaries of the eastern North American Champlainian Series because the focus in both the field and literature aspects of the project was eastern North America where the Middle Ordovician is generally defined as the Champlainian Series. The broad time-stratigraphic framework in which I have worked has been defined by Harland, et al., 1982. North American time-rock stratigraphy was taken from Ross, et al., 1982 (see figure 3), with more detailed information on North American and other continental local rock stratigraphy culled from various smaller scale works.

Environmental Framework

The environmental framework used for this study is similar to that used by Sepkoski and Sheehan (1983), Sepkoski and Miller (1985), and Bottjer, et al. (1988), in previous studies documenting paleoenvironmental histories. Sedimentary structures that reflect the energy of the environment of depositition define a paleoenvironment. The five environments used in this study are nearshore, inner shelf, middle shelf, outer shelf, and slope and deep basin. They are defined and recognized as follows:

Nearshore (NS): subtidal, but above fairweather wave base
  thick, laterally continuous beds
  sand-size and coarser sediments
  common parallel lamination and cross bedding
  fossils disarticulated, abraded, well-bedded
Inner shelf (IS): below fairweather wave base, above normal storm wave base
  common storm beds interbedded with fairweather beds
  fairweather beds are fine grained
  storm beds have parallel laminations or hummocky cross-stratification
  fossils are commonly in storm beds
Middle shelf (MS): below normal storm wave base, above maximum storm wave base
  massive beds, commonly rhythmic; rare storm beds
  fine-grained
  fossils unabraded
Outer shelf (OS): no storm influence, landward of shelf edge
  massive, commonly rhythmic, beds with no storm influence
  fine-grained
  no evidence of slumping, mass movement or turbidites
  fossils unabraded
Slope and deep basin (SDB): Beyond shelf edge
  slumping, mass movement, turbidites, deep sea fan facies geometries
  fossils unabraded; those deposited by mass movement, are not included
(From Bottjer, et al., 1988)

These environments are broadly geographical, but as they are defined by energy considerations, sometimes "nearshore" environments occur offshore of



from Harland, et al., 1982

FIGURE 3

"inner shelf" environments, such as when a relatively quiet water lagoon occurs onshore of a barrier island.

The environments are intentionally very broadly defined on the basis that the literature, which must provide the data for analyses of large-scale trends, is very heterogeneous. In order to colate objectively the information contained in the literature, a consistently applicable set of standards for evaluation must be used. I placed a given coral-bearing bed in an environmental framework on the basis of its sedimentary structures as well as a broader scale facies analysis. When paleogeographic and other information is available, it further informs the placement of rocks in an environmental context. In the course of both the field and literature search for this project, I encountered corals or reports of corals in storm deposits in intertertidal to supratidal environments. Corals found in these deposits are assumed to have been carried from the nearshore or inner shelf environment.

Field Methods

I did field work in three regions: in the Lake Champlain Valley of New York and Vermont, the Black River Valley of central New York, and in the Lexington area of central Kentucky (see figures 4 and 5). I chose the Champlain Valley as a field area because the oldest reported rugose coral has been reported there. The oldest well-documented North American rugose corals are some of the oldest rugosans in the world (the other oldest rugosans are found in Australia where it was not an option to do field work). I chose the Kentucky localities on the basis of their relatively older age among the rocks exposed within reasonable distance of Oberlin. One of the Kentucky localities holds abundant rugose corals that were previously unreported (Miller, pers. comm., 1989).

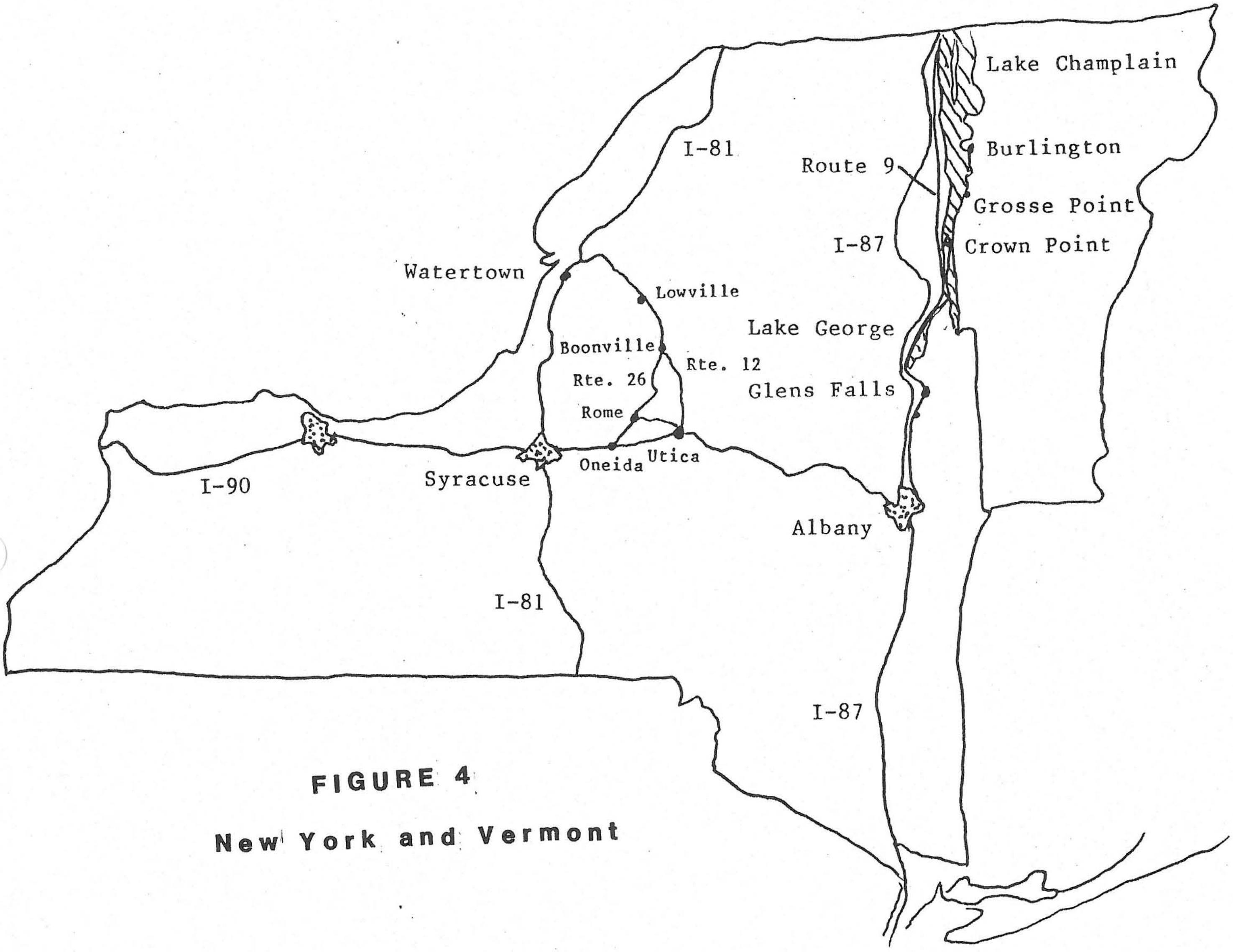


FIGURE 4

New York and Vermont

I did field work in the Champlain Valley at Grosse Point and Crown Point and northeast of Utica.

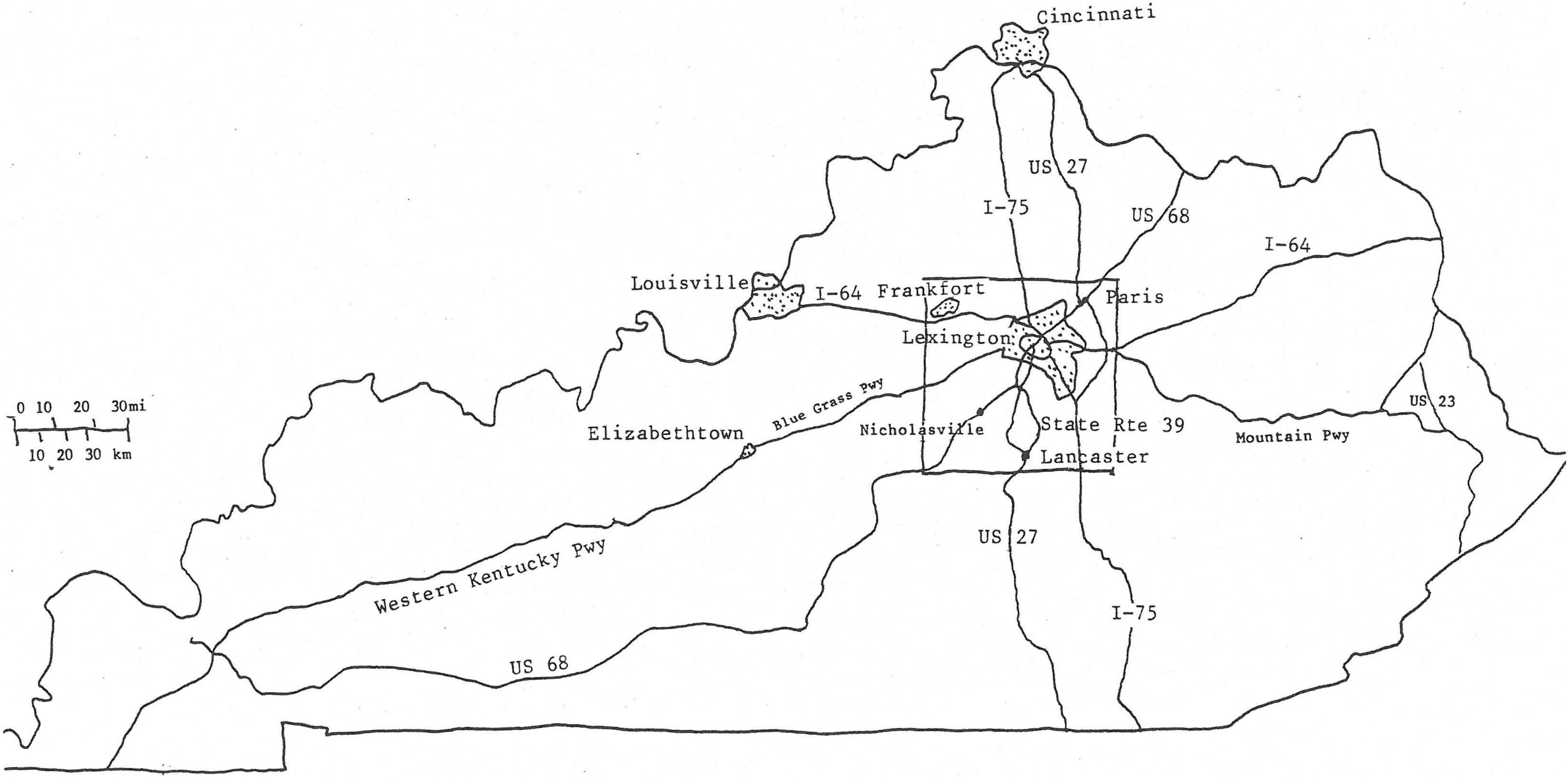


FIGURE 5

Kentucky

The box surrounds the field areas visited in Kentucky for this project.

In October, 1988, I spent several days exploring in the Lake Champlain area to look for corals in areas of published (Welby, 1961) and unpublished (Speyer, pers. comm., 1988) unconfirmed previous reports; and working at established rugose localities to document paleoenvironments. In Vermont, I searched for rugose corals at the previously documented locality of the oldest rugose coral specimen, but did not measure a section as the locality had been previously described and no corals were found. At one known rugose coral locality each in eastern and central New York I measured sections of the coral bearing strata and associated beds. I took lithic samples, coral samples, and photographs. Similar procedures were followed on a three day trip to central Kentucky in March, 1989. Several coral localities were. visited so that environmental determinations could be made. Corals were found at two localities in the Lexington area, but were not found at one site where only a brief stop was made and no new section was measured. At two localities sections were measured and samples and photos were taken.

Literature

The literature for eastern North American coral occurences is relatively completely documented in this paper and for the corals documented sedimentological data was used to identify their environments through the Middle Ordovician. An attempt was made to use environmental data from work published in the last twenty years because, in general, earlier workers did not consistently make the kinds of observations that are useful in determining paleoenvironments as they are defined here. Also, sedimentological data was used only when it was clear that the corals were found within the described facies of a formation. This means that sedimentological data and coral data almost invariably come from the same source. Otherwise, it is usually impossible to be sure in which beds, and hence which facies, the corals were deposited.

Some absences of rugose corals are included. It is necessary to document absences to assure that the positive data points do not just reflect a biased sampling of environments. Absences are gleaned from complete faunal lists which do not include rugose corals, but do record the presence of taphonomically comparable organisms, organisms with mineralogically similar skeletons. Without the taphonomic control, absences might be recorded which are the result of diagenesis rather than environmental restrictions on the living organisms. Tabulate corals, the sponge Receptaculites, calcitic brachiopods (articulate) and bryozoans were used as controls in this study. It is also important to know whether the worker who made the original faunal lists tried to include organisms such as corals in the report. I assume that if a report includes tabulate corals and/or sponges, rugose corals would have been noted, if present.

Some early workers (Bassler, 1950; Okulitch, 1936) identified some colonial corals as rugosans which have subsequently been revised to inclusion in the Tabulata or are now considered indeterminate (Hill, 1981). In several cases the identity of these corals in the revised (Hill, 1981) classification scheme is difficult to discern through the literature. They have not been included in this work.

Geographical and stratigraphical data on corals from Asia and Europe are included, although very incomplete. Language, library, and time constraints prevented a more thorough review.

Systematics

Systematic identification of the corals collected was beyond the scope of this study. The systematic identification of Lambeophyllum profundum, the common, earliest eastern North American rugose coral is problematic.

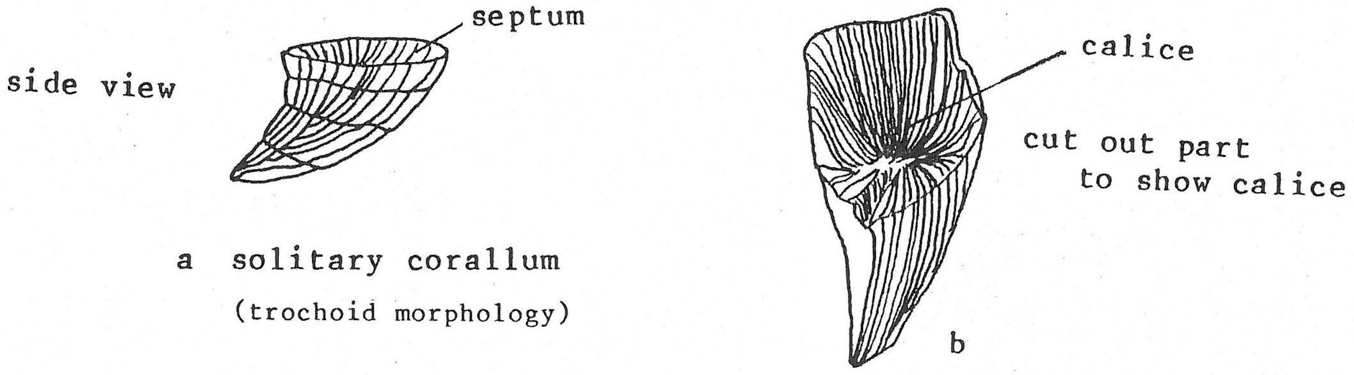
Species of the genus Lambeophyllum have not been rigorously identified in paleontological history, and the systematics need to be rigorously defined and applied by modern workers before they can be utilized in a study such as this (Elias, personal communication, 1988).

Introduction to the Rugosa

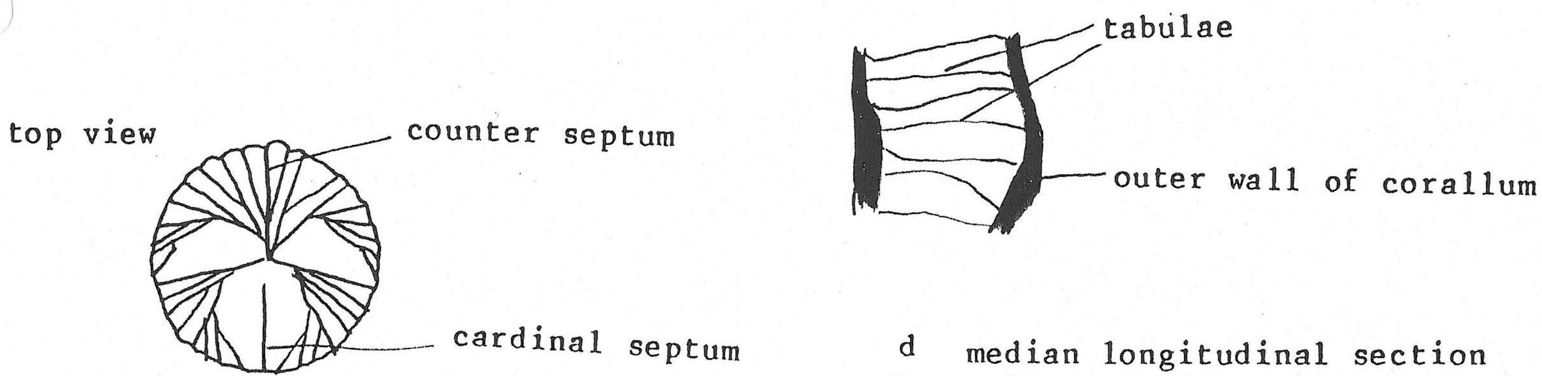
The Rugosa originated in the Middle Ordovician and went extinct at the end of the Permian. Along with the Tabulata and the Scleractinia, they are considered a subclass of the class Anthozoa (Hill, 1981). Like the skeletons of the tabulata and the scleractinia, rugose skeletons are composed of calcium carbonate. Their skeletons are distinguished from those of the Tabulata and the Scleractinia on the basis of septa that are radially arranged, longitudinally oriented partitions within the skeleton. The rugosan method of septal insertion is an important criterion to distinguish them from other corals. The Rugosa have well-developed septa which are inserted in equal numbers in each of four quadrants. When septa are present in tabulate corals, they are tiny; scleractinian septa are inserted symmetrically in groups of six. Another distinction between the major groups of corals is that the Rugosa and Scleractinia have both solitary and colonial members, while the Tabulata are strictly colonial (see figure 6; references for this entire section are Hill, 1981 and Clarkson, 1979).

The classification within the Rugosa is complex and subject to continuing discussion, but is consistently based to some extent on the fine skeletal structures of the fibrous and crystalline septa. The septa are made of aggregates of cylindrical trabeculae that consist of "radiating whorls of tiny fibres" (Clarkson, 1979, p.71). Trabeculae are classified on the basis of the orientation of their axes and the arrangement of their fibers relative to their axes. Septa may be distinguished by the types of trabeculae of which they are composed.

The skeleton of a solitary coral or a coral colony is called a corallum. Coralla are exoskeletons secreted by the soft body of the organism that is assumed to have rested in the calice, a generally bowl-



a solitary corallum
(trochoid morphology)



order of septal insertion can be inferred
c

d median longitudinal section
of corallum showing tabulae
(*Tryplasma sp.*)
from Hill, 1981

FIGURE 6

These diagrams show several skeletal elements of rugose corals.

shaped surface at the top of the corallum. The skeletons are generally shaped like inverted cones, but the shapes of solitary rugose corals range from discoidal to nearly cylindrical. The morphologies of colonial rugosa are also very variable, so that in some genera the individual corallites of the corallum are barely connected and in others corallites are enclosed on all sides by other members of the colony. The morphologies of the coralla as wholes vary as well. The bilateral symmetry of the Rugosa is apparent in the emplacement of the septa in four quadrants around the first-formed septa, the cardinal and counter major septa.

The Rugosa were epifaunal benthic organisms and were most profuse and diverse in carbonate perireefal and reefal environments, but were certainly not restricted to these environments. It is not known whether the Rugosa that lived in the photic zone possessed zooxanthellae. Like other cnidaria, Rugosa were probably carnivores, feeding on zooplankton introduced to the mouth area by the action of cilia or tentacles. Neither solitary nor colonial Rugosa normally cemented themselves to the sea floor and when found in life position, it is generally in sediments that would have been soft substrates. It is suggested that the shape of the skeleton of the solitary horn-shaped corals allowed the organism to anchor itself by partial burial as it sank into a muddy substrate. The convex side of the corallum would have faced down, so the soft body would be supported free of the muddy bottom in which it was stabilized, and thus would be free of sediment, making feeding possible. Colonies are assumed to have stabilized themselves similarly -- by gravity in a soft substrate. Due to this limited means for stabilization, Rugosa were not important to the construction of massive structural reefs, although they were important members of reef communities who inhabited the lower energy subenvironments of Paleozoic reefs.

The Rugosa evolved in five major episodes with one faunal group dominant, but not exclusively represented in each phase. The earliest rugosan phase of development lasted from the Middle Ordovician into the lowermost Silurian when small, solitary corals with simple skeletal structures dominated. Later in the early Silurian, solitary and colonial Rugosa diversified tremendously and became very prolific. They moved into reefal environments at this time. In the Middle to Upper Devonian large colonial Rugosa diversified and became dominant. The climax of rugosan development occurred in the Lower and Middle Carboniferous when both solitary and colonial forms of the family Zaphrentidae were dominant and evolved rapidly. A final radiation occurred in the Permian. The dominant corals were from a family with small, solitary members. Each of these evolutionary radiations involved the development of some of the skeletal elements which complicate the morphology of the Rugosa.

Origin of the Rugosa

The ancestors of the Rugosa are still undetermined (Hill, 1981; Weyer, 1980). A widely discussed idea that the Tabulata gave rise to the Rugosa or that the Tabulata and the Rugosa had a common skeletonized ancestor (Flower, 1961; Ivanovski, 1966, 1968; Webby, 1971; many others) has been generally abandoned (Ivanovski, 1984; Webby, pers. comm., 1988). The consensus among several workers is that the Rugosa descended not from a skeletonized tabulate coral (Webby, 1988, pers. comm.) but from a soft-bodied ancestor (Weyer, 1981; Ivanovski, 1984; Neuman, 1984; Sytova, 1977). The rejection of a tabulate coral as a possible ancestor to the Rugosa stems, at least in part, from a recognition that it is unlikely that a colonial form was the ancestor to the oldest Rugosa, which were solitary (Neuman, 1984). There is also the possibility of an ancestor rugosan or a first rugosan that was skeletonized, but not preserved or not yet discovered by paleontologists.

Although we know that unskeletonized cnidaria lived well before the first Rugosa evolved (they are first well-documented in the Vendian among the Ediacaran Fauna (Ivanovski, 1984); although see Seilacher, 1984), their fossil record is not complete enough to yield specific information on the descent of the Rugosa. Many of the previous assumptions of the relationships between the early soft-bodied cnidaria and later skeletonized cnidaria are invalid because they depend upon broad comparisons of the morphologies of the soft parts of organisms which lived 600 million years apart (the soft-bodied cnidaria of the Pre-Cambrian and Cambrian compared with modern scleractinia) (Ivanovski, 1984). Instead, fauna closely related in time must be studied for clues as to phylogenetic relationships in order to evaluate the role that convergent evolution may have played in producing similar morphologies (Ivanovski, 1984). The fossil record of soft-bodied organisms is limited, so further work in this area will depend first upon luck in finding useful fossils and then upon detailed analysis of their succession and relationships.

The oldest well-documented rugose corals appear within a very narrow range of time on three different continents — Lambeophyllum profundum in North America, Hillophyllum priscum in Australia, and Primitophyllum primum in Europe (Hill, 1981). Due to the limits of stratigraphic correlation between continents, it is not possible at this time to determine precisely the difference in age of these oldest Rugosans or even to say definitely whether L. profundum or H. priscum is the oldest (Webby, 1971; see figure 3). It is fairly clear that the first Australian and North American rugose corals are older than the European P. priscum (Webby, 1971).

The Rugosa diversified rapidly once they made a first appearance. These first Rugosa are classified in different families, as well as different genera (Hill, 1981), and this classification has led workers to several different ideas concerning their genesis and early diversificaton. First, as has been mentioned, it is possible that there existed a first skeletonized rugose coral that was the ancestor to the three genera listed above, and that it has either not been preserved or not been documented. Sytova (1977) has hypothesized the independent development of skeletons for a pre-existing, widespread group of soft-bodied Rugosa based on the rich generic and species compostion of the rugosa in the Middle Ordovician and the penecontemporaneous appearance of rugose corals in widely scattered localities. Because the oldest recorded Rugosa are not closely related, this hypothesis may have some validity. Still, it is not a common assumption that a major group of organisms arose polyphyletically, and others have avoided or rejected this explanation (e.g. Neuman, 1984). A more conventional and more credible hypothesis is that the rugosan skeleton evolved only once, first in either L. profundum or H. priscum, and that geographic dispersal and diversification subsequent to origination occurred immediately and rapidly (Ivanovski, 1984; Neuman, 1984). That all three of the earliest genera have similarly constructed (crystallized) acanthine septa suggests a close unilineal relationship among these corals.

As suggested by Ivanovski (1984), more detailed study of the nature of the early Ordovician cnidarian fauna, skeletonized and skeletonless, is necessary to establish the nature of the rugosan ancestor. Yet, if the ancestor was soft-bodied, its initial preservation and present day identification are unlikely (Weyer, 1980). A more solid identification of the oldest recorded rugose coral could be achieved merely through a finer resolution of time-stratigraphic correlation between continents.

The Mystery of the Oldest Rugose Corals

The identity of the very oldest rugose coral is unresolved due not only to the limitations of the stratigraphic correlation, but to an often cited, but unconfirmed report of a very early Chazyan Stage specimen of *Lambeophyllum profundum*.

Chazyan Stage Corals?

The single oldest report of a rugose occurence is that from the Chazyan Stage Crown Point Limestone in the Lake Champlain Valley of Vermont (Welby, 1961; see figure 4). The Chazyan rocks of Vermont are clearly older than the Australian Gisbornian Stage rocks in which Barry Webby's *Hillophyllum priscum* is confirmed and the New York/Vermont Blackriverian Stage rocks where *Lambeophyllum profundum* is abundant (see figure 3). Charles Welby's *L. profundum* from the Crown Point has been cited for years as the unconfirmed oldest rugose specimen (e.g. Hill, 1981). For this paper, an attempt was made to confirm Welby's report; unfortunately, no success can be reported on this front.

In a paper detailing the systematics of a tabulate coral discovered in the Crown Point and Valcour Formations in the course of Welby's field work for the Vermont Geological Survey in 1956-1959, Welby mentions the occurrence of several rugose corals (Welby, 1961). In a subsequent publication, Welby (1962) includes a photograph of a coral identified as *Lambeophyllum profundum* from the Crown Point Limestone of the same locality. Welby did not seem to be aware that these were the oldest reported rugosans. In his papers Welby gives no further information than the statement of their presence. No systematic description has been done of the rugosans from Crown Point, and no other workers have confirmed their presence.

My own attempts to find rugose corals at Welby's locality and to find Welby's original specimen were unsuccessful. Because I found no corals at Welby's locality, I tried to track down Welby's original specimen. Welby (pers. comm., 1988) tentatively recalled that he listed L. profundum among the fauna at Grosse Point on the basis of one specimen and that he may or may not have collected it. (He did photograph it — it is figured in his 1962 publication.) If he did not collect it and make a thin section, the species identification is invalid. Welby said that if he had collected the specimen it would have been deposited at Middlebury College or in the Vermont State Geological Survey collections which are now held at the University of Vermont. The University of Vermont does not have any collections which are labelled as Welby's work (Dr. Allen Hunt, 1989, personal communication). The Middlebury College collection is not well catalogued, and the catalogue does not list a L. profundum. The collection does include specimens of L. profundum from the Orwell Limestone which is the formation in which early, well-documented rugose corals commonly occur. It seems that if Welby did collect a rugose specimen from the Crown Point Limestone beds, it has since been lost. (The relevant correspondence is included in Appendix A.)

The Australian/North American Question

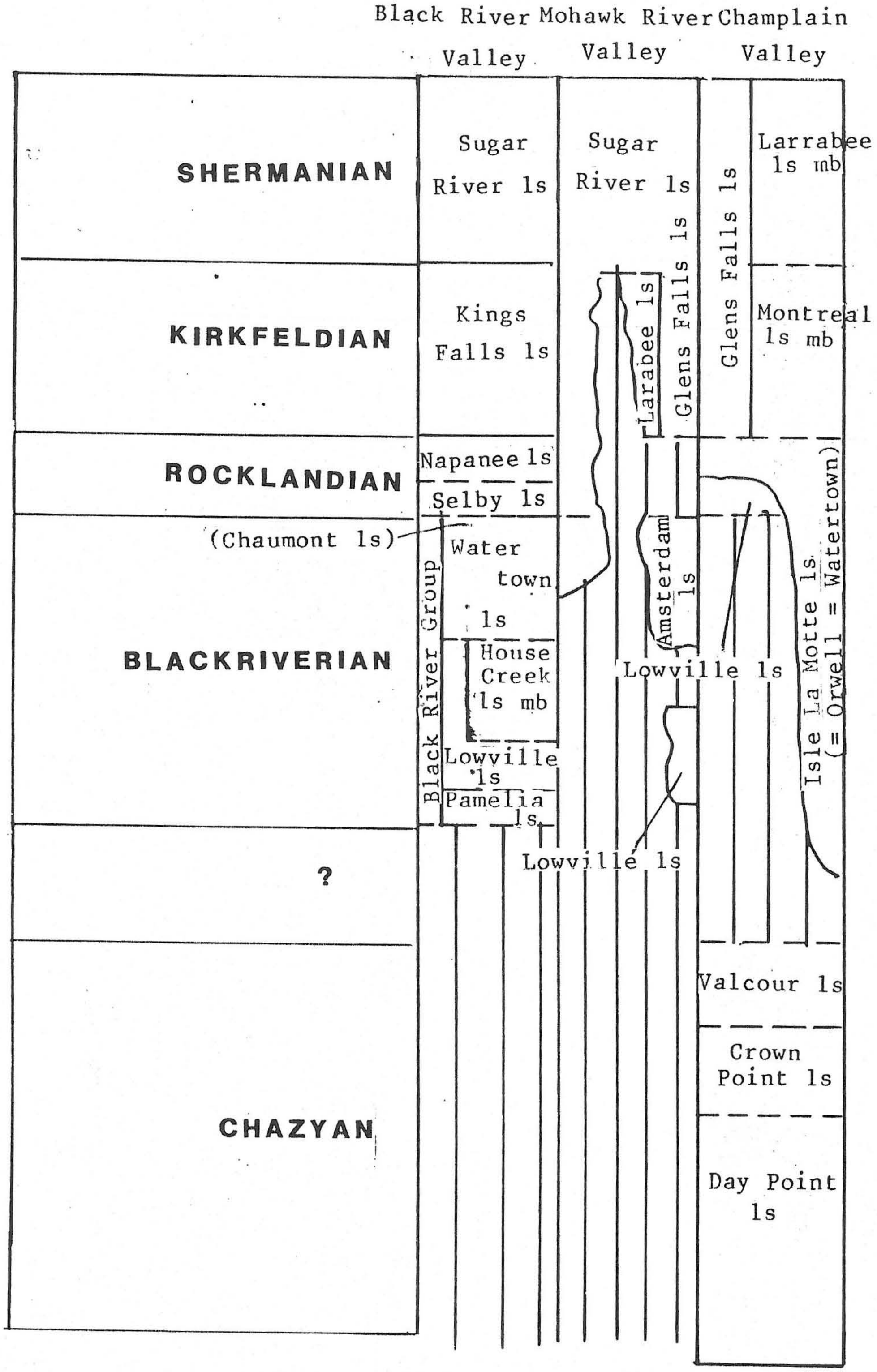
Lambeophyllum profundum from the Blackriverian Orwell and Lowville Limestones of New York State is considered the oldest confirmed rugose coral from North America (Hill, 1981). In the Lake Champlain Valley the oldest Blackriverian Stage rocks are the Orwell Limestone in which L. profundum occurs from the base of its outcrop in the central Champlain Valley (Selleck and MacLean, 1988). L. profundum also occurs commonly in the early Blackriverian Stage Lowville Limestone of the Black River and Mohawk River

Valleys of central New York and in the younger Lowville strata (Rocklandian Stage) of the Lake Champlain Valley (Cameron, et al., 1972; Walker, 1973; Fisher, 1982). (These strata are time-transgressive. See figures 4 and 7). Hillophyllum priscum from the lower Cliefden Caves limestone of New South Wales is the oldest confirmed rugose coral from Australia. H. priscum specimens of about the same age are also documented from the lower Reedy Creek Limestone (Webby, 1971). The Cliefden Caves Limestone is considered to have been deposited throughout the Australian Gisbornian Stage and into the Eastonian Stage, but the oldest coral-bearing strata of these formations are thought to be Gisbornian in age (Webby, 1976; see figures 8 and 9). A more specific age determination of the early coral-bearing beds by identification with index fossil zones has not been done (Webby, 1976).

Because the Australian Gisbornian and the North American Blackriverian Stages are contemporaneous in part (Harland, 1982), and because the dating of the H. priscum bearing beds within the Cliefden Caves Limestone is uncertain, a precise distinction of the ages of the oldest North American and the oldest Australian rugose corals is impossible until a finer stratigraphic resolution is attained.

Semi-formal Descriptions of Early Rugose Genera

Classification of the genus Lambeophyllum and the species belonging to it is in need of revision. Lambeophyllum is listed as a questionable genus in the recently published Supplement to the Treatise on Invertebrate Paleontology (Hill, 1981) where it is suggested that that Lambeophyllum is a possible homonym for Lambelasma. Elias (1983) has said that the identity of Lambeophyllum and its species needs to be evaluated in the context of a comprehensive study of the Middle Ordovician solitary Rugosa of eastern North America. Nonetheless, so that the reader will have a somewhat



from Ross, et al., 1982

FIGURE 7

The time-transgressive nature of the Lowville Limestone of New York is apparent from studying these stratigraphic columns of the Middle Ordovician strata.

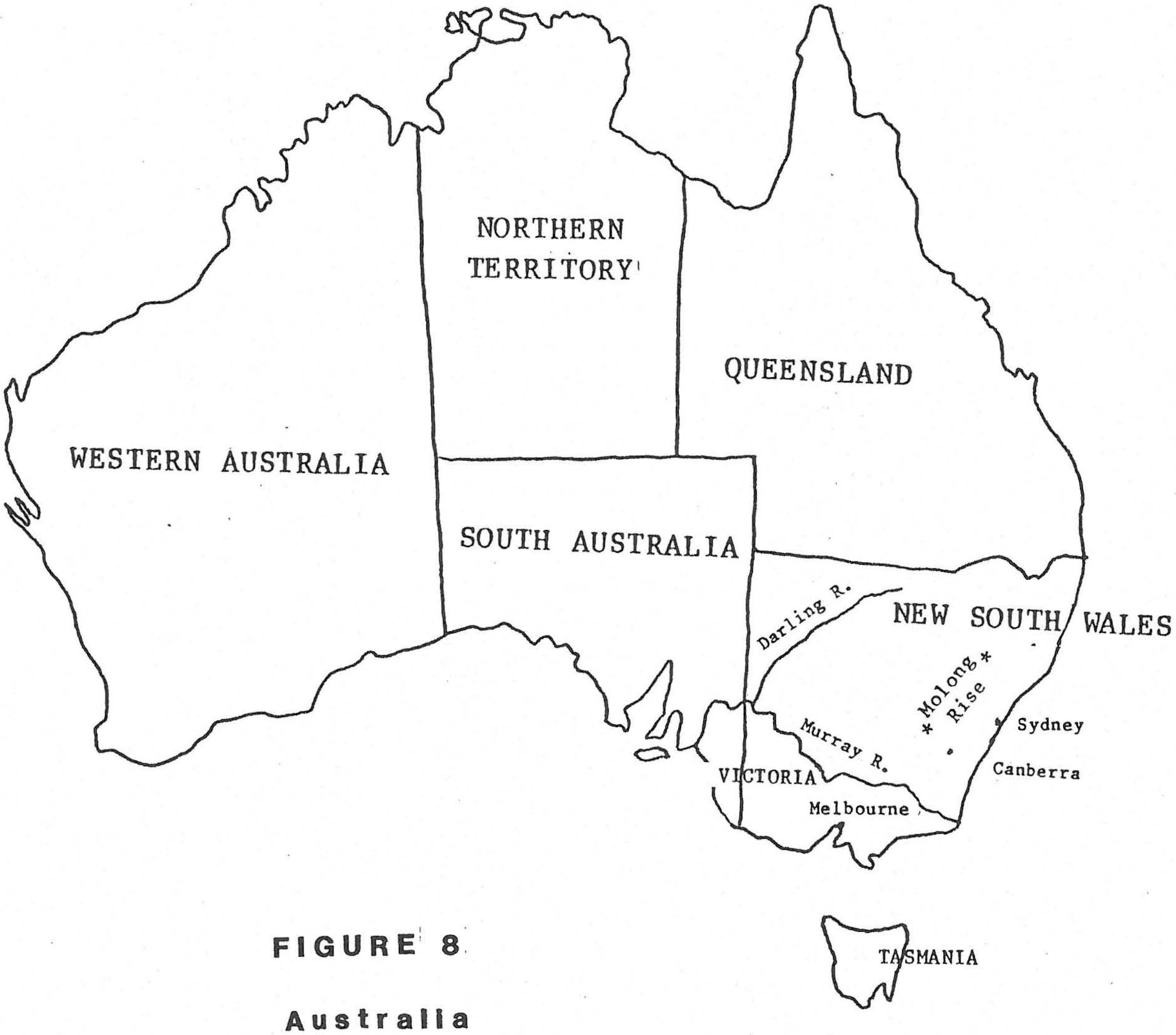


FIGURE 8

Australia

The oldest Ordovician Rugosa in Australia occur in Middle Ordovician strata which outcrop on the Molong Rise.

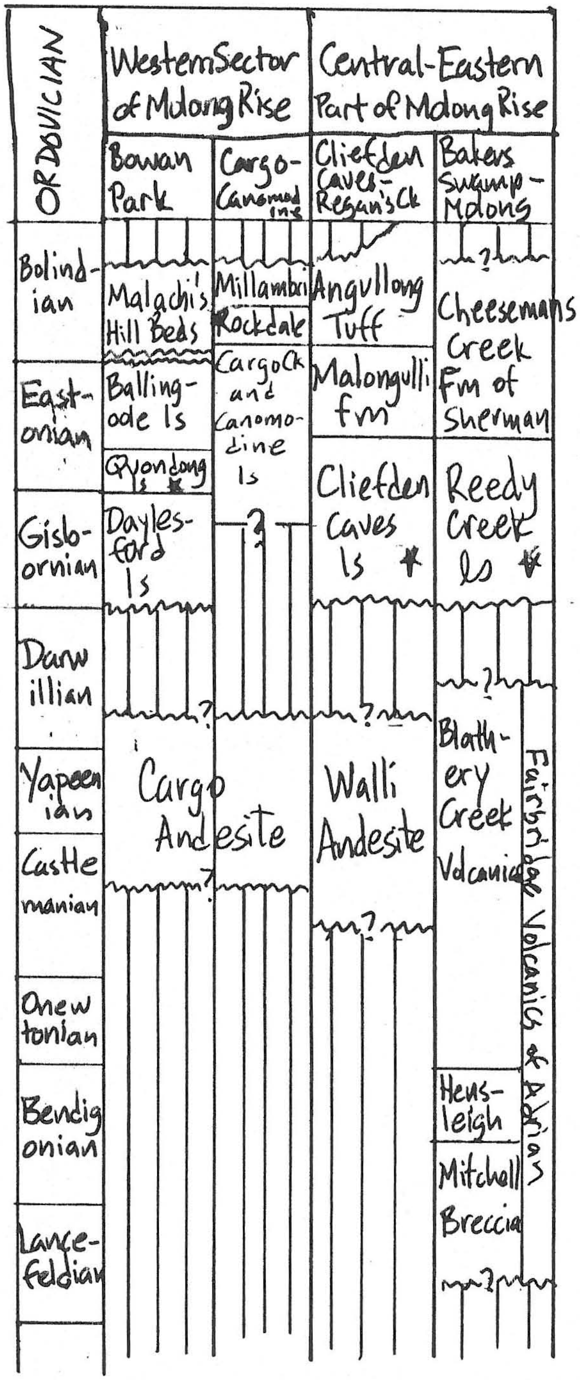


FIGURE 9
Stratigraphy of New South Wales

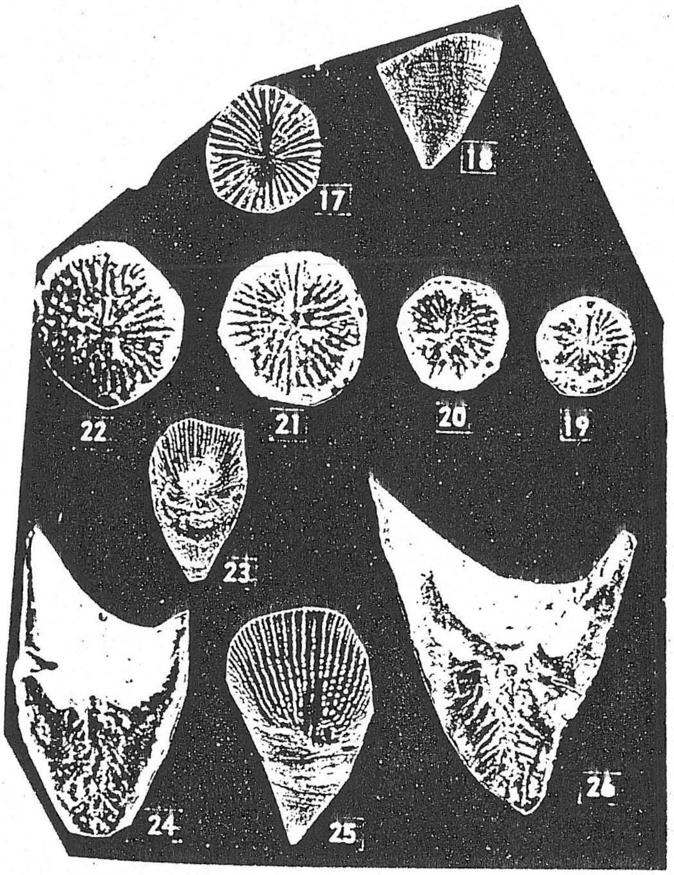
Stars denote the oldest formations in which Hillophyllum has been found. The ages of the Cleifden Caves and Reedy Creek strata in which the corals are found are questionably Gisbornian.

accurate picture of some of the corals discussed in this paper, a brief, general description of *Lambeophyllum* and *Hillophyllum* is included.

Lambeophyllum is small (2-3 cm in length) and strictly solitary. The corallum is conical to trochoid  in shape. The calice, upon which the soft parts rested, is deep, usually about half the length of the corallum as a whole. The septa occur in two distinct sizes, the major septa are longer and thus extend much closer to the central axis than the minor septa (see figure 10; Okulitch, 1938; Hill, 1981).

By contrast, *Hillophyllum* coralla can be solitary or colonial, even within a species (*Hillophylllum priscum* is an example of this). The corallites of the colonial forms are cylindrical and are in limited physical contact with one another. The septa are relatively short, and the major and minor septa are of similar lengths. Tabulae (transverse skeletal elements) are present, as they are in most Rugosa. The calice, as in *Lambeophyllum*, can be up to half the length of an individual corallite (see figure 11; Webby, 1971; Hill, 1981).

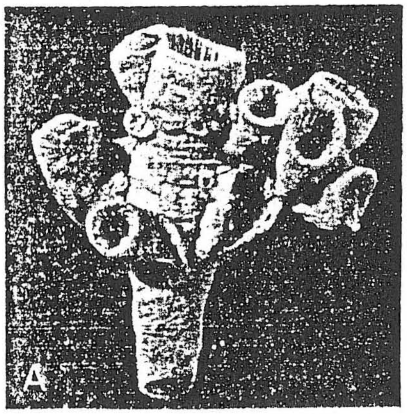
FIGURE 10

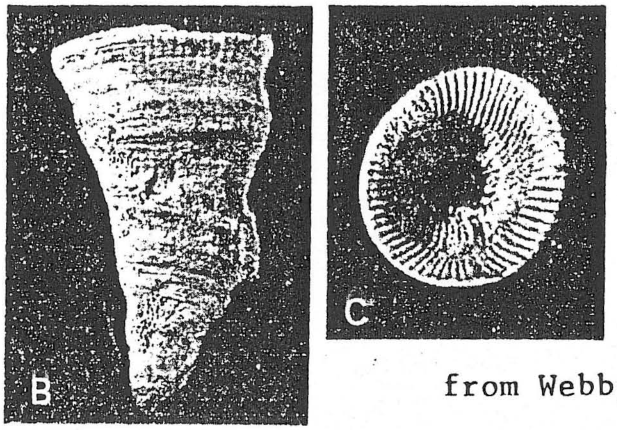


17, 18, 24-26 -- Lambeophyllum profundum   19-23 -- Lambeophyllum apertum

from Stumm, 1963

FIGURE 11





from Webby, 1971

A -- Hillophyllum priscum

B C -- Hillophyllum priscum

Field Studies

Introduction

Geography

Field work for this study was conducted in three regions: the Lake Champlain Valley of New York and Vermont, the Black River Valley of central New York, and in the Lexington area of central Kentucky (see figures 4 and 5). The Middle Ordovician is well-represented in New York state (Fisher, 1977), and rugose corals are reported from many of its strata. In Kentucky, Middle Ordovician outcrops are restricted to the central part of the state (Pojeta, 1979).

Stratigraphy

The coral-bearing strata at the localities visited in New York state belong to the Blackriverian Stage. I went to the areas where the oldest North American rugosa are known to exist. At the Crown Point Historical Site in the Lake Champlain area I looked at corals in the Orwell Limestone (called Isle La Motte Limestone further north). At Inghams Mills in the Mohawk River Valley I looked at corals in the Lowville Limestone. The Lowville outcrops in eastern New York as well, but not as early as the Orwell does (R.J. Ross, 1982). The absolute ages of the formations at their different outcrop areas and the relative ages of the Blackriverian in New York strata vary and often are not clearly determined. This is in part because the Lowville is known to interfinger with the Isle La Motte Limestone, the Watertown Limestone and the Pamelia Dolostone. It _is_ fairly clear that the Orwell strata at Crown Point are slightly older than the Lowville in the Mohawk River Valley (Fisher in R.J. Ross, 1982; see figure 12).

In Kentucky corals were collected from the Tyrone Limestone and the

STRATIGRAPHY OF FIELD AREAS

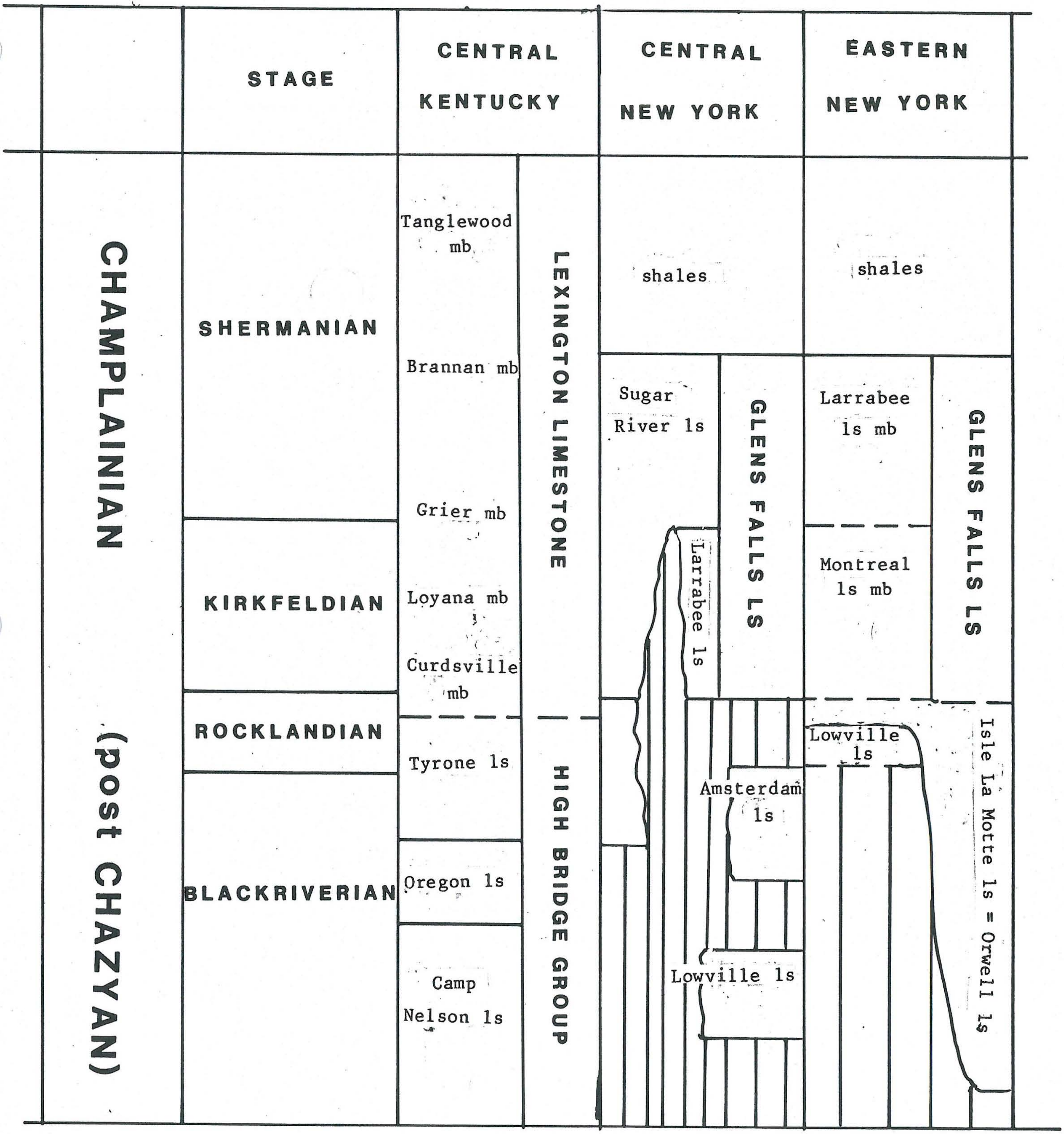


FIGURE 12

from ROSS, et al., 1982

Curdsville member of the Lexington Limestone. The Tyrone is the uppermost formation of the High Bridge Group, and the High Bridge Group has the oldest rocks exposed in Kentucky (Kuhnhenn, et al., 1981). It is overlain disconformably by the Curdsville, but the disconformity does not represent a great period of time (Pojeta, 1979). Based largely on the work of conodont stratigraphers, Pojeta (1979) put the coral-bearing strata of this study in the Kirkfeldian. Ross' (1982) more recent, but more broad scale stratigraphy questionably places the strata in question in the Rocklandian Stage. In any case, the Kentucky strata are younger than the New York strata, as the New York strata are from the Blackriverian Stage and the Kentucky strata are from post-Blackriverian rocks.

The relative ages of the corals at the three localities visited, Little Hickman, Shakertown, and Boonesborough are clarified by reference to the Diecke, Millbrig, and Capitol metabentonites. From Elias' locality information (Elias, 1983), the topmost coral bed at Little Hickman is "about eight meters below the Pencil Cave metabentonite of drillers." The Pencil Cave metabentonite of the Kentucky-Tennessee region is the equivalent of the geographically widespread Deicke metabentonite (Huff, et al., 1986). Similarly, the Mud Cave metabentonite is equivalent to the Millbrig metabentonite (also Huff, et al., 1986). In the field area of the present work, the Deicke occurs in the Tyrone Limestone about seven meters below its upper boundary with the Curdsville member of the Lexington Limestone. The Millbrig occurs at or near the boundary of the Tyrone with the Curdsville. The Capitol metabentonite is found in the upper half of the Curdsville. Because each of the coral occurrences can be described in relation to these metabentonites, their relative ages are easy to determine (see figure 13).

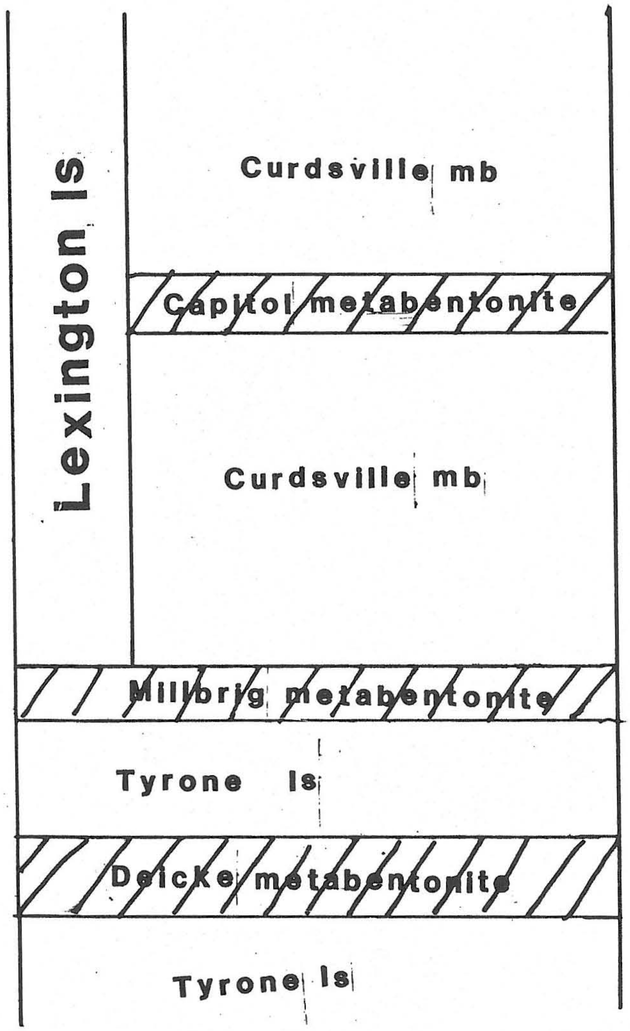


FIGURE 13

based on Huff, et al., 1986

Stratigraphic relationships of the Deicke, Millbrig and Capitol metabentonites in Middle Ordovician rocks in Kentucky

New York Field Localities

Orwell Limestone

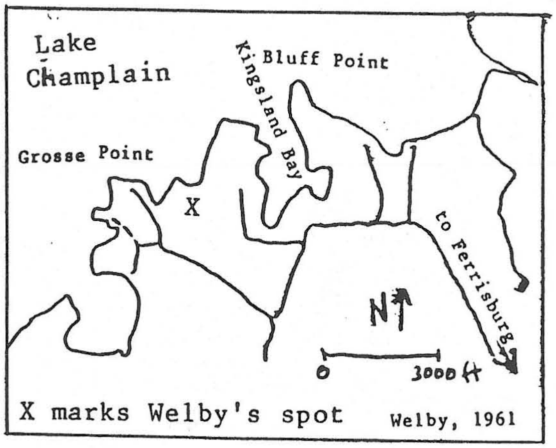
The Orwell Limestone exposed at the Crown Point Historical Site at Crown Point, New York, is among the very oldest outcrops containing well-known rugose corals. The locality is within the Historical Site property (and parts are within the historical site proper; see figure 14a,b). The entrance to the Historical Site is on New York State Route 8 about .2 miles before the road crosses the bridge to Vermont. The base of the Orwell section is past the Visitors Center and the parking lot at the side of the path where the visitors enter the remains of the fort. The section continues across the road toward the lake and then along Lake Champlain. Previous work has been done here on the Orwell by Selleck and MacLean (1988) and Speyer and Selleck (1988) whose work I used to find the section. Selleck and MacLean identified the solitary rugosa which is found there as genus Lambeophyllum, but do not give a species name.

No collecting is allowed at the Historical Site, but a section was measured and photographs were taken of the lowest 4.5 meters (of about 15 meters at the locality) of the Orwell section for this study (see figures 15, 16, and 17). The description of the upper beds is based on personal observation and the discussion of the earlier workers.

In the southern Champlain Valley the Orwell consists primarily of fossiliferous packstones and wackestones. At its base there are sandy dolostones overlain by lime mudstomes with few fossils (Selleck and MacLean, 1988). The formation is said to average 12-15 meters in thickness, but varies, particularly as it thins from west to east (Welby, 1961a).

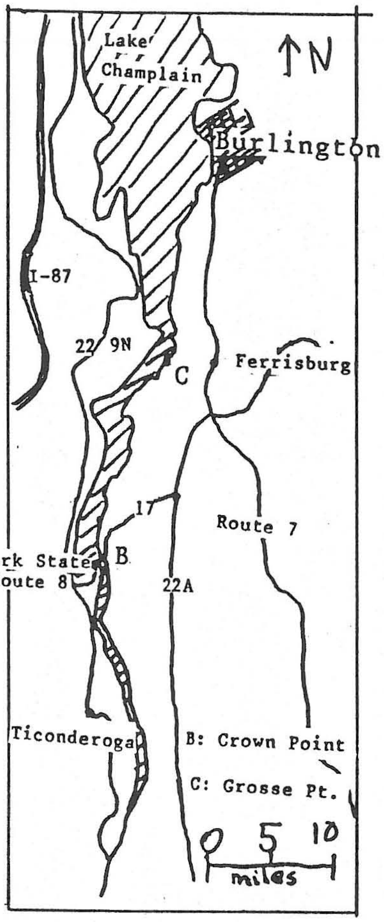
The section of the Orwell is fairly complete at Crown Point; only 2-3 m near the base and about 1 m near the middle are covered. The Chazy Group Crown Point Limestone unconformably underlies the Orwell and the Glens Falls

C) Welby's Chazyan Stage Rugose locality

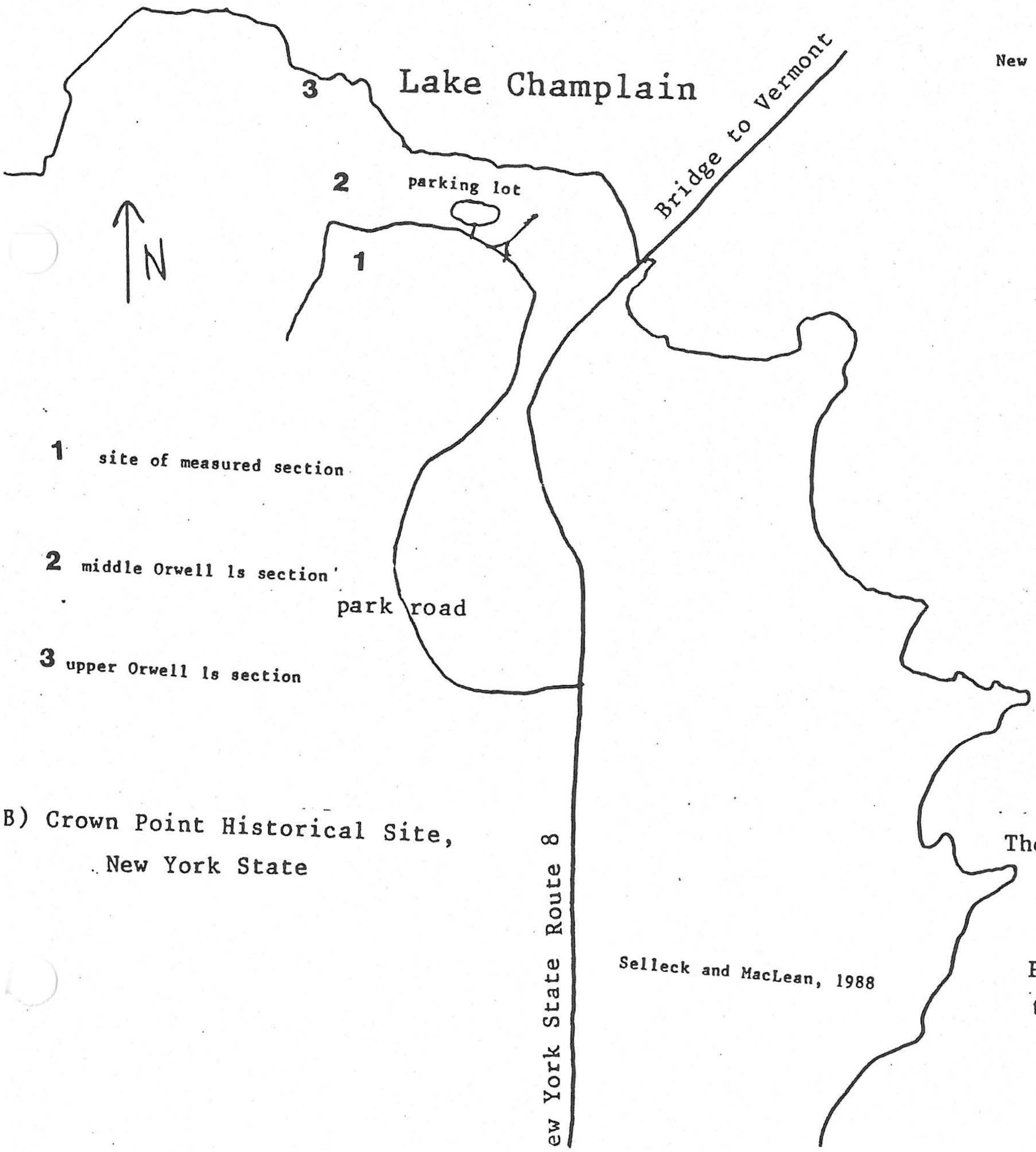


X marks Welby's spot

Welby, 1961



A) shows localities B and C



Selleck and MacLean, 1988

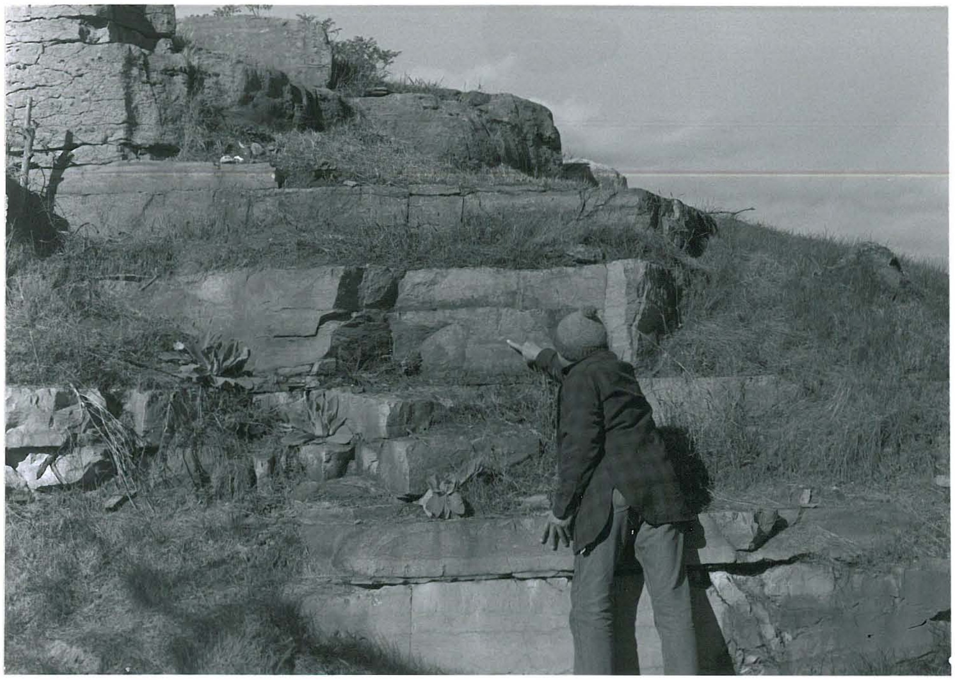
B) Crown Point Historical Site, New York State

FIGURE 14

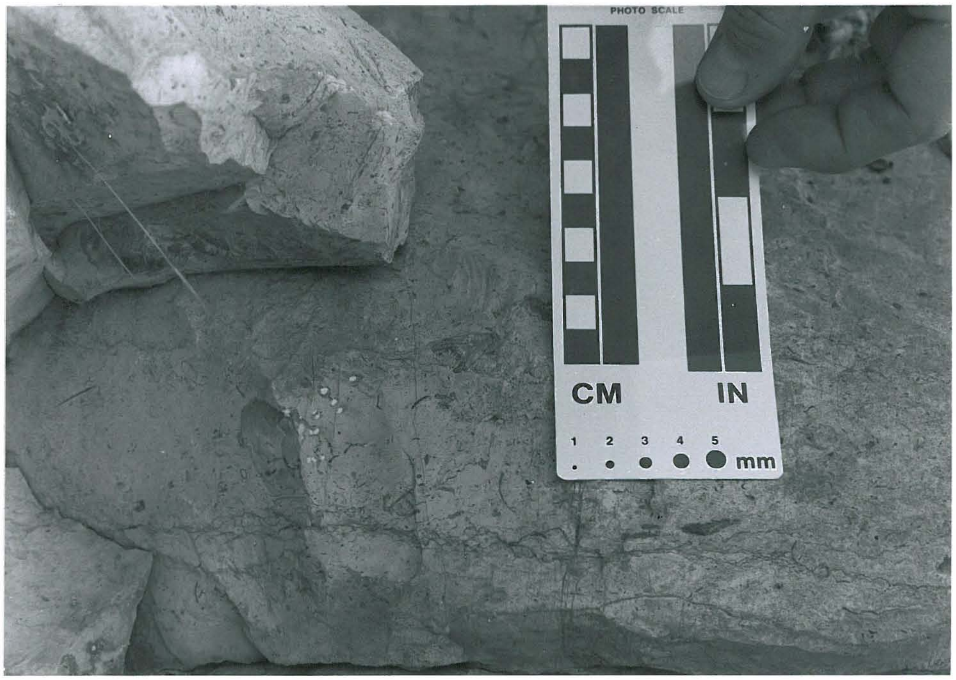
Locality Maps for

Lake Champlain Valle

These maps show the Champlain Valley localities where I looked at the Crown Point Limestone (C) and the Orwell Limestone (B).



a) Larry is pointing to a rugose-bearing bed in about the center of the measured section (photo 4-3).



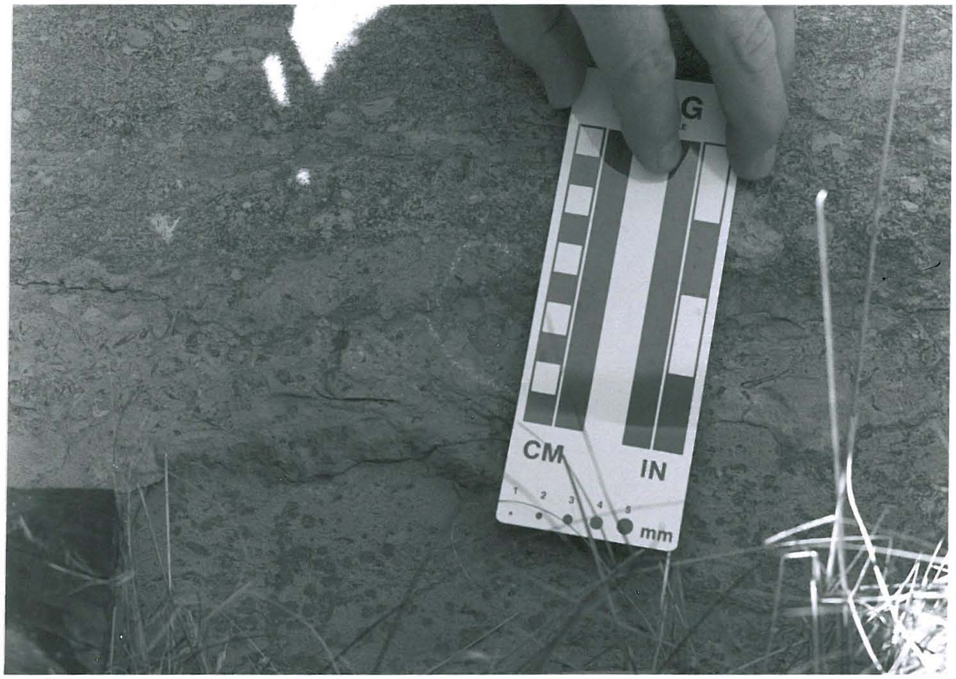
b) Rugose coral is just left of the scale. This is the oldest rugose-bearing bed at Crown Point (photo 4-6).

Figure 15
Orwell Limestone, Crown Point, New York

a) Rugose layer in middle of measured section (photo 5-3).

b) Close-up of a); rugose coral is about one inch to the left of the 2.5 cm mark (photo 5-1).

Figure 16
Orwell Limestone, Crown Point, New York



Beautiful coral (center)!
(photo 4-4)

Figure 16c.
Orwell Limestone, Crown Point, New York

FIGURE 17

Measured section of Orwell Limestone at Crown Point, NY (area 1 on figure 14B).
* denotes rugose corals in bed

Thickness	Rugosa?	Sedimentary information	Fossils
TOP			
120 cm	*	very fine-grained overall homogenous and massive, but at intervals there are planar laminated beds bioturbated -- vertical burrows black chert nodules in layer approx. 30 cm from the bottom	tabulates gastropods cephalopods ostrocods brachiopods rugosans
9 cm			none (?)
19 cm	*	sharp contact at base	abundant rugosa gastropods others(?)
20 cm		rip-up clasts, fossil frags some thin finer-grained beds at base- a jumble of big gastropod & coral frags in fine sed	poorly fossiliferous
50 cm	*	planar lamination in lower part w/in the bed there are 3 different layers of fossil hash	rugose corals common cephalopods, gastropods broken tabulate corals
6 cm		planar lam; bioturbation	fossils rare
55 cm	*	fine-grained with abundant fossils OR packstone?	gastropods common, other unidentifiable fossils rugose (?)
13 cm		very fine sediments w/ small pockets of tiny visible crystals not laminated	gastropods & ostracods not abundant
7 cm		planar lamination; rip-up clasts	ghost structures
60 cm		very fine sediments w/ small pockets of tiny visible crystals no planar lamination bioturbated -- vertical burrows	no body fossils
60 cm		very fine sediments w/ common coarser xls massive generally featureless w/ occasional pockets of tiny visible xls	gastropods & ostracods not abundant

Limestone conformably overlies it (Speyer and Selleck, 1988).

Lambeophyllum first occurs in a bed about 1.5 meters from the base of the section and continues to appear in beds to the top of the Orwell at the historical site. It is most abundant in the middle of the section and rarest near the top.

The basal 1.2 m of the outcrop is composed of thick-bedded to massive lime mudstones with a few gastropods and ostracods. There are spar-filled, vertical burrows near the top of these otherwise featureless lower beds. Within the measured section grain sizes coarsen upwards. In the beds overlying the fairly featureless, basal beds there are several layers of packstones to wackestones containing fossil hash composed of gastropods, ostracods along with solitary rugose and colonial tabulate corals, cephalopods, and brachiopods. The majority of the fossils are concentrated in these layers. They are broken and clearly transported. Other features of these upper layers include common planar lamination, rare cross-lamination and rip-up clasts. At the top of my measured section there are black chert nodules which can be traced across the road to the next higher part of the section.

In the middle part of the section the rocks are still thick-bedded to massive, but the textures are coarser — packstones and wackestones. The diversity and abundance of fossils is greater. Stromatoporoids, nautiloids, bryozoans, and pelmatozoans add to the faunal list. Rugose corals are common (Selleck and MacLean, 1988).

The uppermost Orwell varies little from the middle section. The rocks are fossiliferous packstones and wackestones. There are some ripple cross-laminated grainstone beds. Some trilobite fragments and one species of a byssate bivalve occur (Selleck and Maclean, 1988).

The gradual increase in grain size noted in the lowest third of the Orwell at Crown Point continues to the top, implying an increasingly energetic environment. Selleck and MacLean (1988) suggest a gradual transition from a basal shallow, restricted lagoonal environment to a low energy open marine shelf environment. Their sense of the evolution from a restricted to an open marine environment is based, at least in part, on the increasingly diverse and abundant fauna upsection. The fossiliferous layers in the lower part of the section are storm beds, and it must be noted that the specimens of Lambeophyllum which occur in my measured section are found in these layers, and presumably were transported from further offshore. But, the corals are not particularly abraded or broken, and they occur in rather thin storm beds, which indicates that they have not been transported far and that the storm which carried them there was not large. They are most likely to have been transported from a nearby inner shelf environment which was easily disrupted by small storms.

Lowville Limestone

The Lowville Limestone is the oldest rugose coral-bearing formation in central New York state. Among its many outcrops in the Black River and Mohawk River Valleys is the exposure at Inghams Mills just below a dam on East Canada Creek (figure 13). The section is completely exposed, having been blasted to make the dam. Previous work has been done at this locality by Cameron* (1969; et al., 1972). The rugose corals found at Inghams Mills

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*Although the name Lowville is generally recognized (by Walker, Selleck, Fisher, and others), Cameron, whose work I cite here, uses the name "Gull River Limestone," to avoid the possible confusion of time-rock names — such as Lowvillian substage — with purely rock-stratigraphic terminology. The different names refer to the exact same package of rock. Although I refer extensively to Cameron's work, I will, for internal consistency, use the name Lowville Formation.

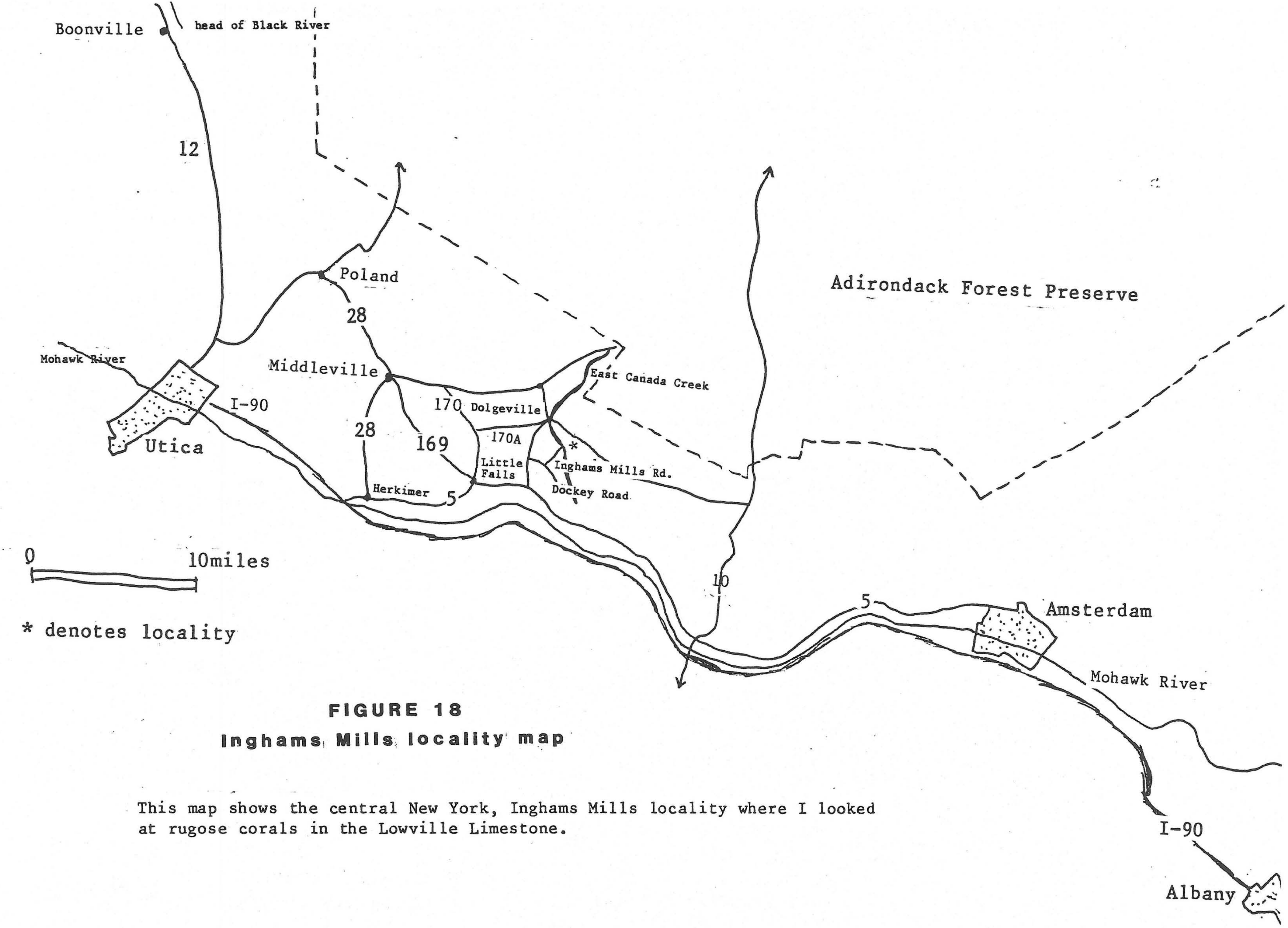


FIGURE 18
Inghams Mills locality map

This map shows the central New York, Inghams Mills locality where I looked at rugose corals in the Lowville Limestone.

were identified in these earlier works as Lambeophyllum profundum.

The Lowville at Inghams Mills is bounded disconformably above and below by the Rocklandian Napanee Limestone and the Cambrian Little Falls Dolomite (Cameron, 1969). The section is about nine meters thick at this locality, and about four meters are included in the measured section (see figures 19 and 20) which was measured down from the upper contact of the Lowville with the Napanee. Lith and coral samples were taken here.

The lithology of the Lowville varies, but it is characteristically a sublithographic lime mudstone or siltstone. In some areas there are large carbonate clasts. There are many stylolites, mud cracks, and birdseye structures. The formation is well-bioturbated with common large, vertical, anthroxolite-filled burrows. There are horizontal laminae produced by current action and by algae (Cameron, et al., 1972).

Lambeophyllum profundum occurs commonly in two facies in the Lowville at Inghams Mills. One of these facies is non-laminated, massively bedded and irregularly burrowed. It is composed of silt-size lime muds. Many fossils are recrystallized, but the fauna include tabulate corals, bryozoans, cephalopods, and trilobites.

The other facies with Lambeophyllum has abundant vertical burrows and contains horizontal algal laminations. There are rip-up clasts. The sediments are fine and very fine lime muds. There is a filled channel up to 7 feet wide and 2 feet deep in this layer (Cameron, 1969). This facies is not in my section.

The Lowville was deposited in supratidal to shallow marine conditions (Cameron, et al., 1972; Walker, 1973). The rugose beds at Inghams Mills can be identified within this framework as shallow subtidal and intertidal to lagoonal respectively. The shallow subtidal environment was a fairly low energy, restricted environment judging by the lack of higher energy

a) Outcrop. Tape measure from 80 cm below the top of the coral bed (photo 1-14).

b) Rugose coral to right of compass. Plan view of outcrop (photo 1-12).

Figure 19
Lowville Limestone, Inghams Mills, New York

Figure 20

Measured section of Lowville Limestone at Inghams Mills, NY (see figure 18*).
* denotes rugose corals in bed.

Thickness	Rugosa?	Sedimentary information	Fossils
50 cm		fine-grained carbonate mudstone beds 2-9 cm thick, generally = 5cm well-laminated bioturbated: U-shaped burrows vertical burrows = 1 cm diam	very rare fossils sponge? Receptaculites
45 cm		massive unlaminated (?) except for thin, wavy, lam layers (dolomotized?) w/in rock (stroms?) some pyrite	cephalopod tabulate colonies
27 cm		fine-grained carbonate mudstone massive	none
5		wackestone to packstone in very fine mud not good bedding or lam dolomotized(?) fine seds in very localized surface lows	abundant broken Tetradium cephalopod other fossils also abundant recrystallized and hard
65		laminated bioturbated	none
30		fine-grained w/ larger clasts (rip-up ?) fossil debris some bioturbation -- vertical burrows	tabulate corals trilobites bryozoans
80	*	calcisiltite massive bedding not laminated	tabulate corals cephalopods, trilobites bryozoans, corals
75	*	calcisiltite massive bedding not laminated	tabulate corals cephalopods trilobites bryozoans rugosans

sedimentary structures and dearth of storm beds. The corals preserved there are only locally transported. The intertidal to lagoonal environment must have been a somewhat higher energy environment based on the presence of rip-up clasts. There was no evidence of subaerial exposure (mudcracks) reported by Cameron (1969) or seen by me in the very shallow Lambeophyllum beds. I do not know whether the rugose corals of this second facies were transported.

Kentucky Field Localities

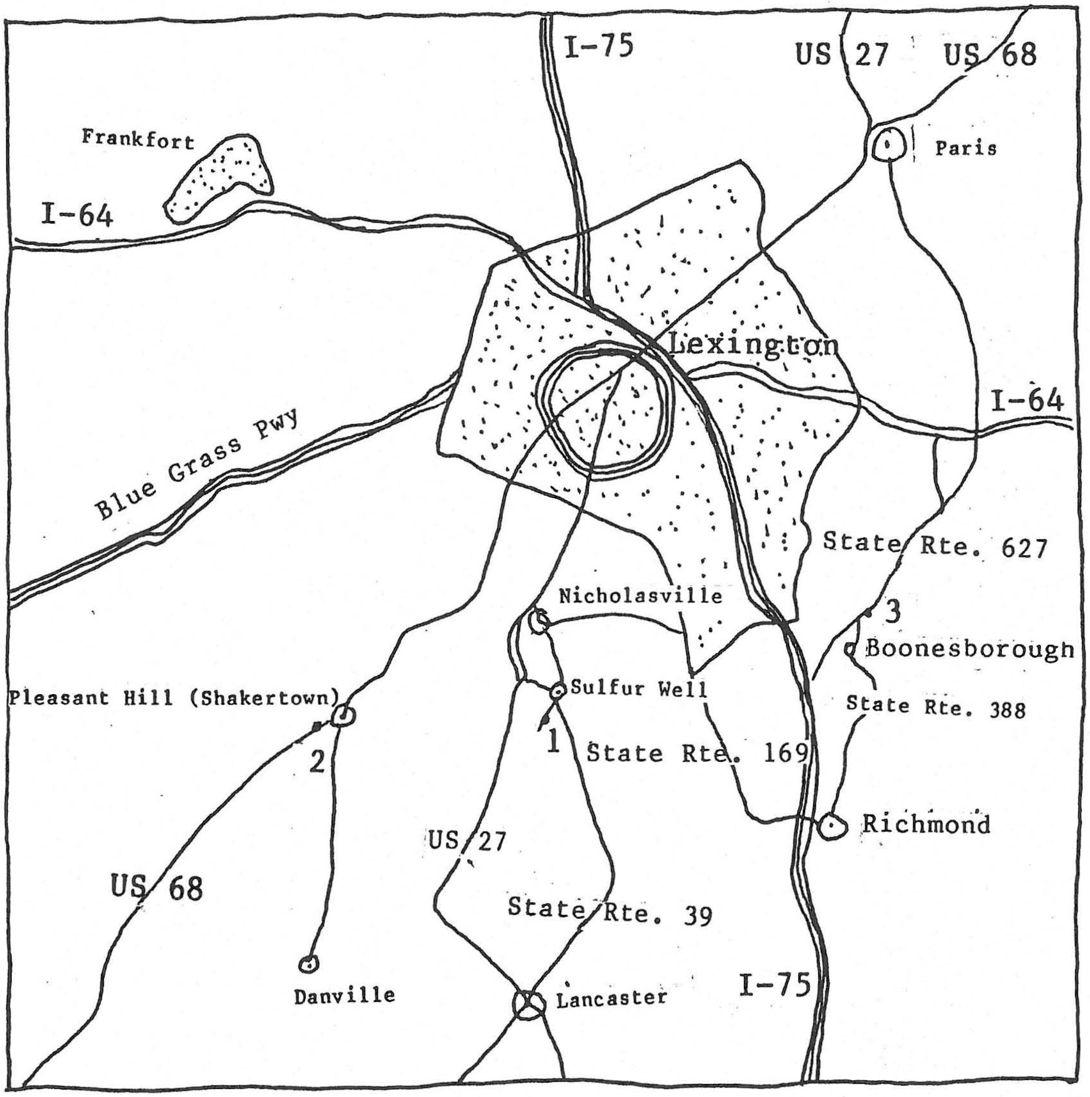
Tyrone Limestone

The oldest corals collected in Kentucky for this project come from the Tyrone Limestone High Bridge Group, Kirkfeldian Stage. The locality visited is exposed in a roadcut on New Watts Mill Road which forks off State Route 39 1.15 miles past Sulfur Wells' center (see figure 21, locality 1). Previous work has been done at this locality in a study of Ordovician paleontology of Kentucky (Pojeta, 1979). From that project the locality is known as the Little Hickman A section and the locality is numbered USGS locality 6034-CO. Corals have been collected from a bed which outcrops .25 miles from the base of New Watts Mill Road at the top of the hill. These corals were identified as Lambeophyllum spp. A and B (Elias, 1983). The sedimentary environment of the Tyrone was interpreted to be tidal flats and lagoons (Pojeta, 1979; Elias, 1983).

The earlier section was not available for this work, so a new one of about twelve meters was measured of beds in approximately the upper two-thirds of the section where rugose corals were found in several beds. The earlier work had identified corals only from the topmost bed. In this study corals were found in several beds throughout the upper section, although the

FIGURE 21

Kentucky locality map



This map shows the area in Kentucky where field work was conducted for this project. Three localities are discussed in the text -- Locality 1 is called Little Hickman; locality 2 is near Shakertown; locality 3 is near Boonesborough.

Locality 1 is on New Watts Mill Road 1.15 miles past Sulfur Well's center;
Locality 2 is on US 68 one mile southeast of the intersection with State Rte. 33, near the entrance to Shakertown;
Locality 3 is just northeast of Memorial Bridge at Boonesborough.

corals are clearly most numerous in the upper bed (see figures 22 and 23).

Three major rock types are present at the Little Hickman locality. The dominant rock type is a very fine-grained, laminated dolomite or limestone that is bedded, massive, and contains few to no fossils. The laminations are wavy and appear to be algal. There are birdseye structures in some of the beds. These characteristics imply a supratidal to intertidal environment for the major lithology at Little Hickman.

A second lithology at this locality is a coarse-grained, cross-bedded (with rarer planar bedding), poorly fossiliferous limestone. No bioturbation is found in these beds. This lithology seems to represent a somewhat higher energy and slightly higher elevation beach environment. All the beds of this lithology in my section occur in about the middle of the section.

A third major lithology at Little Hickman occurs in many beds interspersed between the intertidal and subtidal beds. These rocks are calcareous packstones to rudstones whose coarse clasts consist of generally unbroken fossils (except the crinoids, which are disarticulated). These layers are usually well-bedded and sometimes have definite basal erosion surfaces. These beds are highly fossiliferous and in a given bed, some part of the following fauna can be found: common gastropods, cephalopods,crinoids, brachiopods, and bryozoans. These are the beds in which the rugose corals occur most commonly (the exception — one coral was found in a thin micrite layer just above one of these beds). It is clear that these rugose-bearing beds are storm deposits, and that the fossils depositied in them were not transported very far given their fairly unbroken state.

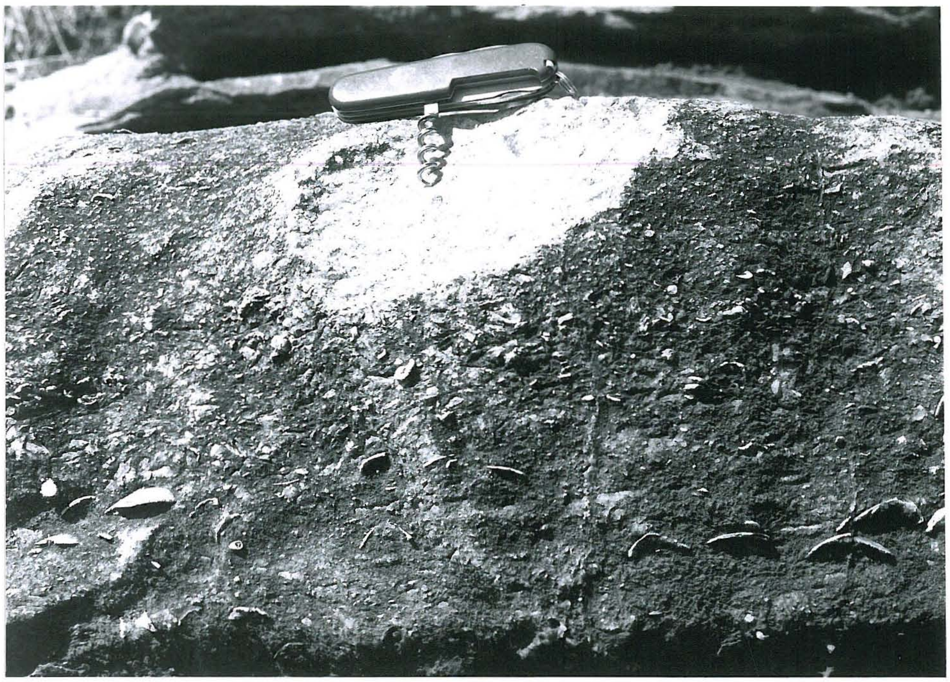
The Pojeta (1979) interpretation of the Tyrone concurs with my findings that the Little Hickman section represents a supratidal to intertidal environment that was affected by storms and includes storm deposits.

Figure 22

Mary Droser and I measured this section of the Tyrone Limestone at the Little Hickman locality in Kentucky.

Thickness	Rugosa?	Sedimentary information	Fossils
8 cm		laminar, stylolites	few fossils include gastropods
14	*	ruddstone	corals, gastropods, crinoids, cephalopods; silicified fossils weathering out
71		very fine-grained dolomite(?) wavy laminations stylolites birdseye structures	none
97		very fine-grained dolomite(?) wavy laminations stylolites birdseye structures	none
12		coarse-grained(?) basal erosion surface (? - weathered at base, so hard to tell)	
covered area crossing field entrance			
87		laminated	poorly fossiliferous
23		extremely fine-grained; no bedding; laminated dolomite (?) very weathered	ghost structures of fossils
22		extremely fine-grained; no bedding; laminated dolomite (?) very weathered	ghost structures of fossils
102		extremely fine-grained; no bedding; laminated dolomite (?) pockets of fossils = 4 cm thick	pockets contain: gastropods, crinoids, brachiopods
49		micrite dolomite (?) beds = 1 cm thick w/ internal lamination; includes thin storm beds with basal erosion and some fossils	fossils present, but not abundant in storm beds - mostly gastropods
41		micrite dolomite (?) mottled = burrow?	
10		planar bedded	

7	*	packstones to wackestones	crinoids, gastropods, bryozoans, rugose
23		x-stratified beds 2-8 cm thick	fossils present, but not abundant
68		x-stratified beds 2-8 cm thick	fossils present, but not abundant
80		coarser sediments planar bedded and x-bedded (x-beds approx. 4 cm thick) not bioturbated	not fossiliferous
covered zone approximately 200 cm			
40		wackestone to packestone well-bedded bioturbated - *Planolites*	fossiliferous, but poorly weathered for fossil ID
38	*	wackestone to packstone 5-10 cm scale bedding	very fossiliferous; rugose coral
15		thinly bedded, laminated - wavy, but not ripple-bedded; wavy laminae approximately 1 cm across	none
97		very fine-grained beds 4-15 cm thick laminated dolomite (?) birdseye structures	very fossiliferous, but fossils not generally identifiable; rugose coral
42		covered, but looks about same; includes 19 cm of extremely fine-grained, well laminated seds, an 8 cm fossil bed w/ an erosional base	
8		fine-grained, laminated	
20	*	packstone w/ a few fine-grained beds w/in well-bedded	
10		thinly-bedded; laminated	
4		thin-bedded	
5	*	micrite; irregular basal surface	coral
33	*	top cm of bed is a packstone; below that it's a wackestone to packestone; irregular basal erosion surface very weathered	corals in top cm; fossils throughout include gastropods, cephalopods
44		very fine-grained w/ some clasts (rip-up) wavy laminations; no ripple marks	



a) Lithology of the uppermost coral bed (photo LH-1).

b) Rugose coral from bed in a) (photo LH-10).

Figure 23
Tyrone Limestone, Little Hickman Quadrangle, Kentuck

Curdsville Member, Lexington Limestone

Shakertown Locality

Corals were collected from Shakertown, Kentucky (see figure 21, locality 2), where basal rocks of the Curdsville member of the Lexington Limestone outcrop on a roadcut on State Route 68 1.0 mile southwest of its intersection with Route 33. The formation was identified at this locality by the presence of the Millbrig metabentonite near the base of the outcrop (Huff, personal communication, 1989). Most of the rugose coral specimens collected at this locality are silicified and had weathered out of their limestone matrix. Others were found, silicified and unsilicified, still imprisoned in the fine-grained limestone of the outcrop.

The section that is included is based on an unpublished section measured by Rodney Watkins and others (see figure 24). The rugose corals at Shakertown first occur sparsely in the beds immediately above the Millbrig metabentonite. They are absent from the next two meters of outcrop, but reappear, and occur commonly, in higher beds.

The corals at Shakertown occur in packstones with low angle cross-stratification defined by bioclast alignment. The lowest coral-bearing bed includes scoured surfaces and is overlain by hummocky cross-stratified beds. Rugose corals occur in association with brachiopods, bryozoans, bivalves, gastropods, disarticulated crinoids, and a few tabulate corals. Brachiopods and crinoids occur throughout the section.

Massive packstones and hummocky cross-stratified packstones throughout the section above the metabentonite are generally non-coral-bearing. The three major lithologies -- low-angle cross-stratified, massive and hummocky cross-stratified -- alternate within the section. This collection of lithologies suggests that the environment was subject to frequent high

Figure 24

This unpublished section of the Curdsville member of the Lexington Limestone at Shakertown, KY was measured by Rodney Watkins and associates with whom I visited the area in March, 1989.

Thickness	Rugosa?	Sedimentary information	Fossils
7 cm		ss packstone, hummocky	gastropods, crinoids, brachs
20		coarse packstone massive	crinoids, gastropods, starfish, brachs
7			
25			
5		coarse packstone, massive	
20		low angle cross-strat, ss packstone	bryozoans, crinoids brachs
20		hummocky x-strat	
45		massive, ss packstone	crinoids, brachs
55		ss packstone hummocky x-strat stylolite surface	crinoids, bivalves brachs
20	*	coarse packstone low angle x-strat	crinoids, bivalves, gastropods, brachs
10		ss packstone; low angle x-strat	gastropods, brachs, crinoids
25		coarse packstone low angle x-strat	gastropods, brachs, crinoids
70		MILLBRIG METABENTONITE	nada
5		silicified mudstone	gastropods, cephalopods brachs, trilobites
33		massive mudstone and wackestone some algal lam	cephalopods, trilobites, bryozoans, brachs,gastro
		birdseye	
12		massive mudstone, birdseye	nada
20		massive mudstone, birdseye	nada
5		mudstone, algal lam, birdseye	nada
10		mudstone, birdseye	nada
5		mudstone, algal lam, birdseye	nada

energy events rather than continuous vigorous beating of waves.

Boonesborough Locality

Rugosa of the genus Streptelasma were reported by Conkin and Conkin (1983) from a roadcut on Highway 627 immediately northeast of Memorial Bridge at Boonesborough (see figure 21, locality 3). A brief examination of the rocks at this locality did not yield any corals for this study. However, the rocks of the coral horizon specified by Conkin and Conkin are not weathered such that fossils or sedimentary structures are easily seen in outcrop.

The outcrop at this locality is questionably from the lower part of the Curdsville. Conkin and Conkin (1983) identified it as the Tyrone, based in part on the identification of the metabentonite that occurs near the base of the outcrop. At a first appraisal, Sheehan and Miller (personal communication, 1989) suggested that the metabentonite was misidentified, and thus the corals at Boonesborough may be in the upper part of the Curdsville rather than near its base. Assuming this stratigraphy, the corals at Boonesborough are younger than those at Shakertown. Conkin and Conkin's stratigraphy would suggest that the Boonesborough and Shakertown corals are approximately the same age.

From Conkin and Conkin (1983), the fauna of the beds in which they reported rugose corals at Boonesborough include abundant crinoids, as well as brachiopods, cephalopods, gastropods, bivalves and bryozoans; the limestone contains some reworked limestone clasts. It is generally medium-grained. It is thin-bedded and does not seem to contain storm beds of wackestones or packstones (personal observation). The "coral beds" are underlain by about two meters of mud-cracked, algal-laminated, bioturbated birdseye limestone. Lower in the section the limestones are finely parallel laminated, and there are some large rip-up clasts.

The beds below the "coral beds" are clearly supratidal in origin, and the reported coral-bearing beds are subtidal. As described by Cressman (1973), the Curdsville was deposited in nearshore and inner shelf environments. Higher and lower energy deposits are interbedded as the result of migrating sand bars. The beds which outcrop at the Boonesborough section represent the lower energy facies of the Curdsville.

Paleoenvironmental Context of Field Localities

The paleoenvironments in which corals were deposited at the localities visited varied from supra- to intertidal mud flats (Little Hickman) to restricted lagoons (Crown Point, Lowville) to marine environments with more open circulation (Crown Point, Shakertown, Boonesborough). Nevertheless, within the environmental framework used for this study, most or all of the corals whose environments were determined in the field lived in the inner shelf environment.

Orwell -- The environments of fossils from both the fine-grained, low fossil diversity beds and the storm beds within them are classified as inner shelf because lagoons have the day-to-day lower energy associated with environments below wave base, but their sedimentary structures reflect even small storms. The corals are found solely in the storm beds though, so may have been transported from outside the lagoon. However, they have not been transported far and are not significantly abraded, and thus are classified as inner shelf. Although the upper Orwell exposed at Crown Point generally consists of coarser fragments, it also may be classified as inner shelf due to the presence of the ripple cross-laminated grainstones, clearly deposited in higher energy events than the more common packstones and wackestones.

Lowville -- The shallow, subtidal rugose-bearing beds are placed in the middle shelf based on the generally low energy and dearth of storm beds. The determination of the environment inhabited by the corals found in the intertidal to lagoonal beds depends on whether or not the corals were transported and how far. If they were buried in or near to life position, they inhabited the inner shelf environment. If they were significantly transported it may have been from the nearshore.

Tyrone -- Because the corals were clearly transported by small storms their original environment is inferred to have been nearshore or inner shelf.

Curdsville, Shakertown -- Based on the alternation of low-angle cross-stratified, massive, and hummocky cross-stratified beds, the environment is inner shelf.

Curdsville, Boonesborough -- As discussed above, the Curdsville outcrop at Boonesborough represents the inner shelf.

Environmental Context of the Rugosa through the Middle Ordovician in Eastern North America

Paleogeography

In the Middle Ordovician, eastern North American was a part of the continent Laurentia, which included the North American craton, Greenland, and the northern parts of Scotland and Northern Ireland (Van der Voo, 1988). Laurentia remained on the equator throughout the Ordovician, but rotated counterclockwise from the Late Cambrian through the Middle Ordovician (Van der Voo, 1988; Scotese, et al., 1979). According to the Middle Ordovician base maps of Scotese, et al. (1979), the the corals that are considered in this report lived south of the equator between about ten degrees and twenty-five degrees south. The published maps show the paleogeography for the Llandelian Epoch to the earliest Caradocian Epoch, while the corals are dated from the early Caradocian through the Ashgillian Epoch. The rotation of Laurentia would have brought the relevant areas closer to the equator through the Middle Ordovician.

Most of eastern North America was covered by "shallow seas" in the Middle Ordovician. There were deep oceans in some narrow bands that run semi-parallel to the continental margin. The land exposed on the continent at this time was low lying and northwest of the areas where corals have been reported, generally in present day Canada (all from Scotese, et al., 1979).

Geography of Middle Ordovician Exposures and Rugose Occurences

Eastern North American Middle Ordovician rocks outcrop along the extent of the Appalachains; around Lake Ontario in New York, Ontario, and Quebec, as well as in a band running northeast of Lake Ontario; in the Upper Peninsula of Michigan and on Manitoulin Island in Lake Huron; in a south-pointing V-shaped belt through parts of Wisconsin, Illinois, Iowa and

Minnesota. They outcrop in central Kentucky; in the area of the Nashville Dome; in a small belt north of the Ozark Plateau; and perhaps on the Ozark Plateau itself (general Ordovician information from Choubert and Faure-Muret, 1976, supplemented by extensive reading on the Middle Ordovician). Rugose corals are documented from all of these areas (except from the Ozark Plateau; see figure 25) in this report.

A chart showing the ranges of the North American genera of the Rugosa subdivided by the geographical area in which they occur through the North American Middle Ordovician is included (see figure 26). The chart is the result of a search of the paleontological and stratigraphical literature which is summarized in Appendix B. Often corals are reported from a particular formation without specific information about where they came from within the formation. In general, therefore, the chart shows even one occurrence within a formation as an occurrence for the formation as a whole. The stratigraphic correlation within and between regions is based on that of Ross, et al. (1982).

The Mystery Revisited

At this point I will consider the environment represented by the lithology of the oldest, Chazyan Stage reportedly rugose-bearing strata and the general environments of the strata between this questionable report and the oldest confirmed report. This information is not included on the time-environments diagram (see below, figure 27). The strata considered here are at least two million years older than those of the next reported occurrence (Ross, et al., 1982). Welby (1961a?) reported Lambeophyllum profundum from the Crown Point Limestone where it outcrops on Grosse Point in Vermont on Lake Champlain (see figure 14). In the northern Champlain Valley the Crown Point Limestone is overlain by the Valcour Limestone. The Valcour underlies

FIGURE 25

RUGOSE CORAL OUTCROPS IN EASTERN NORTH AMERICA

The dots show areas where Middle Ordovician Rugosa have been identified. The information was gleaned from the published literature.

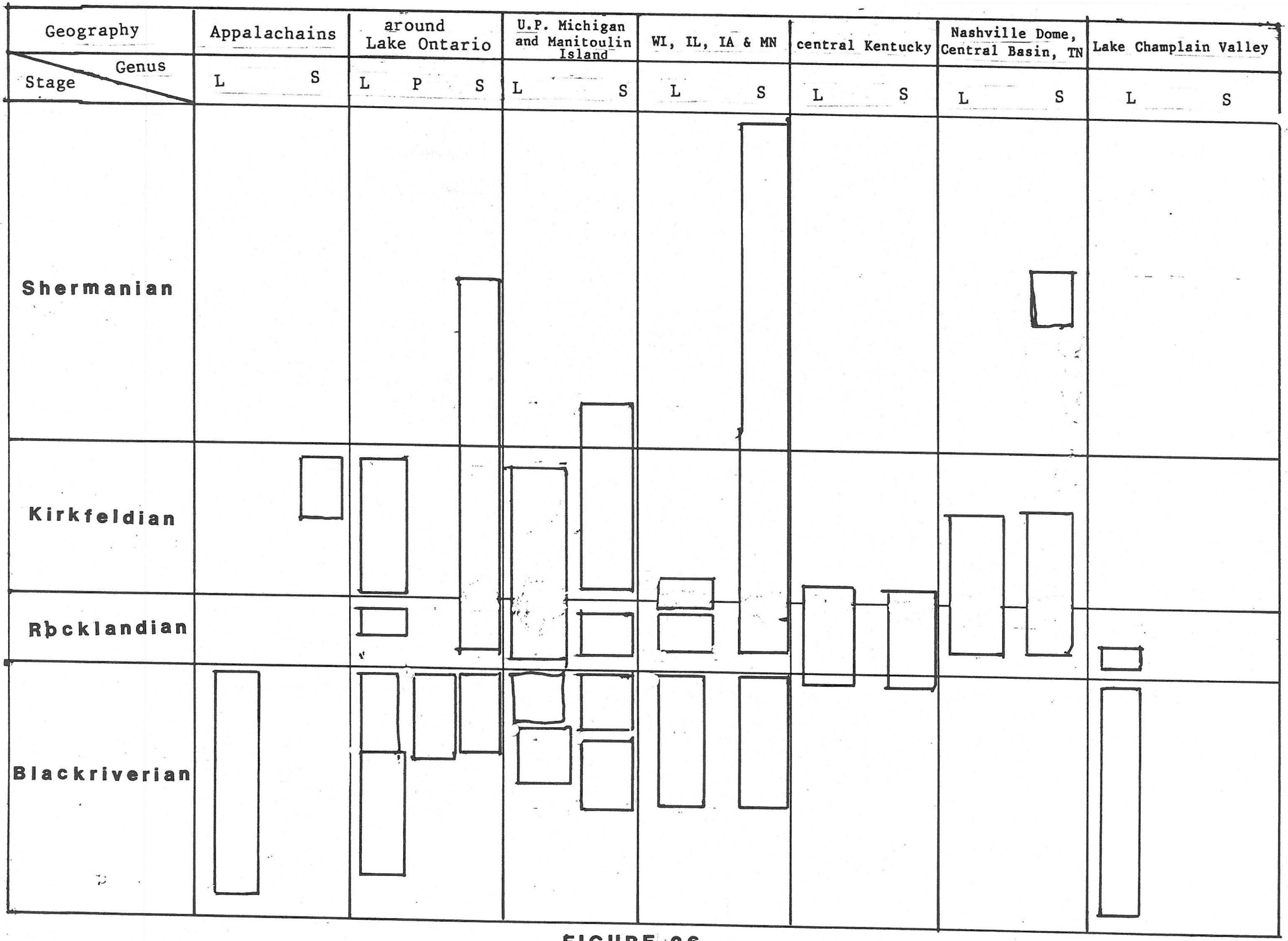


FIGURE 26

TIME-ENVIRONMENT-GENUS DIAGRAM, MIDDLE ORDOVICIAN, EASTERN NORTH AMERICA

☐ = AL OCCURRENCE

L: L eophyllum P: Palaeophyllum S: Strepte sma the Orwell Limestone in which the first well-documented North American Rugosa occur. Although Welby distinguished the Valcour and the Crown Point at the locality in the southern Champlain Valley area where he reported Lambeophyllum (Welby, 1961,bull), later workers have suggested that this distinction cannot be made in the southern area (Selleck and MacLean, 1988) and do not differentiate these Chazy Group rocks. In the southern Champlain Valley the Chazy Group is disconformably overlain by the Orwell Limestone (Selleck and MacLean, 1988).

The Chazy Group in the southern Champlain Valley is characterized by a variety of near shore and inner shelf facies which change rapidly, both laterally and vertically, with no apparent system (Welby, 1961, 1962; Selleck and MacLean, 1988). The rocks of the Grosse Point area where Welby reported Lambeophyllum in the Crown Point Limestone are massive, "sublithographic" limestone/dolostones of very limited fauna and diversity (Welby, 1961; personal observation). Chazyan facies similar to this have been interpreted as tidal flats (Speyer and Selleck, 1988). At the Crown Point Historical Site, about fifteen miles southwest of Welby's locality, the tidal flat facies and a nearshore fossil fragmental packstone to wackestone facies above and below it compose the Chazy Group (Speyer and Selleck, 1988). No rugose corals have been found in these beds (Selleck, Brewster Baldwin, pers. comm., 1988, 1989; and literature). There is a disconformity between the uppermost Chazy Group and the lowermost Orwell in the southern Champlain Valley which is visible at the Crown Point locality (Selleck and MacLean, 1988). The early Blackriverian sediments of the Orwell record a similar nearshore/inner shelf history, the major regional difference being a widespread flooding of the continent which increased the size of the continental shelf (Fisher, 1982). To the west, where Middle

Ordovician rocks outcrop in the Black River Valley, there are no Chazyan rocks (Fisher, 1977), but the Blackriverian Lowville Limestone in which very early corals are reported is underlain by the Pamelia Formation which is also Blackriverian in age. The Pamelia is interpreted as a supratidal to high intertidal environment (onshore of the environments of the time-environment diagram) (Fisher, 1982), and likewise, has had no rugose corals reported from it. It is certainly not expected to find rugosans who inhabited a subaerial environment, like that of the Pamelia, but the environments of the Chazy Group in the southern Champlain Valley are similar to those found later in the Orwell where rugosa are common. If a rugose coral did really live in the Chazyan Crown Point of Welby, its absence from the overlying Crown Point strata is puzzling considering the similarity in environments through the Chazyan and into the Crown Point. For the purpose of identification of the oldest rugose paleoenvironment, the Rugosa in both the Crown Point Limestone and the Orwell Limestone inhabited inner shelf environments.

Time-Environment Diagram

We have arrived (finally) at the TIME-ENVIRONMENT DIAGRAM , the figure which depicts the paleoenvironmental history of the Middle Ordovician North American Rugosa of North America (waste no time in turning to figure 27). The starting data base for the time-environment diagram was the same as that used for figure 20 and is included in Appendix B, but the significance of this figure is in the added environmental information. We can now see that the earliest rugosa were not confined to their environment of origination for more than a couple hundred thousand years, but immediately began to occupy other environments, onshore and off.

The reader will note that there are fewer data points in the time-

IME-ENVIRONMENT DIAGRAM

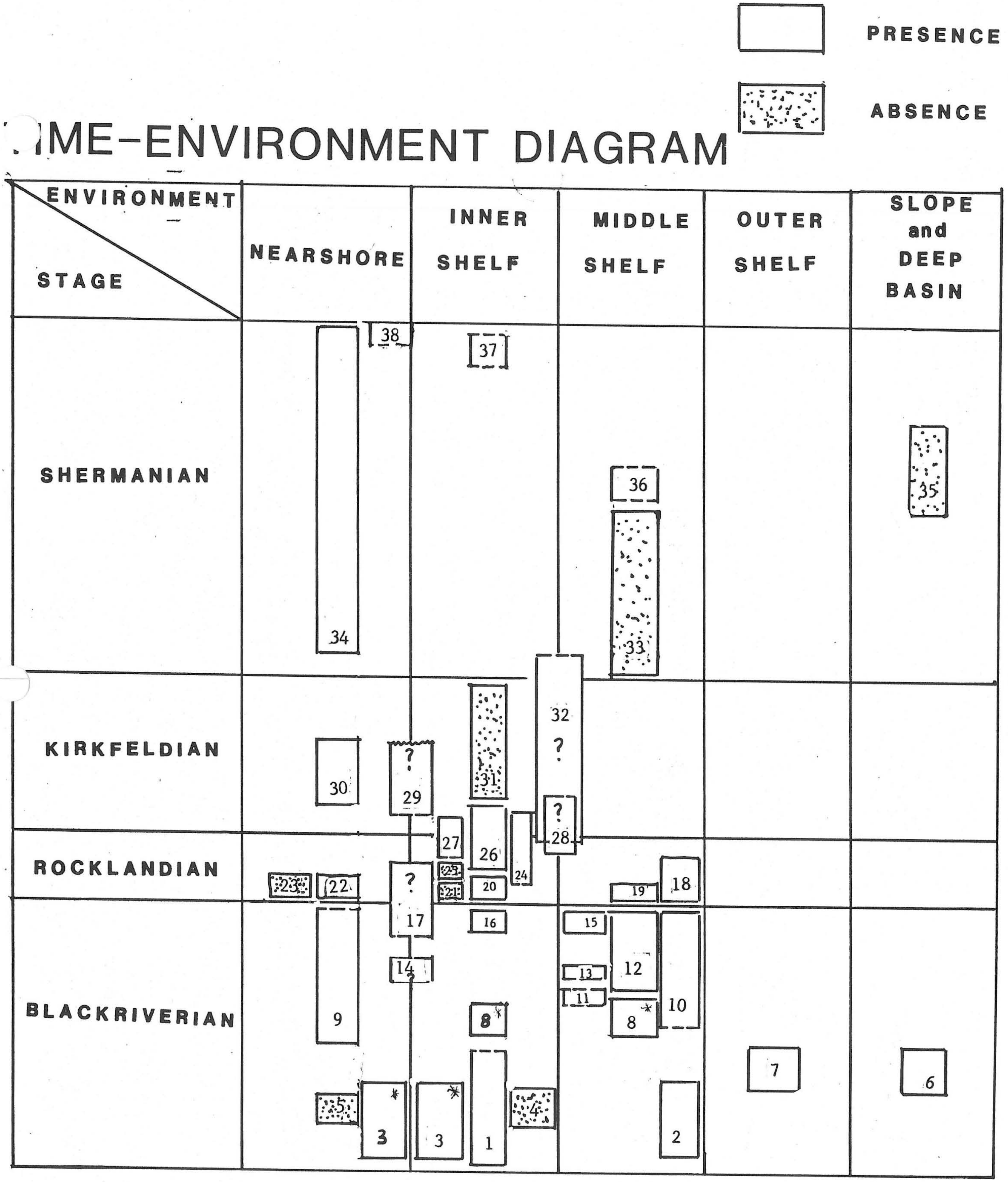


FIGURE 27

*not sure in which facies the corals were deposited

? Environmental information does not permit distinguishing the two environments

Figure 27
Time-Environment Diagram

This diagram was modelled after diagrams by Sepkoski and Sheehan (1983) and Sepkoski and Miller (1985) to show the environmental context of the Rugose corals through the Middle Ordovician. Field work and the published literature provided the sedimentary and fossil information that I used to define the environment for a fossil occurrence. References for the data points are as follows:

1) Selleck and MacLean, 1988, c; this paper, s; Orwell Ls; *Lambeophyllum*; Crown Point, NY.
2) Cameron, c; this paper, s; Lowville ls; *L. profundum*; Inghams Mills, NY.
3) This paper, Cameron, 1969, c+s; Lowville Ls; *L. profundum*; Inghams Mills, NY.
4) Walker, 1972, c+s; Lowville ls, unit D, "subtidal marine pond;" ABSENCE; Black River Valley, NY.
5) Walker, 1972, c+s; Lowville ls, unit D, "subtidal channel community" ABSENCE; Black River Valley, NY.
6) Cooper and Cooper, 1947,c; Read, 1980,s; Edinburg fm, Liberty Hall facies; *Lambeophyllum*; central and northern VA.
7) Cooper and Cooper, 1947,c; Read, 1980,s; Edinburg fm, Lantz Mills facies; *Lambeophyllum*; central and northern VA.
8) Plotnick, personal communication, 1989, c; Fraser, 1976, s; Pecatonica fm (basal Platteville Group); *Streptelasma*; northwestern IL. Note: 2 facies, IS and MS; don' know if one or both has corals.
9) Weiss, 1957, c+s; Platteville Fm, McGregor mb; *L. profundum*; Fillmore County, MN.
10) Wilson, 1949, c+s; Lebanon ls; *S.(?)parasiticum*; Central Basin, TN.
11) Plotnick, pers. comm., 1989, c; Wilman and Kolata, 1978, s; Mifflin Fm; *Streptelasma*; nw IL.
12) Cameron and Mangion, 1977, c+s; Watertown ls; *Lambeophyllum*; northwestern NY.
13) Wilman and Kolata, 1978, c+s; Grand Detour Fm, Forreston mb; *Streptelasma*; Mineral Point, WI.
14) Bretsky, et al., 1977, c+s; Platteville Fm, Mifflin mb; *L. profundum*; sw WI, ne IL, se MN, ne IA.
15) Okulitch, 1939, c; Harland and Pickerill, 1982, s; formation???; *Lambeophyllum profundum*; between Montreal and Quebec City.
16) Okulitch, 1939, c; Harland and Pickerill, 1982, s; formation???; *Lambeophyllum profundum*; between Montreal and Quebec City.
17) Elias, 1983, c; this paper, s; Tyrone Ls; *Lambeophyllum*; Little Hickman, KY.
18) Weiss, 1957, c+s; Decorah Fm, middle and lower; *S. corniculum*, *L. profundum*; Fillmore County, MN.
19) Cameron and Mangion, 1977, c+s, Selby ls; *Lambeophyllum*; Ontario and NY.
20) Cameron and Mangion, 1977, c+s, Selby ls, especially the top 1/3; *Lambeophyllum*; Lowville, NY.
21) Harland and Pickerill, 1984, c+s; Deschambault Fm, fine-grained ls; ABSENCE; north of Quebec City.
22) Harland and Pickerill, 1984, c+s; Deschambault Fm, *Solenopora* gravels; ABSENCE; north of Quebec City.
23) Harland and Pickerill, 1984, c+s; Deschambault Fm, skeletal ls and

coquina: ABSENCE; north of Quebec City.

24) Wilson, 1949, c+s; Carters Ls, lower member; *S. profundum*; Central Basin of TN.

25) Harland and Pickerill, 1984, c+s; Neuville Fm, bryozoan ls; ABSENCE; north of Quebec City.

26) Titus and Cameron, 1976, c+s; Napanee ls, *Triplesia* community; *Streptelasma*; central and northwestern NY.

27) Conkin and Conkin, 1983, c; this paper, s; Lexington Ls, Curdsville mb; *Streprelasma*, also *Lambeophyllum*?; Shakertown and Boonesborough, KY.

28) Hussey, 1952, c+s; Chandler Falls ls (basal); *Lambeophyllum sp.*; Upper Peninsula, MI.

29) Alberstadt, et al., 1974, c+s; Carters ls, adjacent to patch reef; *Lambeophyllum*; Elk River, TN.

30) Titus and Cameron, 1976, c+s; Kings Falls ls, *Liospira* community; *Streptelasma*; central and northwestern NY.

31) Titus and Cameron, 1976, c+s; Kings Falls ls, *Encrinurus* community; ABSENCE; central and northwestern NY.

32) Weiss, 1957, c+s; Galena Fm, Cummingsville mb; *S. corniculum*; Fillmore County, MN.

33) Titus and Cameron, 1976, c+s; Sugar River ls, *Trematic* community; ABSENCE; central and northwestern NY.

34) Weiss, 1957, c+s; Galena Fm, Prosser mb; *S. corniculum*; Fillmore County, MN.

35) Titus and Cameron, 1976, c+s; Kings Falls ls, *Triarthurus* community; ABSENCE; central and northwestern NY.

36) Wilson, 1949, c+s; Hermitage ls, silty nodular ls member; *S.cf.corniculum*; central to eastern Central Basin, TN.

37) Palmer and Palmer, 1977, c+s; Dunleith Fm, Rivoli mb; streptelasmatids; near Decorah, IA.

38) Weiss, 1957, c+s; Galena Fm, Stewartville mb; *S. corniculum*; Fillmore County, MN.

Note:
c = source for coral data
s = source for sedimentological data

environment diagram than in the time-geography-genus diagram depicted in figure 26. This is due to the difficulty of obtaining adequate sedimentological information for every report of a rugosan. Still, it is clear from this diagram that the Rugosa do not exhibit the steady onshore-offshore pattern of expansion that has been reported for evolutionary communities and some post-Paleozoic clades.

There is only a single positive data point and a complete lack of negative data points for outer shelf environments. Similarly, slope and deep basin point are poorly represented here. Descriptions of outer shelf and slope and deep basin environments do exist, but they have not provided enough faunal information to determine coral presence or absence (Titus and Cameron, 1976; Read,1980; Walker, et al., 1980). There are several possible explanations for this, some based on the possibility of a natural bias, another of a bias in the literature. It is certainly possible that the deeper sea deposits of the Middle Ordovician in eastern North America were not not commonly preserved or are not widely exposed. It is also possible that in eastern North America in the Middle Ordovician there was a natural dearth of offshore environments. In general the seas were shallow then. Perhaps the continental slopes began at relatively shallower depths than they have in other times and places in earth history, and there was little or no shelf with the energy conditions of the outer shelf, as defined for this paper, that rugosans (or anyone else) could inhabit. Another possibility is that there has not been much work published on the outer shelf environments of the area. Few of the recently published studies that were used included detailed faunal information so that often no assessment of rugose presence, positive or negative, could be made based solely on these sources. The outer shelf environment is recognized primarily by the absence of structures indicative of either more onshore environments (e.g.

storms, cross-bedding) or the slope and deep basin (e.g. slumping, turbidites). Yet, when evaluating the older literature, I was hesitant to use material that did not offer some positive means to identify the environment. This is because, in much of this older literature, measured sections and lithologic descriptions are very general (e.g. bluish shale, thin-bedded with abundant bryozoa overlying hard, irregularly-bedded, fossil-poor layer), and workers did not use modern terminology to describe the rocks, and were often not keyed into the suites of sedimentary structures that that modern workers (in the age of plate tectonics) would consider diagnostic of a particular environment (and thus might not have noted them).

The positive data points for Lambeophyllum in the outer shelf and deep basin are worthy of some discussion. First, a comment that the lack of the report of later occurrences does not need to imply that they are anomalies. In the deposits of both environments (in the Lantz Mills and Liberty Hall formations of Virginia), Lambeophyllum is not uncommon. They clearly did inhabit offshore environments very early in their evolutionary history. the absence of post-Blackriverian data points probably says more about the limitations of the literature and the preliminary nature of the project than it does about rugosan paleoenvironments. Further work is necessary, of course, to confirm or deny this impression.

Second, the possibility exists that turbidity currents transported Lambeophyllum to the deep basin environment in which it is found. It is impossible to tell from the literature that exists (Ccooper and Cooper, 1947; Read, 1980) whether this might be the case. This uncertainty highlights the fact that, in compiling paleoenvironmental histories, there is often the possibility that an organism was not deposited in its life environment. Nevertheless, it is certain, based on the repeated occurrence of Lambeophyllum in the deep sea facies that this member of the Rugosa did live in a relatively offshore environment, and thus, that these very early rugosans were widespread across marine environments.

Worldwide Distribution of Middle Ordovician Rugosa

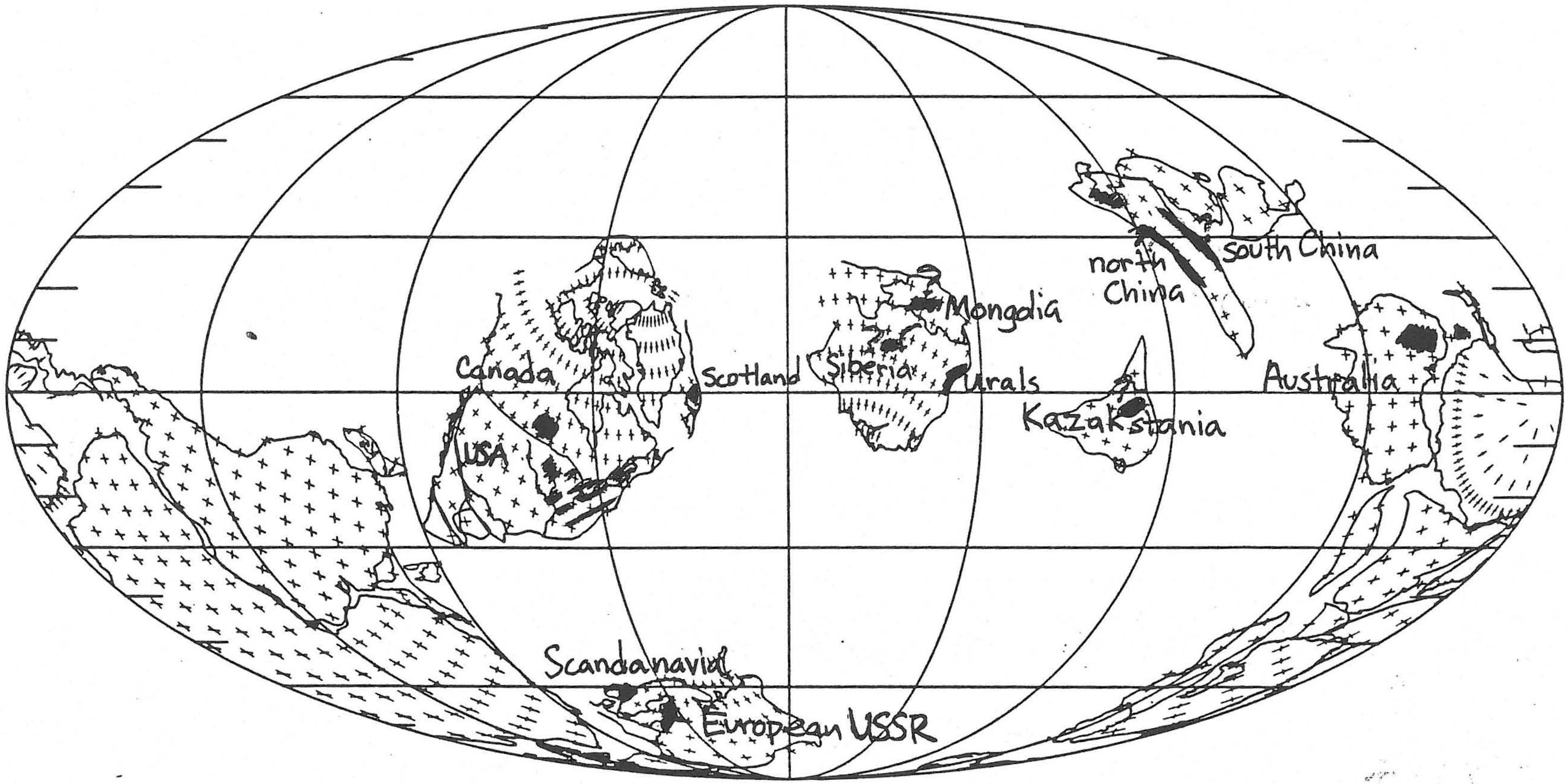
Geographic Occurrences and Broad Scale Paleogeography

A preliminary search of the world literature on the Middle Ordovician Rugosa has shown occurrences in Australia, in Tasmania and New South Wales; in England and Scotland; in Norway and Sweden, on the Balto-Scandian shelf, in Estonia, the Leningrad area; in Kazakstania; in Siberia; and in northern and southern China (see Appendix C). These areas are widely varied in terms of paleolatitudes from about sixty to sixty five degrees south (Scandanavia, Estonia, etc.) to about thirty to thirty-five degrees north (parts of China) (Scotese, 1979; see figure 28).

map is photocopied from Sc se, 1979

place names are from Scotese, 1979

coral info added



-Middle Ordovician (Llandeilian–earliest Caradocian) Base Map. Mollweide projection "front view" (see note on map explanation).

■:corals reported from Middle Ordovician

?: specific area uncertain

FIGURE 28

This Middle Ordovician base map shows the areas where Middle Ordovician Rugosa have been reported. The base map from Scotese, et al., 1979 has had the coral information superimposed on it.

Discussion and Conclusions

Where we are

This work serves as a preliminary study of rugosan paleoenvironments. The environment of the oldest North American Rugosa is established as inner shelf. Welby's (1961) report of a Chazyan Stage Lambeophyllum remains unconfirmed, and in fact should be considered doubtful. Still, the environment of the beds from which the coral was reported is clearly identified as inner shelf, the report is true, the environment of origination is inner shelf. The next oldest Middle Ordovician Rugosa in North America, those of the Blackriverian Orwell Limestone which inhabited the inner shelf. It is unlikely that future workers will concentrate efforts on confirming Welby's report, and unconcentrated efforts have failed to do so thus far. As it stands, we can feel confident that the first North American Rugosa inhabited an "onshore" inner shelf environment, whatever its true age may be. The question remains as to whether the Blackriverian corals pre-date the Australian Gisbornian corals, and thus whether rugose corals truly originated in North America.

Immediately following their first appearance in the Orwell Limestone rugose corals can be found across the shelf. That the rugosa immediately inhabit a range of environments distinguishes rugosan environmental history from that of the evolutionary communities established by Sepkoski (with others, 1983, 1985), as well as from those of previously studied post-Paleozoic clades.

There are absences in all environments. Within an environment absences serve to remind that variables other than the energy level of an organism's environment will determine its ability to live there or be preserved. In the case of the early Rugosa considered in this paper nearshore, inner and middle shelf absences may imply only that the Rugosa were not especially ubiquitous in the Middle Ordovician.

Where we might go

Many questions remain about the paleoenvironmental history of the early Rugosa. Some of these questions can be addressed by a continued study of the literature supplemented by a more aggressive field component to fill in the holes in the literature where they exist. Other problems, such as inexact stratigraphic correlation, or defective systematic classification, await resolution by stratigraphers and systematic paleontologists.

Further work is necessary to clarify the eastern North American situation as well as to identify and compare worldwide patterns. In future work on eastern North America the dearth of outer shelf and slope and deep basin data points must be addressed. An approach to be utilized would be to seek actively sedimentological data on these particular environments and then to find the faunal information either through the literature, or through field studies. It is certainly relevant to this study to define rigorously the role that outer shelf and slope and deep basin environments play -- what is their record, and to what extent are the Rugosa a part of that record?

Fully comprehensive environmental classification of all sedimentary units within the geographic area of the study might clarify the significance of the absences within and between environments. Because the paleogeography and general paleoenvironmental history of the Middle Ordovician of eastern North America is relatively well known, and because supplementary field work would be relatively easy to carry out, this is not as potentially frustrating or impossible a job as it might first sound. Certainly such studies are not feasible or desirable on a broad geographic scale, but a single study of a well-known area might be useful in elucidating the importance and significance of absences.

The interpretation of large-scale trends through the use of this methodology is problematic in some ways, but it is certainly superior to the anecdotal interpretations which have been relied upon in the past. There are gaps and heterogeneities in both the natural record and the published literature which prohibit fully standardized coverage of environments and units of time and geographic areas. The limitations of the rock record cannot be overcome; the limitations of the literature can. As it stands, there is a significant body of literature that is data waiting to be utilized. Important holes can be filled in by immediate field work. Future publication of local paleontological and sedimentological studies will continue to add to the base of information which can be tapped for studies such as this.

With the understanding that ecological relationships are influenced by the evolutionary paleoecological history of an organism within a clade, we can more accurately evaluate short term ecological and paleoecological relationships in future paleoecological studies. The paleoenvironmental histories developed in this and similar projects will provide specific knowledge of clades' evolutionary histories that will be useful in evaluating organisms' paleoecological roles at a given points in their histories.

Acknowledgements

This project would not have been conceived, undertaken, or completed without Mary Droser who has provided immeasureable advice, encouragement, presents, literature, photographs, field "assistance," field funds,....and much more throughout.

Field work was facilitated by the advice and information on local geology of Bruce Selleck at Colgate on the Lowville and Orwell Formations and their outcrops; and Warren Huff and Arnie Miller From the University of Cincinnati who organized a field trip on the Middle Ordovician of Kentucky which I joined. I learned a lot from other participants in the field trip as well. The section measured at Shakertown is a product of that trip. Larry Hampt and Greg Kehm provided field assistance in New York & Vermont.

A tremendous amount of the work for this project required the use of Interlibrary Loan materials. Valerie McGowan-Doyle, of the Interlibrary Loan office should win a prize for helpfulness. Reference libraians were consistently helpful, at Kettering and Mudd and the Texas A&M University Library.

Bob Elias and Barry Webby answered inquiries on their work on North American and Australian Ordovician rugosa. Charles Welby tried to help me track down his Lambeophyllum specimen, as did people at the Vermont Geological Survey, Middlebury College and the University of Vermont. Roy Plotnick informed me of the presence of early corals in northwestern Illinois.

Sue Simonson and MLD lent cameras for field photography. TAMU let me use their GEOREF service. Steve Wojtal and Bruce Simonson answered my questions and suggested and lent references. Ronnie Kusnir, Steve, Bruce, and MLD helped me operate the word processor. Jim Keith slabbed some rocks and made some thin sections of corals collected for this project.

Funds were provided by the Student Projects Fund and the Oberlin Geology Department. I was a guest of Arnie Miller (&MLD) during field work in Kentucky.

Appendix A

Correspondence relating to Welby's 1961 report of a Chazyan Stage specimen of Lambeophyllum profundum

North Carolina State University
College of Physical and Mathematical Sciences

Department of Marine, Earth and Atmospheric Sciences
(919) 737-3711

Box 8208, Raleigh, NC 27695-8208

November 22, 1988

Ms. Gretchen Hampt
Department of Geology
Oberlin College
Oberlin, OH 44074

Dear Gretchen:

This letter is in reply to your November 1 letter, which came while I was out of town.

I have reviewed the *Foerstephyllum* paper and attempted to recall just where the *Lambeophyllum* specimen was observed. I have not been able to locate my notes on the locality. (They're somewhere in the clutter probably.)

My best recollection is that the specimen in question was one-of-a-kind, and I am not completely sure at this point whether the identification was a field identification or whether a portion of the specimen was brought into the laboratory. In any event there probably was only one specimen.

All of the collections from that work were either at Middlebury College or deposited in the geology collections of the Vermont Geological Survey.

I am sorry that I cannot be of more help to you.

Sincerely yours,

Charles W. Welby

Charles W. Welby
Professor

CWW/ch

Department of Geology
Middlebury College
Middlebury VT 05753

3 December 1988

Gretchen Hampt
Department of Geology
Severance Hall
Oberlin College
Oberlin OH 44074-1087

Dear Gretchen:

Ray Coish turned your letter over to me. You inquire about a specimen of *Lambeophyllum profundum* that Chuck Welby collected from the Crown Point Limestone near Grosse Point. I am not aware of this specimen.

We do very little with paleontology here, and so we do not have a very good catalogue of our fossil collection. I believe that most or all of our half-dozen *L. profundum* specimens are from the Orwell Limestone (Black River) from New York's Crown Point State Historic Site (collected before they set a policy forbidding collecting!). If we indeed do have the Chazyan specimen in our collection, it is in the working collection and so has lost the identity you seek.

I've been to the Crown Point Historic Site many times since 1962 and in the past have seen most every layer in the Chazy. I haven't noticed any *L. profundum* below the Orwell beds, though indeed this coral shows up as early as the bottom of the Orwell. Would you send me a copy of the 1961 Welby article that you cited in your letter? Perhaps it has some information that might help.

Cordially,

Brew Baldwin

Brewster Baldwin
cc: Ray Coish

5 Dec— None of our specimens has a catalogue number; our catalogue does not list a L. profundum

Brew

Appendix B

References for Middle Ordovician Eastern North American Rugose Coral Occurences

state	formation	locality	corals	reference
MN	Platteville	Minneapolis	Streptalasma? parasiticum	B
	Platteville	Mantorville	S. corniculum	B
	Platteville ls	Fountain	S. breve	B
	Platteville, McGregor mb	Fillmore Co.	Lambeophyllum profundum	Weiss, 1957
	spechts Ferry, Decorah sh Stictoporella bed	St. Paul	L. prof	Bassler, 1950
	Ion mb Decorah sh Phylloporina&Fucoid beds	St. Paul	L. prof	B
	Ion F&P beds	se MN	L. prof	B
	Guttenberg Decorah sh R&C beds	St. Paul	L. prof	B
	Guttenberg R&C beds	se MN	L. prof	B
	" Rhinidictya, Ctenodonta beds	St. Paul	Streptelasma parasiticum	B
	"	se MN	S. parasiticum	B
	Decorah fm, lower and middle not upper	Fillmore Co.	S. corniculum L. prof	Weiss, 1957
	Galena Fm, 3 mbs: Stewartville Prosser Cummingsville	Fillmore co.	S. corniculum in all 3 mbs	Weiss, 1957
	Prosser mb of the Galena Fm	Cannon Falls	S.corniculum	B

	Prosser ls	Kenyon	S. corniculum	B
IA	Prosser ls	Elkander	S. corniculum	B
	Dunleith fm, Galena Group	near Decorah	streptelasmatids	Palmer&Palmer, 1977
WI	Prosser ls	Green Bay 3 mi nw	S. corniculum	B
	Platteville ls	Beloit	Favistella undulata (prob Favistina)	B
	Platteville	Beloit	L. prof	B
	Platteville ls	?	L. prof	Sturm, 1963
	Platteville	Mineral Point	L. prof	Bassler, 1950
	Platteville	Janesville	L.prof	B
	Platteville	Oshkosh	S. corniculum	B
	Platteville ls	Grant County	L. profundum	Agnew, et al., 1956
	Grand Detour Fm	Lafayette Co.	Streptelasma	W&K, 1978
	Grand Detour Fm, Forreston mb (Galena Gr)	Mineral Point South Wayne	Streptelasma	Willman&Kolata, 1978
	Grand Detour Fm, Forreston mb (Galena Gr)	Martintown in Green Co.	Streptelasma	Willman&Kolata, 1978
IL	Platteville Gr.	Calhoun Co.	L. prof	B
	Platteville Gr.	Calhoun Co.	S. breve	B
	Pecatonica fm (Platteville Gr.)	nw IL	Streptelasma	Plotnick, pers. comm.
	Mifflin fm (Platteville Gr)	nw IL	Streptelasma	Plotnick, pers. comm.
	Grand Detour (Platteville Gr)	Carroll,Ogle Lee &Stephenson Co.	Streptelasma	Willman&Kolata 1978
	Grand Detour, Forreston mb (Platteville Gr)	Oregon & Rochelle in Ogle Co.	Streptelasma	Willman&Kolata 1978
	Grand Detour,	Dixon & sw of	Streptelasma	Willman&Kolata

Forreston mb (Platteville Gr)	Dixon in Lee Co.		1978
Naschua Fm, Eldena mb (Platteville gr)	4 1/2mi. se Durand	Streptelasma	Wilman&Kolata, 1978
Naschua Fm, Eldena mb (Platteville gr)	Rockford	Streptelasma	Wilman&Kolata, 1978
Naschua Fm, Elm mb (Platteville Gr)	1 1/2mi.n of Lowell, La Salle Co.	Streptelasma	Willman &Kolata,1978
Naschua Fm, Everett mb (Platteville Gr)	1 1/2mi.n of Lowell, La Salle Co.	Streptelasma	Willman &Kolata,1978
Naschua Fm, Everett mb (Platteville gr)	4 1/2mi. se Durand	Streptelasma	Wilman&Kolata, 1978
Naschua Fm, Everett mb (Platteville gr)	Rockford	Streptelasma	Wilman&Kolata, 1978
Naschua Fm, Everett mb (Platteville gr)	Oregon in Ogle Co.	Streptelasma	Wilman&Kolata, 1978
Quimbys Mill fm (Platteville Gr)	Pecatonica Valley, Rock Valley, Kendall Co, Oglesby	Streptelasma	Willman & Kolata 1978
Kimmswick ls	Gken Park	S. corniculum	B

IN

Platteville ls	near Kentland	L. prof	B

TN

Hermitage fm	Smith Co.	S. corniculum	B
Hermitage fm "silty nodular ls member"	central basin	S. cf.corniculum	Wilson, 1949
Carters ls	Nashville	L. prof	B
Carters ls	Aspen Hill	L. prof	B
Carters ls	Columbia	L. profundum	B

	Carters ls "Lower member"	central basin	"Streptelasma profundum"	Wilson, 1949

Has this been revised to L. profundum?

	Carters ls	central basin	"Streptelasma profundum"	Wilson, 1949
	Carters ls, adjacent to patch reefs	Elk River in the s. Central Basin	Lambeophyllum	Alberstadt, et al. 1974
	Carters ls, in patch reefs	Elk River	ABSENCE, so far	Alberstadt, et al., 1974
	Tyrone ls	Nashville	L. prof	B
	Lebanon ls	central basin	S. parasiticum	Okulitch, 1936
	Lebanon ls	central basin	S. ?parasiticum	Wilson, 1949
	Lebanon ls	Cumberland City	S.? parasiticum	Okulitch, 1936

KY	Tyrone ls	High Bridge	S. parasiticum L. profundum	B
	Tyrone ls	Frankfort	L. profundum	B
	Tyrone ls	Sulfur Wells	Lambeophyllum sp. A & B	Elias, 1983
	Curdsville mb, Lexington ls	central KY	L. prof S. corniculum	B
	Curdsville mb, Lexington ls	Shakertown	rugosa	new report
	Curdsville mb Lexington ls	Boonesborough	Streptelasma	Conkin&Conkin, 1983?
	Cynthiana ls	central Ky	Favistella	B

VA	Edinburg fm (Lantz Mills facies)	Edinburg Shenandoah Co.	Lambeophyllum	Cooper&Cooper, 1946
	Edinburg fm (Liberty Hall facies)	Shenandoah Co	Lambeophyllum	Cooper&Cooper, 1946
	Edinburg Fm (St. Luke MB)	Frederick Co.	Lambeophyllum	Cooper&Cooper, 1946

Edinburg Fm (Lantz Mills facies)	Frederick Co.	Lambeophyllum	Cooper&Cooper, 1946
Edinburg Fm (Liberty Hall facies)	Frederick Co.	Lambeophyllum	Cooper&Cooper, 1946
*? Edinburg Fm (Lantz Mills facies?)	s. Augsta Co.	Lambeophyllum	Cooper&Cooper, 1946

"Appalachain region"

Leray ls	?	L. prof	Stumm, 1963
Chambersburg ls	MD, Appalachains	L. prof	B

MI & nearby Ontario

Black River	Raynolds Pt., on Drummond Is.	Streptelasma rusticum	Hussey, 1952
Black River (Decorah age)	sulfur Is,Ont	Lambeophyllum sp.	Hussey, 1952
Black River Group	Ontario (prob near the Sault)	L. apertum	Stumm, 1963
Cloche Island fm, lower member	Great Cloche Is., on Manitoulin Is	Lambeophyllum	Copper, 19??
?(Trenton strata)	Escanaba	S. corniculum	Stumm, 1963 and Rominger, 1876
Chandler Falls	Cornell	S. corniculum	Hussey, 1952
Bony Falls ls	?	L. prof L. apertum	Stumm, 1963
Chandler Falls ls?	Bony Falls of Escanaba River	Lambeophyllum sp.	Hussey, 1952
Chandler Falls	3mi. n. of Escanaba	S. corniculum	Hussey, 1952
Chandler Falls ls	3mi. nw of Escanaba	S. husseyi	Stumm, 1963
Chandler Falls	?	S. corniculum	Stumm, 1963
?(Trenton strata)	Sulfur Is.	S. corniculum	Stumm, 1963 and Rominger, 1876
?(Trenton strata)	St. Joseph's Is	S. corniculum	Stumm, 1963 and Rominger, 1876
Hull	West Neebish Channel & s. of Sault Ste. Marie	S. corniculum	Hussey, 1952

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eastern Ontario
and Quebec

is it near Quebec?	Selby ls	look up localtiy	Lambeophyllum	Cameron&Mangion, 1977
	Deschambault fm	Loretteville, just n. of Quebec City	Streptelasma	Harland&Pickerill, 1984

NY

	Orwell, 2 facies	Crown Point	Lambeophyllum	Selleck&MacLean,19??
? check geog^	Lowville (Gull River)	E. Canada Creek, Herkimer co.	L. prof	B (Cameron, 1972)
	Lowville	Crown Pt. and area	S. corniculum	B
	Isle La Motte	Champlain Valley	Streptelasma	Fisher, 1982
	Watertown ls	nw NY	F. alveolata	B
	Watertown ls	nw NY	Lambeophyllum	Cameron&Mangion, 1977
	Watertown ls	Mohawk Valley	Lambeophyllum	Cameron&Mangion, 1977
	Selby ls	nw NY	Lambeophyllum	Cameron&Mangion, 1977
2 facies? (equiv. Lowville)	Gull River	Inghams Mills	L. prof	Cameron, 1972
	Napanee ls	nw NY	S. corniculum Columnaria halli	Titus&Cameron, 1976
	Kings Falls ls	nw NY	S. corniculum	Titus&Cameron,1976
	Kings Falls ls	central NY Sugar River (town)	Lambeophyllum	Cameron, 1972
	Napanee ls	Inghams Mills	L. prof	Cameron, 1972
	Leray ls	?	L. prof	Sturm, 1963
	Amsterdam ls	Canajoharie to Glens Falls	L.profundum	Ross, 1982
	Trentonian Stage	Watertown	S. cornicluum S. multilamellosum	B B
	Trentonian Stage	Trenton Falls	S. corniculum	B

	Trentonian Stage	Middleville	S. crassum, S. parvulum S. corniculum	B
VT	Crown Point ls	Grosse Point	Lambeophyllum?	Welby, 1961
	Orwell ls	Champlain Basin	Lambeophyllum	Selleck&MacLean, 1988
PA	Carlim ls	central	L. prof	B
	Rodman ls	Rodman	L. prof S. corniculum	B
NJ	Jacksonburg ls	Jacksonburg	S. corniculum	B
MO	Kimmswick ls	Glen Park	S. corniculum	B
CA	Johnson Spring, section JS-7, unit8	Johnson Spring	Streptelasmids Palaeophyllum? sp	Ross, 1966
	unit 6		streptelasmids	
	JS-10, unit10		Palaeophyllum "Streptelasma" tennysoni Streptelasmatids horn corals	
	JS-8, coral ls near section		Palaeophyllum sp.2 streptelasmatids	
North America				
	Trentonian	Caradoc	Streptelasma	Hill,1981
	Trentonian	Caradoc	Palaeophyllum	Hill, 1981
	Trentonian	Caradoc	Lambeophyllum	Hill,1981

B = Bassler, 19??

Appendix C

References for Worldwide Middle Ordovician Rugose Coral Occurences Excluding North America

Country	Formation	Stage	Locality	Corals	Reference
Norway	Cyclocrinite beds correspond to L. Hamopsels&U.Hamopse sh &C. wilsoni graptolite zone	younger than Idavere&Johvi		?	Sytova, 19
	Cyclocrinus beds	post Blriv	S. Hadeland	Streptelasma holtedahli	H
	Cyclocrinus beds	post Blriv	S. Hadeland	Streptelasma curvatum	H
	Cyclocrinus beds	post Blriv	S.Hadeland	Streptelasma sp.	H
oldest in Norway✓	Cyclocrinite beds (l.Hamopse ls, u.Hamopse shale)	L.Caradoc	?	Leolasma (eg. S.corniculum HILL)	S,1977
	Mastoporas beds	post Blriv.	Mjosa region	Streptelasma holtedahli	H
	Encrinite ls	post Blriv.	Gjerpen-Langesund district	Tryplasma basaliforma	H
	Encrinite ls	post Blriv.	Gjerpen-Langesund district	Tryplasma brevikense	H
	Sphaeronid ls (Chasmops ls)	post Blriv.	S. Hadeland	Streptelasma holtedahli	H
	Sphaeronid ls (Chasmops ls)	post Blriv.	Toten S.Hadeland?	Streptelasma compactum	H
	Sphaeronid ls (Chasmops ls)	post Blriv.	Toten S.Hadeland?	?Streptelasma curvatumm	H
	Sphaeronid ls	post Blriv.	S. Hadeland	?Grewingkia sp.	H
	Sphaeronite ls	equiv.to Keila&Vasalemma	?	Coelostylis compactum	W, 1971
	?	m.M.Ord.	?	coelostylis	Hill,1981
Sweden	?	M.-U.Ord	?	Helicelasma	Hill, 1981

	Macrourus beds equiv.to Keila&Vasalemma		?	Coelostylis	
	?	m.M.Ord	?	Coelostylis	Hill,1981
USSR - Estonia	Rakvere horizon (prob. Cincinnatian >U. Ord)	U.Viruan	?	Lambelasma narvaense	Weyer, 1983
	Johvi horizon	M.viruan	Baltoscandian shelf region	Lambelasma dybowskii	Weyer, 1981-t
	Johvi horizon	M.Viruan	Leningrad area	Primitophyllum primum	Weyer, 1981-t
	Keila	u.L.Caradoc	Leningrad	Primitophyllum	N,1985
	Idavere	u.L.Caradoc	Leningrad	Primitophyllum	N,1985
	Johvi	u.L.Caradoc	Leningrad	Primitophyllum (primum)	N,1985 (S,1977)
	Johvi	u.L.Caradoc	Estonia	Lambeophyllum dybowski	W, 1971
	lower Johvi horizon	?	Madise, Balto- Scandian shelf area	Primitophyllum primum	Weyer, 1981-t
	Idavere horizon	?	Unikula, Balto- Scandian shelf region	Primitophyllum primum	Weyer, 1981-t
	Oandu horizon = Vasalemma horizon	M.Ord	s. of Tallin, Estonia	Estonielasma praecox	Weyer, 1979
	?	M.Caradoc	Estonia	Estonielasma	Weyer,1979
	Idavere	m.L.Caradoc	Estonia	Primitophyllum (primum)	N,1985 (Webby,1971)
	Idavere	L.Caradoc	Estonnia	"Lambeophyllum" dybowskii	S,1977
	Idavere	L.Caradoc	Leningrad	"Lambeophyllum" dybowskii	S,1977
	Johvi	u.L.Caradoc	Estonia	Lambeophyllum profundum	S,1977
	Johvi	u.L.Caradoc	Leningrad	Lambeophyllum profundum	S,1977
	Johvi	u.L.Caradoc	Estonia	Primitophyllum (primum)	N,1985 (S,1977, Webby, 1971)

Keila	l.M.Caradoc	Estonia	Primitophyllum (primum)	N,1985 (Webby,1971)
Keila	l.M.Caradoc	Estonia	Leolasma sociale	Webby,1971
Keila	l.M.Caradoc	Estonia	Leolasma reimani (maybe = Coelostylis)	Webby, 1971
Vasalemma beds	l.M.Caradoc	Estonia	Leolasma reimani (maybe = Coelostylis)	Webby, 1971
Wesenburg fm	?	Estonia	Lambeophyllum profundum (possible occurrence)	B
?	M.-U.Ord	Estonia	Helicelasma	Hill,1981
? (corresponds to Cincinnatian)	Vormsi	Estonia	Estonielasma	Hill,1981
Johvi horizon	M.Viruan	Baltoscandia	Lambelasma dybowskii	Weyer, 1983
Johvi horizon	M.Viruan	east Baltic area	Leolasma	N,1985
Rakvere horizon	U.Viruan	Baltoscandia	Lambelasma atavum	Weyer, 1983
?	u.M.Ord	Baltoscandia	Neotryplasma	N,1985
?Ppleistocene erratics from Baltoscandia			Dybowskinia	Hill,1981

note: Sytova thinks the genus Lambeophyllum was wrongly assigned to the coral Lambeophyllum dybowski from this area.

Europe

Keila horizon	?	?	Primitophyllum primum	Weyer, 1981-t
?	"Trenton age"	Europe	Primitophyllum	Hill,
?	"Ttrenton age"	Europe	Neotryplasma	Hill,1981
Kokruse horizon	basal Caradoc	Europe	ABSENCE	Weyer, 1981-t
?	"Trenton age"	Europe	Streptelasma	Hill,1981
?	"Trenton age"	Europe	Palaeophyllum	Hill,1981
?	"Trentom age"	Europe	Favistina	Hill, 1981
?	?	Pin Valley, Spiti, central Himalayas	Streptelasma corniculum?	B

	?	L.Caradoc	Europe?	?Primitophyllum primum	Weyer,197
	?	L.Caradoc	Europe?	Lambelasma dybowski	Weyer,1979
	?	M.Caradoc	Europe?	Lambelasma atavum	Weyer,1979
	?	M.Caradoc	Europe?	Coelostylis toerquisti	Weyer,1981
Germany	An erratic of Wesenberg ls	?	from Estonia?	Lambelasma narvaense	Weyer, 1983
	erratics in Pleistocene drift	u.M.Ord	?	Coelolasma	Hill,1981
	erratics in Pleistocene drift	m.M.Ord	?	Coelostylis	Hill,1981
Australia	l.Cliefden Caves ls	U.Gisbornian, possibly Eastonian	Molong Rise	Hillophyllum priscum	M&W
	l.Cliefden Caves ls	Gisbornian	s. of Molong	Hillophyllum priscum	W,1971
	u.CliefdenCavesls	L. Eastonian U.Gisbornian?	centralN.S.W.	Hillophyllum 2 sp.	W
	u.CliefdenCavesls	L. Eastonian U.Gisbornian?	centralN.S.W.	Palaeophyllum proliferum	W
	u.CliefdenCavesls	U.Gisbornian or L.Eastonian	Molong rise	Palaeophyllum sp.	Webby,1971
	mid Bowen Park ls	U.Gisbornian or L.Eastonian	?	Palaeophyllum sp.	Webby,1971
	(?	L.Eastonian	?	Paleophyllum	N, 1985)
	Billabong Creek ls	L.Eastonian or U. Gisbornian	?	Hillophyllum priscum	M&W,
	Billabong Creek ls	L.Eastonian or U. Gisbornian	?	Hillophyllum sp.	M&W
	Quondong Fm	L. Eastonian or U.Gisbornian	Quondong, N.S.W.	Hillophyllum 2 sp.	W
	Quondong fm	L.Eastonian or U.Gisbornian	Quondong, N.S.W.	Palaeophyllum proliferum	W

U.Regan's Creek ls	L. Eastonian U.Gisbornain?	central N.S.W.	Palaoephyllum proliferum	W
?	U. Gisbornian	?	?Palaeophyllum patulum	S&U also M&W
?	"Trenton age"	?	Palaeophyllum	Hill,1981
?	"Trenton age"	?	Hillophyllum	Hill, 1981
?	U. Eastonian	New South Wales	Palaeophyllum crassum	S&U
?	U. eastonian	?	Favistina	Webby,1971
?	U.Eastonian	?	Streptelasma	Webby,1971
m.Bowen Park ls	U.Gisbornian or L.Eastonian	?	Hillophyllum sp.	W,1971
u.Cliefden Caves ls	U.Gisbornian or L.Eastonian	?	Hillophyllum sp.	W,1971
?	U.Gisbornian or L.Eastonmian	Billabong Creek, wsw of Parkes	Hillophyllum priscum	W,1971
l.Reedy Creek ls	Gisbornian	s. of Molong	Hillophyllum priscum	Webby,1971
m. Cliefden Caves (more massive parts)	Gisbornian	s. of Molong	Hillophyllum priscum	Webby,1971
Regan's Creek ls (more massive parts)	Gisbornian	s. of Molong	Hillophyllum priscum	Webby,1971
u. Cliefden Caves ls	Gisbornian	s. of Molong	Hillophyllum priscum	Webby,1971
m. Bowen Park ls	Gisbornian	s. of Molong	Hillophyllum priscum	Webby,1971
Tasmania				
Gordon Group Lithofacies IX	Black River? Kirkfeld?	Ida Bay	solitary corals	Burrett, et al.,1984
USSR				
Typyl horizon	m. Ord	Urals	Grewingikia altaica	S&U
Typyl horizon	m. Ord	Urals	Streptelasma duncani	S&U
?	m-u Ord	Urals	Neotryplasma shuryginae	Weyer, 1982

	?	M.Ord	Urals	Vischeria	Hill, 1981
	?	"Trenton age"	Kazakhstan	Proterophyllum	Hill, 1981
	?	"Trenton age"	Kazakhstan	Kenophyllum	Hill,1981
	?	?	Goruaga Shoria, w. Siberia	Columnaria= Paleophyllum halysitoides	B
Great Britian					
	Coniston ls	?	?	Streptelasma aequisulcatum	H
	Bala-Craighead ls	?Caradoc	Craighead, Ayrshire, Scotland	Streptelasma (Palaeophyllum) aggregatum	B
	Bala-Craighead ls	?Ccaradoc	Craighead, Ayrshire, Scotland	Streptelasma craigense; europaeum; fossulatum	B
	?	M.-U.Ord	?	Helicelasma	Hill,1981
China					
	Yanwashan Ls	late M.Ord	Jiangshan County, Zhejiang province	Palaeophyllum irregulare	LB
	Yanwashan Ls	late M.Ord	Jiangshan County, Zhejiang province	Yohophyllum zhejiangense	LB
	?	M. Ord	N.China	Tryplasma	YiNung
	?	M.Ord	N.China	Favistella	YiNung
	?	M.Ord	S.China	Favistella	YiNung
	?	M.Ord	S.China	Palaeophyllum	YiNung
	?	M.Ord	S.China	Calostylis	YiNung
	?	M.Ord	S.China	Brachylasma	YiNung
	?	M.Ord	S.China	Ningnanophyllum	YiNung
	?	M.Ord	S.China	Yohophyllum	YiNung
	?	M.Ord	nw China	Protozaphrentis	Weyer 1973
	?	M.Ord	Kueidon district, Szechwan	?Yohophyllum	Hill, 1981
	?	"Trenton age"	Mongolia	Protozaphrentis	Hill,

				1981
?	M.-U.Ord boundary	country???	Kenophyllum	I,1968
?	Ord. or Sil.	Karakorum Mtns.	Kenophyllum asiaticum	B
?	"Trenton age" (u.M.Ord-U.Ord)	Szechwan-Kweichow	Calostylis (possibly the earliest Calost.)	Hill,1981
?	M.Ord	Szechwan-Kweichow	?Ningnanophyllum	Hill,1981

M&W = Maclean and Webby, 1975
S?U = Sytova and Ulitina, translation
W = Webby
H = Hill, 1953
LB = Lin Baoyu, 1980
Yi Nung + Yi Nung, 1974
Weyer, 1981-t = weyer, 1981, translation
N, 1985 = Neuman, 1985
S, 1977 = Sytova, 1977
W, 1971 = Webby, 1971
I,1968 = Ivanovski,1968

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