

Heliophyllum

A Study in Survival



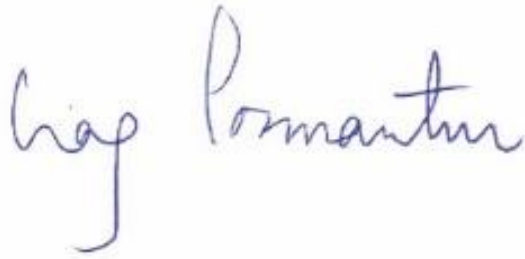
Buffalo Geological Society

Education Committee Bulletin - December 2019

ACKNOWLEDGEMENTS

The Buffalo Geological Society thanks the members of our Education committee for their time and effort in producing what we hope to be the first of many informational bulletins on various facets of our hobby. Committee chairman Walter Drabek coordinated the project with the able assistance of several club members. Photography and photographic design were provided by Paul Leuchner whose nature photography is widely acclaimed in Western New York. Long time club member and amateur paleontologist Joseph Sullivan was responsible for technical review, enlisting the expertise of Dan Krisher of the Rochester Academy of Science and ensuring factual integrity. Mr. Krisher is a local coral expert who has worked with numerous organizations to produce fossil related publications and other educational events. Mark Castner of Canisius College provided editing and readability review as well as technical production support. Thin sections and acetate peels were produced at the Buffalo Museum of Science by Joseph Butch currently on the faculty at Buffalo State College and photographed by Michael Grenier of the Rochester Academy of Science. Specimens appearing in this pamphlet, that are not otherwise designated, are from the collections of various Club members. Finally, the Officers and Board need to be acknowledged for their support and critiquing of the final version.

We dedicate this inaugural work to Bruce and Ruth Banick, Life Members of our organization and avid fossil collectors. The generous and ongoing commitment of their time and knowledge to our organization along with their extensive field work and the exhibition of their collections at numerous club events over the course of many years has inspired countless members to “keep on digging” and learning along the way.

A handwritten signature in blue ink that reads "Craig Posmantur". The signature is written in a cursive style with a large, looped initial 'C'.

Craig Posmantur
President, Buffalo Geological Society

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INTRODUCTION

The objective of this bulletin is to provide the amateur fossil collector with a comprehensive, non-technical examination of the extinct rugose coral genus *Heliophyllum*. Our research is restricted to species found in select members of the Hamilton Group of Western New York. For purposes of this work we focused on outcrops in Erie, Genesee, Wyoming, and Livingston counties. Although *Heliophyllum* have been found as far away as South America, North-West Africa and South-West Europe, this region represents the area of greatest abundance and largest stratigraphic range.

Unlike most genera of invertebrate fossils collected in our area, *Heliophyllum* exhibits a great deal of intra-species diversity in terms of size and shape making it unique among its cohabitants. In this work we will explore how this adaptability, coupled with some distinct morphological features, allowed this amazing creature to survive in the Devonian seas of Western New York. We will examine how its survival was threatened from its earliest days as a minute larva, but it somehow managed to flourish in an environment unquestionably unsuited for its sessile lifestyle.

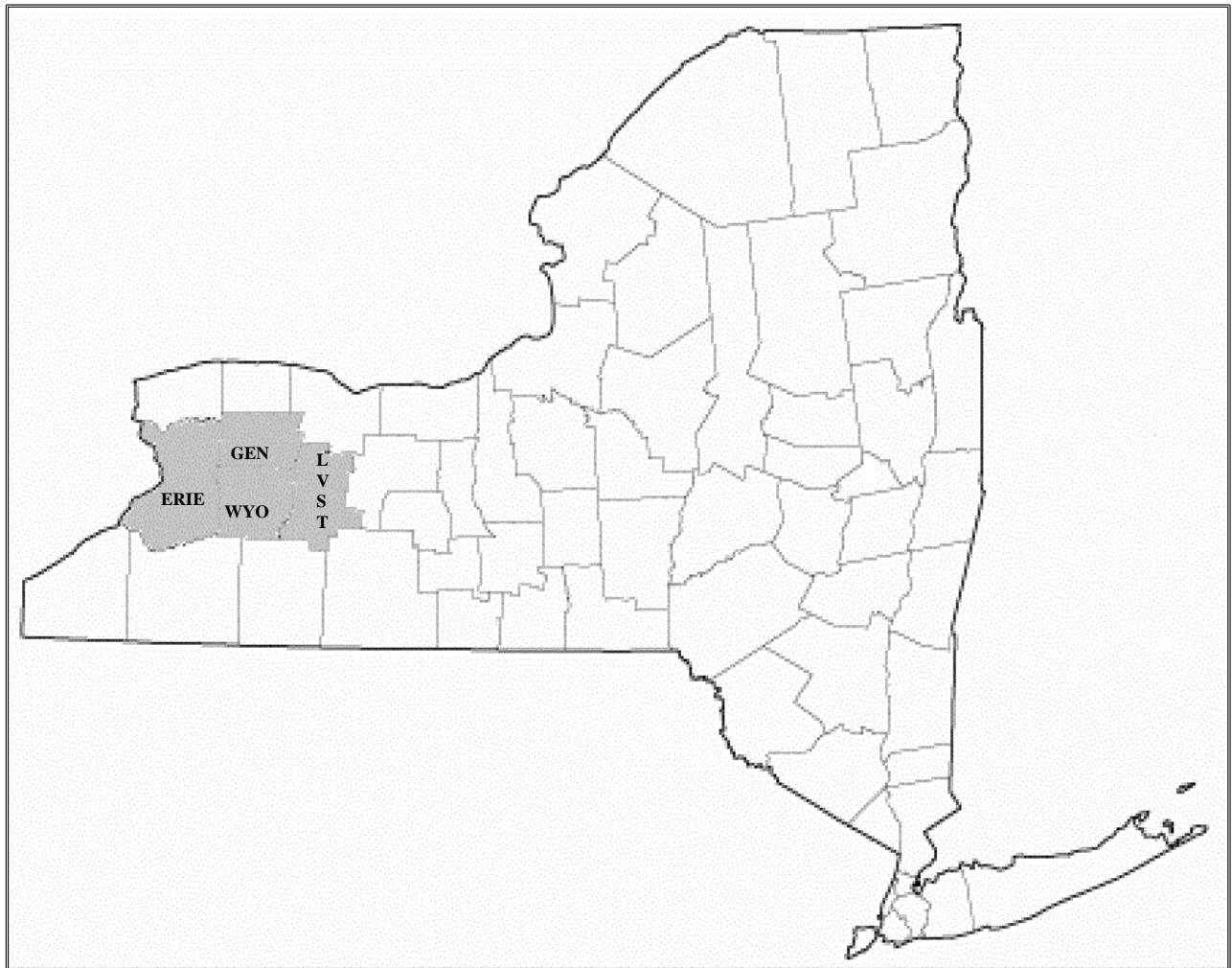


FIGURE 1

STRATIGRAPHY

HAMILTON GROUP	MOSCOW FORMATION	WINDOM SHALE MEMBER
		KASHONG SHALE MEMBER
		MENTETH LIMESTONE MEMBER
		DEEP RUN SHALE MEMBER
		TICHENOR LIMESTONE MEMBER
	LUDLOWVILLE FORMATION	JAYCOX SHALE MEMBER
		WANAKAH SHALE MEMBER
		LEDYARD SHALE MEMBER
		CENTERFIELD LIMESTONE MEMBER

The rock units investigated are of Middle Devonian age deposited approximately 385 million years ago during the Givetian Stage. The Devonian System was named in 1839 by Roderick Murchison and Adam Sedgwick for a series of sedimentary rocks they examined in the Devonshire province of England.

These rocks are a succession of fissile (property of rocks to split along planes of weakness into thin sheets) sedimentary gray shales and limestones. The sediments are clastic (rocks that are composed of fragments of rocks broken off of other rocks) as they were weathered from the mountain forming Acadian Orogeny to the east. As water levels rose and fell over the period of deposition, the limestones represent a noticeably clearer and sediment starved environment than the shales.

The Hamilton Group is approximately 280 feet thick at Lake Erie in western New York, thickening to over 3,000 feet as you move east, and is thought to represent approximately 5 to 7 million years of deposition.

THE PALEO-ENVIRONMENT

Throughout the Middle Devonian, Western New York sat just south (20 to 30°) of the equator in the Appalachian Basin. On the east, the basin was flanked by the Acadian Mountains which were the result of the Avalon landmass colliding with North America causing the continental plate to crumple and push upwards. This geologic event is referred to as the Acadian Orogeny. On the west stood the continental crust. A shallow inland sea, named the Kaskaskia Sea, covered the basin positioning Western New York in a well oxygenated near shore environment. The sea sat on a sloping bottom deepening to a trough in Central New York. It exhibited general subtidal conditions, including a consistent temperature, high nutrient levels, constant water cover, and enough sunlight for photosynthesis to occur. A tropical paradise, the region was teeming with warm water organisms which found their habitat in the bio-herms and reefs that were both numerous and robust. Days were shorter (the Devonian year had 400 days, making each day only 22 hours long) and the carbon dioxide level was more than six times higher than it is today. Isolated from the surrounding oceanic “Old World” waters, the fauna was very provincial, meaning that many of the existing species tended not to expand beyond this confined area and were therefore unique to our region.



FIGURE 2

TAXONOMY

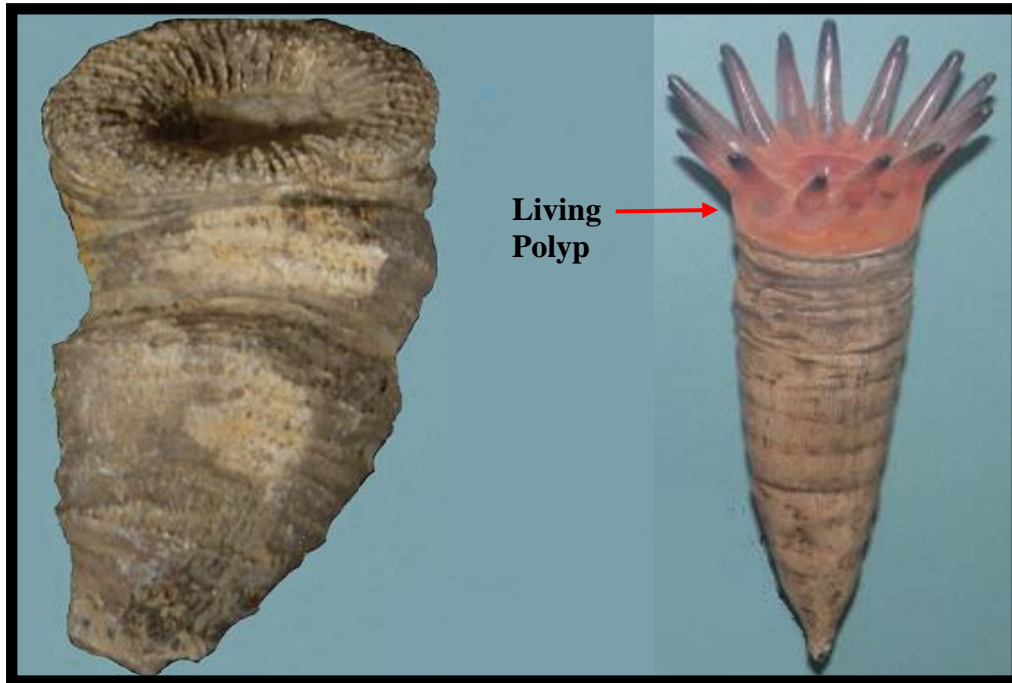
KINGDOM	Animalia
PHYLUM	Cnidaria (Hatschek 1888)
CLASS	Anthozoa (Ehrenberg 1834)
SUBCLASS	Zoantharia (de Blainville 1830)*
ORDER	Rugosa (Milne-Edwards & Haime 1850)
FAMILY	Zaphrentidae (Milne-Edwards & Haime 1850)
GENUS	Heliophyllum (Hall 1846)

* In place of Zoantharia, the term Hexacorallia is widely used, though not universally, by biologists studying modern corals. On the other hand, paleobiologists tend to use the term Hexacorallia in a more restrictive sense than do biologists to refer only to Scleractinians.

Since the science of classifying life was first outlined by Carl Gustav Linnaeus in the 1700's, the classification of species has been constantly reworked by researchers. No single organization sets the standards for the systematic organization of organisms in the fossil record. Instead, taxonomy is revised as a result of the work of scholarly researchers and general acceptance by their peers. All corals for example were originally classified by Aristotle in his "Scala Naturae" as "zoophyta" ("plant-animals"), animals that had characteristics of plants and were therefore hypothetically an intermediate between animals and plants. In fact, categorizing corals outside the animal kingdom continued to be the accepted placement until the eighteenth century when William Herschel used a microscope to establish that coral had the characteristic thin cell membranes of an animal. They were later placed in the phylum Coelenterata (Frey & Leuckart 1847) and Cnidaria was designated as their subphylum. In the late 1980's Coelenterata as a phylum began to be disputed, eventually being replaced by Cnidaria. The result shown in the chart above is currently recognized by most researchers as the accepted standard taxonomy for Heliophyllum.

Each grouping is meant to represent distinguishable characteristics, for the most part using morphology to identify individuals to be of the same kind.

While the order Rugosa under which Heliophyllum falls is first known from the Middle Ordovician in North America and extended through the Permian, Heliophyllum is restricted only to the Lower and Middle Devonian. Their early ancestors were non-skeletal sea anemones dating back to the Precambrian.

MORPHOLOGY

Fossil Rugose coral *Heliophyllum halli* reconstructed with living polyp

FIGURE 3

Since *Heliophyllum* is an extinct species and soft tissue in general is not preserved in the fossil record, all descriptions on the make-up of the polyp (the living part of the organism) itself are extrapolated from modern scleractinian corals. In this case, it inherits many of its characteristics from its formerly recognized parent phylum *Coelenterata* (*coel*, hollow; *enteron* gut).

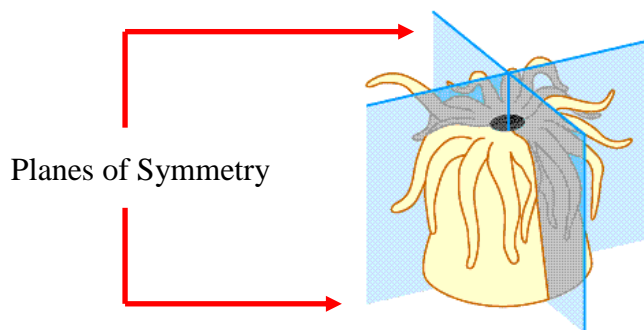


FIGURE 4

The sack like body cavity or enteron exhibits radial symmetry which means the polyp has identical body halves around a central axis. As such it has no right and left and no front and back. This distributes sensory organs around the whole-body surface instead of concentrating in one particular region, giving them the ability to sense danger from their prey from any direction.

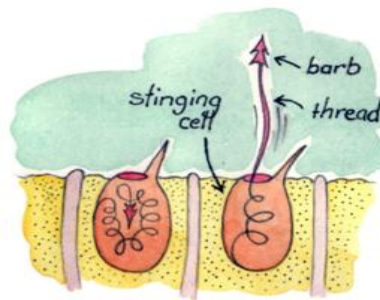
The body itself, although diploblastic, meaning two layered, is in fact composed of three layers; the inner endoderm and the outer ectoderm both consist of living cells while the intervening mesoglea is a gelatinous, non-cellular substance. It has only one opening, at the top, which functions both as a mouth and an anus.

A central nervous system is absent but a diffuse network of nerve cells is embedded in the mesoglea which enables coordinated body movement. Like all other cnidarian, the Heliophyllum were aquatic and carnivorous with no heart, respiratory, excretory, or circulatory systems.

Being Cnidaria, it is also believed their cells were organized into tissues. Since the presence of tissues allows similar cells to work together to perform a discreet function, efficiency and structure is added to critical tasks.

The subphylum name Cnidaria comes from the Greek word "*cnidos*" which means stinging nettle. So as one would expect, the most significant characteristic of the phylum is the presence of "stinging cells."

The outer layer of the body called cnidoblasts that capsules known as confined to the tentacles that sensory hair on the outside vibrations in the water, discharge when an organism thread is propelled with organism allowing poison to defensive and a feeding



NEMATOCYSTS

FIGURE 6

wall houses these stinging cells contain microscopic discharge nematocysts. They are usually surround the mouth. A small of the nematocyst senses causing the nematocyst to passed close by. The barbed such force that it penetrates the be injected. This is both a mechanism.

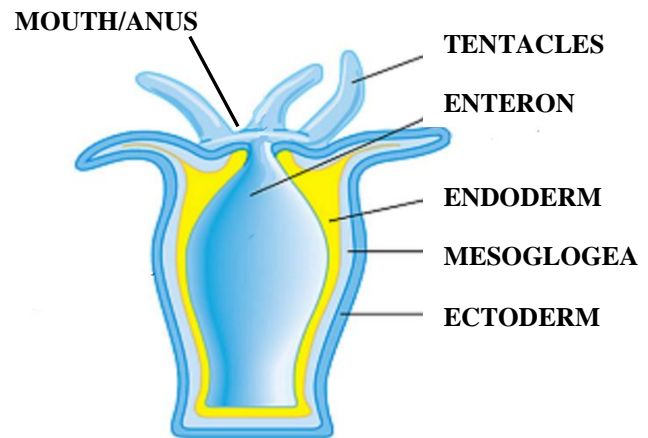


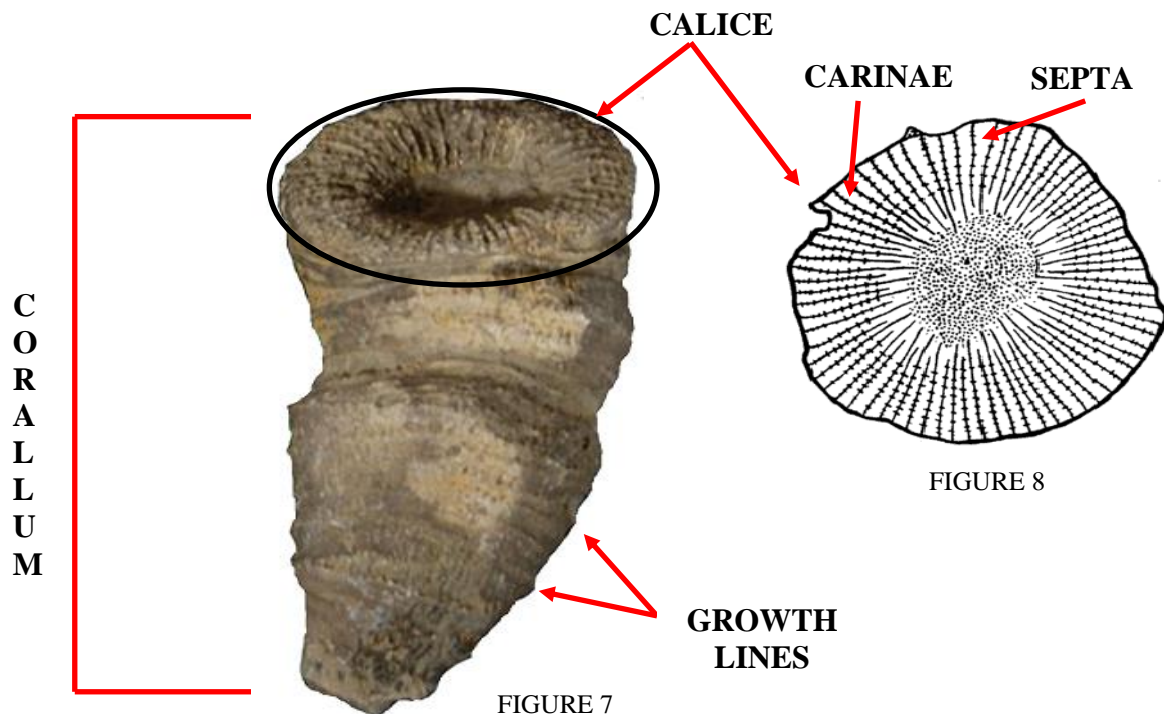
FIGURE 5

Generally believed to be passive predators, Heliophyllum fed on prey that blundered into their tentacles. This method of nutrient intake is commonly known as suspension feeding. As such, the polyp was probably entirely carnivorous, relying on a food supply consisting of tiny planktonic (floating) and nektonic (swimming) animals that were ensnared by the motion of their tentacles.

Rugose corals also assume the characteristics of the class Anthozoa. The name comes from the Greek words *ánthos*, "flower" and *zóa*, "animals." Hence *anthozoa* equals "flower animals," a reference to the floral appearance of their perennial polyp stage.

EXTERNAL FEATURES

As the polyp grew it created an external skeleton by removing calcium carbonate from the sea water and converting it to calcite. While most Paleozoic corals, including Heliophyllum, are composed of calcite, some later corals may have originally included aragonite which is not stable and over millions of years recrystallizes to calcite. This skeleton is referred to as the corallum, synonymous in the case of solitary corals such as Heliophyllum with the term corallite. The outer “skin” layer of the corallum is called the epitheca. Their shape varied greatly and at least partly reflects the ecological conditions in which it lived. Their most common form being horn shaped, they acquired the popular moniker of “horn coral.” Heliophyllum was placed in the Order “Rugosa” (which is derived from the Latin “ruga” for wrinkle) because of its wrinkled looking texture which resulted from the daily growth rings on its corallum.



The top of the corallum, called the calice, provided a cup-like shelter and a place of attachment for the polyp. Two distinguishing features of Heliophyllum occur inside this calice. The first are called septa. These are vertical plates radiating out from the center and extending to the corallum wall and are used to strengthen the calice. In the early growth stages, the corallite had only two opposing septa, known as the cardinal and counter septa which define the plane about which the polyp is bilaterally symmetrical. Next, two alar septa were inserted on either side of the cardinal septa, which in combination with the first two divided the corallite into four sectors. These original four are called the protosepta and were inserted very quickly during the early life of the coral. As the calice grew, new septa were added, four at a time, in sets of two, alternately, in mirror quadrants to help maintain a rigid structure. As a result, these are sometimes referred to as tetracorals – tetra meaning four. The newly added septa pairs include a long metasepta and a short catasepta that is split off from the just formed metasepta. It is also worth noting that the catasepta never split off from any of the protosepta.

Recognition of conventional life cycle stages is somewhat impractical in *Heliophyllum*. Consensus is that the brephic or first post-embryonic stage of *Heliophyllum* was characterized by the development of the protosepta which typically occurred within the first two millimeters of growth. The next stage called the neanic was where all the morphological features of the adult began to develop. It started with the addition of the first metasepta, but its transition point to the adult or ephelic stage was capricious. The ephelic stage is often estimated by using the average number of septa in large specimens as the demarcation line. Oliver and Sorauf in their 2002 work settled on a calice diameter of approximately 20 mm and a septa count from 22 to 36 based on locality. Environmental and genetic factors may very well have played a role in the septum variance as well as in the size at which the polyp achieved the ephelic level.

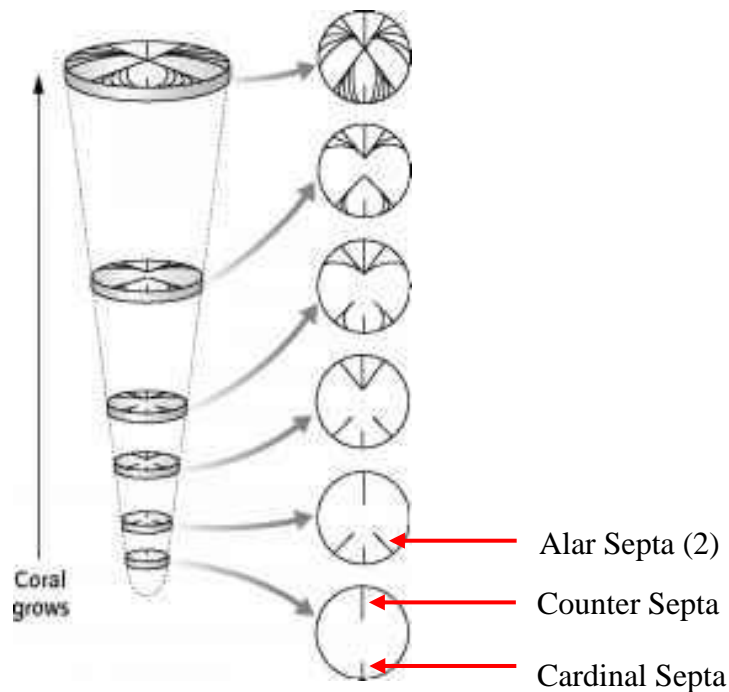
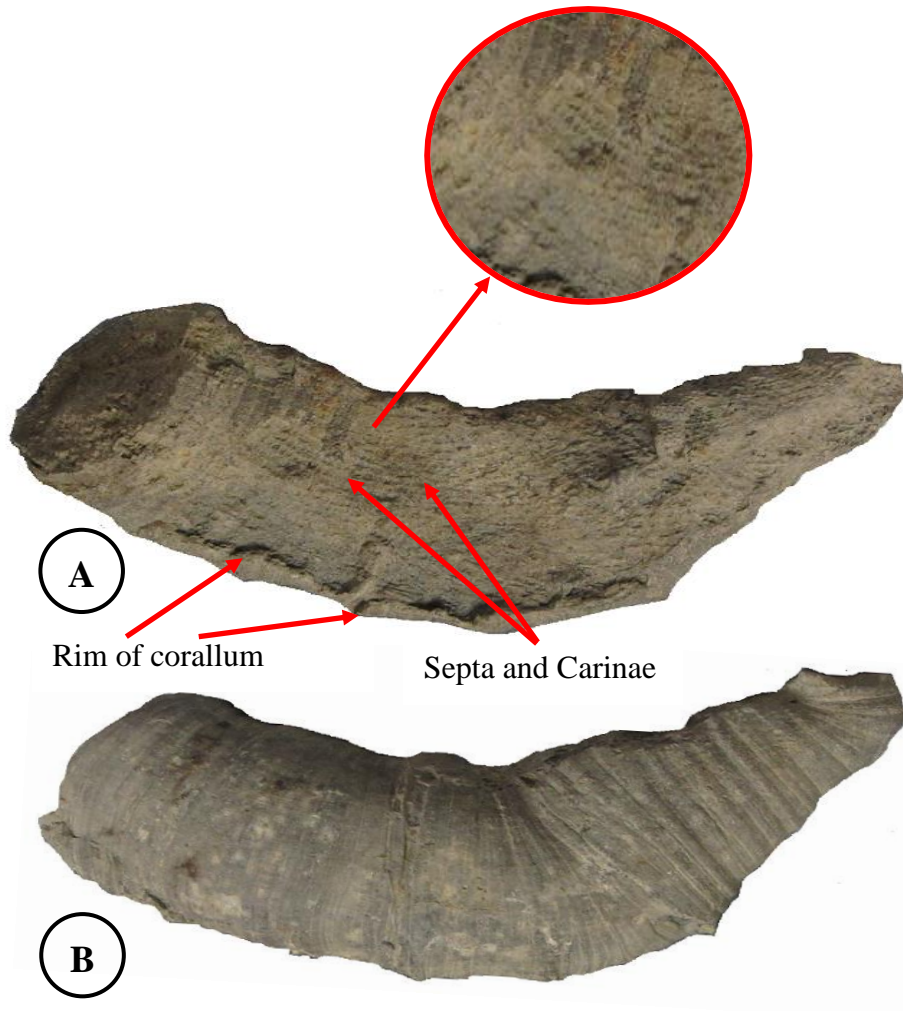
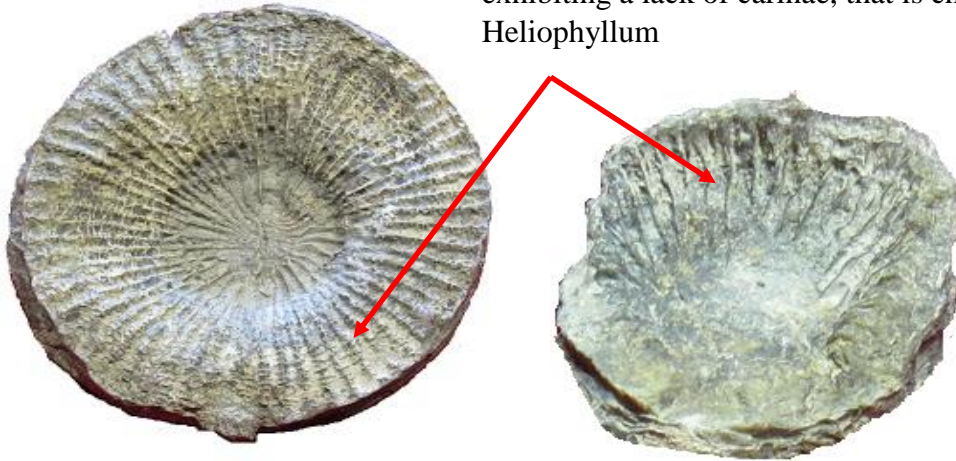


FIGURE 9

In *Heliophyllum*, the septa are crossed by horizontal structures known as carinae. Often referred to as having a “yard-arm” appearance, these developed at the upper margin of the septa each time the septa was extended. In all but one species of *Heliophyllum* these carinae extend just short of touching the adjacent septa. The attachment of the polyp to its skeletal upper surface was probably facilitated by these two structures.

Blothorophyllum, a different species of coral, exhibiting a lack of carinae, that is characteristic of Heliophyllum



A

Rim of corallum

Septa and Carinae

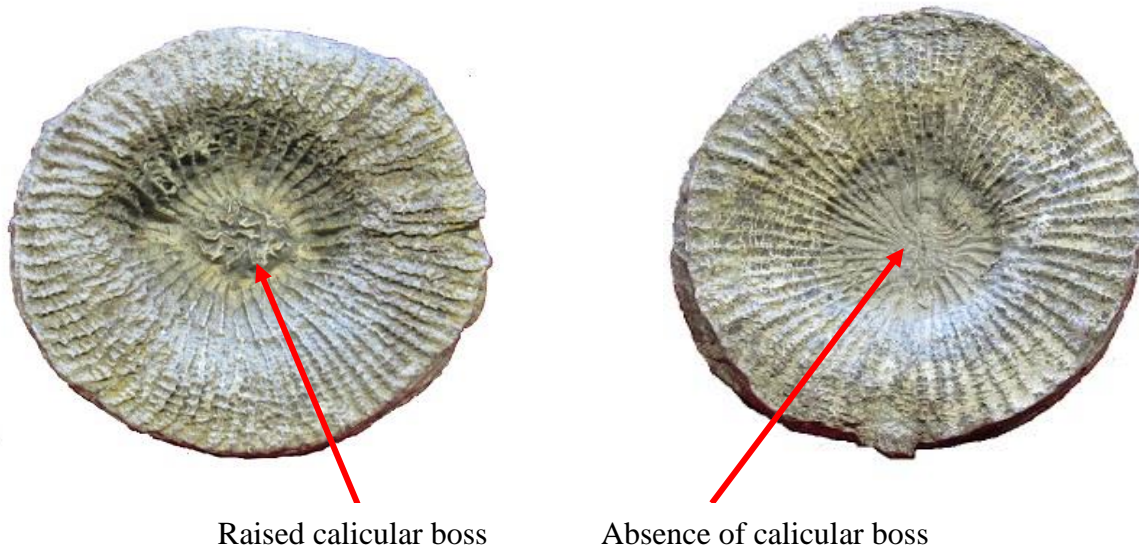
B

Shown on the left are two sides of the same coral. Side **A** was exposed to weathering on the surface while side **B** was buried in the sediment.

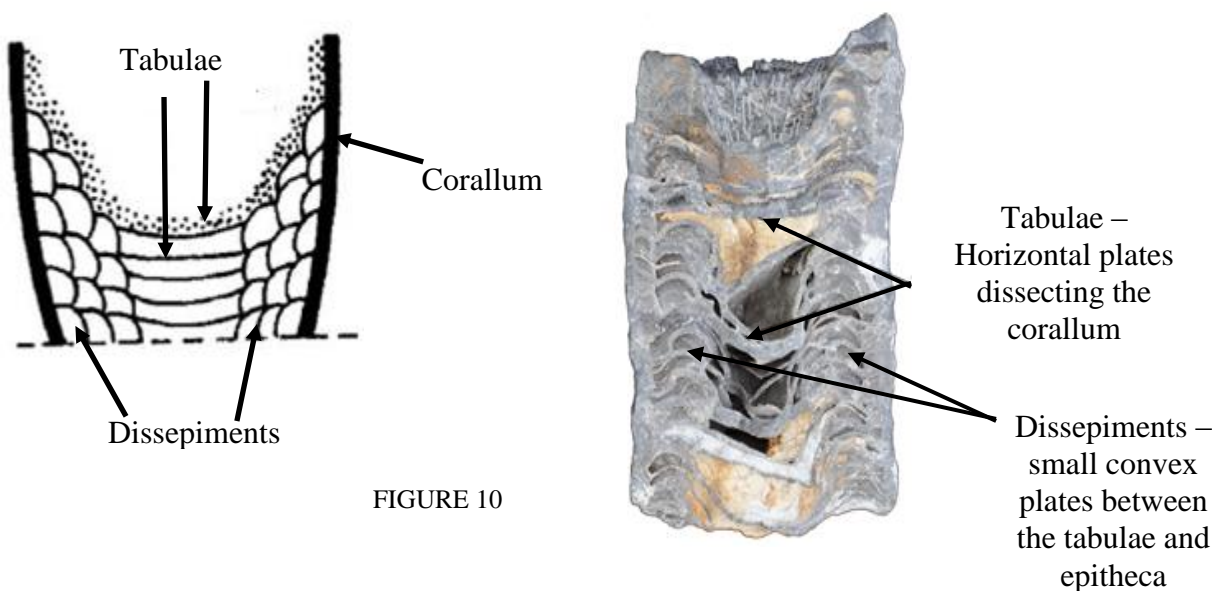
The weathering exposes the septa and carinae and the rim of the corallum where the coral was exposed to the elements.

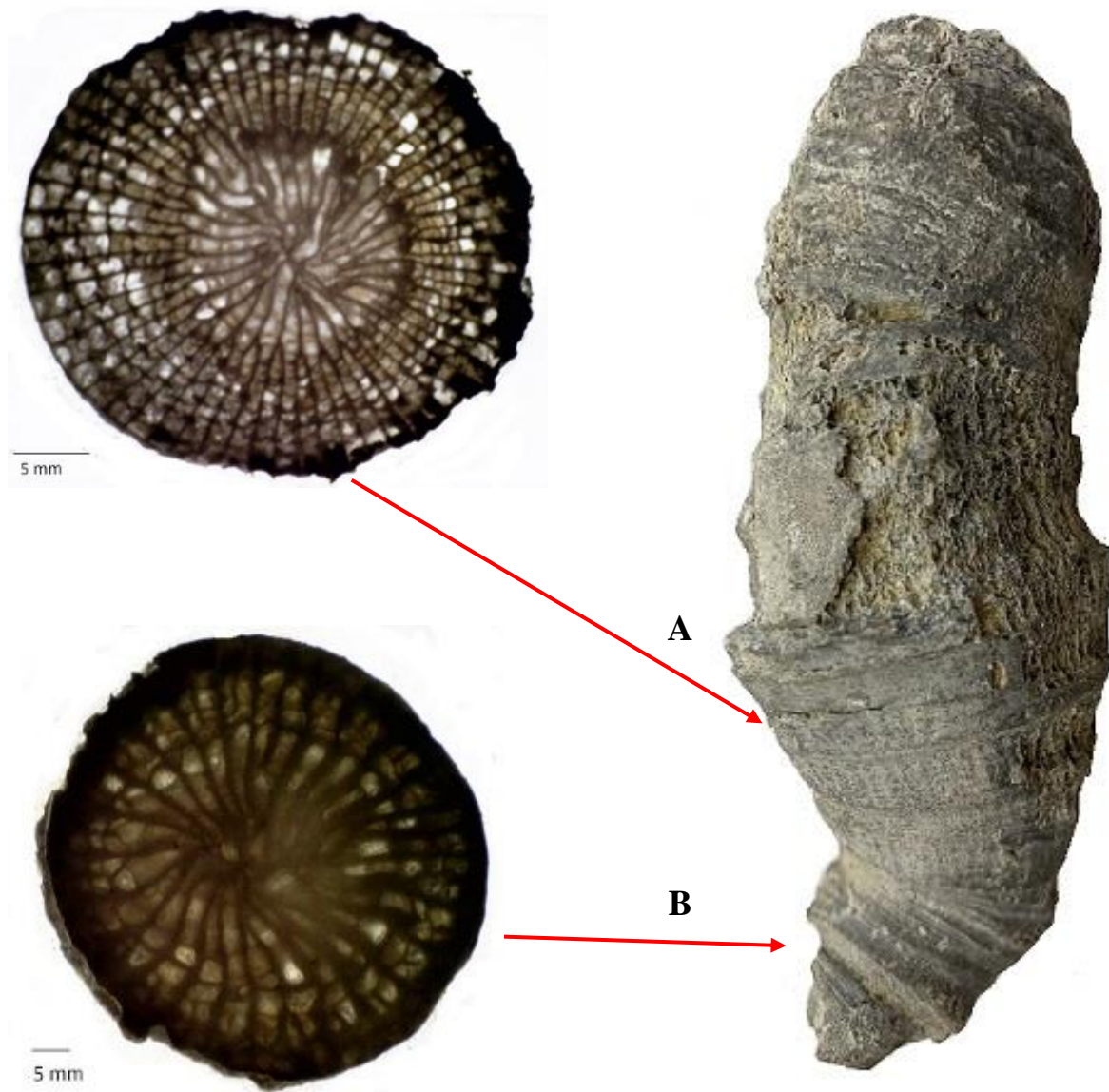
Lack of epibionts on the weathered side indicates it probably was not exposed for too extensive a period of time.

In some specimens, the septa join together at the axial base of the calicular pit to form a protruding structure sometimes called a calicular (axial) boss. However, it is most often referred to in the literature as simply an upwardly arched calice floor. The function of this construct, although often used in species descriptions, is not well defined. It is atypical, however, for a single species to display both the presence of this structure in some specimens and its absence in others. It's difficult, in *Heliophyllum*, to ascertain which form is more prevalent, since the structure can only be seen in specimens with completely clean calicular pits, thereby not allowing for well-founded population sampling.

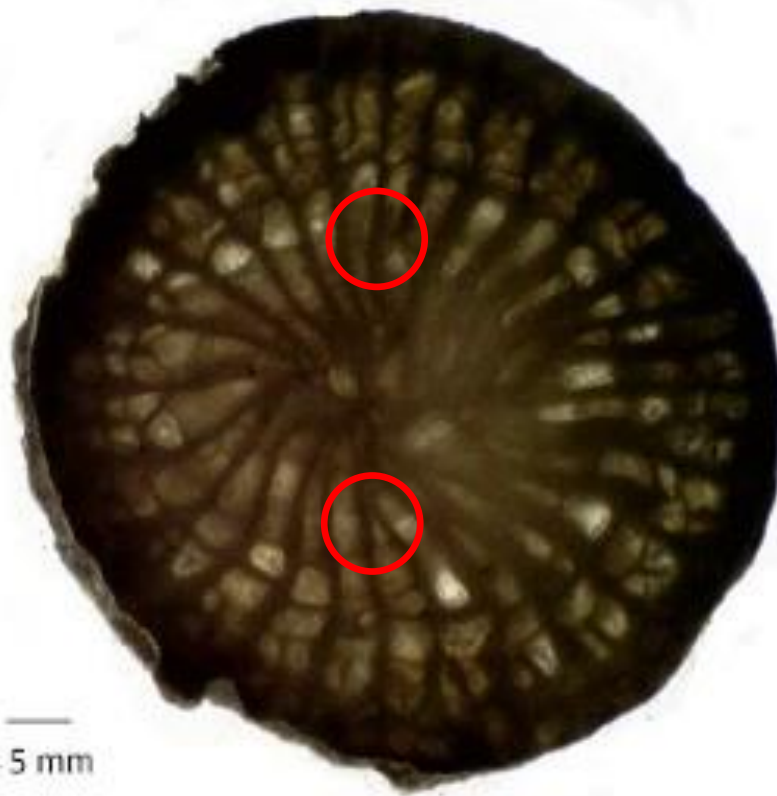


When vertically thin sectioned, horizontal plates known as tabulae become visible. These tabulae are gently domed plates which represent the floor like structure on which the polyp sat. As the corallum grew, new tabulae were created, sealing off the earlier now unoccupied parts of the corallum, always keeping the organism near the top of the calice. The tabulae, however, do not fill in the entire space in the corallum. Dissepiments, which are small blister-like carbonate plates, pack the remainder of the empty room created as vertical growth advances.

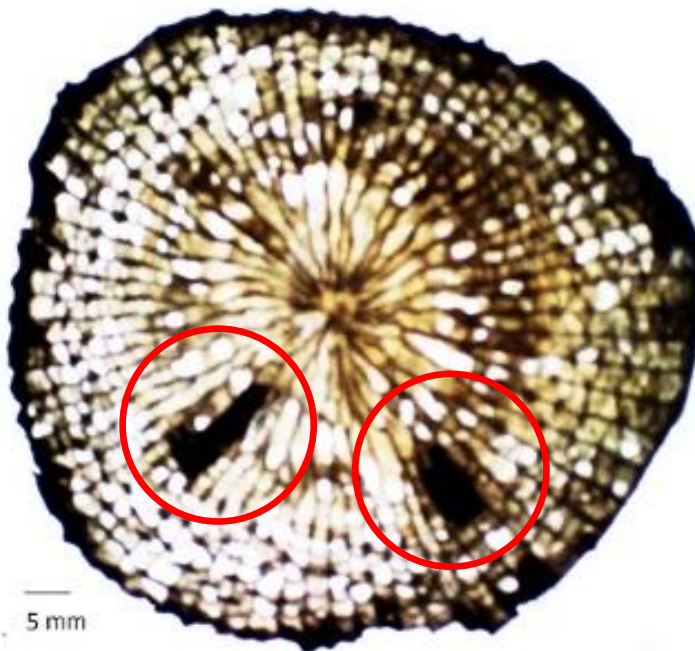




The two horizontal thin sections above show the increase in septa as the coral grew. Early in its life cycle, as shown in the lower thin section, approximately 27 septa were present. By the time the coral grew to the point where the upper thin section was taken, 65 septa exist.



Expanding the lower left image from the previous page clearly shows proto-typical catasepta which split off from longer septa.



Dark spots showing up in a thin section taken slightly above point "A" above possibly represent living areas of predators.

Root-like extensions of the basal skeleton known as talons helped attach corals to the substrate, holding them in a nearly upright position. As toppling occurred, new talons were often excreted to help stabilize the coral in its preferred posture.



GROWTH LINES AND PALEOZOIC TIME

As noted previously, Heliophyllum corals altered calcium carbonate to excrete calcite in order to build their external skeleton (corallum). This skeletal growth took place by laying down distinct bands at the top of the calice on a periodic basis. The bands are themselves made up of narrower bands that seem to represent monthly growth and were probably related to the tides and the monthly cycle of the moon. In 1963, Dr. John W. Wells, Professor of Geology at Cornell University, proposed that the still finer ridges found within these bands represented daily growth. He based his hypothesis on observation of modern day scleractinians which are an order of modern coral that lay down a new layer of carbonate on the top of their calices each day.

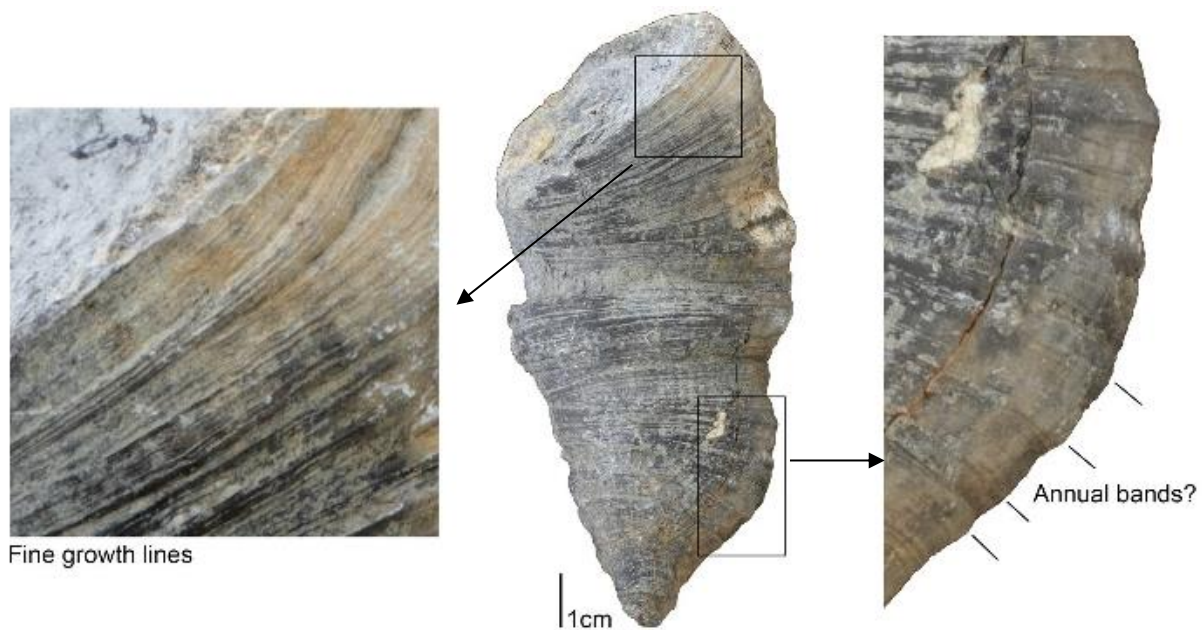


FIGURE 11

Examining predominantly Heliophyllum, along with a few Eridiophyllum and Favosites collected in Bethany, NY, Dr. Wells attempted to derive the number of days in the Devonian year by counting these finer bands within the annual rings. This was no simple task as these bands vary in distinctness, and it is often difficult to see where one band ends and another begins. Corrosion of the epitheca (see page 9) can also make the collection of usable specimens challenging. Despite the obstacles, his analysis determined the number of rings ranged between 385 and 410 per year with an average of 400, generally assigning a length of 400 days (each approximately 22 hours) to the Devonian year.

British paleontologist Colin T. Scrutton repeated Dr. Wells' work using different corals and obtained similar results. His work matches with the more theoretical research by astrophysicists who believe that in the past the Earth rotated more quickly around its axis. Their analysis does not change the length of the year (the time it takes the earth to orbit the sun) but does suggest the length of the day (the rotation of the earth on its axis) is slowing down by approximately 2 seconds every 100,000 years. This is believed to be the result of the gradual and continual application of the "tidal brake" exerted by the moon's gravity.

REPRODUCTION

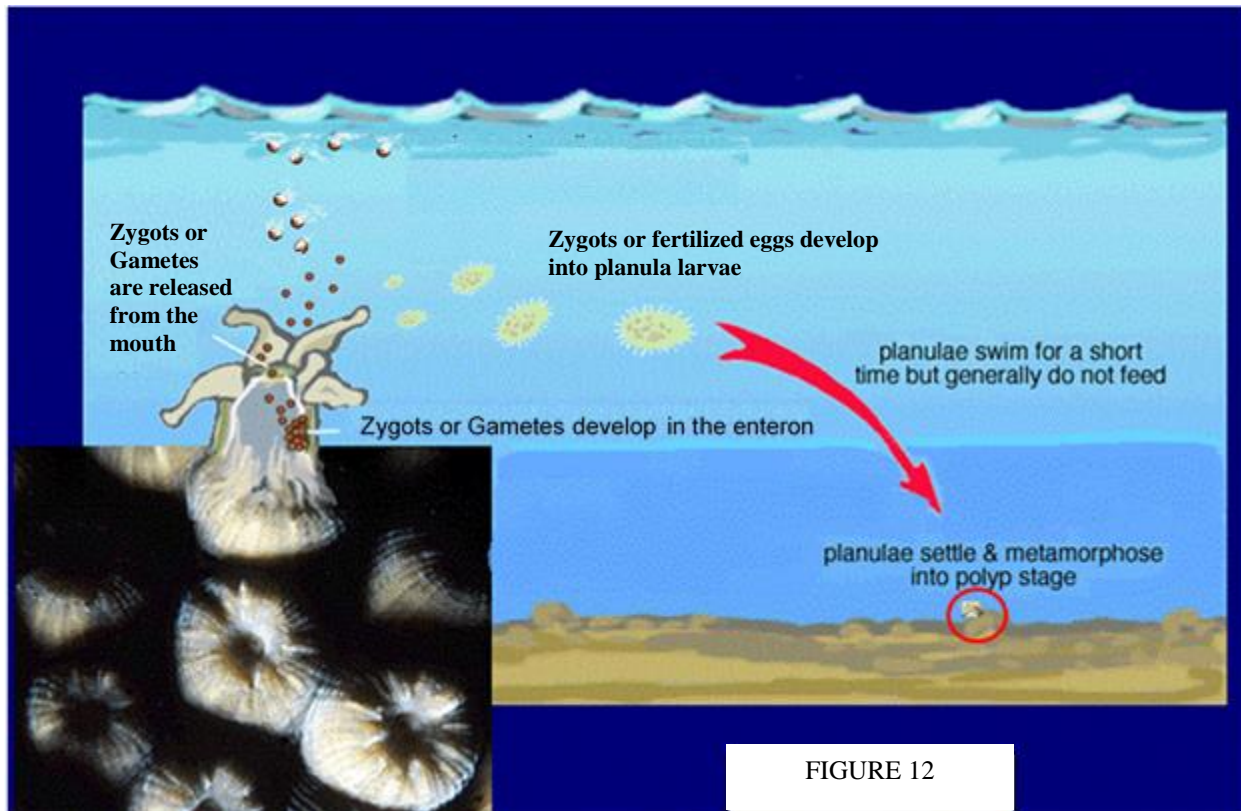
Extrapolating from the life cycle of modern corals, Heliophyllum almost certainly employed both sexual and asexual strategies of reproduction in order to survive in their dynamic environment. Although it is unknown as to whether Heliophyllum were hermaphrodites, in which case each polyp was both male and female, or gonochoric, where each organism is a discrete sex, they must have employed either broadcast spawning or brooding for sexual reproduction. As a point of reference, only one-third of all modern corals are gonochoric.

Broadcast spawners usually release gametes of either eggs or sperm in mass spawning events on a regular schedule. The released gametes drift to the water surface where fertilization takes place. Commonly after a few days, the embryos will have developed into coral larvae. By contrast, brooding coral species perform internal fertilization and embryogenesis before releasing zygots which are settlement ready larvae. In both cases, the microscopic ciliated larvae are referred to as planula. Approximately 75% of all modern corals employ broadcast spawning, while the remainder are brooders.

While brooded larvae are immediately ready for settlement and typically settle close to the parent, the larvae from broadcast spawning may float long distances in the water for several weeks. Either way, the larvae eventually swim to the sea floor and search for a suitable settlement substrate.

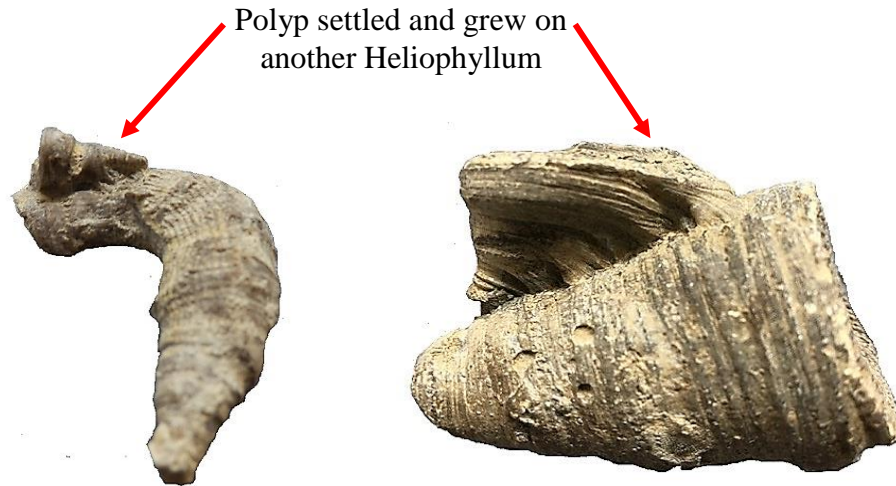
Thousands of these larvae can be formed by an average size assemblage to enhance the odds of species survival. Many believe that the Devonian seas may have been home to a form of broadcast spawning known as synchronous. Under this process entire colonies release their gametes or zygots within a short period of time, usually at night. Cued by lunar fluctuations and possibly chemical catalysts, this discharge may have been so extensive that it clouded normally clear waters.

The pre-larval and larval stages are obviously the most vulnerable in the early life cycle of the polyp. In addition to the hazards faced while drifting defenselessly in open water, the young planula faces a limited prospect for survival should it not find some hard ground or accumulation of shelly material on which to attach and grow.



Even those planulae fortunate enough to find an appropriate place to settle still faced modest odds of enduring. Once attached, they quickly metamorphosed into a tiny polyp, usually not more than one millimeter in size, and the sessile life stage of the Heliophyllum began. They could still easily be buried by sediment, fall prey to the omnipresent threat of predation, or fall victim to one or more of the many diseases that may harm or kill the sensitive organism.

As a result, the following weeks were a crucial period for the minute polyp that needed to quickly increase in size to improve its chance for existence.



In some cases, after surviving its early life cycle challenges, environmental conditions faced by the polyp lead to asexual reproduction. In the case of Heliophyllum, this took the form of budding or gemmation. Effectively this may be termed cloning as an identical polyp is created through the process. This can result from either **fragmentation** or **division**.

Fragmentation occurred as a result of disarticulation of the polyp by either wave action, storms, or predation. In fragmentation, the disarticulated mass landed somewhere either on the corallum or in the outer rim of the calice (called the septate zone) and regenerated the missing tissue resulting in a complete polyp clone. Sometimes referred to as tissue regeneration, this would be similar to the ability of a few species of starfish that can grow an entirely new starfish just from a portion of a severed limb.

Division, often thought of as a controlled reaction, can fall into any of three categories based on the location of the budding. The original calice is called the protocorallite while the new clones are referred to as offsets. This is believed to have been an attempt on the part of the polyp to survive, most likely triggered by some life-threatening event.

The most commonly seen form of budding in Heliophyllum is termed **peripheral increase**. In this case the offsets occurred in the septate zone of the protocorallite allowing the original polyp, at least temporarily, to survive. If the offsets grew too large, they may have eventually infringed on the territory needed by the protocorallite to capture food, resulting in its demise. **Axial increase** looked somewhat similar, but with the growth arising within the existing calice. In this case, the polyp divided down the middle yielding two or four new polyps while life of the original polyp

ceased immediately. Since this resulted in the death of the “parent” polyp, many researchers believe that axial increase did not exist but was rather rejuvenation of the protocorallite reacclimating to better surroundings after experiencing more difficult conditions.

The final form of increase is labeled **lateral increase** and was the only true non-parricidal form of increase. The offsets in this case projected laterally through the side wall of the corallum and rarely occurred other than in *H.halli* confluens and *H.delicatum*.

It is not uncommon in examining large populations to observe combinations of multiple forms of budding in the same Heliophyllum and it is often impossible to distinguish between fragmentation and division.

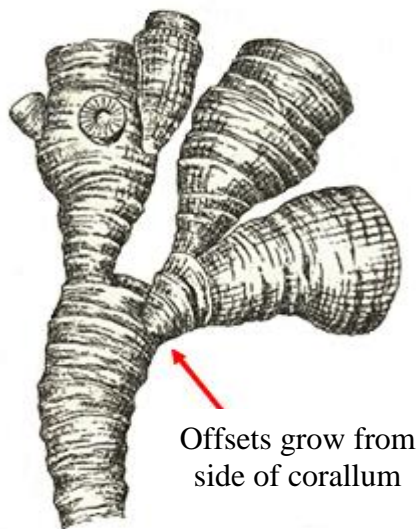
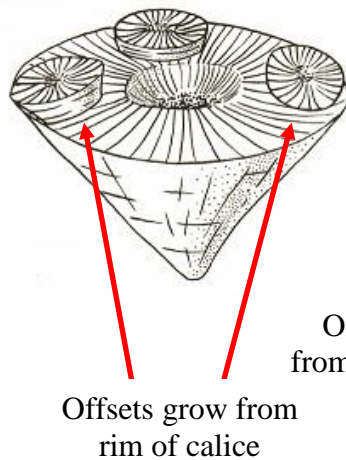
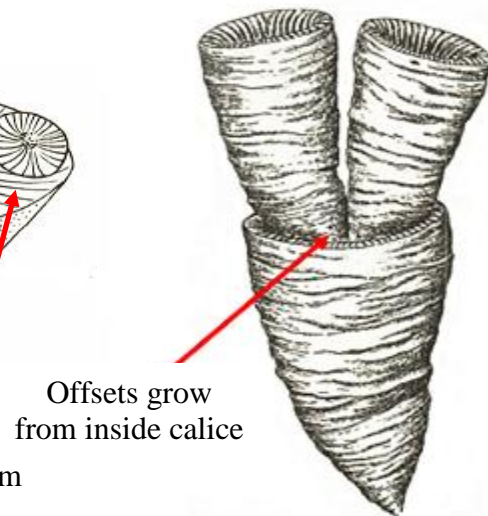
LATERAL**PERIPHERAL****AXIAL**

FIGURE 13

Examples of Multiple Budding on the Same Specimen

**COLOR**

Since Heliophyllum are an extinct species and no specimens preserving their soft tissues are known, we can only extrapolate from modern corals what the Devonian seas may have looked like. Figure 14 shows an example of a modern reef, but most likely Heliophyllum were far more drab looking than what is pictured here, most probably shades of tan and gray. Colors in modern corals are the result of the presence of zooxanthellae which are a group of single-celled microscopic plants that live in the tissue of modern corals. Like most plants, they use photosynthesis to convert the sun's energy into food. Without these symbiotic plants, modern coral polyps would be unable to obtain enough nutrients to build their calcium carbonate skeletons. Researchers, however, doubt the existence of zooxanthellae in Heliophyllum, mostly based on the sediment laden, turbid conditions in which they lived. Generally speaking, modern zooxanthellae tend to exist only in sediment starved waters with low turbidity.



FIGURE 14

SPECIATION

James Hall was the first to recognize the genus *Heliophyllum* in 1846. However, three years earlier in 1843 he described a coral he named *Strombodes helianthoides*, which later in 1850 was reclassified as *Heliophyllum halli* by Milne-Edwards and Haime.

Worldwide the area of greatest abundance of *Heliophyllum* was in the Eastern Americas Realm, although as mentioned previously, they also existed in South America, Northwest Africa, and Southwest Europe. *Heliophyllum* first appears in Western New York in the Lower Devonian Bois Blanc Formation. This formation, which is positioned just below the Onondaga, is part of the Emsian stage of the geological time scale. The genus ranged through the Middle Devonian Tully Formation which sits just above the Hamilton in the Late Givetian stage. Although the Devonian world was very provincial, it is most likely that the numerous other species of *Heliophyllum* found outside New York will eventually be synonymized with *H.halli*. This assertion is based chiefly on the history of speciation in our study area.

In the late 19th century, the establishment of new species was based primarily on external morphology. Armed with only this non-comprehensive approach and spurred on by the appeal of being the first to name more new species than one's rivals, early paleontologists churned out numerous dubious species. Many of these have subsequently been synonymized through the use of more modern techniques, none more so than those generated by the early work on the genus *Heliophyllum*.

In late 1876, Dr. Carl Rominger, the State Geologist of Michigan, was on the verge of releasing his comprehensive work on Michigan corals. James Hall, Director of the New York State Museum of Natural History at the time, recognizing the similarity of many of Rominger's specimens to those occurring in New York, issued hurriedly, without text, his own work: *Illustrations of Devonian Corals*. This edition, consisting of only 130 bound copies, listed five new species, one existing species, and two varieties of Heliophyllum.

Hall based his work on the fundamental tenant of the day espoused by Amadeus Grabau. According to Grabau: The environment can influence the shape of the same species if the variations occur in different localities, however, "Where morphological variation exists in the same locality, it must be regarded as expressing a fundamental even if slight, inherent difference in the organism that may lead to the development of distinct genetic series." As such, the impact of external factors influencing shape were often overlooked when describing species. While Grabau's paradigm certainly influenced Hall's assessment, by far the greatest shortcoming in Hall's work on Heliophyllum was the small population size he used in his analysis.

It wasn't until nearly 60 years later in 1937 that Dr. John W. Wells, recognizing these limitations, undertook a re-evaluation of Hall's work. Increasing the sample size significantly revealed intermediate stages and trait combinations between Hall's species and variations, such that no clear dividing line could be drawn between any two of them. Dr. Wells recognized the morphotypes as gradients of a spectrum of variation and not discrete points. In an effort to explain the variation, Dr. Wells attempted to correlate Hall's species to the coral's growth strategies and adaptation to its environment. He converted many of Hall's species and variety names and added a few of his own to what he referred to as **formae**. These represented morphotypes or groupings of external skeletal shape. The term *formae*, however, does not have any formal standing in zoological nomenclature and thus left his analysis unsettled. His work resulted in the naming of 11 *formae* and one variety (*confluens*) of *H.halli*.

Another 60 plus years passed before Dr. James E. Sorauf's work in 2001 revisited this topic. Collaborating one year later with Dr. William A. Oliver Jr., their efforts resulted in what is currently recognized as the Heliophyllum species group of the Hamilton occurring in our study area:

- (1) *H.halli* Milne-Edwards & Haime 1850
- (2) *H.halli formae praecoquus* Wells 1937
- (3) *H.halli confluens* Hall 1877
- (4) *H.delicatum* Oliver & Sorauf 1994
- (5) *H.cribellum* n. sp. (Oliver & Sorauf 2002)

Sorauf and Oliver could find no internal characteristics that correlated with the corallum's shape and thereby could not support any species separation, beyond the segregation of *H.delicatum* and *H.cribellum*. Although given no formal standing, *H.halli formae praecoquus* was given recognition as a separate synonym of *H.halli* from the other *formae* due to its frequent citing in the literature. *H.halli confluens* were relegated to a subspecies. A subspecies is sometimes referred to as a variety and essentially represents a group within a species that is somewhat physically and perhaps genetically different from the rest of the group but that is still more similar to the parent species than any other known species.

Heliophyllum halli Milne-Edwards & Haime 1850

Although the holotype illustrated by Hall in 1843 is now lost (named *Strombodes helianthoides* by Hall in 1843 and synonymized by Milne-Edwards & Haime in 1850), the neotype is housed in the Museum National d'Histoire Naturelle, Paris, France, distinguished by the yard-arm carinae described previously. The type locality for the species is recognized by most as being the Ludlowville formation at York in Livingston county New York.

Dr. Wells described the largest specimens as being up to 8 cm in diameter with a height of 22.5 cm. Working with specimens with an average height of 10 cm, he estimated a life span of a specimen of that size to be approximately 13 years. Extrapolation would lead us to the hypothesis that larger individuals may have lived for over 25 years. The vast majority of locally collected specimens are under 8 cm, with any over 15 cm an uncommon find.

ENVIRONMENTAL THREATS

As the work of Drs. Wells, Oliver, and Sorauf explained, the pronounced variation in *H.halli* morphology is largely due to environmental adaptation. Silt levels, current velocity, and substrate instability are most frequently cited as the main contributors to the survival challenges experienced by these corals. Either individually or in combination, these factors resulted in the various “formae” enumerated earlier.

During the Devonian, the muds in the shallow waters covering western New York were extremely soft and easily disturbed by storms or strong currents, resulting in turbid water and an unstable substrate. Whether the coral remained upright or toppled, suffocation from the encroaching silt became the polyp's main threat to life.

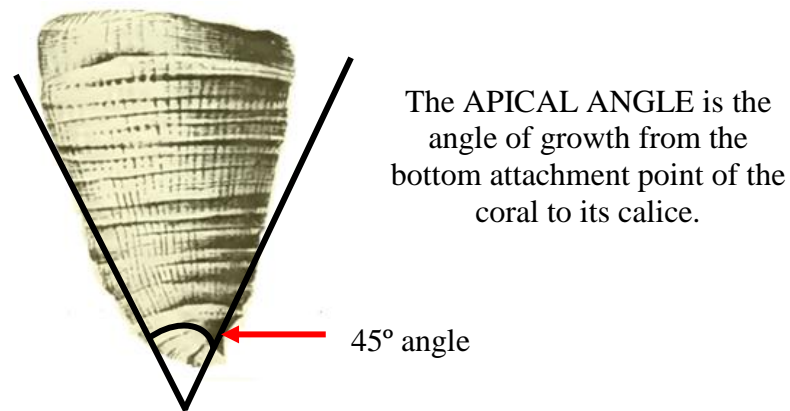
Researchers suggest that *Heliophyllum* had multiple mechanisms for dealing with these life threatening conditions. It is believed the coral's ectoderm was highly ciliated and capable of excreting a dense mucus material. Finer particles could be removed by the wave creating action of the cilia as well as by entanglement in the mucus which could then be sloughed off. Larger particles would have been removed by controlled distension (swelling) of the polyp. Repeated, coordinated inflation and deflation of the polyp created a wave-like motion that would disrupt and remove particles. Tentacular motion would have created similar wave action further dispersing silt particles infringing on the organism. The large number of septa suggest numerous tentacles, and polyp distention could very well have been facilitated by the numerous septal carinae in the calice which would have provided the polyp a better grip on its base

Substrate instability was worsened by the fact that the already water-saturated muddy sea bottom was frequently reworked by bioturbation, the alteration and disturbance of the substrate by living organisms. These included burrowing, feeding motions, and the ingestion and excretion of sediment grains. Even during periods of successful growth, coral toppling could be expected as a result of top heaviness created by the weight of the increased coral skeletal mass, anchored to an unpredictable and unstable substrate foundation.

Once toppled, the silt particles invaded the living space of the polyp, frequently resulting in suffocation.

TOPPLING

Theoretically, one of the preferred growth forms for a solitary coral such as *H.halli* would be what Wells referred to as **FORMAE: OBCONICUM**. This would be best described as a narrow cone shaped corallum with no curves or bends. The **apical angle** of this group of Heliophyllum would not exceed 45° and represents a stable living environment with limited influence being exerted by the sediments and surrounding wave action. It would have sat with its calice above the sediments stirred by the currents and avoided toppling.



Since this would require a stable attachment in the substrate, researchers believe the coral must have lived with most of its corallum buried in the sediment. J.A.E.B. Hubbard suggests that this could only be achieved if only one-third or less of the corallum were exposed above the wave base.

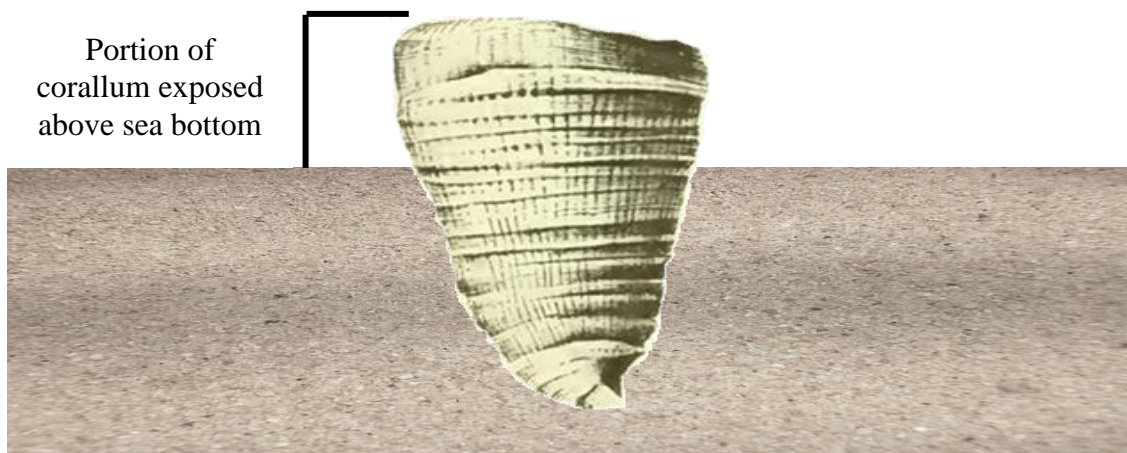


FIGURE 16

The specimens used by James Hall to illustrate what Dr. Wells termed **FORMAE: OBCONICUM** reflected only *H.halli* with a cone shaped corallum. Review of larger populations, however, reveal a range of forms from the cone shape shown previously to a more cylindrical shape. All, almost certainly, represent a similar growth strategy and living environment where the sedimentation rate was rapid and steady. The polyp may have failed to grow, demonstrated by the lack of expansion in calice diameter, due to its need to expend significant energy to maintain a considerable height above the sediment surface to avoid suffocation.

Examples of a more cylindrical form, which yields the tallest specimens found in our area, are shown below. The center specimen is 24.77 cm high with a calice diameter of 3.175 cm.

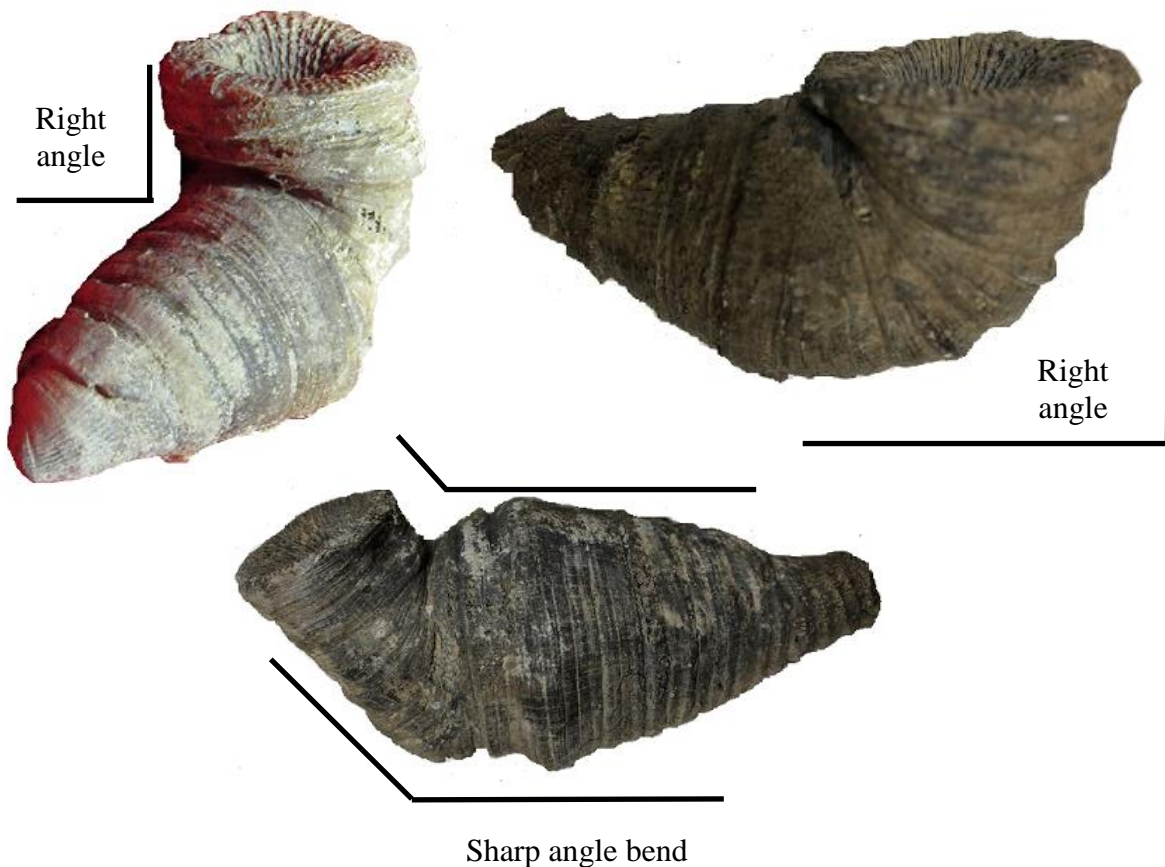


Not all *H.halli* were fortunate enough to experience steady, upright growth throughout their life. In fact, as the name suggests, the vast majority adopted what Wells described as the **FORMAE: TYPICUM** life style. Toppling was no doubt a fact of life in this environment. Once knocked over, the coral was forced to deal with the sediments that threatened to suffocate the polyp. Obviously, the coral's goal was to avoid smothering and return to its optimal life position with the upper rim of its calice situated a comfortable distance above the sediment. In the best-case scenario, the coral could gradually re-direct its growth by developing a curve in its corallum, then continuing with its upward growth.

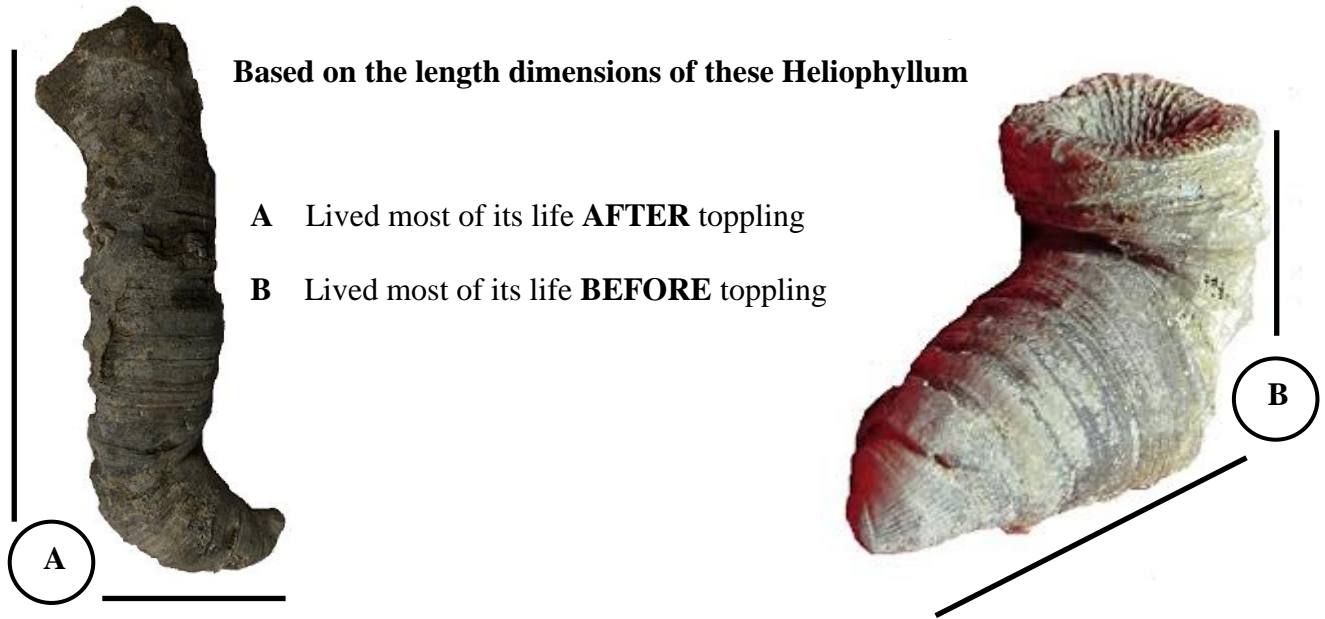


FIGURE 17

The degree of curvature varied from case to case based on the depth the calice sunk into the sediment and the amount of time available before suffocating. A more moderate curvature resulted in the classic “horn” shape, most frequently associated with *H.halli* and the shape Wells labeled FORMAE: TYPICUM. A curvature at a sharp angle close to 90° is often referred to as **geniculation**. In these cases, the polyp was most likely partially in contact with the sediment after toppling and a rapid directional change was necessary to wall off the onslaught of sediment. To facilitate the direction change, the polyp excreted a skeletal wall, repositioning and closing off access to the calice. This construct is easily identified by its lack of growth rings. Examples of geniculation are shown below.



The portion of the coral’s life spent before and after toppling can be extrapolated by the relative length of its corallum before and after the bend. In some cases, the coral flourished after redirecting growth and lived most of its life after the adjustment. Of course, the opposite was also true, as are a multitude of intermediate instances. The examples on the next page represent cases at the two extremes.



Toppling, however, was not always a one-time event during the tumultuous existence of a coral living on an unstable substrate. Numerous twists and bends would result from the constant succession of tumbling, redirection, and growth. Given the lack of consistency and the uniqueness of each resulting shape, the term **FORMAE: IRREGULARE** is an appropriate description for these true survivors.



FORMAE: IRREGULARE as illustrated by James Hall

FIGURE 18

Like most FORMAE: IRREGULARE, the uncommon tight U-shaped outcome illustrated below could have developed from multiple toppling events. Starting upright as shown in A, the initial toppling event positioned the coral as shown in stage B of the diagram. Growth would have been redirected upward to avoid suffocation. Shortly thereafter, a sinking substrate, possibly caused by wave induced turbidity, bioturbation, or scouring by currents, again repositioned the coral as shown in C with its axial end pointing upward. Reacting to an influx of sediment into its calice, the coral once again redirected its growth. This, combined with an environmental change to conditions more favorable for polyp growth, causing the diameter of the calice to expand, could have resulted in the tight U shape.

An alternative hypothesis centers on the pliability of the corallum either “pre” or “post” mortem. Researchers know that *H.halli* could modify the direction of its growth by laying down new calcium layers. However, evidence that the polyp could adjust any existing exterior skeleton does not exist. It is likely that the hard, brittle calcium composition of the corallum would crack before bending under the stress of pressure in a post-mortem burial situation, making this theory non-plausible.

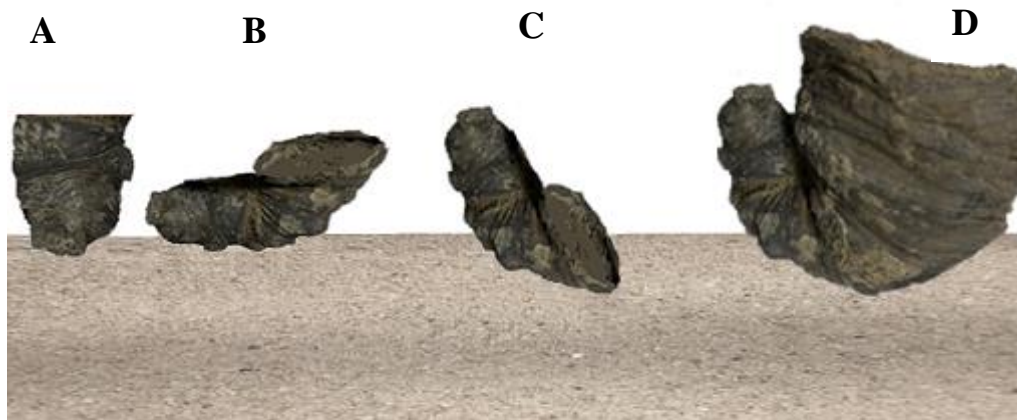


A – The coral grew upright before toppling.

B – It redirected its growth to again grow upright and avoid suffocation from the sediment.

C – Then as the result of a weakened substrate, possibly from bioturbation, the coral settled deeper into the sediment.

D – Once again the coral redirected its growth upright, while at the same time as indicated by the increased diameter of its calice, the polyp grew larger.





Another seldom encountered growth form of Heliophyllum is referred to as scolecoïd or worm shaped. This was most likely caused by multiple toppling, where recovery did not require extreme geniculation.

CONstriction, REJUVENATION, AND GERONTISM

While toppling may have been the most severe threat to their survival, even those polyps that managed to elude this consequence still faced several smaller hazards throughout their existence. According to Clarkson (1979), a short period of nutrient deficiency may have resulted in the polyp reabsorbing some of its own tissue and consequently reducing the diameter of its corallum. This process is referred to as **constriction**. When the constriction occurred rapidly, the epithelial wall could not keep pace and the existing calice was not gradually narrowed but rather was altered by the construction of a new wall.



Start of *rapid* constriction.

Partition formed to wall off constricted area of calice inhabited by polyp.



Both sides of wall built by polyp early in the process of rapid constriction.

Once environmental conditions cleared up, there was often renewed growth resulting in a gradual increase in diameter. This cycle is referred to as **rejuvenation**. When this combination occurred multiple times on a seemingly regular basis over the life of the polyp, Wells applied the name **FORMAE: PRAVUM** to the specimen.

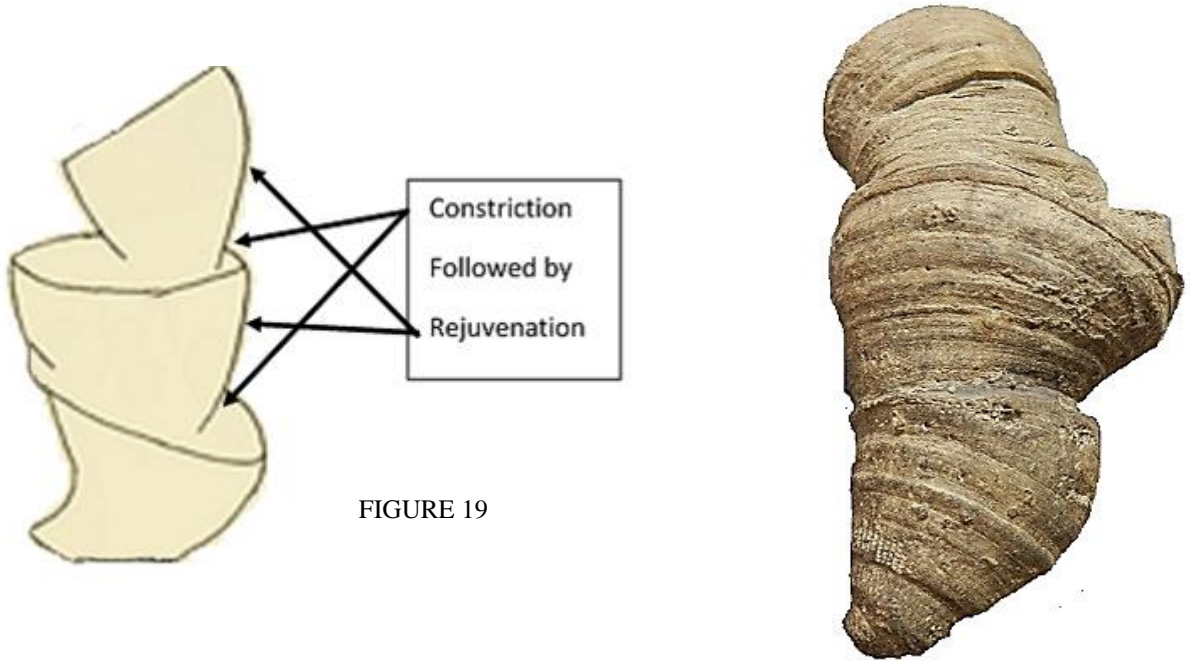


FIGURE 19



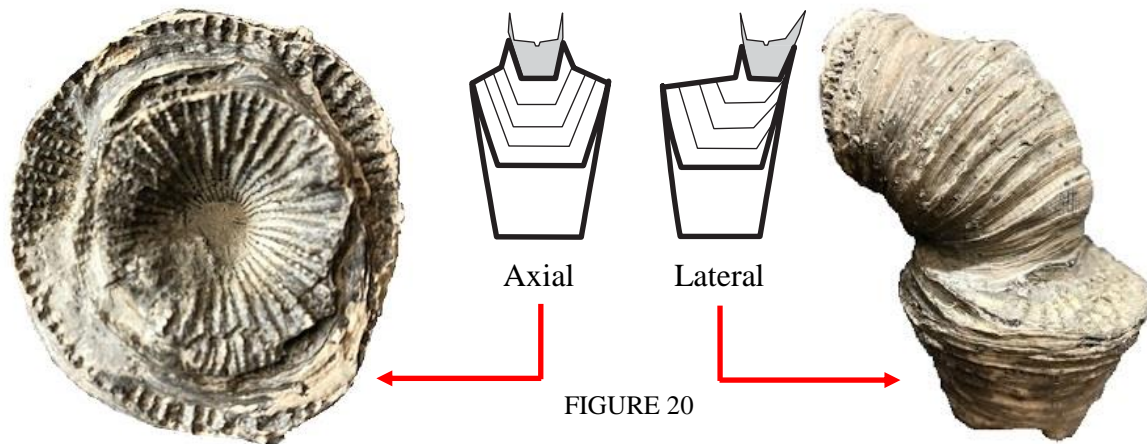
Top view

Axial constriction/rejuvenation



Short-termed constriction and rejuvenation re-occurring consistently over the life of the coral.

Cases where constriction/rejuvenation did not extend beyond the outer rim of the calice are referred to as Axial and are associated with a polyp affliction resulting from nutrient deficiency or a genetic abnormality. Instances where the constriction/rejuvenation resulted in a directional change were the result of toppling and were a defensive strategy to avoid suffocation. This is called Lateral constriction/rejuvenation.



Unfortunately, conditions did not always clear up and the polyp did not survive long enough for rejuvenation to occur. In these cases when the constriction was the final stage in growth, whether sudden or gradual, Wells referred to the specimen as **FORMAE: DEGENER**. By definition, the ending calice in these cases would need to be one-half or less that of the maximum diameter of the corallum. An alternative explanation to environmental stress is simple lack of vitality due to gerontism (old age).

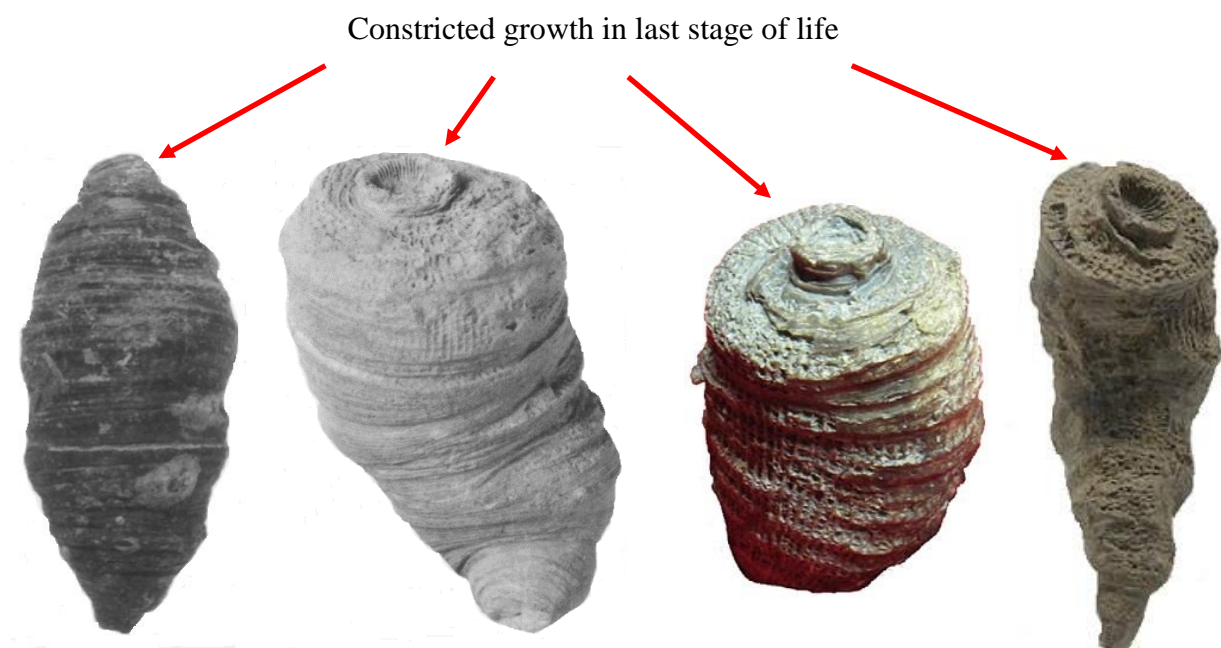


FIGURE 21

In rare occasions, the constricted corallum remained completely within the existing calice (most likely rapid constriction), never growing above the current rim. Additionally, a flat capping of the calice appears, leaving only a very small central opening. Apparently, the polyp then died. According to Sorauf, it is not apparent whether this capping could have been advantageous to the polyp or if it is only a by-product of a shrinking diameter in a smothering polyp. This process is referred to as Epithecal Capping.

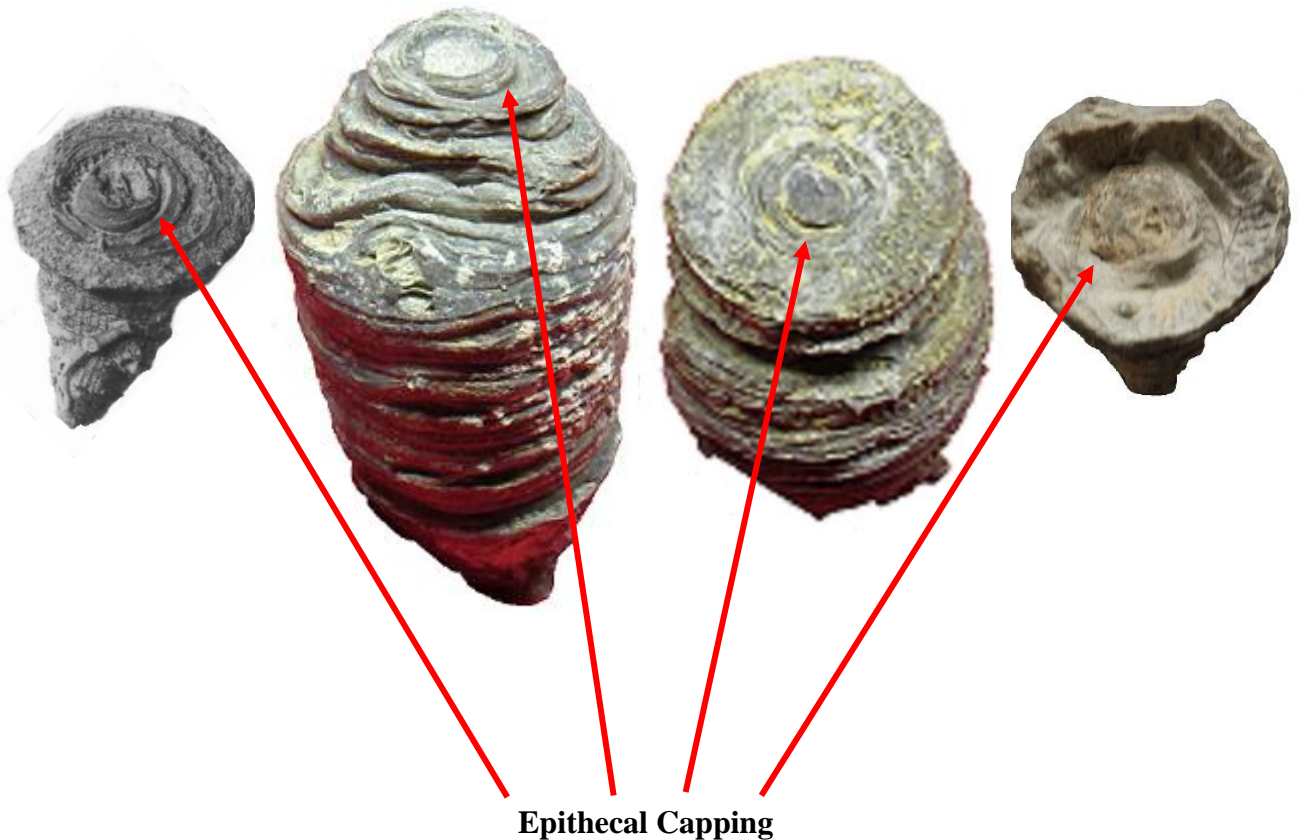


FIGURE 22

CALICE VARIATION

For most *H. halli* the calice is described as bowl shaped with the outer margin at the highest point of the corallum. In the case of **FORMAE: REFLEXUM**, however, the highpoint is at the inner rim of the calice where the septa begin their slope to the interior bottom of the calice. The resulting concave (down turned) protruding calice may again have been an attempt to avoid suffocation. Having septal carinae further from the center of the calice would have provided additional grasping points for more efficient distention and may also have provided for additional cilia to aid in the removal of silt particles. A less causal explanation could be that the peripheral section of the polyp that produces the epitheca simply lagged behind the lumen (central portion of the polyp) in the deposition of the skeleton. This may be a genetic variation or the result of a physiological defect.

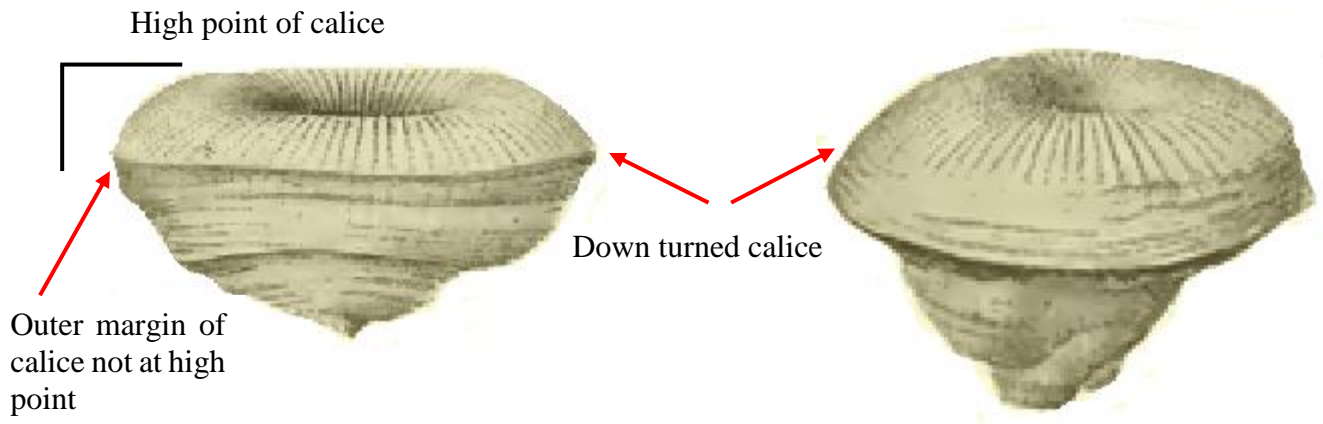
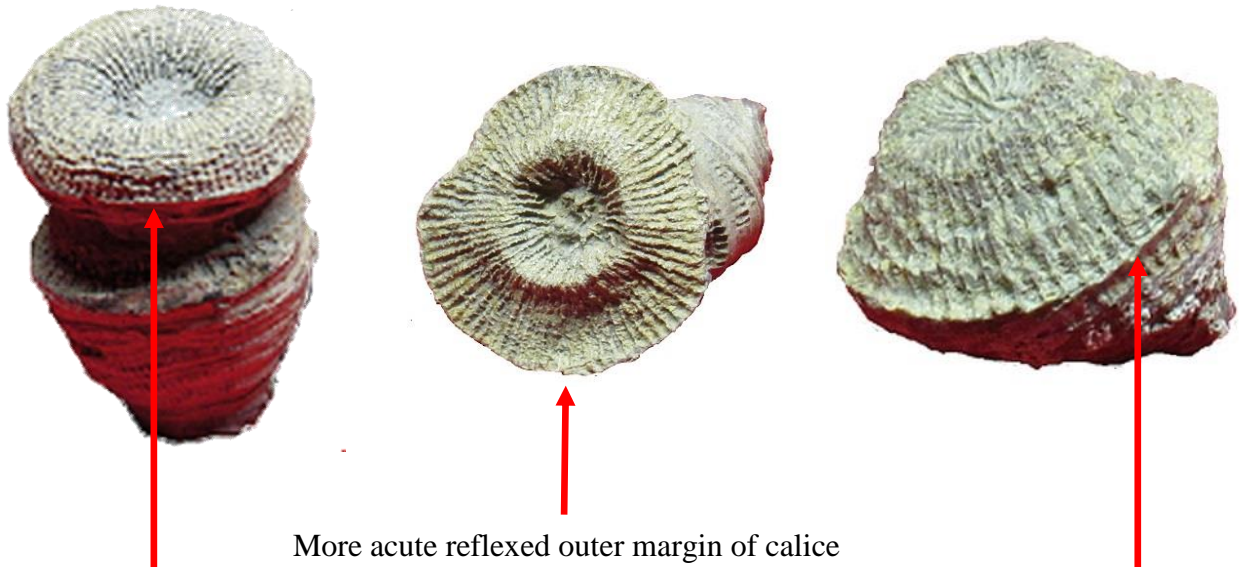


FIGURE 23

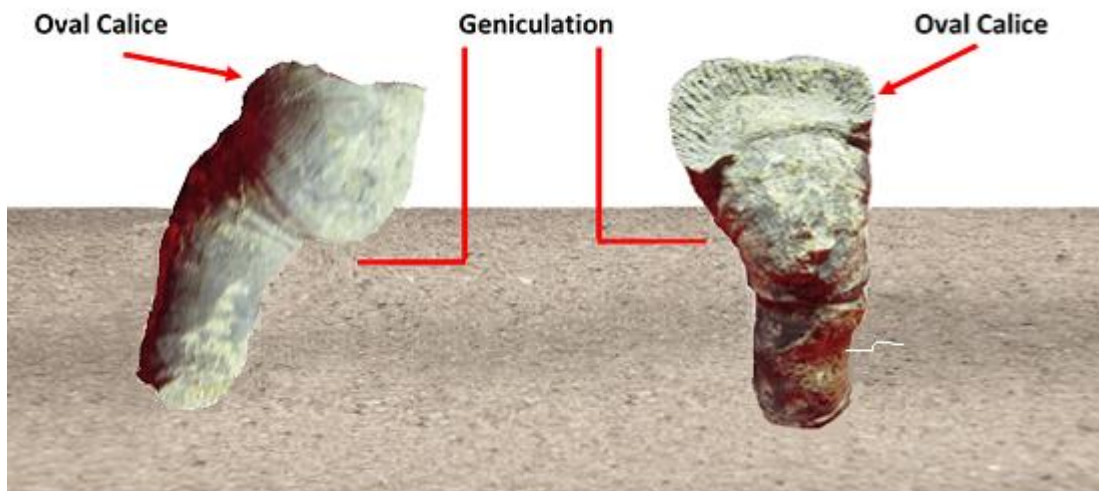




Typical reflexed outer margin of calice

Extreme reflexed outer margin of calice

Although the vast majority of *H.halli* exhibit a round bowl shaped calice, on occasion it can take on an oval appearance. This occurs in cases where the polyp did not survive much beyond the start of geniculation. It appears to represent a transition form, taken on by the coral as it begins to revert back to its typical bowl shape shortly after the curvature of geniculation takes place. Unfortunately, the polyp failed to survive long enough for the transition to be completed.



As mentioned previously, a brittle calcite corallum would not be pliable under pressure and in all likelihood would crack rather than modify its form. Thus, any sort of post-mortem compaction may be ruled out as a cause of the contorted shape. However, there is an alternative hypothesis that maintains that the polyp may have been attempting to develop in a confined space and needed to adjust its shape to fit the available area. However, this would have required the polyp to modify its own shape as well as that of its corallum. Such a metamorphism in polyp form remains questionable.



Corallum cracking under pressure



Oval calice always occurring after bend

SKELETAL PRODUCTION RATE

In a “typical” *H.halli*, the growth rates in height and width of the corallum are uniform, implying a similar growth pattern of the polyp. This results in the typical cone shape with an apical angle of approximately 45°.

When the growth rate of the polyp exceeded that of the corallum and the coral still maintained a conical appearance but with a broad calice, the growth form is referred to as **FORMAE:**

ARACHNE. In instances where this difference was extreme enough to produce a short, dish shaped corallum (referred to as patellate) the term **FORMAE: APLATUM** is applied. However, as Dr. Wells pointed out, analysis of extensive populations shows a continuum of one form to the other. A defined break point was never established and the exact transition point from “dish” shape to “top heavy cone” is subjective. A good rule of thumb, however, would be to define **FORMAE: APLATUM** as specimens where width noticeably exceeds height. While a wide calice most likely represented a nutrient rich environment, allowing the polyp to grow uncharacteristically, it occasioned other challenges for the polyp.

In **FORMAE: ARACHNE** the broad calice would have increased the risk of toppling due to its top-heavy structure. The shorter than normal height may have helped in this regard, but being low to the substrate, the coral would have been more prone to suffocation from extensive inflows of silt. The reflexed calice common in specimens of this form may have been an adaptation to assist in removing the silt particles. An environment with limited wave action would also have helped in avoiding the perils presented by this low-to-the-substrate growth form.

FORMAE: APLATUM faced similar life challenges. Rapid increase in diameter relative to height provided a flat base that would resist overturning while allowing the polyp to better distribute its weight. However, since the polyp remained low to the ground, the obvious shortcoming of this structure was once again its susceptibility to a rapid influx of large amounts of sediment. This could quickly suffocate the polyp with little time to adapt. Many **FORMAE: APLATUM** also exhibit a reflexed calice margin similar to the **FORMAE: ARACHNE**, indicating a dependence on distension and ciliary action to resist burial.

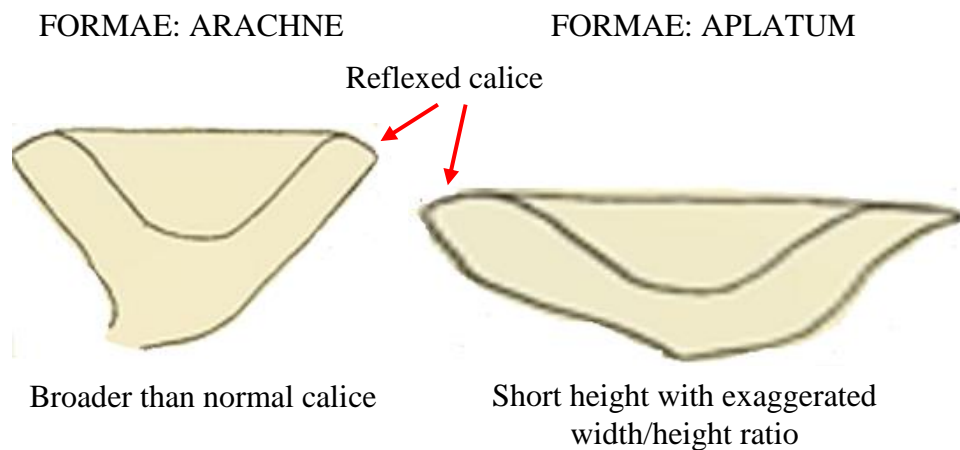


FIGURE 24

Growth rate of calice (diameter)
exceed standard rate of 45°



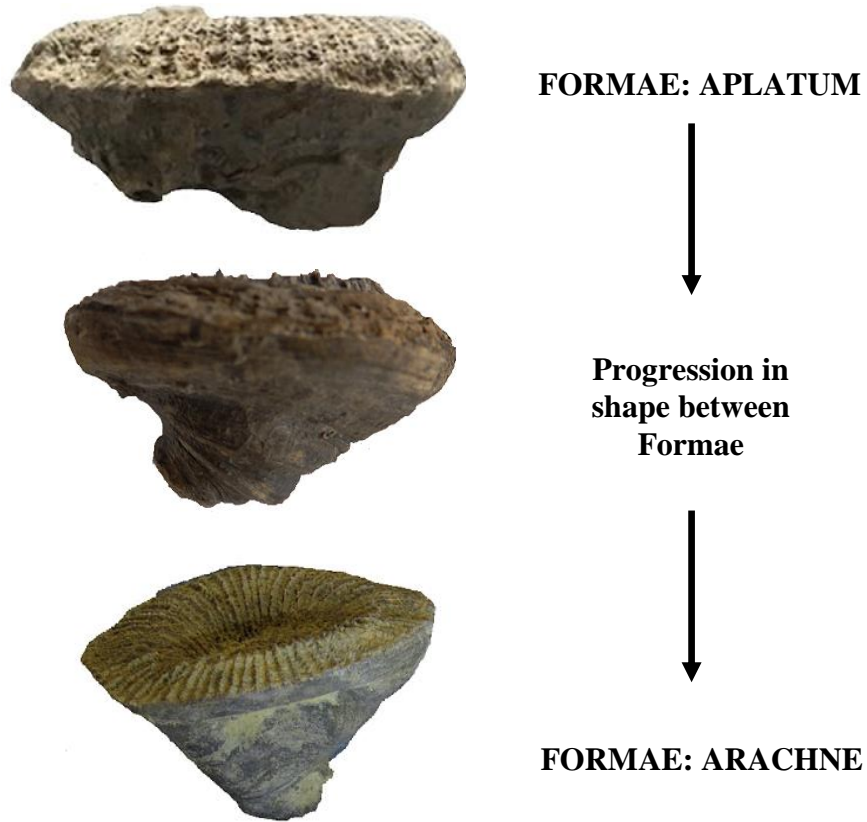
Bottom of another specimen.
Note width to height ratio



Calice and apex of specimen exhibiting polyp growth exceeding that of corallum



FORMAE: ARACHNE exhibiting geniculation



In cases where the peripheral epitheca grew faster than the internal portion of the coral, a funnel shaped corallum would result. A deep calice pit would develop between the tabulae (bench where the coral sat) and the upper edge of the calice. Wells described the typical calice as having a width to depth ratio of 3 or more. Any pit deeper than this (a ratio less than 3) would qualify as an anomaly. Researchers have not linked this growth form to any specific environmental conditions, but some conclude that slight physiological disturbances in the polyp would have been the most likely cause. This abnormality is referred to as **FORMAE: INFUNDIBULUM**.

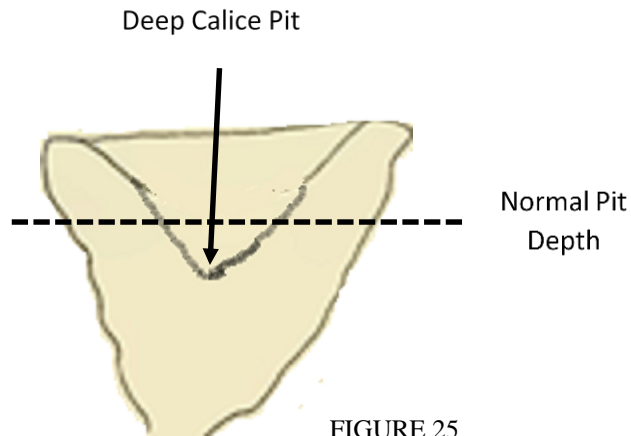


FIGURE 25



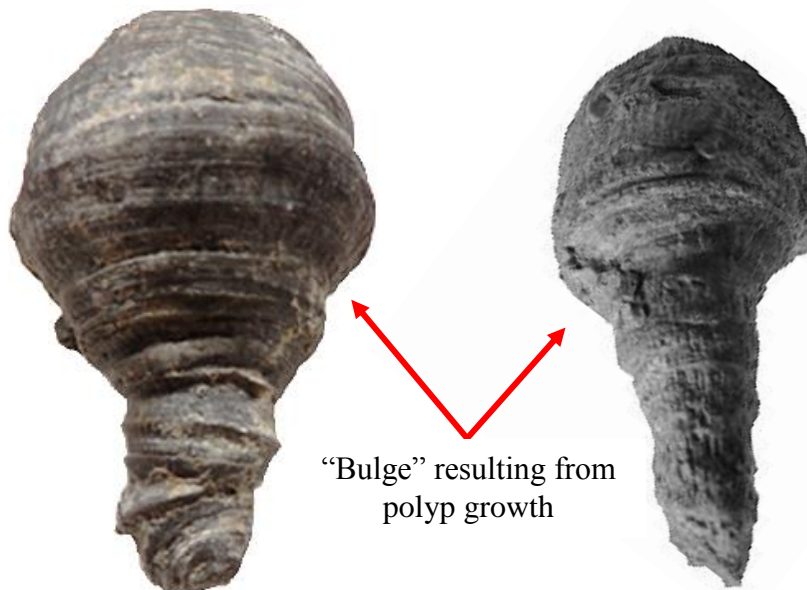
Normal Calicular Pit
Width: 2.858cm Depth: 0.178cm
Ratio: 16.06



Deep Calicular Pit
Width: 3.175cm Depth: 1.111cm
Ratio: 2.86

GROWTH IN RICH ENVIRONMENTS

Conditions were not always unfavorable for the Heliophyllum polyp. On the other hand, the polyp may have, at least temporarily, experienced a lush environment, rich in nutriment with quiet waters. In places like this, the polyp would have expanded disproportionately to its standard growth rate, resulting in a bulging corallum. Such conditions may have continued throughout the remaining life of the polyp or may have ended just as abruptly as they arose.



“Bulge” resulting from
polyp growth

THE IMPACT OF BUDDING ON SPECIATION

Dr. Wells originally described one subspecies, *H.halli confluens* and two “formae,” **FORMAE: PROLIFERUM** and **FORMAE: PRAECOQUUS** based on budding. All three were defined as resulting from peripheral increase.

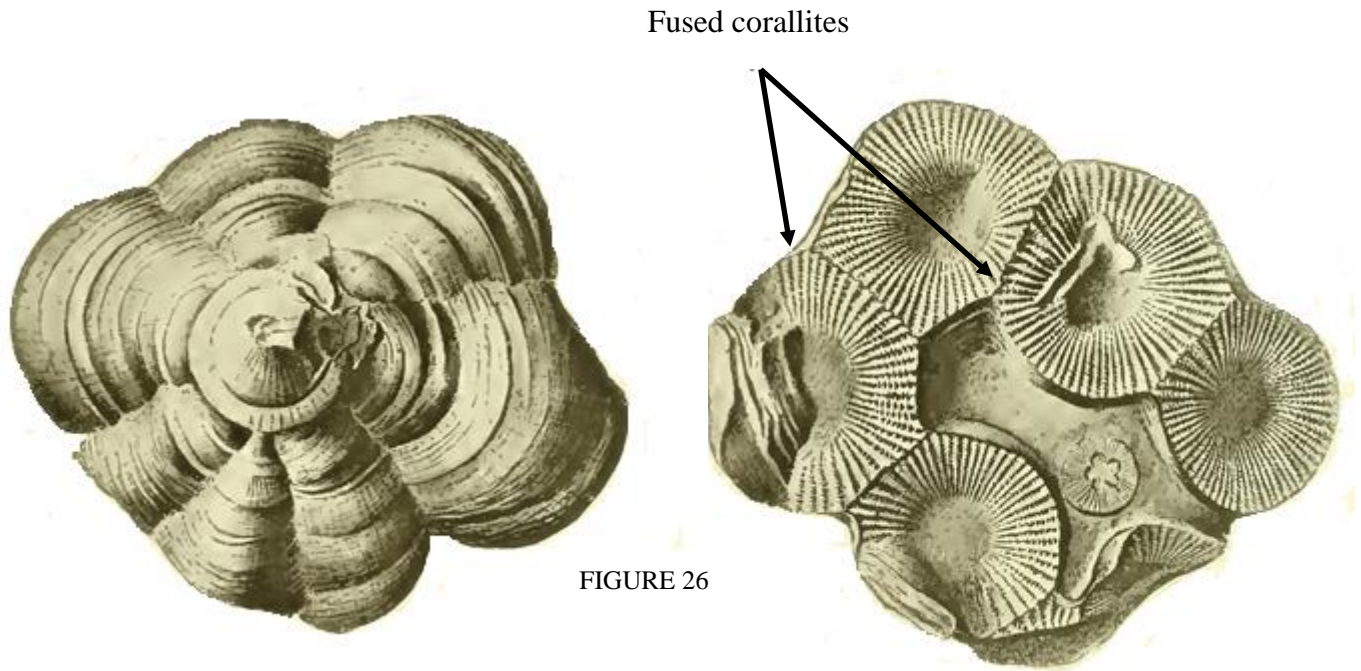
The subspecies *H.halli confluens* was distinguished from the two formae by the fact that its offsets fused laterally forming a solid cabbage-like coral head and by the rapid obliteration of the parent polyp as the neo-polyps expanded rapidly to mature diameters. Early researchers limited *H.halli confluens* to only specimens produced exclusively by peripheral increase. More recent work, however, by Oliver & Sorauf also included lateral increase in the definition in conjunction with peripheral increase. This results in not all calices being fused, making identification more difficult. Exact identification in specimens with non-fused calices requires sectioning the specimen. By current definition, at least two calices must share an outer wall, a structure termed astreoid, to be classified as *H.halli confluens*.

Colonies consisting of two to over fifty corallites that are over 20 cm in diameter have been discovered. Each corallite exhibits the distinguishing yard-arm carinae. Occurrence of *H.halli confluens* is believed to be restricted to the Green’s Landing coral bed in the lower portion of the Jaycox. Reports of discoveries in the upper Jaycox just below the Tichenor may be the result of misinterpreting the stratigraphy due to the erosional beveling that occurs as you move west. Occurrences outside the Jaycox have not been recorded. *H.halli confluens* shares its type locality, the Ludlowville formation at York in Livingston county New York, with *H.halli*. While Hall never designated a holotype, the lectotype selected by Dr. Wells in 1937 resides in the Walker Museum at the University of Chicago.

The two formae are distinguished from each other based on when they occurred in the life cycle of the coral and the life span of the offsets. **FORMAE: PRAECOQUUS** is distinguished by the development of multiple short offsets, in the range of 1 to 2 cm, during the early stages of development of the coral. As a result, the protocorallite is also small with a diameter no larger than 4.5 to 5.0 cm. Researchers attribute the rapid and extensive cloning to the polyp reacting to an external life-threatening event, in effect, a “preservation of the species” strategy. If this is in fact correct, it would explain the small size of the offsets, since they would also have been caught up in the same life-threatening circumstances that lead to their creation.

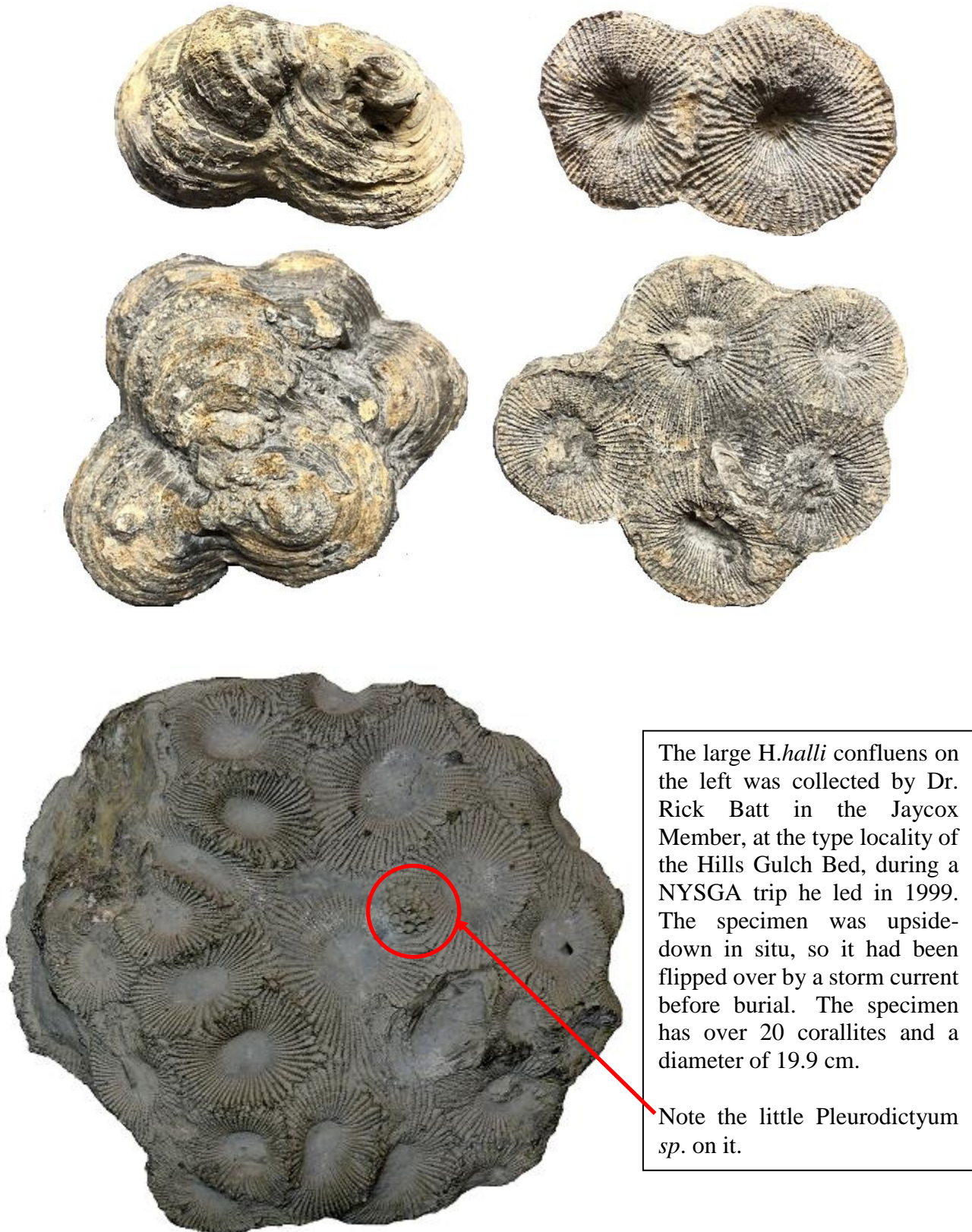
FORMAE: PROLIFERUM budded at a later stage in life and its offsets also lived to grow to a more robust state. This resulted in a specimen with a taller corallum than **FORMAE: PRAECOQUUS** or an *H.halli confluens* with longer offsets and without calice fusion.

It is not difficult to envision a continuum composed of the three configurations. Continued calice expansion in the two formae could result in the fusing seen in *H.halli confluens* and the ensuing obliteration of the parent polyp. Since no internal differences have been observed in the three growth forms, it would be safe to conclude that any specimen with multiple buds, not found in the Deep Run Shale, should be identified as *H.halli confluens* or simply an *H.halli* with budding.



Top and bottom views of a traditional *H.halli* confluens

Additional examples of traditional *H.halli* confluens showing 2 and 5 corallite specimens.



Examples of possible *H.halli* confluens showing non-fused corallites



Heliophyllum delicatum Oliver & Sorauf 1994

H. delicatum, the only true colonial species of Heliophyllum found in our collecting area, occurs only in the Deep Run Shales. *H. delicatum* is described as a derivative of *H. halli*, in which budding occurred most frequently through lateral increase, during a late period in the life of a “mother” polyp. The buds rarely fused and the “mother” polyp survived the budding. The corallites are long and gently tapering with very delicate internal structures with thin walls, septa, and carinae, thereby earning the name delicatum. The holotype, housed in the Smithsonian Institute in Washington, D.C., was collected from the Deep Run Shale member of the Moscow Formation in Darien, New York. Oliver & Sorauf described colonies with over 20 corallites that were over 46 cm in diameter.

Front and back view of Holotype of *H. delicatum*

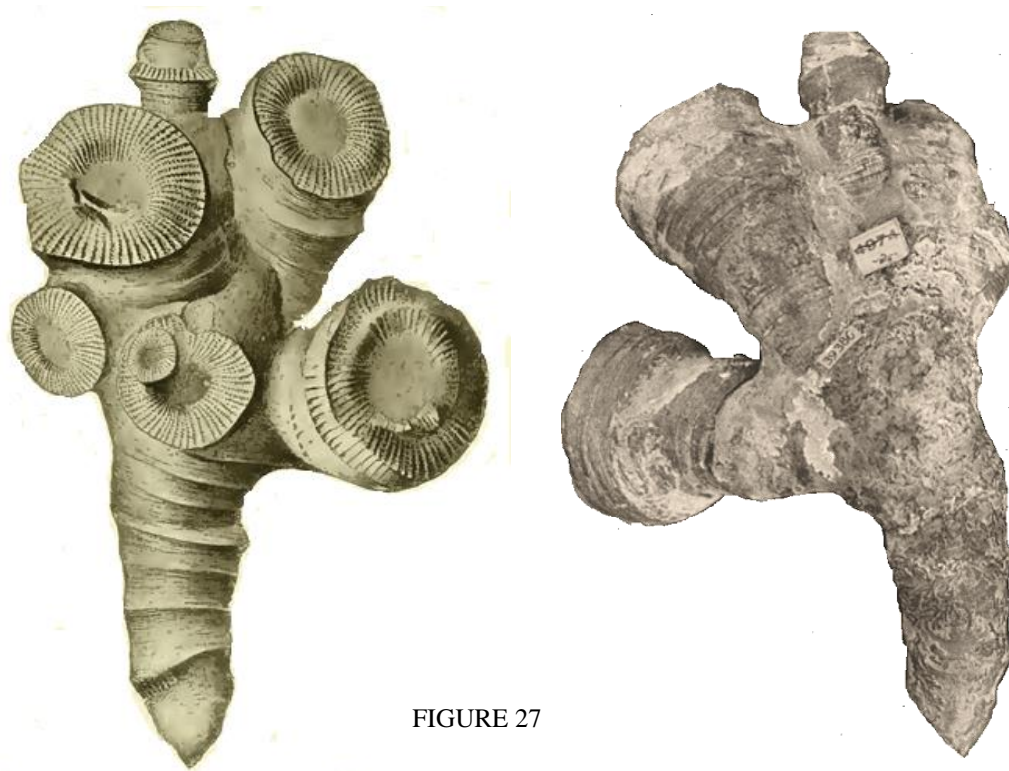


FIGURE 27

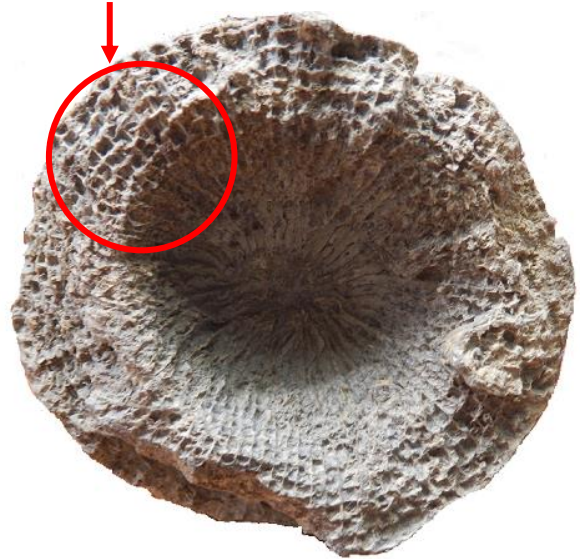
Heliophyllum cribellum Oliver & Sorauf

The most recent species of Heliophyllum to be described was by Oliver & Sorauf in the August 2002 *Bulletins of American Paleontology*. The holotype, housed in the Smithsonian in Washington, D.C., was collected near East Alexander, New York, in the Centerfield Member of the Ludlowville formation.

Essentially, it is described as a small, horn shaped *H.halli* with long and thick septal carinae that connect to those of adjacent septa forming a box-like appearance. Size is a helpful feature in identifying *H.cribellum*, with Oliver & Sorauf citing roughly 75 mm as the maximum observed length and 22 mm as a maximum calice diameter, ruling out larger specimens. The calice pit is shallow, being less than half the diameter of the calice. Although external morphology may be used for a rudimentary identification, internal features are the main basis for its separation into a new species. Principally short major septa and grid-like dissepimentarium, which can only be seen in traverse sections, are designated as the distinguishing characteristics of the species.

All currently known specimens have come from the Centerfield. Larger specimens of *H.halli* with strong carinae can easily be confused with *H.cribellum*.

Strong carinae touching both adjoining septa resulting in “box” shape



SYMBIOSYS WITHIN SPECIES

Heliophyllum was an incredibly adaptive and efficient genus of coral. The specimen below does not readily fit into any of the standard adaptation scenarios described previously, but rather appears to represent two polyps that settled and grew in close proximity to each other. We know Heliophyllum was capable of developing talons and sharing a calice wall (*H.halli* confluens). One possible theory is that these polyps bonded together in fast moving water to prevent toppling, much like first responders lock their arms together when attempting rescues in rivers with strong currents.

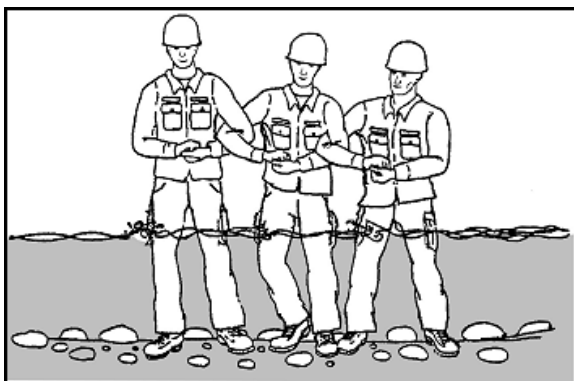


FIGURE 28



PREDATION

All creatures large or small fall somewhere on the universal food chain. Heliophyllum is no exception and had its share of predators. Two in particular left behind their mark, gastropods and sponges.

Gastropod drill holes in Heliophyllum are small, ranging from 1 to 2 mm in diameter, circular, and extending perpendicularly into the corallum. Gastropods have a special feeding organ called a radula, which is a rough structure used for scraping food. They also have the ability to secrete a chemical to soften the shell of their prey as they scrape with their radula. Since it is the “meat” of the polyp that is their target, it would be expected that these holes would be found near the calice. However, they are also known to exist substantially below the part of the corallum which was inhabited by the polyp. Most likely these represent failed borings, survived by the polyp which continued to thrive and grow after the attack. This sometimes occurs with modern oysters that can expend an inordinate amount of effort drilling into a shell only to miss the “meaty” part of its victim.

Failed **gastropod** borings.



Typical **sponge** borings on the coral *Stereolasma* *sp.*



Sponge borings, appearing like troughs cut tangentially into the corallum, are the result of the sponge looking to make a home in the calcium carbonate skeleton of the Heliophyllum. Using chemicals, they etch into the corallum and then mechanically wash away the small chips, slowly spreading the holes within the skeleton and across its surface, forcing the coral to deal with a weakened corallum. In some instances, the boring may have continued until the interior of the Heliophyllum became essentially hollow except for a few pillars of calcium carbonate stretching across a series of hollow cavities. The weakened corallum would have been more vulnerable to the pressure of fast-moving currents as well as to the incursion of opportunistic borers. Eventually,

these holes and tunnels could play a major role in the death of the polyp. Since boring sponges obtain their food from sources other than the host, the death of the Heliophyllum would not have a negative impact on the sponge because the calcium carbonate corallum would remain. Based on the observation of living species, the sponge could have continued to live within the corallum until such time as the entire skeleton collapsed. Brachiopods such as *Athyris spiriferoides* and the coral *Stereolasma sp.* appear to be favorite targets for these predators and are rarely seen on Heliophyllum.

The originators of both these trace borings, however, have recently come under scrutiny. Some researchers now lean toward replacing sponges with annelids (worms) as the architect of the troughs and argue the drill-holes attributed to gastropods were made by some other unknown organism.

EPIZOAN

Just like the planula of Heliophyllum which sought a hard surface to attach to and grow, other species of invertebrates did the same. It is common to find organisms that have encrusted or attached themselves to other host invertebrates. Attachment could occur either on a living host, in which case the association could be either symbiotic or antagonistic, or after the host's death. These organisms, when secured to another animal, are referred to as epizoans or epibionts. Some examples of commonly observed epizoan groups include bryozoans and phoronids (which are the most common), as well as inarticulate brachiopods, corals, tubicolous worms, and pelmatozoans. A result of either their size or simply their preponderance in the community, Heliophyllum were frequently found serving as hosts to a variety of epizoan.

In general, the reasons for the epizoan to attach to the Heliophyllum include:

- **Chance** – The epizoan may have settled on the host quite accidentally because it constituted an available hard surface needed for growth.
- **Protection** – Attachment to a surface that sits high enough above the substrate would avoid suffocation from silt stirred up by water currents.
- **Feeding Advantage** – Some organisms may have benefitted by extracting scraps from feeding currents generated by the host.
- **Source of Food** – The epizoan may have sought to bore into the shell and eat away at the soft tissue of the host.

Most relationships were believed to be commensal, meaning the epizoan neither harmed nor benefitted the host Heliophyllum. From the host's perspective, the primary value, when one existed, of the relationship was camouflage, concealing the host from predators. Another benefit involved commensal creeping bryozoan or phoronids, such as *Hederella*. In such instances the organism commonly encrusted much of the corallum to the exclusion of other predatory epizoans.

Chemicals present in the sediment that interacted with the calcium carbonate corallum resulted in a surface corrosion noticeable on most Heliophyllum. Since the corrosion process would have taken some time to occur, it is evident that most toppled Heliophyllum had a long exposure on the sea floor. As such, the corallum of a dead Heliophyllum would have served just as favorably as a substrate for attachment as a live one. In most instances it is impossible to determine whether the Heliophyllum was alive or dead at the time of attachment and growth of the epizoan. Attachment

on a worn corallum would indicate a post-mortem event. However, attachment to a well preserved one does not rule out post-mortem attachment followed by rapid burial.

The position of the attachment may provide some evidence of the state of the host during the association but not necessarily to the state of the coral at its onset. Encrustation of the calice of a coral substantiates that the epizoan was alive after the death of the host, as the polyp would have prevented colonization or extension into these regions. It is, however, not conclusive evidence that the relationship began with the Heliophyllum in a post-mortem state or that the epizoan was responsible for the death of its host.

Examples of typical epizoan attachments

Pelmatozoan (An Echinoderm, most likely a crinoid) Holdfast



Tabulate Coral



Coral – *Aulopora sp.*



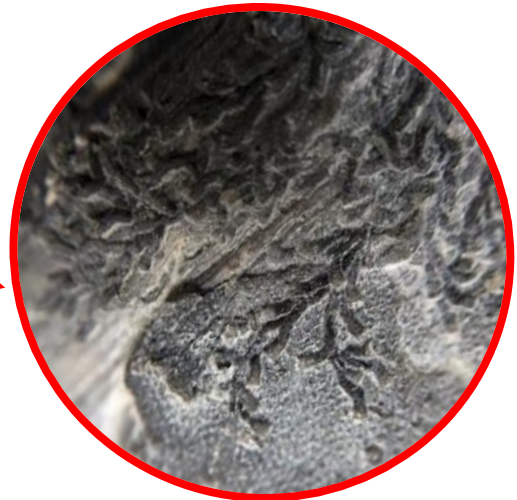
Bryozoan



Tabulate Coral



Bryozoan – *Leprotrypella amplexans*



Phoronid - *Hederella sp.*





Phoronid - *Hederella sp.*



Coral - *Aulopora sp.*

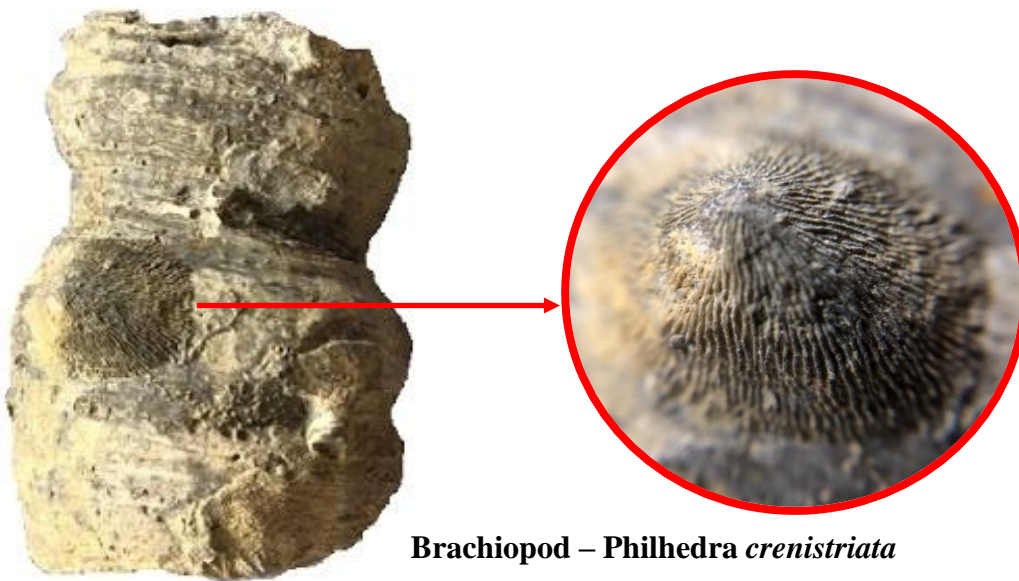




Phoronid – *Hederella sp.*



Bryozoan – *Leprotrypella amplectens*



Brachiopod – *Philhedra crenistriata*

Often what appears to be an epizoan living on a Heliophyllum is actually the result of storm action common in the Devonian waters of our area. In the case below a gastropod seems to have attached itself to the rim of the calice of a coral. It is sitting in living position and they have been known to assume a similar position on crinoids, living off the waste of their host. However, looking at the specimen from another angle shows that part of the base extends beyond the outer rim of the coral. This would represent a precarious and non-functional position for the gastropod. In fact, these two organisms were blown together, most likely post-mortem, by a storm and buried in the muds that cemented them in the mishmash below.



Part of the gastropod would have been living unsupported outside the rim of the coral.

At first glance the specimen below appears to be another example of post-mortem aggregation, with one already deceased coral blown into the calice of another. However, a more likely scenario is that a polyp still in its larval stage landed in the calice of another already deceased coral, attached to the inside, and grew.



Top View



Side View

While we can never be absolutely certain of what occurred during the Devonian, specimens like those above provide us with countless thought-provoking opportunities.

FIGURES

1. Verified December 2019 from <http://www.yellowmaps.com/map/new-york-blank-map-129.htm>
2. Verified December 2019 from <https://web.archive.org/web/20110605135422/http://jan.ucc.nau.edu/rcb7/namD385.jpg>
3. Verified December 2019. Reconstruction image from North American Museum of Ancient Life in Lehi, Utah, https://www.geocaching.com/geocache/GC51XAP_a-tropical-reef-in-utah?guid=c8d901eb-18c9-47a1-9868-d841d7005fa0 and from Bruce Avera Hunter, <https://www.usgs.gov/media/images/horn-coral-heliophyllum-halli-0>
4. Verified December 2019 from <http://biologytricks.blogspot.com/2012/05/animal-kingdom.html>
5. Verified December 2019 from <https://www.geol.umd.edu/~tholtz/G331/lectures/331coral.html>
6. Verified December 2019 from www.askiitians.com/biology/animal-kingdom/phylum-coelenterata.html
7. Verified December 2019 from <https://www.usgs.gov/media/images/horn-coral-heliophyllum-halli-0>
8. Taken from *Annals of the New York Academy of Sciences* (1877) Page 104
9. Verified December 2019 from Dennis Larson <https://www.fossilhunters.xyz/fossil-classification/rugose-corals.html>
10. Hand drawing taken from online class notes for University of British Columbia, EOSC 326 module c, no longer online. Transverse section verified December 2019 from <https://www.digitalatlasofancientlife.org/learn/cnidaria/anthozoa/rugosa/>
11. Verified December 2019 from <https://www.digitalatlasofancientlife.org/learn/cnidaria/anthozoa/rugosa/>
12. Verified December 2019 from <http://www.virtualcoralreefdive.com/recruitment.php>
13. Hand drawn illustrations adapted from Fenton & Fenton, “The Fossil Book” and Raymond C. Moore, “Treatise on Invertebrate Paleontology,” Part F
14. Verified December 2019 from <https://www.fromthegrapevine.com/nature/hawaii-just-banned-some-types-sunscreen-protect-coral-reefs>
15. Summary of work by Oliver & Sorauf 2002
16. Adapted from James Hall’s “Illustrations of Devonian Corals” – Plate XXV
17. Taken from work of James Sorauf 2001 – Figure 3
18. Adapted from James Hall’s “Illustrations of Devonian Corals” – Plate XXIV
19. Adapted from John W. Wells 1937 – Figure 15
20. Adapted from Blajez Berkowski 2012 – Figure 3
21. First two specimens pictured in the work of James Sorauf 2001 – Figure 5
22. First specimen pictured in the work of James Sorauf 2001 – Figure 5
23. Adapted from James Hall’s “Illustrations of Devonian Corals” – Plate XXIII
24. Adapted from John W. Wells 1937 – Figures 19 and 30
25. Adapted from John W. Wells 1937 – Figure 29
26. Adapted from James Hall’s “Illustrations of Devonian Corals” – Plate XXVI
27. Front view taken from James Hall’s “Illustrations of Devonian Corals” – Plate XXVI and back view taken from Oliver & Sorauf 1994 – Figure 3
28. Verified December 2019 from <https://www.globalsecurity.org/military/library/policy/army/fm/3-97-61/ch9.htm>

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