Exceptional new fossil of *Siphonophrentis gigantea*

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**Abstract**

Rugose Corals, often referred to as Horn Coral, are an extinct order of stony corals in the phylum *Cnidaria*. They lived from the Ordovician period to the end of the Permian period, and can be found worldwide. A new fossil of *Siphonophrentis gigantea*, a species of Rugosa in the family *Streptelasmatidae*, has been recovered from the Devonian strata of the Lucas Formation. The fossil gives clues towards the paleobiology of *Siphonophrentis*, revealing it to have likely anchored itself to the sea bed in the ocean depths. *Siphonophrentis gigantea* likely had no relationship with *Zooxanthellae*, a kind of Dinoflagellate that gives modern extant coral their colour and allows them to photosynthesize. These single celled organisms appear to be absent in *Siphonophrentis*, and it instead received nutrients from a rich amount of biological debris that fell into its habitat. Further comparisons can be made between *Siphonophrentis* and the extant, cold-water coral *Lophelia pertusa*.

**Introduction**

*Rugosa* (Edwards et Haime, 1850), commonly known as “Horn Coral”, is an order of extinct marine animals that thrived from the Ordovician to the Permian period. They are called Horn Coral in reference to the concave depression (called a calice or calyx) on the tops of their fossils, which in life would have served as a living chamber for polyps. Rugosans ranged in size, with typical specimens usually preserving the calice and reaching a few centimetres in length. They can be identified by the pattern made by their septa, visible in the calice. Septa are the vertical plates inside the walls of the rugose coral, radiating from the centre (Sprung, 1999). It is unique from other corals in that the septa pattern is bilaterally symmetrical, with a rod running through the center providing extra support to the often solitary corals (Ulrich et al, 1983).

*Siphonophrentis gigantea* is a taxon belonging to the group Rugosa. It is typically found in the Devonian strata of Ontario and New York. *Siphonophrentis gigantea* is relatively rare and is perhaps one of the largest species of Rugosa in Ontario. A specimen of this animal was recently recovered from a quarry in Beachville Ontario and represents a relatively complete and well-preserved fossil of this animal preserved in three dimensions. Using previous research, we can learn more about the life cycle and history of this individual specimen, including its breeding cycle and growth rate.
Materials and Methods

**Figure 1**: CMBB-0001 locality, Beachville ON. Map retrieved from the Pit and Quarry finding tool on the ontario.ca website.

**CMBB-0001**

*Siphonophrentis gigantea*, a rugose coral (also known as Horn Coral) from Devonian strata. The fossil is approximately 21 centimetres long, and approximately 7 centimetres in diameter. The rock was found with some exposed surface area of the fossil exposed, indicates by the erosion visible on one side of the fossil. The rest was cleared after collection, exposing a less eroded surface. This surface shows the calcite exterior of the fossil, as it would have appeared in life.
The apex and calice of the specimen were not preserved or were broken away from the primary piece of the rock presented here. Because of this, the septa and tabula of the fossil are not readily visible. The septal grooves of the fossil are typically 1 centimetre wide. Various fractures can be found on the newly exposed surface of the fossil (Figure 2-a). These were not caused by accidentally striking the fossil, although they may have been inflicted as the fossil surface was exposed. They are not damaging to the stability of the fossil, being only a few millimetres long at most.

The fossil was collected near a small stream, but was relocated here from the Lafarge quarry (Figure 1). The rock is Devonian in age, and after a phone call with the person who brought these rocks to the stream, it was confirmed that the rock came from the Devonian topstone of the Lafarge limestone quarry. In this area, the largest Rugose coral that matches the description of CMBB-0001 is a species of large Rugosa called *Siphonophrentis gigantea*. Fossils of this taxon can be found at the ROM (ROM94MRB). This species is relatively rare, compared to the abundant rugosa that belong to other Rugosa genera such as *Stereolasma* (Simpson 1900) and *Heliophyllum* (Hall 1846).

**Experiments**

Because of the preservation of the epitheca (outer wall of the rugosan) of CMBB-0001, we can learn much about its life history. Colin T. Scrutton suggests in his 1963 paper “Periodicity in Devonian Coral Growth” that the texture of rugosa epitheca correlates directly with time passed, largely inspired and based upon prior research on an extant species of cold-water coral that grows upwards like a tower called *Lophelia pertusa* (Linnaeus,1758), similar to the morphology of Rugosa. He suggests that each band (the largest ridges on horn coral) represent approximately 30.59 days passed, with each day indicated by a smaller diurnal ridge which is less likely to be preserved. This study also concluded that a Devonian year was approximately 399 days in length. The bands are divided clearly by a sudden drop in the diameter of the coral, followed by a gradual rise until the next drop. These bands are likely created when an event deprives the coral of resources necessary for additional growth, such as breeding, lunar tides, and lack of nutrients. By dividing the number of days in a Devonian year by the number of days represented in the growth ridges of the bands in horn coral, he calculated that these events took place 13 times during a Devonian year, every 30.59 days. The author used these calculations in an attempt to find out roughly how much growth the exposed fossil portion represents. The author counted the bands on the specimen, and used the equation \((30.59 \times B) / 399\) to find out how many diurnal ridges were present in the fossil. This was then translated into devonian years, and multiplied by the length of the specimen divided by the number of bands,

Let \(B\) represent the number of bands on CMBB-0001, and let \(L\) represent the length.
\[
(L ÷ B) \times ((30.59 \times B) \div 399)
\]
Using CMBB-0010, a *Heliophyllum* specimen collected from limestone rocks of the same strata as CMBB-0001, and a less complete specimen of *Siphonophrentis gigantea*, an experiment was conducted in order to provide clues towards the habitats of both species. A chip of rock was taken off of each matrix and submerged in white vinegar for upwards of 3 hours. The resulting reaction between the Calcium Carbonate (\(CaCO_3\)) and the Hydrochloric Acid (\(2CH_3COOH\)), a primary component of vinegar, removed the Carbon Dioxide (\(CO_2\)) from the rock, and replaced the \(CaCO_3\) with Calcium Acetate (\(CA(CH_3COO)_2\)). Because \(CaCO_3\) is primarily made up of microfossils (Omari et al, 2016), and is one of the primary factors affecting growth rates of modern corals as it is necessary for the further construction of the limestone skeleton (Osinga et al, 2011), it was predicted that finding the percentage of this compound within the matrix would provide insight to the accelerated growth rates of these corals. The results, while inconclusive, may indicate higher nutrient content in the habitats of growing *Siphonophrentis*. The experiment
could not be conducted using the previously mentioned samples of *Heliophyllum*, as they were legally collected from the Arkona Shale in Rock Glen, which is not limestone.

**Results**

By using the calculations brought forth by Scutton and in the Materials and Methods section on CMBB-0001, we can learn about the lifecycle of this particular *Siphonophrentis*. Of the animal preserved in the fossil, we can count 17 bands (see figure 3) on one side of the fossil. Because there is little variation in the number of diurnal growth ridges given by *Scrutton*, we can assume that it had approximately 30.59 growth rings in each band. The fossil is somewhat eroded, and the preservation is not sufficient to show these small growth rings. Based on the number of bands on this fossil, and the research of Scrutton, it can be assumed that the fossilized section of CMBB-0001 represents 520.03 days (30.59 • 17), or approximately >1.3044 Devonian years (520.03 ÷ 399). Dividing the length of the specimen (~19.9 centimetres) by its estimated lifespan, we can calculate that it grew by approximately 15.22 centimetres every year.

\[
(19.9 ÷ 17) • 13.044
\]

(length divided by the number of bands times the number of lunar months in a Devonian year)

\[
= 15.2176 \text{ cm / year}
\]

This is a considerable amount faster than the growth rates of modern corals of this size (Barnes, 1987) which average at about 7.5 centimetres per year. *Lophelia pertusa*, a cold-water, deep sea coral grows at a rate of only a few millimetres a year.

*Figure 3: showing the bands on the concave side of the specimen (17 bands in total)*
Using a large sample of rugose corals from the genus *Heliophyllum*, growth values and lengths were collected and put into a graphing tool (Desmos). Based on these measurements, it would appear that the average growth rate for *Heliophyllum* is roughly around 7.8 centimetres per year. Below is a chart of the values collected.

![Chart of growth values collected. Growth Rate is the Y-axis, Length of specimen is X-axis. The green dots represent Heliophyllum, and the Purple dots represent Siphonophrentis. The orange dot represents the average of the Heliophyllum (green) data. The orange line represents the line of best fit.](image)

**CaCO₃ + 2CH₃COOH → CA(CH₃COO)₂ + CO₂ + H₂O**

*Formula for the chemical reaction between Calcium Carbonate and Hydrochloric Acid*

<table>
<thead>
<tr>
<th>Sample</th>
<th>Mass (before)</th>
<th>Mass (after)</th>
<th>Percentage lost</th>
</tr>
</thead>
<tbody>
<tr>
<td>CMBB-0001</td>
<td>9.7g</td>
<td>9.6g</td>
<td>1.031%</td>
</tr>
<tr>
<td>CMBB-0002</td>
<td>3.9g</td>
<td>3.2g</td>
<td>17.949%</td>
</tr>
<tr>
<td>CMBB-0010</td>
<td>3.0g</td>
<td>2.9g</td>
<td>3.334%</td>
</tr>
</tbody>
</table>

*Figure 5: chart showing the results of the limestone and vinegar experiment. CMBB-0001/2 are of the genus Siphonophrentis, while CMBB-0010 is likely of the genus Heliophyllum. All rocks were limestone.*
Discussion

This experiment (Figure 5) might indicate that the waters which *Siphonophrentis* inhabited were richer in nutrients. The second specimen of *Siphonophrentis* gigantea reacted the most violently, fizzing rapidly and turning the vinegar a brownish colour. The low percentage shift of CMBB-0001 could be explained by its comparatively higher starting mass, which could have prevented the Hydrochloric Acid from reaching its core. All samples were roughly the same size, though the CMBB-0001 chip was much thicker. Another possible explanation for its lower concentration of *CaCO₃* could be indicated by the shape of CMBB-0001. This specimen is noticeably constricted on both ends. I propose that this oval shape could be a result of environmental change rather than warping in the process of fossilization. Perhaps a shift in its environment lead to the animal being unable to grow in diameter, and eventually leading it to its death. This may have caused or been caused by a drop in nutrient concentration in the waters.

These tests indicate that *Siphonophrentis* gained its rapid growth rate and larger size by living in deeper waters than its reef-dwelling relatives. Nutrient contents in modern oceans are at a much higher concentration in deeper waters, due to so-called “Marine Snow”, in which biological debris fall into the depths of the ocean (Miller, 2004). The three primary factors affecting the growth of extant coral are photosynthesis, heterotrophic feeding, and calcification (The Biology and Economics of Coral Growth, Ronald Osinga). No evidence for or against the mutualistic relationship between Rugose Corals and *Zooxanthellae* has been identified as of yet, as *Zooxanthellae* do not fossilize. In extant corals, these microorganisms allow the host organism to photosynthesize, providing a reliable source of energy for reef coral.

These organisms also give extant coral their vibrant colours (Birkeland, 1997), and explain why these colours are absent in deep-water coral species such as *Lophelia pertusa* (Shaw et al, 2014). Because this relationship is unlikely in Paleozoic rugose corals, it can be assumed that these extinct corals did not have a relationship with *Zooxanthellae*. The limestone experiment mentioned earlier indicates that *Siphonophrentis gigantea* lives in a deepwater habitat, and thus is even less likely to have a relationship with *Zooxanthellae*. It must have gotten all of its nutrients from the latter two sources; heterotrophic feeding and calcification. The richness of marine snow which can be inferred from *CO₂* content in limestone therefore provides an explanation for the accelerated growth of *Siphonophrentis gigantea*.

The research conducted in this paper provides information on the lifecycle and biology of *Siphonophrentis*. It is likely that *Siphonophrentis*, despite its larger size, grew at a faster rate than extant coral. This could be because of its more primitive nature or need to grow faster than modern coral, for whatever reason. However, the calculations of growth rate and timespan represented are not concrete figures. The growth lines and bands vary in dimension due to the life history of the specimen. If the animal fell into its side or needed to adjust itself in accordance
to the shifting substrate it is growing upon, it may shift and turn, and grow more in certain areas to regain proper position sooner (Scrutton, 1963).

Because the fossil shows only a gentle curve to the side, and little variance in the width of the bands throughout (Figure 6), it can be assumed that this specific individual didn’t experience very much of these interruptions. It shows that it likely anchored to an area where it remained stable for most of its lifespan, and thus, the calculations presented here should be mostly reliable.

The width of the specimen varies throughout, with one noticeably wider spot located in the middle section of the fossil. Although this could be interpreted as one of the aforementioned disruptions in its growth, it could also indicate a seasonal or environmental change. This study has limitations that the author, as a citizen scientist with no funding or access to advanced technology, cannot overcome. The author is unable to confirm the exact amount of CaCO$_3$ that was present in the samples, and their measurements will not be accurate past one decimal point, and the number of bands is intrinsically chaotic when the coral shifted direction or laid more limestone skeleton on one side rather than the others. The author encourages others to conduct similar experiments and calculations to either confirm or debunk their findings.

**Conclusion**

As concluded by Scrutton, the growth rate calculations indicated by the bands and ridges in Rugosa coral cannot be confirmed without more investigation into the growth patterns of the coral species *Lophelia pertusa*. There is an unfortunate lack of information available on Devonian fossils from Ontario, despite the fossiliferous nature of the local strata. With any luck, this article will contribute to the knowledge about Rugose Corals. This paper indicates that *Siphonophrentis gigantea* had no relationship with *Zooxanthellae*, and was thus colourless. It lived in deep, cold water, with access to large amounts of biological debris and nutrients. It used this for energy, rather than Photosynthesis.

*Figure 6: full image of CMBB-0001*
References


