Symbiotic Relationships Among Benthic Invertebrates from the Ludlowville and Moscow Formations (Hamilton Group) in New York State: A Closer look at Faunal Interactions

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ABSTRACT

Paleontologists and amateurs alike are privileged to collect fossils within the Finger Lakes region of upstate New York, among the best-preserved Devonian fossils worldwide. The paleontological record preserved in these sediments of western and central New York includes remarkable specimens of cnidaria, brachiopods, bryozoans, gastropods, trilobites and echinoderms, including crinoids and blastoids. Both the fossils and lithostratigraphic units have been studied for well over 150 years (Hall, 1843, Hall, 1861, Grabau, 1899, Baird, 1979, Brett et al., 1986, Brett et al., 2013, Zapalski, 2014, Vinn, 2017 and numerous others). Fossils from the dense and diverse assemblages also illustrate some of the best documented cases of interactions among ancient organisms including examples of overgrowths, commensalism, parasitism and predation that have been studied for more than a century (see Clarke, 1908). This field trip and accompanying guidebook paper will provide a look at some of the more interesting species and their interactions in some key fossiliferous, stratigraphic intervals of the Ludlowville and Moscow Formations, Hamilton Group, including the Centerfield Limestone, Jaycox Shale, Deep Run Shale and Kashong Shale members.

GEOLOGIC SETTING

Approximately 380-385 Ma, during the Middle Devonian (Givetian), eastern North America was affected by the breakup of Gondwana and the amalgamation of terranes and orogenic events (Benton, 2004). The convergence and subsequent collision and accretion of Avalonia to Laurentia (Blakely, 2008) resulted in intense crustal deformation giving rise to the Acadian Mountains and concurrent loading was predominately responsible for the subsidence of the Appalachian Foreland Basin (Van der Voo, 1983, 1988, Ettensohn, 1985). Westward erosion of these mountains resulted in siliciclastics and carbonates to accumulate in a shallow epeiric sea. The total thickness of the sequence of Hamilton Group strata in New York State ranges from 250 ft at Lake Erie shore to over 2500 ft in eastern New York, in Ulster and Green counties, as well as thicknesses range from outcrop to 8,000 feet in depth in southeastern New York, Sullivan County (Martin, 2006).

KEY FOSSILIFEROUS UNITS

Although there are numerous fossil-rich intervals in the Hamilton sediments we will only be looking at a few stratigraphic horizons during this trip. These intervals are associated with the ends of regressive successions or the beginnings of ensuing initial transgressions. In places these two types of successions appear nearly gradational and their facies successions seem to form mirror images of shallowing and deepening patterns. It is particularly within these shallow, relatively clean water associations that some of the most diverse fossil assemblages in western New York occur and just here fossil evidence of organism interactions becomes most apparent.

Ashantee Member (Skaneateles Formation) and Centerfield Limestone Member (Ludlowville Formation)

The Centerfield "cycle" extends across western NY through Seneca County with exceptional exposures in Livingston County. The detailed correlation of the "lower Centerfield" with the coarsening upward succession of the Chenango Siltstone-Sandstone Member (Skaneateles) in central New York led to the recognition that these packages both represent local manifestations of a forced regression (falling stage) at the end of sequence Giv-1. Hence, Brett et al. (2023) propose the name Ashantee Member for the former "lower Centerfield". The Ashantee Member records gradational changes in litho- and biofacies from dark gray, poorly fossiliferous shales to gray, calcareous fossiliferous mudstones with thin limestones.

Centerfield Member (Ludlowville Formation)

A slight discontinuity separates the upper coral-rich beds of the Ashantee from a distinctive limestone, placed at the base of the Centerfield Member (Ludlowville Formation;

sequence Giv-2). This unit is recognized as the basal transgressive limestone of the Ludlowville Formation. The Schaeffer Creek Submember passes up (almost symmetrically with the Ashantee) into coral-rich beds (Crooked Creek Coral Bed), then back through diverse brachiopod biofacies and finally into sparsely fossiliferous, dark gray shales (Ledyard Member). This sequence indicates a regressive-transgressive cycle with a shallow water deposited middle limestone (Savarese et al., 1986). The Centerfield contains typical Hamilton Group taxa including tabulate and rugose corals, crinoids, brachiopods, bryozoans and gastropod faunal associations.

Jaycox Shale Member (Ludlowville Formation)
The Jaycox Shale Member is an eastwardly thickening variably fossiliferous calcareous mudstone at the top of the Ludlowville Formation that is exposed in outcrops between Erie County and Cayuga County, New York. Like the Ashantee Member, the Jaycox records the final falling stage of sequence Giv-2. The Jaycox is noted for its two regionally widespread coral beds, the lower or Green's Landing Coral Bed and the upper or Cottage City Coral Bed, both containing a very rich diversity of marine organisms (Mayer, 1989, Mayer et al., 1994). The Jaycox Member records an overall gradual regressive sequence with minor transgressive fluctuations, which culminates in erosional downcutting and concurrent deposition of the overlying Tichenor Limestone.

Deep Run Shale Member (Moscow Formation)
The Tichenor Limestone, which forms the base of the Moscow throughout the region, grades upward into the lowermost beds of the Deep Run Shale Member. The Deep Run is also an eastwardly thickening calcareous siltstone that is exposed in outcrops between Erie County and Cayuga County, New York. In western sections, the Deep Run Shale is a condensed unit only a few feet thick, which balloons in the Canandaigua Valley, and thins again in the Cayuga Valley. A series of thin highly fossiliferous layers, comprising the basal Kipp Road Bed (Mayer et al., 2017) are, in turn, overlain by barren to sparsely fossiliferous mudstones of the upper Willard Siltstone of the Deep Run. The Kipp Road sediments were deposited in an overall transgressive sea at the base of the Moscow Formation (shallow enough to support a rich diversity of marine organisms).

Kashong Shale Member (Moscow Formation)
The Kashong Shale Member also extends from Erie County to Seneca County thinning towards its western and eastern margins but ballooning in thickness in the Genesee Valley. In the Kashong, we will see an unnamed layer, correlated with the so-called *T-T* (*Thamnoptychia-Taeniopora* beds) of Genesee County. The interval is rich in *Tropidoleptus carinatus* (Conrad, 1839) brachiopods covered by epibionts as well as *Pleurodictyum americanum* Roemer, 1876 corals that typically have grown on gastropods and other shells. This layer is laterally replaced by the *Rhipidomella-Centronella* (RC) Bed, which is a regionally widespread shell bed that contains a rich diversity of benthic organisms (Baird, 1979, Lukasik, 1984).

PALEOECOLOGY

The North American continent was lying below the equator between 25-30 degrees south latitude (Van der Voo, 1988), and was affected by a subtropical climate. This warm subtropical marine environment supported a diverse fauna. It is difficult to ascertain the real extent of the diversity of species that existed in this epeiric sea but a complex ecosystem must have existed at times within shallower water settings. Vast gardens of crinoids were interwoven with thickets of bryozoans living amongst solitary and colonial corals. Brachiopods filter fed on plankton drifting with the currents and gastropods attached to crinoids consumed nutrients derived from their waste products. Not only did these organisms live their lives as benthic and pelagic sea creatures, but they also interacted with each other. Excellent examples of organism interactions recorded in the Hamilton Group include evidence for predation (organisms killing and consuming other organisms), competition, and symbiosis.

ORGANISM SUBSTRATE RELATIONSHIPS

In the shallow water facies of the Hamilton Group numerous organism skeletons served as substrates for the growth of others that required at least a small patch of hard substrate for larval settlement and initial growth (Brett et al., 2008a). In many such cases, it is uncertain whether the skeletal substrate was simply the skeletal remains of other organisms or a living host. In the latter case, it is often impossible to tell whether the co-occurrence of another organism provided any benefit, harm or no effect at all. Probably a majority of such cases were simply an illustration of simple co-occurrence with organisms occupying the same environment but not interacting in any way. And yet, the very existence of skeletal hard substrates be they living or dead organisms undoubtedly promoted diversity in Hamilton shallow marine communities. It should be noted that distinctive assemblages of hard substrate encrusting organisms (sclerobionts) on particular shell types, termed "sclerobiofacies" by Brett et al. (2008a) occur at particular combinations of inferred water depth and sedimentation rates. The sclerobionts are often more sensitive to the environment than the substrate organisms. They form a spectrum of decreasing diversity offshore into deeper, dysoxic facies.

Because many organisms that require hard substrates themselves secrete skeletons there is a positive feedback, which means that shelly substrates tend to buildup and promote increased complexity of shelly organisms. This process has been called "taphonomic feedback" (Kidwell and Jablonski, 1983) and promotes increasing diversity in seafloor communities even though it often results from the interaction of living organisms with dead skeletons. Taphonomic feedback also enables the buildup of shell rich beds during times of low sedimentation so that shells do not get rapidly buried (Brett et al. 1986; 2008b; Dattilo et al., 2008).

Crinoids and related echinoderms provide a special case of skeletal substrates and permit many opportunities to examine organism substrate relationships as well as interactions, because their skeletons are actually endoskeletons capable of modification in response to local conditions. Crinoids comprise a significant proportion of the ecosystem preserved in the Deep Run Shale Member. At least four different species of crinoids are moderately common in the basal Kipp Road Beds in the Canandaigua and Seneca Lake Valleys. Blastoidea are uncommon although intact thecae are occasionally encountered. Like crinoids, they had a slightly flexible stem or column made up of stacked disc-shaped columnals and attached to the seafloor by a holdfast. Unquestionably, blastoid stems are mixed together with crinoid stems but due to their similarities, columns of crinoids and blastoids are difficult to distinguish, hence we may term them pelmatozoan columns.

The vertical elevated portions of pelmatozoans had strongly varied lengths from a few centimeters (e.g. small blastoids and inadunate crinoids) to more than a meter (large camerates like Dolatocrinus liratus Hall, 1862 and *Gennaeocrinus nyssa* (Hall, 1862). This variable elevation permitted crinoids to feed from different portions of the water column and benefit from different food resources and reduced possible competition among different taxa. This pattern of different feeding heights, has been called tiering (Ausich and Bottjer, 1982). Crinoids with branched, pinnulate arms, like most camerates, required stronger water currents for most efficient feeding; these typically had longer stems. Other types of crinoids such as some inadunates, and blastoids, were probably adapted for weaker currents and tended to have shorter stems.

The elevated columns of living crinoids also may provide opportunities for secondary tiering: encrusting organisms benefit from elevation above the substrate, reducing competition for space and providing stronger current action for suspension feeding (Peters and Bork, 1998). Many Hamilton crinoid and probably blastoid columns show abundant encrustation at various levels by varied invertebrates, including rugose and tabulate corals, cornulitid worm tubes, bryozoans and even other crinoids.

The robust crinoid subclass Camerata is represented by large rhizome-like stems of *Dolatocrinus liratus* and *Megistocrinus depressus* Hall, 1862. The stems range up to 1.5 feet (45 cm) in length and 0.5 inches (1.27 cm) in diameter and tightly overlie one another throughout the Kipp Road Bed. These crinoids often showed "runner type" distal columns that evidently lay horizontally on the seafloor as holdfasts and interacted with their substrates (Brett, 1981). As echinoderm skeletons are invested in living tissues, these crinoids were able to produce outgrowths of stereom where they came in contact with objects including other organisms skeletons on the seabed; these probably increased the anchorage of the stems. In addition, these runners provided a substrate for benthic encrusting organisms including other crinoids with discoidal holdfasts, bryozoans and microconchids (formerly termed *Spirorbis*).

Based on the very great abundance of columns, including the runners, it would be expected that an equally large number of calyces would also be observed; however, to the contrary, the calyces are relatively rare. This is consistent with other observations of a strong bias against calyx preservation in most crinoid faunas. An abiotic explanation for the lack of calyces could be due to taphonomy. The soft tissues binding the calcitic plates of the calyx may have been more prone to decay causing the calyx to disarticulate prior to fossilization than the tightly sutured columns (Brett et al., 1997). In addition, storm-related underwater disturbances may have torn apart more fragile crinoid crowns while burying columns, particularly the runners which were already attached to the substrate (see Brett et al., 1986 for a detailed discussion of storm-generated sedimentary units in the Hamilton Group).

It is also possible that the preferential loss of crinoid calyces may in part reflect the increased intensity of predation by durophagous predators, which greatly increased with the evolutionary development of gnathostome fishes in the Middle Devonian (Brett, 2003, Syverson et al., 2018). Moreover, Syverson et al. (2018) noted that Devonian predators preferentially targeted camerate crinoid soft tissues housed in calyces and tegmens.

SYMBIOTIC RELATIONSHIPS

Symbiosis is any type of long-term biologic interaction between two different organisms often inhabiting the same spaces and sharing or competing for the same resources. These associations were termed "dependent relationships" (Clarke, 1908). Three interactions are recognized which include mutualism, commensalism, and parasitism. Each of these relationships is observed in the fossil record and will be discussed separately.

Mutualism

Mutualism refers to the interaction between two species where each has a net benefit. A well-known example between extant species is the clownfish (*Amphiprion ocellaris* Cuvier, 1830) and its host, the Magnificent Sea Anemone (*Heteractis magnifica* Quoy and Gaimard, 1833). The clownfish feeds on small invertebrates which otherwise have the potential to harm the sea anemone and the fecal matter excreted from the clownfish provides nutrients to the sea anemone. In turn, the sea anemone protects the clownfish from predators by the anemone's stinging cells to which the clownfish is immune. A still more important form of mutualism involves marine invertebrates, especially corals and sponges and tiny modified dinoflagellates termed zooxanthellae. Not only do the algae benefit by deriving nutrients from their host's tissues but they also aid their host's growth. The coral provides the zooxanthellae with a protected environment and nutrients the algae need for photosynthesis, while the zooxanthellae produce oxygen and food and aid the coral by removing waste products and in more rapid skeletal secretion (Karako et al., 2004). Hence, this mutualism is vital to modern reef ecosystems.

Symbiosis in Devonian corals may have been common as it is in modern reef corals and has been the focus of recent studies (Tapanila, 2005, Vinn, 2017). A study conducted by Zapalski (2014) strongly suggested mutualism existed between the tabulate favositid corals (13 different species) as well as representatives of four other tabulate suborders with zooxanthellae, microscopic algae inhabiting the host coral's soft tissues. Zapalski analyzed $\delta^{18}O$ to $\delta^{13}C$ isotopes in modern photosymbiotic scleractinians compared with Paleozoic tabulates and found stable ratios were very similar, providing evidence that symbiosis with algae existed as early as the Silurian. Although stable isotope analysis was not conducted specifically for *Favosites* from the Middle Devonian of New York (**Figure 1**), it is reasonably interpreted that such a mutualistic relationship also existed between this favositid and the zooxanthellae algae.

Another example of mutualistic "peaceful coexistence" was examined by Zapalski (2014) between auloporid coral and zooxanthellae using the same stable isotope methods. Zapalski came to the same conclusions as with the favositids. Furthermore, auloporid corals are frequently observed encrusting other organisms, particularly fistuliporid bryozoans (**Figure 2**).

Figure 1. *Favosites argus* Hall, 1876. Green's Landing Coral Bed, Jaycox Shale Member, Ludlowville Formation, Canandaigua Lake.

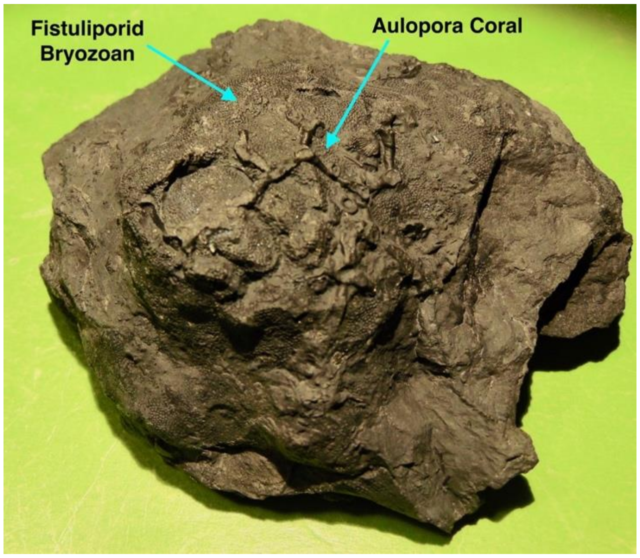

Figure 2. Auloporid coral encrusting fistuliporid bryozoan, Green's Landing Coral Bed, Jaycox Shale Member, Ludlowville Formation, Canandaigua Lake.

Vinn et al. (2020) examined the relationship between rugose corals and the cystoporate bryozoan *Fistulipora* in the latest Silurian of Estonia and interpreted the associations were most likely mutualistic. Here the tabulate coral *Aulopora* sp. is interpreted to be mutualistic with *Fistulipora* sp. for the same reasons as Vinn et al. (2020) concluded about the rugose corals and the bryozoan colonies. Mutualism is evident in the lack of malformations and lack of a decrease in the size of the bryozoan zooids near the auloporids, which suggests there were no strong negative effects of the auloporids on the bryozoan. The coral benefited from the bryozoan, which served as an anchor to stabilize the coral in the underwater currents, while the bryozoan colony may have benefited from protection against some predators. Zapalski et al. (2022) examined bryozoan auloporid interactions within the Silurian and similarly determined that the auloporids benefited from feeding currents created by the host bryozoan, while the latter benefited from the protection from predators afforded by the coral's stinging cells (cnidocytes).

An association commonly observed in the coral-rich beds of the Ludlowville and Moscow Formations is the encrustation of epibionts on rugose corals. Particularly bryozoans appear to have an affinity for *Heliophyllum halli* (Milne-Edwards and Haime, 1850), often encrusting large areas of the coral epitheca (**Figure 3**).

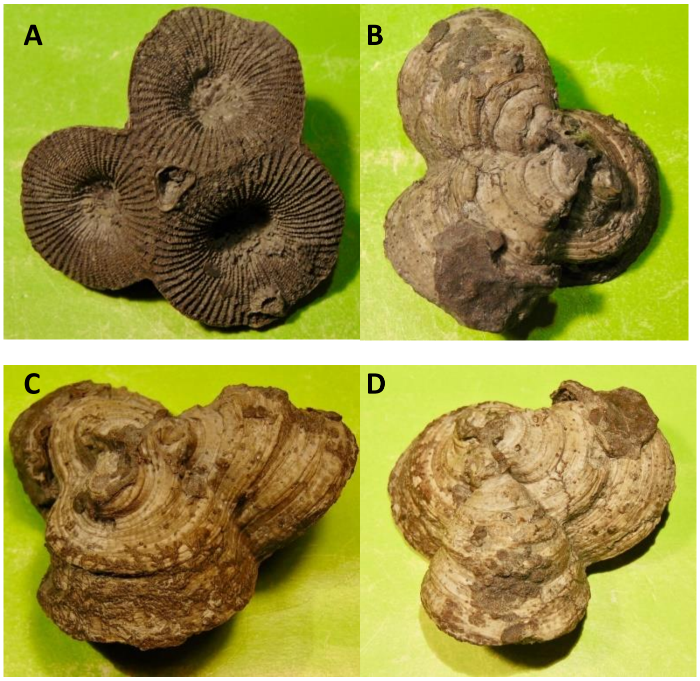

Figure 3. Calyx (A) of *Heliophllum halli var. confluens* Hall, 1876, and apical end (B-D) rotated 120° with three different bryozoan epibiont species encrusting all three corallites. B) *Leptotrypella amplectens* (Grabau, 1899), C) *Hederella canadensis* (Nicholson, 1874), and D) *Botryllopora socialis* Nicholson, 1874 all are interpreted to have a mutualistic symbiotic relationship with the host coral. Green's Landing Coral Bed, Jaycox Shale Member, Ludlowville Formation, Canandaigua Lake.

Auloporids are frequently found encrusting and spreading across rugose corallites. McKinney et al. (1990) interpreted similar associations of *Aulopora* and the bryozoan *Leioclema* from the Early Devonian of western Tennessee to have been mutualistic. This interpretation can also be made for the coral-bryozoan association observed in the Ludlowville faunas. This symbiotic relationship provides the benefits of raising the epibionts off the crowded substrate and into a higher realm of suspension feeders; this has been called secondary tiering (see Peters and Bork, 1998).

Moreover, the attachment of crinoid holdfasts to corallites (**Figure 4**) similarly elevates the crinoid in the water column. It is highly unlikely that the larval crinoid would have actively sought out this position, but it would have certainly aided the animal in growth during filter feeding allowing it to capture more food particles than otherwise would have been available closer to the substrate.

Figure 4. Large crinoid holdfast attached to *Heliophyllum halli*, Deep Run Shale Member, Moscow Formation, Deep Run, Canandaigua Lake (specimen courtesy of Gary Thomas).

Commensalism versus Competition

Commensalism describes the interaction between two species where one benefits and the other is not significantly harmed or helped whereas competition describes the relationship between species where one species benefits and the other is harmed.

Commensalism between cnidarians and brachiopods may have preferentially favored the corals. This is interpreted with the cnidarians *Amplexiphyllum* and *Favosites* which have attached themselves to the surface of the strophomenid brachiopod *Megastrophia.* This permitted the corals to reach and bring nutrients to their mouths from an increased food supply suspended higher in the water column without harming the brachiopod (**Figure 5**). However, is this a case of competition? *Megastrophia* may

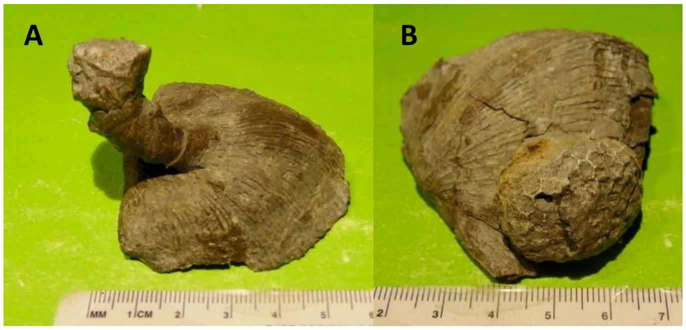

Figure 5. A) Side view of the rugose coral *Amplexiphyllum hamiltoniae* (Hall, 1876) and its host, the brachiopod *Megastrophia concava* (Hall, 1857), and B) side view of the tabulate coral *Favosites argus* encrusting *Megastophia concava*.

indeed be harmed by the loss of food particles (captured by the corals) as well as the burden of opening and closing its valves with such a large, attached encrustation. Since both the pedicle and brachial valves are intact, this demonstrates that the brachiopod was still living at the time of the cnidarian encrustation but did the brachiopod reach its large size prior to or after the attachment of the corals? Among other issues, the occurrence of corals on the convex pedicle valves of these strophomenid brachiopods provides support for the controversial hypothesis that the brachiopods were commonly oriented convex upward during life (see Lescinsky et al., 1995; Dattilo et al., 2008).

A second example of commensalism bordering on competition is between auloporid corals, bryozoans and brachiopods. Mistiaen et al. (2012) documented more than 40 brachiopod species encrusted by living auloporids in the Devonian. In this case, the coral *Aulopora* sp. and the bryozoan *Atactotoechus furcatus* (Hall, 1876) are epibionts on the host spiriferid brachiopod *Mediospirifer audaculus* (Conrad, 1842) (**Figure 6**). Zaplaski (2005a) interpreted the coral brachiopod association may have been competitive because corals use water currents produced by the brachiopod's lophophore intercepting food particles and thus depleting the brachiopod's food supply (Alvarez and Taylor, 1987). Similarly, the bryozoan zooids would have captured suspended food particles.

Figure 6. *Aulopora* sp. and bryozoans on *Mediospirifer audaculus*, Deep Run Shale Member, Moscow Formation, Canandaigua Lake.

Parasitism

Parasitism describes the relationship in which one organism, the parasite, lives in or on another organism (its host) and benefits by obtaining nutrients at the other's expense. It is somewhat similar to predation except that in parasitism the symbiont relies on a living host for its food and produces harmful effects without killing the host for considerable periods.

Tabulate corals attached to crinoid stems were examined by Berkowski and Zapalski (2014). They determined that the coral damaged the stem of the living crinoid causing it to lose flexibility. However, the corals benefited by being able to access food sources that were suspended in a higher tier in the water column. They interpreted this as a form of parasitism. Brett (1999) described the tabulate coral *Antholites* attached just below the crinoid crown in *Dolatocrinus*. This suggests a similar symbiotic relationship between the corals and crinoids may have occurred in some shallow water environments such as those recorded by the Deep Run Shale Member.

The platyceratid gastropods *Naticonema lineata* (Conrad, 1842) and *Platyceras sp.* occur abundantly throughout the basal Kipp Road Beds of the Deep Run Shale Member. These species are invariably found amongst *Dolatocrinus* and *Megistocrinus* calyces and stems (**Figure 7**). It is known that snails engaged in coprophagous behavior (Brett, 1999; see review in Thomka and Brett, 2021), dining on fecal matter excreted by the crinoids. No damage has been observed to these crinoid bodies, thus it appears that the snails did not harm their hosts. This suggests that the snails formed a commensal relationship with the crinoids.

Figure 7. *Dolatocrinus liratus* with nearby *Naticonema lineata* gastropod. The snail may have been dislodged from the crinoid tegmen due to water currents prior to fossilization, calyx 4 cm.

However, a study conducted by Gahn and Baumiller (2003) concluded differently. They studied two species of Middle Devonian camerate crinoids, *Gennaeocrinus variabilis* (Kesling and Smith, 1962) and *Corocrinus calypso* (Hall, 1862) collected from Alpena, Michigan and Arkona, Ontario, Canada respectively, with and without attached platyceratid gastropods. Their results indicated that for both species of crinoids, those with attached snails were much smaller in size than those without attached snails. Gahn and Baumiller (2003) interpreted this interaction between the gastropods and crinoids as parasitism and a consequence of nutrient stealing.

In addition, Brett (1978a, 1985) described a form of probable host-specific parasitism involving crinoids and other echinoderms and a yet undetermined pit forming organism which evidently gained a living site and possibly nutrients by infesting the living epidermis and stromal tissue in the echinoderm endoskeletons. These parasites imbedded in host tissues of specific crinoid species and in some cases produced tumor like swellings. Brett (1985) termed the circular parabolic pits produced by these parasites *Tremichnus.* Such pits though common in some Silurian crinoids (e.g. in the Rochester Shale of NY, Brett, 1978a) are rare in the Hamilton Group. Nonetheless, a few spectacular examples are known including a crown of *Synaptocrinus* (**Figure 8**) probably from the Deep Run Shale at Seneca Lake, which was riddled with large circular pits attributed to *Tremichnus*.

Figure 8. Two views of waterworn crown of *Synaptocrinus nuntius* (Hall, 1862) riddled with large pits (about 1-2 mm diameter) attributed to *Tremichnus*, embedment pits of an unknown but host-specific parasite. Found in beach gravels probably derived from lower Deep Run Shale Member, Seneca Lake, west shore south of Dresden, NY; scale bar = 1 cm (specimen courtesy of Nikki Gottschall-Chase; PRI number 76684).

An exemplar of parasitism and commensalism within the Ludlowville and Moscow strata is the association of a platyceratid gastropod, a crinoid, a bryozoan and barnacles, first investigated by Baird et al. (1990). Fragile crinoids belonging to the group Flexibilia (now considered a superorder of the cladida; Wright et al., 2017) are encountered in the Kipp Road Bed. Most notable is *Taxocrinus lobatus* (Hall), which is frequently found with the platyceratid gastropod *Naticonema lineata* attached to the crinoid tegmen (**Figure 9**). Moreover, these gastropods often display borings, which the researchers attributed to acrothoracic barnacles. These borings are consistent with the ichnogenus *Zapfella* (Tomlinson, 1969, Baird et al., 1990). In addition to the borings, snails are often encrusted by the bryozoan *Palaeschara incrustans* (Hall, 1874), which may overgrow the borings or be perforated by the borings.

Figure 9. Well preserved example of commensalism and parasitism displayed n a single association of epizoans and hosts. *Taxocrinus lobatus* with attached *Naticonema lineata*. Note also the bryozoan *Palaeschara incrustans* covering the gastropod. In this specimen, borings may be overgrown by the bryozoan colony. Kipp Road Bed, Deep Run Shale Member, Hopewell Gully, near Canandaigua Lake.

These biologic interactions between these four organisms demonstrate both commensal and parasitic symbiotic relationships. *Naticonema* exhibits coprophagous behavior with *Taxocrinus*; *Palaeschara* is suspected to have used *Naticonema* as a mobile substrate to gain access to a higher tier in the water column and ready supply of suspended food particles; and the barnacle borings indicate parasitism.

Thomka and Brett (2021) have noted the two most common forms of evidence of parasitism of pelmatozoans are shallow pits and platyceratids sometimes directly overlying borings in the crinoid tegmens. These circular borings are not to be confused with the teardrop shaped barnacle borings and instead were apparently made by the gastropods to obtain fecal matter (coprophagy), gametes (gametophagy) and undigested food (kleptoparasitism) (Baumiller, 1990; Baumiller and Gahn, 2002). Gastropod drilled boreholes have not been observed in the crinoid in Figure 9 of the specimen of *Naticonema* attached to *Taxocrinus*. But the possibility certainly exists that other specimens would have these boreholes beneath the gastropod shells, thus supporting parasitism of the host.

Predation

Predation is the organism relationship in which an organism benefits from the other by killing and consuming prey species. Two forms of evidence for probable predation are recognized in the Hamilton Group, based upon trace fossils, durophagous predation marked by bite marks and predatory drilling, which produced the trace *Oichnus* (Bromley, 1981).

Modern marine gastropods drill boreholes into occupied shells to obtain food. Moreover, Smith et al. (1985) documented 20 non-ribbed brachiopod species from the Ludlowville and Moscow Formations having drilled boreholes (**Figure 10**) resembling borings produced by Triassic age and later naticid gastropods (trace called *Oichnus*). These boreholes have been attributed to the Middle Devonian Givetian-age platyceratid gastropods such as *Naticonema* (Brett, 2003). Holes appeared to be targeted into the more central areas of the valves away from the edges and blisters covered incomplete drill holes indicating predation on living shells (Brett and Walker, 2002). The non-ribbed, smooth shelled brachiopods such as *Athyris spiriferoides* (Eaton, 1831), and finely costate taxa such as *Protodouvillina inequistriata* (Conrad, 1842) and *Rhipidomella* spp. were preferentially targeted, whereas the coarsely ribbed species *Mucrospirifer mucronatus* (Conrad, 1841) and *Tropidoleptus carinatus* were avoided due to more rigid, reinforced shells (Brett and Walker, 2002).

Figure 10. Naticid-like drill hole in a *corroded Spinocyrtia granulosa* (Conrad, 1839). Kashong Member, West Bethany Submember, *Rhipidomella-Centronella* (RC) Bed, Menteth Gully, west side of Canandaigua Lake; PRI number 104875.

Moreover, sharp jagged breaks attributed to bite marks have been found on certain bivalves (**Figure 11**), particularly the pterineid *Ptychopteria* within the Ludlowville-Moscow strata (Nagel-Myers et al., 2009, 2013). In this case, evidence of healed breakage was attributed to various decapod crustaceans. The frequency of bite marks is nearly constant through the mid-Hamilton suggesting relatively stable predator-prey systems (Nagel-Myers et al., 2013).

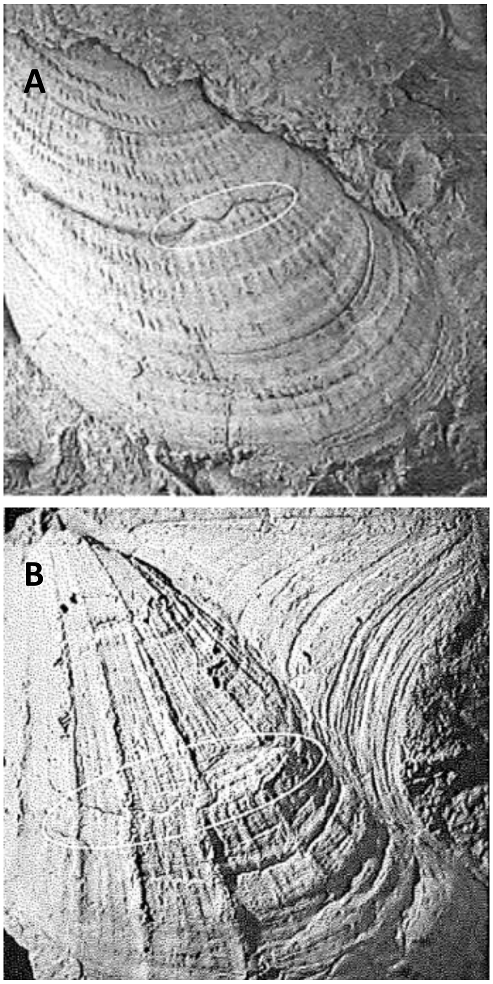

Figure 11. Healed bite marks on (A) *P. (Actinopteria) decussata*, PRI number 9809, with jagged marks and (B) *P. (Ptychopteria) flabella*, PRI number 9811, with shell rib misaligned. From Nagel-Myers et al. (2009).

Finally, the appearance of increased spinosity in some Devonian crinoids, especially those with platyceratid gastropods commonly attached, as well as productid brachiopods and some mollusks may represent an evolutionary response to the rise of predatory fishes and other organisms in the Devonian Period (see Brett, 2003, Syverson et al., 2018).

SUMMARY

Examples of all three symbiotic relationships including mutualism, commensalism, and parasitism, as well as evidence of competition and predation are recognized in key fossiliferous beds within the Middle Devonian Ludlowville and Moscow formations. Particularly evident are interactions between various species of tabulate and rugose corals, bryozoans, brachiopods, crinoids, gastropods and even barnacles with each other and their environment. Ecosystems were clearly thriving and diverse in Middle Devonian shallow seas with organism interactions similar to those that occur in modern marine environments.

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illustrated in the figures, as well as provided encouragement in the preparation of this manuscript. Both Gary Thomas and Nikki Gottschall-Chase willingly offered specimens that they collected and were illustrated in Figures 4, 12 and 8 respectively.

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THE SEARCH FOR SYMBIONTS

ROAD LOG AND STOP DESCRIPTIONS

Starting Point: SUNY Brockport, 350 New Campus Drive
Starting Point Coordinates: 43. 21293, -77.94687
Starting Time: 8:30 AM

Cumulative Miles	Incremental Miles	Route Description
0	0	Leave SUNY Brockport
		Turn right onto Rt. 19 (Main Street)
0.7	0.7	Turn Left onto Rt. 31 E
5.6	4.9	Becomes Spencerport Expy Rt. 531 E
13.1	7.5	Enter onto I-490 E
32.6	19.5	Take exit for Rt. 96 S (Pittsford-Victor Rd.)
38.8	6.2	Turn right onto Rt. 332 S.
46.6	7.8	Turn left onto Routes 5 & 20 E
48.4	1.8	Left into Walmart - Canandaigua

Meeting Point: Walmart - Canandaigua, 4238 Recreation Drive
Meeting Point Coordinates: 42.87450, -77.24101
Meeting Time: 9:30 AM

		Proceed out of Walmart parking lot across Routes 5 & 20 straight onto Lake Shore Dr.
48.9	0.5	Turn left onto Rt. 364 S
52.5	3.6	Turn right into Deep Run Park, carpool from here
53.4	0.9	Proceed south past Hall Road
53.5	0.1	Stop # 1 - Very limited parking at creek overpass

STOP # 1: Unnamed Creek South of Hall Road - Deep Run Shale Member

Location Coordinates: 42.80516, -77.26014

The first cutbank immediately upstream from (east of) Route 364 bridge exposes the Cottage City Coral Beds. This is the upper of two coral beds within the Jaycox Shale Member, which yields a high diversity of taxa including large *Heliophyllum halli* and favositid corals, brachiopods, bryozoans and pelmatozoans in a calcareous mudstone. This unit records a shallow water facies (Mayer, 1989); the varied and abundant fossils suggest that symbiotic interactions must have occurred between the living organisms. The Cottage City Coral Beds and approximately 2 feet of succeeding Jaycox Member shales are disconformably overlain by the Tichenor Limestone, which marks the base of the Moscow Formation and, in turn, grades upward into the Kipp Road Bed of the Deep Run Shale Member.

The Kipp Road Beds are the focus of Stop #1 where we will concentrate our search for symbionts in about 4-5 ft. of highly fossiliferous calcareous shales. Particularly evident are the very abundant rhizome-like stems of the camerate crinoids *Dolatocrinus liratus* and *Megistocrinus depressus*, which overlap one another throughout the unit. Moreover, fragile crinoids belonging to the superorder Flexibilia, including *Taxocrinus lobatus* are occasionally found with platyceratid gastropods attached to the crinoid tegmen (see discussion above). Another crinoid species, *Synaptocrinus nuntius* also occurs in this unit, but less frequently. One specimen of this crinoid was found with parasitic boreholes covering the crown. The most remarkable crinoid discovered thus far (**Figure 12**) belongs to the subclass Inadunata. George McIntosh, Rochester Museum and Science Center, Curator Emeritus, (pers. comm) has identified it as

Poteriocrinites multicosta (Goldring, 1954), but also observed that the ornamentation is slightly different than others he has seen. Therefore, he believes that it could be a new undescribed species.

Complete blastoid fossils are uncommon, although intact theca, are occasionally encountered. Like crinoids, they had a cylindrical stem or column attached to the seafloor by a holdfast. It is likely that blastoid stems are mixed together with crinoid stems in the Kipp Road Beds but due to their similarities are very difficult to distinguish.Three species *Devonoblastus leda* Hall,1862, *Nucleocrinus powelli* Reimann, 1935 and *Eleutherocrinus cassedayi* Shumard and Yan, 1855 occur infrequently in these shale layers.

Platyceratid gastropods *Naticonema lineata* and *Platyceras sp.* are found attached to or in very close proximity to these various pelmatozoans suggesting parasitic and/or commensalistic relationship. Furthermore, the corals *Heliophyllum halli* and *Favosites sp.* as well as brachiopods, bryozoans and pelecypods are encountered in the Kipp Road Beds each exhibiting different symbiotic interactions as described in the discussion above. Lastly, proetid and phacopid trilobites occur throughout the beds and together with all the other phyla formed a complex interrelated ecosystem.

Figure 12. A possibly new crinoid species related to *Poteriocrinites multicosta* (specimen courtesy of Gary Thomas)

Cumulative Miles	Incremental Miles	Route Description
54.5	1.0	Return to Deep Run Park, Pick up vehicles
57.1	3.6	Right onto Lake Shore Drive
57.6	0.5	Turn right onto Routes NY 5 & US 20 E
70.2	12.6	Turn right into Geneva McDonald's This is a Lunch/Restroom stop
73.5	3.3	Head on Rts. NY5 & US 20 E, turn right onto Rt. 96A
75.1	1.6	Turn right onto East Lake Road at Ventosa Winery
80.2	5.1	Turn left into Seneca Lake Camp

STOP # 2: Reeder Creek - Centerfield Limestone Member

Location Coordinates: 42.78390, -76.92698

One interesting piece of history, albeit only 223 years old, is the ruins of the grist mill (**Figure 13**) standing adjacent to Reeder Creek. The mill was built in 1800 by Benjamin Dey, a land surveyor, who was granted the land by Cayuga County a few years earlier (Gable, 2015). He also constructed the first house in Romulus in 1794. Then Benjamin Dey passed away in 1824 and the property was willed to his son Alexander H. Dey, who sold the property to Dr. Henry Reeder, for whom the creek was later named. Dr. Reeder died November 14, 1880 and is buried in the West Fayette Cemetery.

Fissile, medium gray shales of the Centerfield Member are exposed along Reeder Creek. Several species of rugose corals including common *Heliophyllum halli, Heterophrentis simplex* and *Eridophyllum subcaespitosum* are easily found in the shales whereas the tabulate coral *Favosites* are much less abundant. Fossil assemblages also contain numerous phacopid trilobites, *Eldredgeops* and *Greenops*, various brachiopods including *Athyris, Protodouvillina, Mediospirifer, Mucrospirifer* and *Rhipidomella*, fenestrate bryozoans and the platyceratid gastropods *Platyceras* and *Naticonema.* These species and many others interacted with each other and their environment constituting a dynamic ecosystem.

Figure 13. Grist mill on Reeder Creek.

		Leave Seneca Lake Camp, turn left onto E. Lake Rd.
81.1	0.9	Turn left onto Hahnel Road
82.5	1.4	Turn right onto Rt. 96A, proceed south
89.1	6.6	Exit from Rt.96A, stay straight onto Rt. 132 A
89.3	0.2	Right onto Main Street in Willard, Rt. 132
90.3	1.0	Park vehicles on left at pulloff at Seneca Lake shore
90.5	0.2	Continue walking 950 ft. to bridge over creek

STOP # 3: Indian Creek - Kashong Member

Location Coordinates: 42.68390, -76.88261

Indian Creek is structurally complex with at least 2 faults cutting diagonally across the main channel. As a result of these faults the topmost few inches of the Deep Run Member are exposed near the fork between north and south branches of Indian Creek. In turn, these lowest beds are overlain by the Menteth, Kashong and Windom Members of the Moscow Formation. At this stop, we will concentrate on the Kashong Shale Member and in particular the RC Bed and shales immediately below it.

Immediately east of (upstream from) the bridge over Indian Creek near its mouth at Seneca Lake, large irregular shaped concretions are concentrated in the West Bethany (upper) Submember of the Kashong Shale. Scattered fossils are mixed amongst the concretions suggesting this concretionary zone formed diagenetically after burial of the organisms on the substrate.

Still further upstream, at a Y-junction, a south tributary enters the main channel and exposes an unnamed mudstone layer, rich in the orthid brachiopod *Tropidoleptus carinatus*. Microconchid coiled worm? tubes and *Hederella* (formerly regarded as a bryozoan and now considered a colonial tube dwelling phoronid) commonly occur as epibionts on the convex surface of *Tropidoleptus*. Moreover, the examination of over 2500 brachiopods in the Hamilton Group of New York by Bordeaux and Brett (1990) revealed that *Tropidoleptus carinatus* and athyrids are among the most heavily encrusted shells by epibionts. This commensal relationship suggests the epibionts were aided by elevating them into a higher suspension feeding tier.

The tabulate coral *Pleurodictyum americanum* also commonly occurs in the unnamed Kashong mudstone layer. Another example of commensalism in the Ludlowville and Moscow Formations was demonstrated by Brett and Cottrell (1982). Their detailed research showed the tabulate coral *Pleurodictyum americanum* was a semiselective epifaunal organism that favored the dead shells of the gastropod *Palaeozygopleura hamiltoniae* (Hall, 1843), which were secondarily occupied by sipunculid worms. This strategy allowed the settlement of some larvae on mobile substrates assuring an ample supply of suspended food while remaining above the sediment-water interface as the coral grew.

The RC Bed (*Rhipidomella-Centronella* Bed) is a distinct 2 ft. thick ledge outcroping along most of the banks and directly above this unnamed mudstone layer in Indian Creek. Brett and Bordeaux (1990) noted that worm borings attributed to *Vermiforichnus* as well as encrustation by the epibionts *Hederella* and *Microconchus* (formerly *Spirobis*) preferentially covered the brachiopods *Spinocyrtia granulosa* (Conrad, 1839) and *Rhipidomella spp.,* thus providing additional evidence of parasitism and commensalism respectively. They further interpreted the RC Bed to have recorded multiple episodes of seafloor burial followed by winnowing of sediments, as evidenced by the poor preservation of the fossils, but at any one time symbiotic relationships between several organisms prevailed. These shallow water facies tend to have fewer epibionts on most shells because the shell surfaces were exposed to corrosion which tended to erase fragile encrusters.

End of Trip: Return to SUNY Brockport