

PROVISIONAL PALEOECOLOGICAL ANALYSIS OF THE DEVONIAN ROCKS OF THE COLUMBUS REGION

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INTRODUCTION

To anyone who collects carefully from the Devonian rocks in the Columbus region, it is soon evident that while there are many fossils that occur in all of the zones of the limestones, there is none that extends from them upward into the overlying Olentangy and Ohio shales. Further study shows that many species are found only in certain sets of strata of the Columbus and Delaware formations. There are two reasons for this distribution: time and change. The time that elapsed while the limestones and shales were being deposited was very long, possibly as much as 20,000,000 years. During this time many species died out (extinction), new species developed (filiation), other species came in from elsewhere (migration), and some species carried on without significant change (propagation). But all during this time conditions in the local seas were constantly changing—minor changes during the deposition time of the Columbus formation, distinct changes beginning with the Delaware, and great changes in Olentangy and Ohio time. The environments and sea-climates in which the marine communities (biocoenoses) lived changed. Many species could live only in certain conditions of bottom (sediments), depth, temperature, dissolved oxygen, illumination, salinity, neighbors, etc. When all of these, or any of these, changed, species either died out if they could not become adjusted to the new situation, or migrated elsewhere. The long-ranging forms (tycoen), such as *Leptaena*, *Atrypa*, *Megastrophia*, evidently could make these adjustments and stuck it out until the situation became too difficult even for them. Short-ranging types (eucoen), like *Nucleocrinus*, *Goldringia*, colonial corals, and many other zone fossils, flourished only while their environment remained at an optimum. To distinguish between the effects of time and change in segments of the geologic past is never easy, and here an attempt will only be made to point out some of the significant environments (biotopes) and their organic communities (biocoenoses) as they are revealed by the rock records of the environments (lithotopes) and their fossil contents (thanatocoenoses). The complete reconstruction of an ancient community is of course practically impossible for a lithotope never contains fossils of all the various organisms of the original biocoenose, only the remains of the few forms equipped with shells or skeletons of some sort.

The analytical columnar section (Figure 1) for the Devonian rocks of the Columbus region will serve to focus the relative positions of the lithotopes to be discussed below. The alphabetical zonation is that established by C. R. Stauffer in 1910; the zone fossils are in part his, and in part, suggested here.

DISCUSSION OF LITHOTOPES AND BIOCOENOSES (THANATOCOENOSES)

Normal Limestone Lithotope:

Here are included the relatively pure limestones of the Delhi member (Zones E, F, G, H), throughout which the same general type of fossil assemblage persists with faunule modifications due to the time factor. The biotope during this time was nearly constant,—warm, clear, shallow, well-illuminated, quiet sea-water

of normal salinity.¹ The richly-specified faunules were composed of mostly benthonic types, comprising several interlocked layer-societies or associations of different bottom levels; the burrowing animals, especially pelecypods (*Conocardium* and *Modiomorpha*); forms living directly on the bottom, fixed or crawling, such as brachiopods, small corals and bryozoa, gastropods and trilobites; forms raised off the bottom by stems or ramose growth modes, such as blastoids, crinoids, large horn corals, colonial corals; and the bottom hugging swimmers (nektobenthon), the frilled, breviconic, and orthoconic cephalopods.

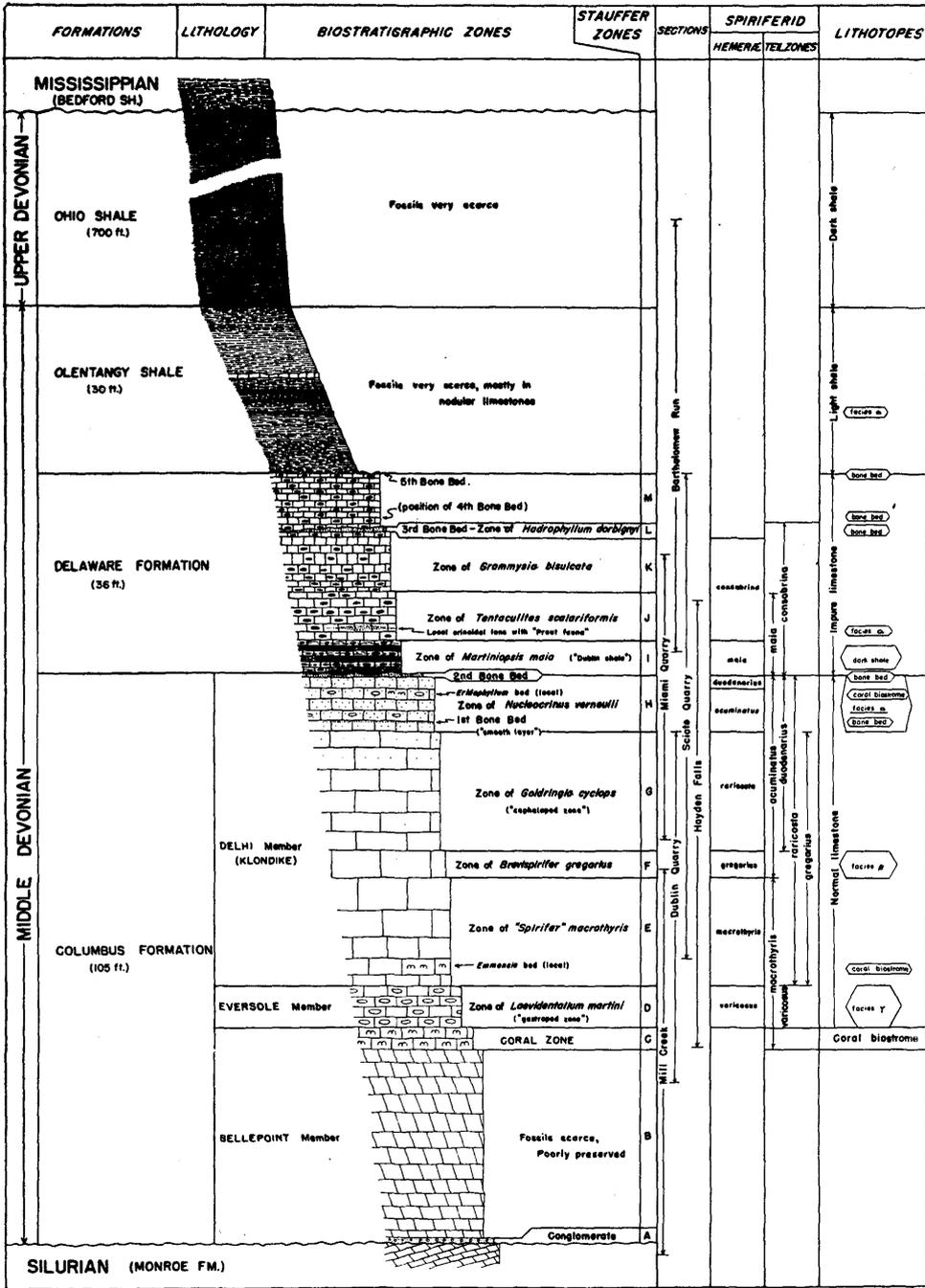
In this "normal" environment flourished the large, heavy-shelled gastropods (*Pleuronotus*, *Turbonopsis*, *Palaeotrochus*) and large nautiloides,—forms which are almost completely absent from higher or lower beds. The corals of this biotope are almost exclusively types suited to a soft bottom lacking solid points for fixation: many species of horn corals and such honeycomb corals with pear-shaped colonies as *Favosites hemisphericus*, all of which lay loose on the substratum. This is in strong contrast to the bushy and sprawling types with fewer free horn corals of the coral biostromes of Zone C.

The mottled weakly pelmatozoic limestones of Zone G show pronounced differential weathering due to the presence of thick, finger-like, anastomosing networks of finer, more-easily weathered material. This may be the highly triturated faecal material of crawling or burrowing detritivores analogous to the modern holothurians, but there is no more direct evidence of these lowly members of the "normal" communities.

Facies α . An interesting facies of the normal environment exists in the upper part of the Delhi member (Zone H). Layers of limestone are composed largely of pelmatozoan remains,—*Nucleocrinus*, crinoid and blastoid stem fragments, and occasional large crinoid heads (*Dolatocrinus* and *Megistocrinus*). Other members of the "normal" biocoenose are not lacking, but are reduced in numbers. From time to time during the deposition of Zone H large patches of the bottom must have been covered by "colonies" of crinoids and blastoids swaying on their stems, the dominants of this society. Sediments accumulated so slowly that rapid burial, necessary for preservation of blastoids and crinoids with stems still attached, did not obtain. The action of scavengers in disarticulating stems and other parts made such preservation even more unlikely. The crinoids were all camerates with stout stems and large calices about the size of peaches. A special associate of these crinoids was the large spiny gastropod, *Platyceras dumosum*. This handsome species belongs to a Devonian genus whose species nearly always occur with crinoids, often actually attached to the calice. This constant association is often considered to have been parasitic but may well have been the more mutually beneficial arrangement, symbiosis.

Another example of Facies α , the crinoid-*Platyceras* layer society, is the thin crinoidal lens in the lower part of the Delaware formation at the Miami quarry, on the Olentangy River two miles north of Bartholomew Run. This is a very restricted occurrence and seems to represent a temporary and local re-establishment of Columbus (Delhi) biotopic conditions. The crinoids are small, and likewise all specimens of *Platyceras* and the closely related *Orthonychia* are small. This thanatocoenose, however, is not a recurrence of any of those of the Delhi, and is quite distinct from those of the rest of the Delaware. It is analogous to that of Zone H, and homologous to that of the Prout limestone of northern Ohio,—a nice instance of homologous lithotopes with analogous thanatocoenoses due to the time factor.

¹That is, normal salinity for the seas of Devonian times, which must have been appreciably less saline than modern seas.



BIOSTRATIGRAPHIC ANALYSIS OF COLUMBUS DEVONIAN SECTION

FIG. 1. Biostratigraphic analysis of Columbus devonian section.

Facies β . The concentration of *Brevispirifer gregarius* in vast numbers of Zone F represents another facies, one characterized by bottom-lying brachiopods,—a “brachiopod bank.” This species is found not only in this zone, but also in the ones just below and above but in much smaller numbers. During the time of Zone F in this region, however, *B. gregarius* reached its local acme and flourished almost to the exclusion of other forms,—a single dominant layer-society. This distribution is a good example of the biostratigraphic concept of the hemera, the acme time of a species, the epibole, the deposits accumulated during the hemera, and the biozone (or more accurately, teilzone), the complete duration, in strata, of a species, thus: the *gregarius*-biozone (teilzone) extends through Zones E, F, and G, the Zone F epibole was deposited during the *gregarius*-hemera. Similarly Zone E is the *macrothysis*-hemera, Zone G the *ravicosta*-hemera, while Zone H includes two hemerae, the *acuminatus* in its lower part, the *duodenarius* at its very top, all based upon spiriferids.

The occasional occurrence of conchs of *Goldringia* in the midst of these departed brachiopod hosts of Zone F suggests that this cephalopod may have been a raider that found these banks especially good feeding grounds.

Facies γ . The Eversole chert member, just below the Delhi member, with its lithotope facies of fossiliferous white or gray chert, contains the largest number of species of any unit. Among the 85 species now known, many of those of the “normal” limestone lithotope make their first appearance. Environmental conditions of this lithotope, except for the still practically unknown factors that brought about the periodic accumulation of layers of silica, were the same as for the normal limestones. It would seem that the richness of the faunule is due to the chert rather than a biologic factor. That is, the benthonic biocoenose of the Eversole differed from later ones only insofar as the time factor is involved; the thanatocoenose, however, because of more favorable conditions of preservation, contains many forms unknown or very scarce in other lithotopes.

The most important feature of the Eversole facies thanatocoenose is the large number of species of gastropods,—30, about triple the usual number of the “normal” limestones. Especially abundant are bellerophontids and pleurotomariids. The thinness of the shells of these forms made them particularly liable to destruction before burial and elimination during diagenesis. In the limestones it is rare to find a gastropod with some of its replaced shell. Most are steinkerns. The same applies to the pelecypods, with the exception of the heavy-shelled *Conocardium*.

Chert is not confined to the Eversole member, and is common in Zone H and throughout the Delaware formation. However, in these higher horizons it is almost wholly unfossiliferous except in the bone beds. In the Eversole member the chert was probably a syngenetic silica gel; in the higher members it is of secondary origin, replacing the limestone and appearing as concretionary masses.

Coral Biostrome Lithotope:

True coral reefs do not occur in the limestones of the Columbus region, but in Zone C, the upper few feet of the Bellepoint member, corals are so numerous as to form a large part of the zone and qualify as a biostrome. The lithotope, a brown magnesian limestone with a thanatocoenose of many species of tabulate and rugose corals and stromatoporoids, represents an environment especially favorable for the development of hermatypic corals. Two layer-societies are here commingled, the primary one being that of bottom-hugging types such as horn corals and innumerable large sprawling stromatoporoids, with many of the usual benthic forms of the “normal” limestone biotope. This basal society provided firm sites for the fixation of larger coral colonies which grew away from the bottom to a

height of two or three feet; colonial rugosa such as *Diphyphyllum*, *Synaptophyllum* and *Cylindrophyllum*, large massive and ramose tabulates such as *Favosites*, *Emmonsia*, and *Cladopora*. The stimulus for the development of these lotic types was probably more agitated water than prevailed during the deposition time of the higher members.

At a few localities small biostromes of the secondary colonial coral layer society, usually the species *Eridophyllum seriale*, occur a few feet from the top of the Delhi member. One such occurrence is in the old Marble Cliff quarry on the east side of the Scioto River, and similar ones in apparently the same stratigraphic position are found sporadically as far north as Sandusky. Limited biostromes of the massive tabulate, *Emmonsia*, are found at a few places a few feet above the Eversole chert member.

Bone Bed Lithotopes:

The five bone beds of the Columbus and Delaware formations are records of a biotope distinctly different from the preceding. They are thin layers of fragmentary fossils, mostly of small size, and mostly crinoidal or pelmatozoic, mixed with bones, scales, teeth and bits of armor plate of fishes, button corals; the whole forming a coarsely granular, "sandy" limestone. They represent, not the lime-mud depositing conditions of the great bulk of the limestones, but epochs when the sea-bottom was above the base of wave action and fine-grained muds could not accumulate. Erosion (subaqueous) rather than deposition was the order of the day. Under these conditions the bone beds are the concentrated coarse residue of perhaps many feet of lime muds. In places they rest on mud-cracked limestones, indicating occasional exposure.

The bone bed lithotopes record a sandy bottom biotope, a favorable environment for certain benthonic communities. But the composition of these biocoenoses is poorly known because of the slowness of burial and effects of detritivores and scavengers. The fish remains are all of fresh-water forms borne in from Cincinnati. They are thinly diffused throughout the limestones and concentrated in the bone beds. They are not records of periodic catastrophic annihilation of shoals of marine fishes, as often supposed. Most of the other fossils are the regular eurytropic species of the limestone lithotopes,—species widely adapted to a variety of benthonic situations. In other words, the bone beds have no special faunules, with the possible exception of ostracods, for whom the sandy bottoms were evidently suitable, and the curious stenotopic button-coral, *Hadrophyllum d'orbigny*, which flourished only on sandy bottoms.

Impure Limestone Lithotope:

This lithotope extends generally through the Delaware formation and especially in Zones J, K, and M. It consists of argillaceous blue to brown limestones, with many scattered dark chert bands, and represents a biotope much less favorable to organisms than the clear waters of the Delhi member. The water was still shallow, but cooler and turbid with fine mud. The thanatocoenoses of less than half as many species in the various zones compared with those of the Delhi member indicate equally reduced biocoenoses. Notable is the practically complete absence of groups common in the normal limestone lithotopes: tabulates, rugose corals, stromatoporoids, blastoids, crinoids, gastropods, cephalopods and trilobites. The faunules consist mostly of brachiopods and pelecypods. The impoverished biocoenoses comprised three main layer-societies: the bottom burrowers or plowers such as *Lingula*, *Grammysia*, and *Nyassa*, the sessile benthonic forms such as most brachiopods and *Glyptodesma*, and occasional shoals of nektonic gastropods (pteropods) such as *Tentaculites*. The stratal distribution of these is different

from that in the normal limestones. Instead of being well-mixed assemblages of many species, species commonly occur singly but in large numbers of individuals. Slabs of the Delaware are commonly found covered by hundreds of *Tentaculites scalariformis*, or *Leptaena rhomboidalis*, or Spirifers, *Grammysia*, *Glyptodesmae*, etc. This fewness of kind with local abundance of individuals is characteristic of waters of abnormal salinities, boreal environments, or very muddy bottoms, as against the abundance of kind with fewer individuals of warm, clear, normally-haline environments. In the present case there is some indication of subhaline conditions during Delaware time, such as the shale facies of Zone I, which has, however, a thanatocoenose distinct from those of the more calcareous lithotopes under consideration. Colder water may account for the great reduction or disappearance of such stenothermic types as corals and crinoids, but not for such eurythermic forms as trilobites, gastropods, and cephalopods. Further and closer study of the Delaware faunules is necessary before a satisfactory resolution of the biotopes can be made, but it is likely that they were subhaline, not so much as in Zone I, and somewhat cooler and decidedly muddier than those of the Delhi. The occurrence in the Delaware of layers such as the bone beds and other crinoidal lenses, containing normal-haline clear-water thanatocoenoses, further emphasizes the distinctness of this lithotope.

Dark Shale Lithotope:

These are exemplified by the Ohio shale and the "Dublin shale" phase of Zone I of the Delaware, and are essentially nearly unfossiliferous bituminous shales. The Ohio shale is black; that of Zone I is dark brown. Both are lithotopes indicative of brackish-water environments; both contain analogous thanatocoenoses of a few species of thin-shelled brachiopods (*Leiorhynchus*, *Lingula*, and *Orbiculoidea*) with occasional euryhaline wanderers. *Lingula*, a mobile form, lives in muddy bottoms, the others were sessile and probably fixed to seaweed. Conditions were quite impossible for other groups such as corals, crinoids, trilobites, cephalopods, etc. They were less rigorous in the Dublin shale biotope than in that of the Ohio shale, where the blackness of the deposit with much pyrite indicates foul water with very low oxygen content. Fossils are fairly common in the Dublin shale and have the characteristic brackish-water facies of few species and many individuals. In the Ohio they are very scarce, and are significant only in the Bellefontaine outlier some 50 miles to the west of the Columbus region, nearer the old shore of Cincinnati. Here there are several layers near the base of the formation crowded with individuals of *Lingula*, *Orbiculoidea*, *Leiorhynchus* and *Chonetes*, together with the vast numbers of *Styliolina*. The last may represent pelagic dwellers in the better-aerated surface waters. The fish remains of the Ohio, like those of the Middle Devonian limestones, are not those of endemic marine forms, but remains of stray carcasses drifted in from the streams of Cincinnati. The same origin also applies to the occasional plant remains in the Ohio. Some of the silicified logs of *Callixylon* bear traces of attached or entangled crinoids (*Melocrinus*) that they bore while floating at the surface of the foul-bottomed sea.

The Dublin lithotope is a dark shale facies which passes laterally into the impure limestones of Zone I. These limestones carry the usual thanatocoenoses of the higher zones of the Delaware. Species of the Dublin thanatocoenose likewise pass laterally into the limestones, but those of the limestone do not extend into the shale. The screening off of the biocoenose of the lime mud areas from that of the contemporaneous dark mud areas was probably due to differences of bottom, salinity, and aeration, but mingling in the opposite direction was possible because of the greater environmental tolerance of the species of the brackish-water biotopes.

Light Shale Lithotope:

The Olentangy shale, a slightly calcareous gray-green clayey shale with thin layers of impure limestone, is nearly unfossiliferous. Fossils, except for microscopic forms (ostracods, conodonts, and plant remains), are found almost exclusively in the nodular pyritiferous limestones. The presence of one or two thin layers of black shale in the Olentangy and of occasional layers of green shale in the lower part of the Ohio shale suggest that the Olentangy is a basal phase of the Ohio. Its thanatocoenose consists of a very few forms indicative, not of the brackish-water biotope of the Ohio, but a very impoverished nearly normally saline but uncongential biotope; one or two small rugose corals, a few bryozoans, several tolerant brachiopods (*Lingula*, *Chonetes*, *Ambocoelia*), an orthoconic nautiloid, and goniatites (*Tornoceras* and *Manticoceras*), and a few others. Neither species nor individuals are abundant. Seemingly this was a depauperate biocoenose of the normal benthonic type eking out a ragged existence against stifling fine muds, most of the time driven out by mud, returning during the brief intervals of reasonably clear water represented by the thin limestones. Occasional crinoid plantations did exist, notably the one at the type locality of the shale near Delaware,—a lens several inches thick of comminuted remains of the large *Melocrinus bainbridgensis*, a species also found in the green layers near the base of the Ohio shale and the probable pseudobenthonic associate of the *Callixylon* logs of that formation.

SUMMARY PALEOECOLOGICAL ANALYSIS BY LITHOTOPES

1. *Normal limestone lithotope*: fine-grained to somewhat crystalline nearly pure limestone, usually thick-bedded, locally weakly pelmatozoic.

Biotope: normally saline, warm, quiet, clear, shallow water below base level, bottom mainly mud.

Biocoenose (thanatocoenose): richly speciated benthonic multilayered society of rugose corals, crinoids, byozoans, brachiopods, large gastropods, large cephalopods, and trilobites.

Distribution: Delhi member.

Facies:

α —crinoidal limestone.

Biotope: as above, but sandy bottom.

Biocoenose (thanatocoenose): crinoid-blastoid-*Platyceras* layer society dominant.

Distribution: Zone H of Delhi member, and Miami Quarry lens of lower Delaware formation. Also the thin crinoid lens in the Olentangy shale at Delaware.

β —brachiopod limestone (*gregarius-hemera*).

Biotope: as above.

Biocoenose (thanatocoenose): sessile brachiopod layer-society dominant.

Distribution: Zone F of Columbus formation, Delhi member.

γ —fossiliferous gray-white chert.

Biotope: as above.

Biocoenose (thanatocoenose): multi-layered benthonic society, richly speciated, gastropods dominant.

Distribution: Eversole chert member.

2. *Coral biostrome lithotope*: brown magnesian limestone crowded with corals.

Biotope: as in normal limestone biotope, but water more agitated.

Biocoenose (thanatocoenose): dual-layered, lotic coral society dominant.

Distribution: Zone C; minor occurrences in Zones E and H.

3. *Bone bed lithotope*: crinoidal limestone with heavy concentration of fish remains.
Biotope: as in normal limestone, but water agitated, bottom sandy and above wave base.
Biocoenose (thanatocoenose): dual-layered society, mostly eurytropic forms, dominant.
Distribution: five bone beds in Delhi member and Delaware formation.
4. *Impure limestone lithotope*: argillaceous blue-brown limestone with chert layers and thin shale bands.
Biotope: salinity slightly subnormal, cool, muddy water below wave base.
Biocoenose (thanatocoenose): triple-layered benthonic societies, restricted faunules, few species, individuals locally abundant.
Distribution: generally throughout Delaware formation.
5. *Light shale lithotope*: slightly calcareous green-gray shale with thin layers of impure, pyritiferous limestone.
Biotope: normally saline, warm, but very muddy water below wave base, subnormal oxygen content.
Biocoenose (thanatocoenose): depauperate, multi-layered society, species and individuals few.
Distribution: Olentangy shale.
6. *Dark shale lithotope*: brown to black, often pyritiferous, bituminous shale.
Biotope: brackish water, often foul and poorly aerated except superficially, muddy, below wave base.
Biocoenose (thanatocoenose): few species of thin-shelled types, with individuals locally numerous, forming two or three layer-societies (surface, on bottom, and in bottom).
Distribution: Ohio shale and locally in Zone I of Delaware formation.