PATTERNS OF PHYLETIC EVOLUTION IN THE TRENTON GROUP

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INTRODUCTION

The Trenton Group has been the subject of 60 years of continuous biostratigraphic study since Marshall Kay began his work during the early 1930's. The unit displays a remarkably rich and diverse fossil assemblage which, along with its facies patterns, is now quite well known. The Trenton Group is thus very well suited for research directed at understanding patterns of evolution. This ongoing research program is currently focused on recognizing patterns of intraspecific clinal variation and relating these to facies change in order to develop comprehensive records of evolutionary events. Two case studies are now complete. Evolution within the crinoid genus *Ectenocrinus* has been described (Titus, 1989). A similar paper on the brachiopod genus Sowerbyella is pending (Titus, 1992). This field guide will serve as an appendix to both of those papers.

PATTERNS OF EVOLUTION

The two broadest categories of evolutionary patterns are cladogenesis and anagenesis. Cladogenesis occurs when a population is divided and, from the two isolates, separate species are derived. This is also called allopatric speciation. Cladogenesis is multiplicative, as two or more taxa are descended from a single ancestral form. Anagenesis, or phyletic evolution, is not. It consists of evolutionary change within an undivided lineage. It is driven by natural selection and thus conforms to Darwin's original view of evolution. Virtually all recent workers agree that both patterns do occur and much of the current debate centers over their relative frequencies and macroevolutionary significance.

The Trenton Group is well suited for the study of anagenesis. The unit is well exposed across an outcrop belt extending from Canajoharie to Ontario (Figs. 1, 2). Deposition of the unit spanned a period of at least 8 million years without any significant breaks in the record. There is a rich and diverse fossil fauna which is very well preserved. These assemblages are found within a diverse facies mosaic (Fig. 3). The author has spent 20 years studying the Trenton and has documented its facies patterns and the biostratigraphy of over 200 of its species (Titus, 1986, 1988). This provides a wealth

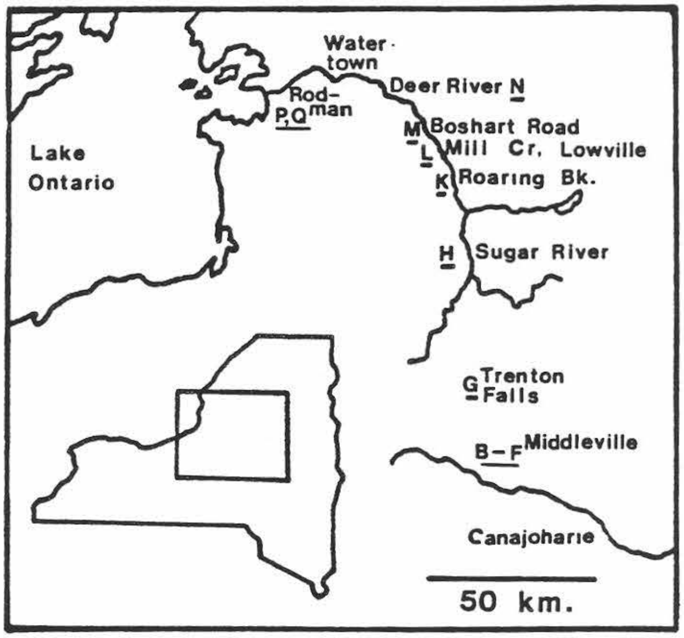


Figure 1. Map of the major locations of the Trenton Group.

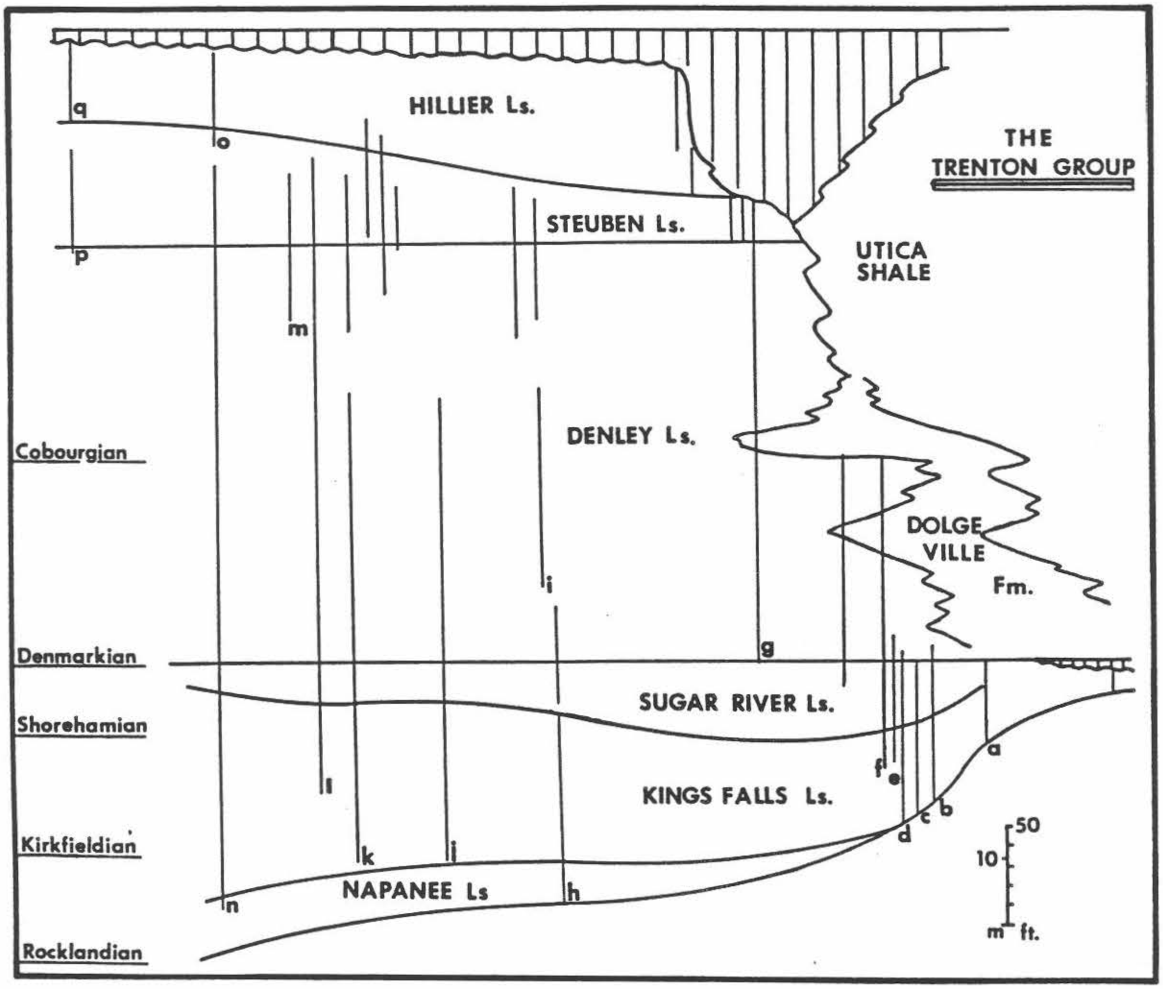


Figure 2. Stratigraphy of the Trenton Group. Letters refer to Fig. 1.

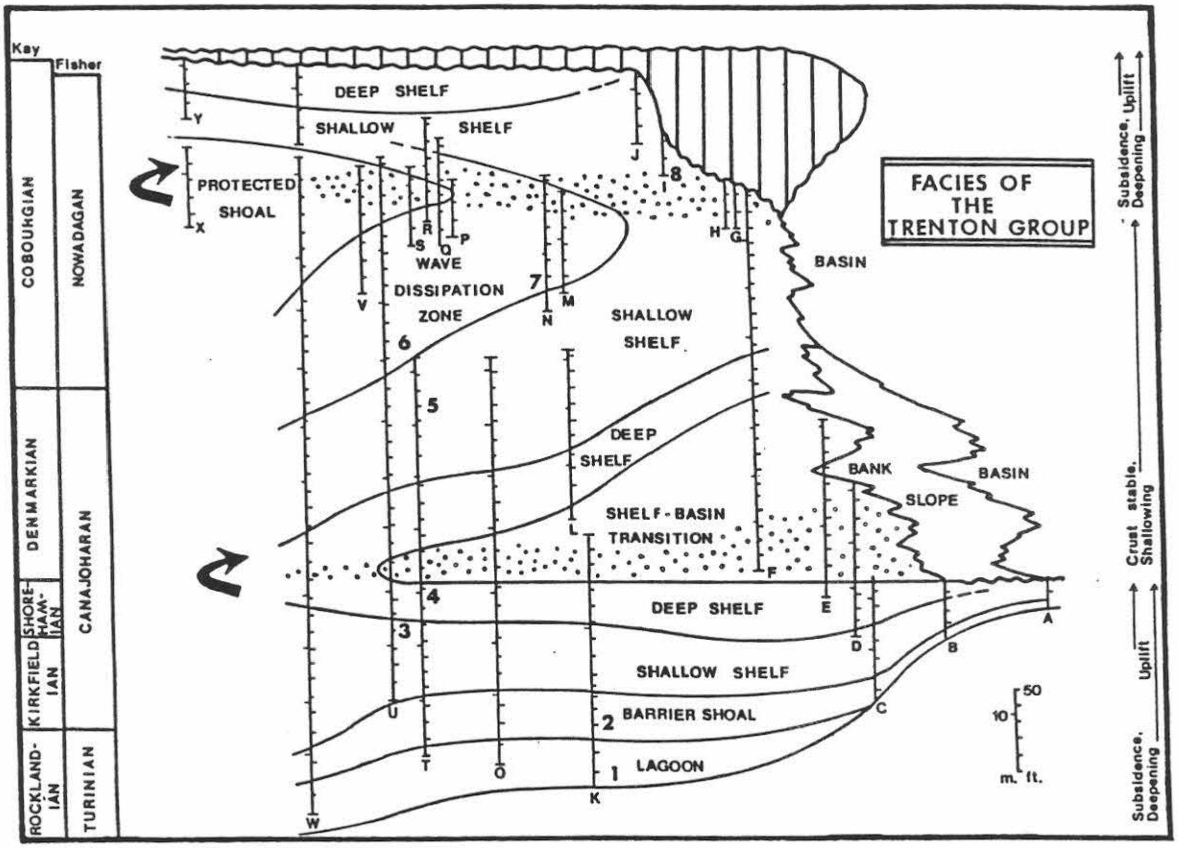


Figure 3. Facies of the Trenton Group. Arrows and stipples define the facies bottlenecks. Stippled areas display very few specimens of *Sowerbyella*. Numbers are trip stops. Stop six is approximate.

of background information. Thus any lineage can be knowledgeably traced through the entire Trenton Group and any phyletic evolutionary change can be observed.

The Trenton Group is not well suited for the documentation of cladogenesis. The carbonate platform is not likely to have any significant reproduction barriers and thus allopatric separation and cladogenesis is unlikely. It has not yet been observed. No examples of punctuated equilibrium have yet been demonstrated, although several possibilities are being investigated.

PHYLETIC EVOLUTION IN THE TRENTON GROUP

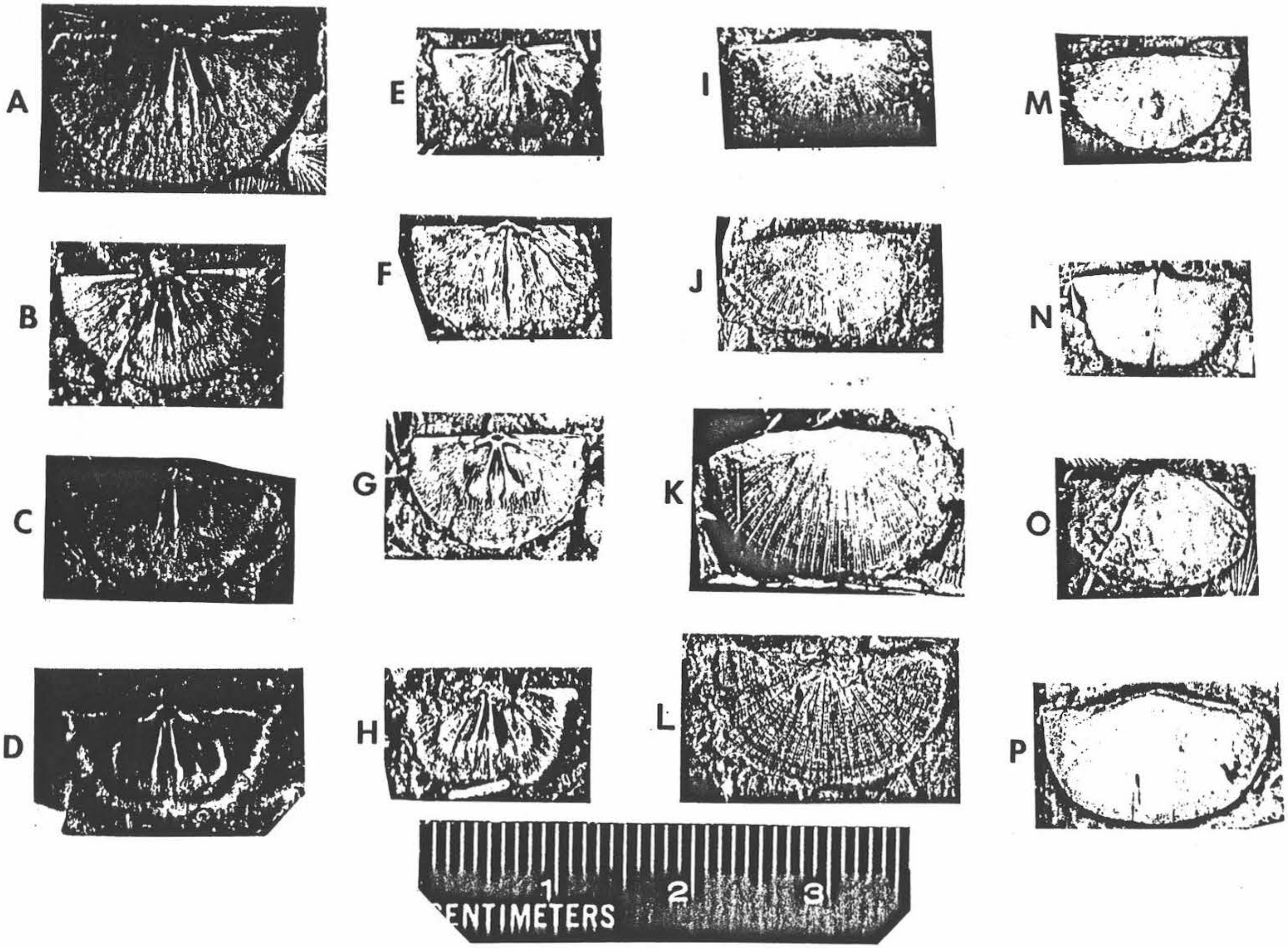
Phyletic evolution, as observed in the Trenton Group, can be described as continuously changing clinal variation in a continuously changing facies mosaic. Clinal variation is systematic geographic or ecologic variation within a species. Although such variation is commonplace among modern species, it has not often been reported in the fossil record (however, see Cisne et al. 1980a, 1980b & 1982 for other Trentonian examples). Recent studies in the Trenton Group suggest that clinal variation plays an important role in phyletic evolution: directional evolution through substantial episodes of time.

The following three models relate clinal variation to phyletic evolution: First, during times when facies are expanding and diversifying, species widen their ranges by evolving clinal variants adapted to the newly available environments. They become eurytopic by polymorphism. Second and conversely, at times when there is restriction of available facies, species experience cline sorting. Polytypic species pass through a facies bottleneck. Morphologies linked to disappearing environments are selected against and the species become stenotopic. In the third variation species can experience a form of clinal orthoselection when environments are deteriorating at one end of a species range while opportunities are expanding at the other end. Continuous, adaptive and directional selection occurs and the species evolves.

EXAMPLES OF PHYLETIC EVOLUTION

Model One

The lower Trentonian brachiopod *Sowerbyella curdsvillensis* illustrates the first model. This brachiopod evolved considerable clinal variation when a variety of environments became available during the lower Trentonian transgression. In quieter, mud-bottomed environments the species evolved a small morphology with a simple brachial valve interior (Fig. 4a). The pedicle exterior has a medial fold and alate corners (Fig. 4i).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CENTIMETERS

This form prevails in the nearshore lagoon and offshore deeper shelf facies (Fig. 3). In the adjacent wave swept, barrier bar facies *Sowerbyella* is much larger and its brachial interiors are quite ornate (Fig. 4d). They display septa, subperipheral thickenings, muscle scars and abundant and well developed vascular markings. The pedicle exteriors are often flattened or broadly rounded. These morphologies grade into each other in what is called a sloping cline. In the past this intergradation was not recognized and the plain, quiet water form was called *S. punctostriatus*.

During deposition of the middle Trenton Group a diversity of environments appeared in shallowing facies pattern (Fig. 3). Once again a model one pattern of clinal variation evolved. Plain brachial interiors occur in the quieter, muddier bottom environments while ornate brachial interiors are found in more agitated settings. This is a striking parallel to the lower Trentonian cline. There are differences, however. A new cline is seen in the morphology of the pedicle exteriors. In the middle Trentonian, deep and shallow shelf facies pedicles tend to have medial folds as was the case in similar lower Trentonian facies. In the barrier facies, however, pedicle exteriors tend to be more rounded and inflated. In the protected shoal facies there tends to be a broadly rounded medial fold. Thus, the overall structure of the middle Trentonian *Sowerbyella* cline is different and this cline should be recognized as a new species.

Model Two

Model Two occurs when there is cline sorting which accompanies times of facies restriction. Such an event would affect a species when facies change reduces its suitable habitats to a minimum. Perhaps a transgression would reduce suitable shallow water habitat, greatly restricting a species range. If polytypic forms pass through such a facies bottleneck, they are subject to intense natural selection. Inadaptive traits are selected against; these disappear and the species emerges from the facies bottleneck altered.

This is illustrated in the *Sowerbyella* populations of the middle Trentonian. Twice, there were times when the range of *Sowerbyella* was greatly restricted (stippled zones on Fig. 3). First, at the close of the lower Trentonian transgression, shallow water habitats had disappeared. The large forms with ornate brachial interiors were selected against and they are not seen above the facies bottleneck (Fig. 3). The middle Trentonian *Sowerbyella*, as noted above, closely parallels the lower Trentonian *S. curdsvillensis*. Both have plain, quiet

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Figure 4. a-d, *Sowerbyella curdsvillensis*, brachial interiors; e-h, *Sowerbyella*. n. sp., brachial interiors; i-l, *S. curdsvillensis*, pedicle exteriors; m-o, *S.* n. sp., pedicle exteriors; p, *S. subovalis*, pedicle exteriors.

water forms grading into ornate types found in agitated facies. However the middle Trentonian *Sowerbyella* is not as big as in the lower Trentonian form and it only very rarely displays well developed vascular markings (Figs. e-h). Large size and vascular markings are traits associated with shallow waters and selected against, within the deep water bottleneck, when the shallow facies disappeared.

A similar facies bottleneck is found at the top of the middle Trentonian Denley Limestone. During deposition of the Denley a well defined, east-to-west and deep-to-shallow *Sowerbyella* cline had evolved (see above). *Sowerbyella*, however, is virtually absent in the lower Steuben Limestone (stippled area, Fig. 3) except in the far west at Rodman. Lower Steuben depositional environments were evidently too agitated for *Sowerbyella* except in the quieter western protected shoal facies (Fig. 3). Only one clinal variant is found there. This form is recognized by the broadly rounded medial fold on the pedicle exterior (Fig. 4p) and plain brachial interior. This clinal variant made it through the western facies bottleneck (arrow on Fig. 3) and became a founding population for *Sowerbyella subovalis*, the most common species of *Sowerbyella* seen in the upper Trenton Group. The broadly rounded pedicle exterior is what most characterizes *S. subovalis*. The trait was, evidently, inherited from the bottleneck population.

Model Three

The columnals of the crinoid genus *Ectenocrinus* record an example of Model Three clinal variation. *Ectenocrinus* is first found in the deeper shelf facies of the Sugar River Limestone (Fig. 3). There it is commonly recognized by its nearly triangular columnals with triangular lumina (Fig. 5n-s). It passed, without effect, through the same facies bottleneck that generated the middle Trentonian species of Sowerbyella (arrow on Fig. 3). During the middle Trentonian, in a Model One case, it evolved a variety of clinal variants, which ranged in distribution from deep shelf to shallow water extremes (Fig. 5). The newly evolved shallow water clinal variants forms have round columnals with pentagonal lumina (Fig. 5a-c). The middle Trentonian records a long episode of shallowing facies. This included the carbonate bank margin which was shallowing and steepening (Titus, 1986, Fig. 7). Thus while new shallow water facies were opening up in the west, the old, deeper shelf facies were being restricted in the east. The result was a form of clinal orthoselection. As deep water environments shrank, the triangular forms disappeared. At the same time shallowing facies favored the round columnal forms and they eventually were the survivors. The transition is between the species *E. triangulus* and *E. simplex*. The transition is gradual and both facies and clines are central to this event.

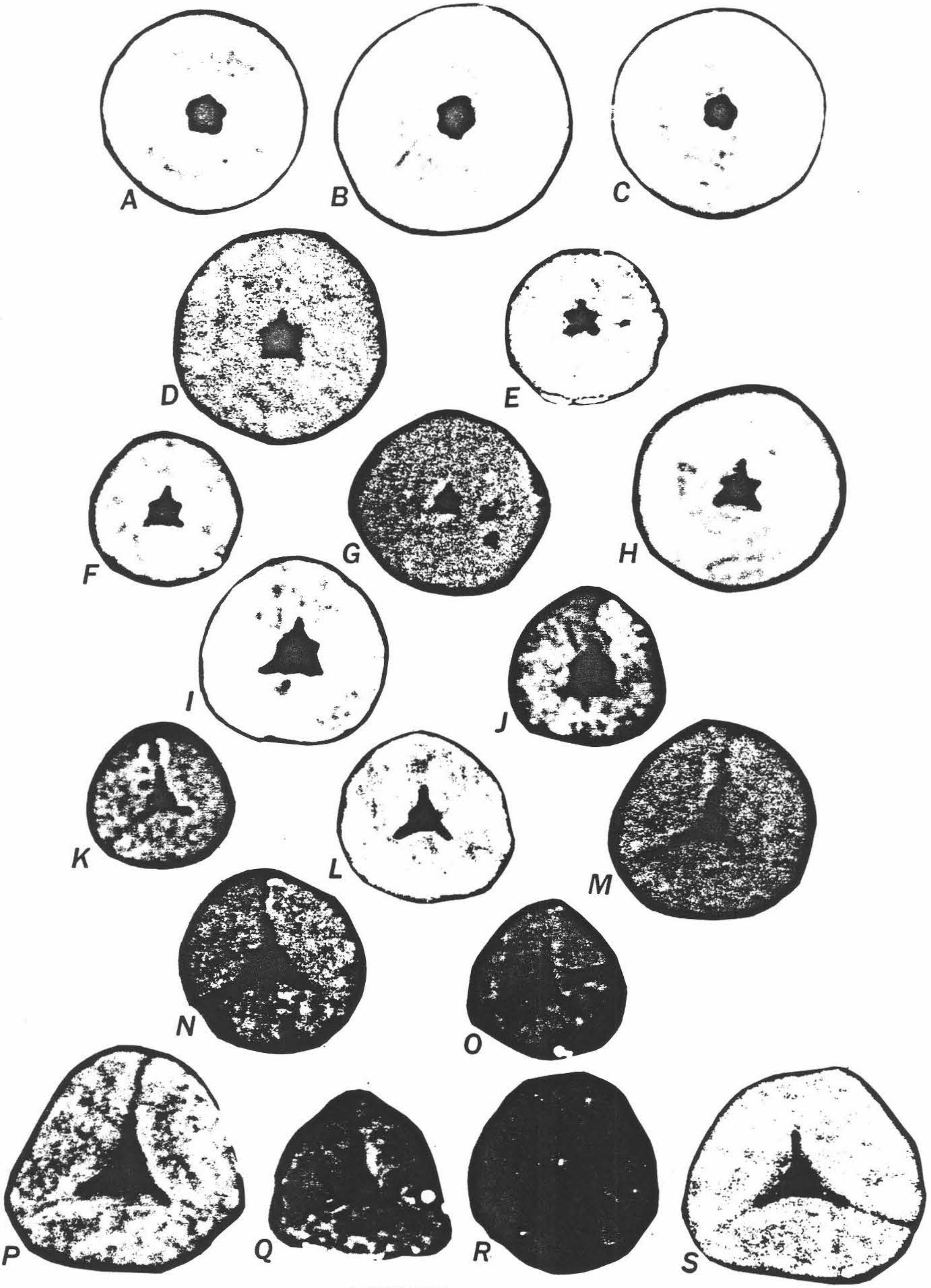

FIGURE FIVE

CRYPTIC VARIATION

An interesting problem which was raised but not solved in Titus (1992) was the disappearance and reappearance of the ornately sculptured brachial valve interiors that Sowerbyella possesses in the agitated facies in the lower and, then again, in the middle Trenton Group. These valves with their well-developed muscle scars are adapted to life in a rugged environment where individuals, from time to time, are overturned and must right themselves (there is no pedicle in *Sowerbyella*. Ornately sculptured valves are commonplace in the barrier shoal facies of the lower Kings Falls Limestone. They become rare in the deeper water facies of the upper Kings Falls and disappear in the deep shelf Sugar River Limestone. Later the trait reappears in the agitated facies of the Denley Limestone. Where did this trait go during the interval? Did it endure genetic extinction? Did it then re-evolve? If not, then where was it? The problem is a difficult one for a paleontologist who normally does not investigate the genetics of fossil species. Inferences, however, can be made.

A potential solution to the problem is to regard the ornate traits as going through cycles of being manifest and cryptic. Cryptic traits exist in the genotype but are not expressed in the phenotype. There are numerous genetic mechanisms which can preserve the genetics of a trait while, at the same time, preventing its expression. Traits can exist in a cryptic state as recessives. Stabilizing selection can keep a trait cryptic by eliminating the deleterious recessive homozygotes which express the trait. Heterosis will preserve cryptic diversity. Modifier genes can serve to mask the expression of traits while preserving them. There are ecological means of preserving cryptic variation as well.

Cryptic traits serve to maintain a maximum of species genetic diversity with a minimum of risk to the individual (any deleterious effect is masked). The benefit to the species is that the cryptic genetic diversity may sometime prove valuable as the environment shifts. any concept of species diversity thus has two facets. Expressed diversity is the sum total of traits which work successfully in whatever environment does exist. Cryptic variation represents a reserve of traits which may be potentially valuable in some future environment. Genes and species cannot foretell the future, but natural selection is most likely to preserve those species which ahve enough diversity to sustain themselves through the vicissitudes of change that always occur with time.

The on and off distribution of the ornate brachial interiors of *Sowerbyella* may well represent cycles of being manifest and cryptic traits. Indeed this may be key to accounting for the long-term success of this taxon. This issue of cryptic variation deserves much more attention. It is better illustrated in the strophomenid genus *Rafinesquina*. Future work will focus upon this.

CONCLUSIONS

In the half century since clinal variation was first described by Huxley, paleontologists contributed little to our understanding of this concept. There needs to be a greater awareness of clinal variation in the definition of fossil species and as a factor in phyletic evolution. To date, biologists have done most of the work but they have viewed clinal variation only in terms of geography and ecology. Paleontologists can explore the temporal dimension. This is being done in the Trenton Group where we can observe clines through time as well as through space. We see in the Trenton Group that, by the standards of geologic time, clinal variation is immediately adaptive to changing environments. It is through clinal variation that species can track facies change through time. Finally it is the linkage of clinal variation and facies change through time which appears to define phyletic evolution.

FIELD DISCUSSION TOPICS

Our trip gives us an opportunity to examine, in the field, evidence pertinent to some of the most difficult issues confronting paleontologists as we try to understand the fossil record of evolution. At the end of this trip we might well take time to discuss some of them. Two issues are outlined below.

This field trip illustrates some of the basic problems that paleontologists face in recognizing fossil species. We have always relied too much on the typological approach to species recognition. The two lower Trentonian species of *Sowerbyella*, which have been traditionally recognized, are *S. punctostriatus* and *S. curdsvillensis*. As we have seen, they turn out to be intergrading clinal variants of a single species. The typological approach has failed us, but when we employ a polytypic approach to species recognition other difficulties appear. The polytypic middle Trentonian form, *Sowerbyella*. n. sp., is an example. This form has a clinal variant which is identical to the deep water forms of the lower Trentonian species. It also has a clinal variant which is identical to the upper Trentonian form, *S. subovalis*. What is unique about the middle Trentonian form is the *combination* of clinal variants. Is this a proper criteria for species definition? I think so. How do you react?

A number of workers vigorously deny that phyletic evolution can produce new species. Species, instead, are regarded as sharply bounded spatiotemporal entities. No matter how much evolution may occur within a phyletic lineage, they argue that only one species should be recognized. Adherents of this point of view would thus argue that only one species of *Sowerbyella* can be recognized in the entire Trentonian sequence. I believe that I am observing phyletic evolution producing change at the species level and thus that phyletic change does result in macroevolution. I suspect that species generally are not spatiotemporally bounded entities and therefore that species are emphemeral, evolving continuously through time. You have seen some of the evidence basic to my argument. How do you react to this issue?

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ROAD LOG

The first three stops are designed to display a model one pattern of clinal variation. The brachiopod *Sowerbyella curdsvillensis*, by evolving several different clinal variants, was able to occupy most of the environments seen in the lower Trenton Group. It became a polytypic and eurytopic form.

TOTAL MILES	MILES FROM LAST POINT	ROUTE DESCRIPTION
0.0		Trip meets and organizes at the

		prominent outcrop of the Napanee Limestone just west of the bridge where Rt. 12 crosses the Sugar River, 3 miles west of Boonville. The group will walk up the west side of the stream and gather at the outcrop of the Napanee beneath the railroad bridge.

STOP 1 THE NAPANEE LIMESTONE

The strata here are primarily thick bedded, black micrites which have been interpreted as a nearshore lagoon facies. *Sowerbyella* is abundant. This form has traditionally been identified as *S. punctostriatus*. It is herein reinterpreted as the quiet water, mud bottom clinal variant of *S. curdsvillensis*. Examine the brachial interiors and see the preponderence of simple forms. Medial septa can be seen but muscle scars, vascular markings and subperipheral thickenings are uncommon. The pedicle exterior usually displays alate corners and a well developed medial fold giving this valve a peaked appearance.

0.0	0.0	Return downstream and cross the Rt. 12 bridge to the outcrop of the Kings Falls Limestone east of the road.

STOP 2 THE KINGS FALLS LIMESTONE

The lower strata here are primarily thick bedded, coarse grained biosparites which have been interpreted as a barrier shoal facies, lying offshore of the Napanee lagoon facies. Toward the top of the outcrop the facies grades into a shallow shelf facies. While, at this location, these strata overlie those of the lagoon facies, presumably there were contemporaneous lagoonal facies elsewhere. *Sowerbyella* is very abundant at the base of this outcrop. This form is larger than the one in the lagoon facies. Most of the brachial interiors are quite ornate. They have medial septa, muscle scars, vascular markings and subperipheral thickenings. The pedicle exteriors have blunt corners. They don't often show medial folds. Instead they tend to be flattened or broadly rounded. This form has traditionally been identified as *S. curdsvillensis*. It is herein reinterpreted as the agitated facies clinal variant of a more broadly defined *S. curdsvillensis*. By collecting enough brachial interiors at these two outcrops, an assemblage of forms can soon be put together that show the gradation between the lagoon and the shoal clinal variants.

21.1	21.1	Drive north on Rt. 12 to Lowville. Turn left in Lowville to remain on Rt. 12.
22.0	0.9	Drive north on Rt. 12. Cross Mill

		Creek bridge and park immediately. Climb down to creek and walk to exposure east of and about 50m below the bridge.

STOP 3 THE SUGAR RIVER LIMESTONE

There is a prominent re-entrant below the bridge which can be traced downstream. This is a thick bentonite which lies 10 m (32 ft.) below the top of the Sugar River Limestone. *Sowerbyella* is rare in the deeper water facies above this bentonite, but common in the shallower facies below. Examine the strata several meters below the bentonite. The common form of *Sowerbyella* here is the mud bottom, quiet water form. Although some of the brachial interiors are ornate, most are plain. Medial septa are seen but other features are uncommon. The form is relatively small. Pedicle exteriors often display a medial fold and alate corners. This location records a return of both quiet water conditions and the quiet water clinal variant of *Sowerbyella*. Upstream into the highest strata of the Sugar River Limestone, and for a considerable distance into the overlying Denley Limestone, *Sowerbyella* is quite scarce. This zone is part of the first *Sowerbyella* bottleneck.

The next location is designed to display an example of model 3 clinal variation. The middle Trentonian crinoid genus *Ectenocrinus* occupied a shallow to deep shelf range of environments. Because of bank margin steepening, the deep end of its range was deteriorating while shallowing facies offered opportunities for *Ectenocrinus* in shallow water environments. The result is a kind of clinal orthoselection.

23.3	1.3	Turn around and return, on Rt. 12 through Lowville. Take the right fork onto Rt. 26.
26.7	3.4	Follow Rt. 26 through Martinsburg. Turn left onto Glendale Ave.
27.5	0.8	Turn left and enter Whitikers Falls Town Park. Park and follow one of the trails down to Roaring Brook and then climb down to the top of Whitikers Falls.

STOP 4 THE SUGAR RIVER AND DENLEY LIMESTONES

At the base of the falls a re-entrant can be seen. This is the same bentonite which was observed at Mill Creek in Lowville. Here it is also 10 m (32 ft.) below the top of the Sugar River Limestone. The bentonite is a marker bed which is found at the same level at all outcrops from Mill Creek, Lowville to Sugar

River. It has not been found at Deer River or at any of the Mohawk Valley locations.

Examine the several meters of strata above the falls. *Ectenocrinus* is represented by moderately abundant columnals. Look carefully as these columnals are small. It is very helpful to bring a water container and pour water on columnal rich beds. This brings out the contrast between the columnals and their micritic groundmass. *Ectenocrinus* is easily recognized by its trimeric morphology. Each columnal is composed of three elements fused together along faintly visible sutures. The most common form is a triangle with very rounded corners. At first glance the lumina appear to be triangular, and many are. But you will soon notice that many also have very poorly developed 4th and 5th points, along with three long and attenuated points (Fig. 5i-5m). All specimens at this level belong to the species *E. triangulus*.

Climb to the level above where the trail intersects the stream. Here and for quite a distance upstream *Ectenocrinus* columnals are different. Now they are generally rounder and the lumina are composed of more equal sized points (Fig. 5s-5v). Forms at this level are intermediate between *E. triangulus* and its descendent *E. simplex*. Continue upstream and observe the increasingly abundant columnals of *Ectenocrinus*. The transition from *E. triangulus* to *E. simplex* is not just one of morphology. *E. triangulus* was a relatively stenotopic form which never became especially abundant. The descendent, *E. simplex*, was altogether different. It was eurytopic and one of the dominant forms in the upper Trenton Group, a "weed" crinoid. This evolutionary event records an ecological transition from the K-strategist ancestor to the r-strategist descendent.

The last locations are designed to illustrate model 2 examples of clinal variation. *Sowerbyella* passed through two facies bottlenecks, one at the base of the middle Trentonian and one at the base of the upper Trentonian (Fig. 3, arrows). The best place to study the *Sowerbyella* of the middle Trentonian is at Mill Creek, Lowville, but as that outcrop extends for such a long distance along the stream, it is not practical to include this location in a one-day trip. We will examine middle Trentonian forms at other locations, stops 5 and 6.

		Return to the cars and drive back to the park entrance.
27.7	0.2	Turn left and travel to bridge where Glendale Road crosses Roaring Brook. Climb to the exposure immediately above the bridge.

STOP 5 THE DENLEY LIMESTONE

At this level the transition to *Ectenocrinus simplex* is complete. Virtually all *Ectenocrinus* columnals, upstream from the bridge, are round with pentagonal lumina (Fig. 5 z-5aa). *Sowerbyella* is not common here but the specimens which can be seen are of interest. They are nearly identical to the quiet water lower Trentonian forms. They have plain brachial interiors; the pedicle exteriors have medial ridges and alate corners.

28.9	1.2	Turn around and travel back towards Martinsburg. Turn right on Rt. 26.
30.8	1.9	Turn left onto B. Arthur Rd.
32.7	1.9	Turn left onto W. Martinsburg Rd.
32.8	0.1	Stop at large road outcrop on the right.

STOP 6 THE DENLEY LIMESTONE

The exposure here is of the middle Denley Limestone. The facies are the shallow shelf possibly grading into the barrier (Fig. 3). Several types of *Sowerbyella* can be recognized from the brachial interior structure. Many have plain interiors. While medial septa are present, none of the other internal structures are seen. The other type has an ornate brachial interior. Medial septa, muscle scars and subperipheral thickenings can be seen, some or all, on the same interiors. The plain forms found at this outcrop are typical of the Denley's deeper shelf facies while the ornate forms, although never very common, are typical of the more shallow and agitated facies. Significantly, vascular markings are quite unusual and these ornate forms are never as large as their lower Trentonian equivalents. Pedicle exteriors are more inflated and rounded. This is *Sowerbyella* n. sp.

33.9	1.1	Continue south on West Martinsburg Road. Turn left onto West Road.
51.4	17.7	Head east on West Road. At Whetstone Gulf State Park bear right onto Rt. 26. Continue east on Rt. 26 past its junction with Rt. 12D. Continue on 12D until the bridge over Sugar River at Talcottsville. Park, descend dirt path to outcrop.

STOP 7 THE UPPER DENLEY LIMESTONE

The best location to see *Sowerbyella* next is at the outcrop of the lower Steuben Limestone on Rt. 177 just west of Rodman, but this is too far away for our trip today. The Rodman exposure shows *Sowerbyella* within the second bottleneck (Fig. 3, arrow). Specimens there are small and have a well developed, broadly rounded medial fold. At Talcottsville we can see *Sowerbyella* in the barrier facies just below this second bottleneck. The form is abundant up to the base of the falls and then quite a bit less common in the bottlenecking beds above. The specimens here are, for the most part, characterized by well inflated pedicle exteriors which sometimes display the broadly rounded medial folds typical of the second bottleneck. Brachial interiors are generally plain. Notice the magnificent display of large symmetrical ripple marks (pararipples) here.

55.4	4.0	Continue south on Rt. 12D. Enter Boonville; enter Rt. 46 at its junction with Rt. 12D (no turn).
69.7	14.3	Follow Rt. 46 south to Frenchville. Turn left onto Rt. 274.
70.8	1.1	Park just west of the bridge over Big Brook. Descend to outcrop east of the brook.

STOP 8 THE HILLIER LIMESTONE

The Hillier Limestone is exposed all along Wells Creek and Big Brook. The environment of deposition was quiet deep shelf and the deposits are mostly biomicrites. This location is above the second facies bottleneck and a third species of *Sowerbyella* is exposed. The form, *S. subovalis*, is characterized by a greatly inflated pedicle exterior with a broadly rounded medial fold. Brachial interiors are mostly plain. Medial septa are seen, and sometimes poorly developed subperipheral folds can be found, but muscle scars and vascular markings are absent. These traits are apparently inherited from the clinal variants of S. n. sp. which made it through the second bottleneck. The ones on Big Brook are larger than their middle Trentonian ancestors.

END OF FIELD TRIP