The Cambrian Ecotone: Dynamics of a Major Evolutionary Discontinuity

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Abstract.—The biotic diversification of the Early Cambrian is now constrained by radiometric dates to have occurred over the span of only a few million years, during which time the marine fauna experienced unprecedented evolutionary change. Three mathematical models have been presented to describe the Cambrian event. Two of the models, here called the logistic and cell type models, are shown to be inconsistent with the latest geological estimates of the duration of the Cambrian diversification. The third or ecotone model employs a version of the Verhulst equation, in which the initiation of predator-prey relationships is modeled as a transmission of information from one species to another. This model permits estimation of its Malthusian parameter, a parameter used to describe the number of ecological "message deliveries" per unit time. The ecotone model passes the test of the geological age calibration, and gains support from recent results demonstrating the brevity of what has been called the Cambrian "explosion."

KEY WORDS: Cambrian diversification, evolution of early animals, Verhulst equation, Malthusian parameter, paleoecology, transformation of prey to predator

Several mathematical models have been offered to describe the dynamics of the Cambrian evolutionary radiation. Although, on first inspection, these models might appear difficult to test, with each advance in our knowledge of the Cambrian paleobiological event, our ability to test these models improves. In this paper I will elaborate a recent mathematical model (McMenamin 1992a) for the Cambrian event, and follow with a test of this and competing models. The model described here is called the ecotone model.

The Cambrian evolutionary radiation of animals (often referred to as the Cambrian "explosion") is the most conspicuous discontinuity of the entire fossil record. This event poses two crucial puzzles to students of evolution. The first puzzle asks why the Cambrian radiation was so fast. The second asks why the radiation occurred when it did.

Predators and the onset of macropredation have been implicated in three of the proposed answers to the latter puzzle. Earliest of these proposals was Evans' (1910) suggestion that Cambrian skeletons resulted from the influence of Cambrian predators on an already well-diversified marine fauna. Evans (1910, p. 545) argued that the "absence of hard parts in the pre-Cambrian fauna can only be satisfactorily accounted for on the hypothesis that at that time there was no reason why the organism should secrete them." Six decades after Evans' (1910) work, Stanley (1973) proposed that the cropping pressure of Cambrian predators triggered the evolution of diverse animal forms. Stanley (1973) envisioned direct links between cropping pressure, maintenance of unoccupied patches of seafloor by removal of occupants by predators, improved chances of recruitment from a variety of marine larvae on these unoccupied patches, and resultant diversity increase of animals at a high taxonomic level. Stanley's (1973) paper argues that this predator-induced patchiness of the environment was the main impetus to the Cambrian macroevolutionary radiation. This explanation seems insufficient by itself to account for the evolutionary changes seen at the beginning of the Cambrian, especially if these changes are constrained to occur within a short interval of geologic time.

McMenamin (1988) linked the appearance of Cambrian predators to a high taxonomic-level diversification by the switch in function of antipredatory traits (such as shells) from items of defense to tools for gaining access to new food resources. In this view, numerous function switches occurred in different clades at or nearly at the same point in geological time.

The three different hypotheses (of Evans [1910], Stanley [1973] and McMenamin [1988]) are quite distinct, but not necessarily mutually exclusive, as portrayed in figure 3.3 of McMenamin and McMenamin (1994). For example, McMenamin's "function switch" hypothesis requires a component of Evan's "simple predator defense" to initiate the evolutionary process.

Solving the first puzzle posed above, why the Cambrian radiation was so rapid, is the primary object of this paper. Following is a mathematical description of the dynamics of the Cambrian event, showing how rapidly such an event could occur given several assumptions regarding the onset of abundant metazoan predators. The ultimate goal of this work is to uncover the proximal cause of the Cambrian evolutionary event. The ecotone model suggests that it was due to the evolution of a single predator species that set into motion a paleoecological transformation unprecedented in earth history.

THE ECOTONE MODEL

The term “ecotone” was coined in 1905 by F. E. Clements, who defined it as a narrow transition zone or “line” between two qualitatively defined discrete habitats or ecosystem types. More recently, ecotones have been quantitatively defined by Fortin (1994, p. 956) as “long narrow regions of high rates of change.” As used by ecologists, “ecotone” bears a primarily geographic usage. I recently (McMenamin 1992a) borrowed the term from the ecologists and imparted to it a temporal connotation. The term is well suited to this purpose, for as correctly predicted by McMenamin and McMenamin (1990), the transition from the Proterozoic to the Cambrian was a short interval of high rates of paleoecological and evolutionary change. Of particular interest is the appearance, during this interval, of the first macropredators.

The initiation of predator-prey relationships can be viewed as a transmission of information from one species to another. Classic mathematical tools are available for such an analysis. The iterated growth equation, first introduced by P. F. Verhulst (1838), has been applied to describe the spread of a rumor (McCarty 1976) and is the generating equation for the well-known bifurcation diagram of May (1976). A version of the Verhulst equation was employed to develop the ecotone model of Cambrian diversification (McMenamin 1992a).

This model is useful for the study of the spread of information “units” or ecological “messages”. The onset of macropredation is the ecological message considered here, with the implication that the macropredatory habit can be acquired by triploblastic animals. An animal species changing permanently from non predator to predator, as a result of itself being newly subjected to predation pressure, constitutes receipt of the ecological message. Of course, no conscious awareness of the evolutionary process is implied here for the animals in question.

Several assumptions will be required to model the spread of information through an ecosystem. These assumptions will be discussed in detail below, after a general presentation of the model.

Assume at the beginning a world filled with primary producers and first order consumers, and no (or a negligible number of) higher order consumers. Introduce one larger predator to a biota free of megascopic predation. Assume this predator attacks two species per million years. Each first order consumer prey species develops aggressive behaviors which in turn allow it to attack, as a predator or parasite, two more species per million years. If $M(t)$ is the number of species attacked at time t, out of a population of first order consumer species V, then every million years each one of them will attack on average:

$$2(1-\frac{M(t)}{V}) \qquad (1)$$

species not yet preyed upon. Consider the following differential equation:

$$\frac{dM(t)}{dt} = M(t)\,[2(1-\frac{M(t)}{V})] \qquad (2).$$

The variables are separable, and the equation can be rewritten:

$$\frac{dM(t)}{dt} = [\frac{2V - 2M(t)}{V}] \qquad (3);$$

$$\frac{dM(t)}{dt} = M(t)\frac{2}{V}(V - M(t)) \qquad (4);$$

$$\frac{dM(t)}{dt} = \frac{2}{V} M(t)(V - M(t)) \qquad (5);$$

$$\frac{V}{M(t)(V - M(t))} \frac{dM(t)}{dt} = 2 \qquad (6).$$

The solution to equation (6) will be (*C* a constant):

$$\int \frac{V}{M(t)(V - M(t))} \frac{dM(t)}{dt} dt = \int 2\, dt = 2t + C \qquad (7).$$

Such a differential equation is said to have separable variables because it can be written in the form:

$$P(y)y' = Q(x) \qquad (8).$$

The solution will be of the form:

$$\int P(y)y'\, dx = \int Q(x)dx \qquad (9).$$

where the indefinite integral $\int Q(x)dx$ represents a family of antiderivatives of functions whose derivative is $Q(x)$.

Proceeding with

$$\int \frac{V}{M(t)(V - M(t))} \frac{dM(t)}{dt}\, dt = \int 2\, dt = 2t + C \qquad (7)$$

observe that, for integrating the left-hand side:

$$\frac{V}{M(t)(V - M(t))} = \frac{1}{M(t)} + \frac{1}{V - M(t)} \qquad (10).$$

Integrating both sides of equation (10)

$$\int \frac{V}{M(t)(V - M(t))} \frac{dM(t)}{dt}\, dt = \int \frac{\frac{dM(t)}{dt}}{M(t)}\, dt + \int \frac{\frac{dM(t)}{dt}}{V - M(t)}\, dt \qquad (11)$$

gives

$$\int \frac{\frac{dM(t)}{dt}}{M(t)}\, dt + \int \frac{\frac{dM(t)}{dt}}{V - M(t)}\, dt = \ln|M(t)| - \ln|V - M(t)| + C \qquad (12).$$

Since

$$0 \le M(t) \le V \qquad (13)$$

the absolute value symbols may be dropped, yielding

$$\ln M(t) - \ln(V - M(t)) = 2t + C \qquad (14).$$

Thus:

$$\ln\left(\frac{M(t)}{V - M(t)}\right) = 2t + C \qquad (15);$$

$$\frac{M(t)}{V - M(t)} = e^{2t+C} = e^{2t}e^{C} = ke^{2t}\text{ , } k > 0 \text{ and with } k = e^{C} \qquad (16).$$

Solving for *M* as a function of *t* gives:

$$M(t) = ke^{2t}(V - M(t)) \qquad (17);$$

$$M(t)(1 + ke^{2t}) = kVe^{2t} \qquad (18);$$

$$M(t) = \frac{kVe^{2t}}{(1+ke^{2t})} = \frac{kVe^{2t}}{(1+ke^{2t})}\frac{e^{-2t}}{e^{-2t}} = \frac{kV}{e^{-2t}+k} \qquad (19).$$

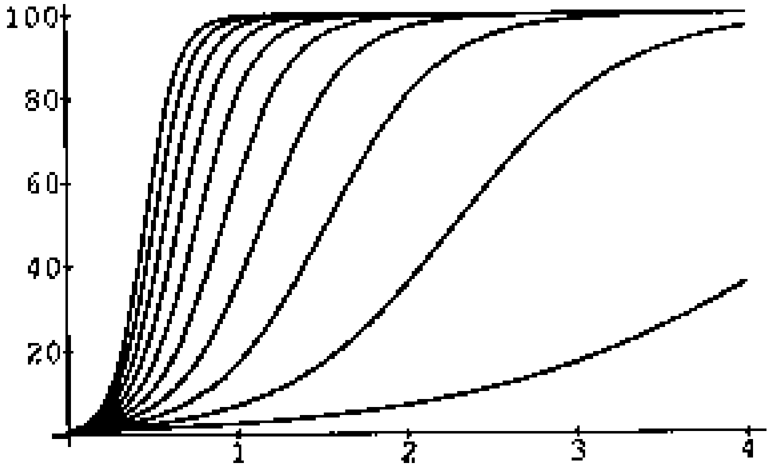
Note that

$$\text{as } t \rightarrow \infty,\ M(t) \rightarrow V;$$

$$M(t) = \frac{kV}{k + e^{-2t}} \qquad (20),$$

$$\text{or more generally, } M(t) = \frac{kV}{k + e^{-\ddot{o}t}} \qquad (21).$$

where *ö* (odereisis) represents the number of “message deliveries” per unit time. Figure 1 shows a sample family of curves for equation (21) with *ö* varying from one to ten.



ESTIMATING Ö

In his study of diversification functions and the rate of evolution, Walker (1985) employed the logistic equation:

$$\frac{dN}{dt} = r\left(1-\frac{N}{k}\right)N \qquad (22).$$

Equation (22), like equation (2), is a variant of the Verhulst equation. In the former case *r* is the Malthusian parameter (intrinsic rate of diversification) and *k* is some limiting or equilibrium value (such as carrying capacity) of the habitat for the taxon in question. The Malthusian parameter is introduced into the ecotone model as *ö* in equation (21).

Walker (1985) was able to solve for *r* from the solution of equation (22):

$$r = \frac{1}{t}\ln\left[\frac{k-N(t_o)}{N(t_o)}\right] + \frac{1}{t}\ln\left[\frac{N(t)}{k-N(t)}\right] \qquad (23).$$

Walker (1985) then searched for a way to simplify this equation. He noted that one cannot use $N \geq k$ since *N* never reaches or exceeds *k*. Nonetheless, it makes most sense to choose the largest value of *N* which makes equation (23) computable, and this would generally be the value $N(t')=k-1$, in other words, the population value that is one less than the equilibrium level or carrying capacity. Not only will this give the most accurate estimate, it will simplify Equation 2 to the form:

$$r = \frac{1}{t'}\ln\left[\frac{k-N(t_0)}{N(t_0)}\right] + \frac{1}{t'}\ln\left[k-1\right] \qquad (24).$$

The expression k-1 is dimensionless. Walker (1985) assumed that the evolutionary radiation proceeded from a single ancestral species. Thus $N(t_0)=1$ and:

$$r = \frac{2}{t'}\ln[k-1] \qquad (25).$$

Walker's (1985) attempt was the first time that the logistic model had been used to calculate an intrinsic rate of increase. Equation (25) can be adapted (McMenamin 1992a) for the ecotone model (assuming a single, initial, bilateral, megascopic animal predator) as:

$$\ddot{o} = \frac{2}{t'}\ln[V-1] \qquad (26)$$

$$\text{for } M(0) = 1 \text{ and } M(t') = V - 1.$$

Equation (26) would be applied in the following fashion. The unit of time in this case will be one million years. Say, for ease of calculation, that the time interval (t') during which the ecotone transformation occurs lasts only two million years. V represents the total population of animals liable to be affected by the ecotone transformation. In other words, these animals are the ones capable of changing from a peaceful neighbor to a predator or a parasite.

Most animals near the Cambrian boundary were afflicted by large predators. Responses in prey animals varied from secretion of spiny scleritomes (Bengtson 1994) to secretion of chemotoxins (McMenamin 1992b). The animals of variable V manifested a different response; a combination of aggressive behavior and newly acquired predatory (or if they began as micropredators, macropredatory) feeding strategy.

With $t'=2$ and $V=100$ species:

$$\ddot{o} = (1)(\ln[99]) = 4.6 \qquad (27).$$

For *V*=1000 species:

$$\ddot{o} = (1)(\ln[999]) = 6.9 \qquad (28).$$

Interestingly, an order of magnitude change in *V* requires only a relatively slight increase in *ö* to keep the ecotone interval constant. Stretching *t'* to twenty million years changes *ö* to 4.6 and 6.9 for *V* = 100 and *V* = 1000, respectively.

THE TEST

Three mathematically-oriented descriptions of the Cambrian evolutionary event will now be tested. The first is the logistic hypothesis of Sepkoski (1992). This hypothesis posits the Cambrian radiation to the exponential phase, following an early lag phase, of logistic equilibrium growth in early animal taxa. It differs from the ecotone model by relying on intrinsic, within-taxon diversification to generate the Cambrian explosion.

Second is the cell type hypothesis of Valentine (1994). In this hypothesis, the Cambrian explosion owes to attainment of a threshold number of cell types (40-50) and ensuing radiations of several animal clades. Third is the ecotone hypothesis described above.

The test is provided by a recent recalibration of the age of the beginning of the Tommotian stage of the Cambrian. Bowring et al. (1993) placed the point of “exponential” increase in Cambrian taxa at the base of the Tommotian, and calculated this horizon to be 530 million years in age. The Tommotian-Atdabanian interval of taxonomic increase lasted, according to Bowring et al.’s (1993) calculations, only 5-6 million years. The duration of this interval constitutes the test for the three mathematical descriptions above.

Sepkoski (1992, p. 559) estimated the duration of the “exponential diversification” interval to be 15 million years. With Sepkoski’s estimate cut in third by the new recalibration, the logistic/equilibrium hypothesis is falsified by the fact that there is no longer enough time for even the exponential phase of logistic growth. Even without the new limitation imposed by the length of the exponential phase, the logistic model fails because a high per-taxon rate of diversification would have to be manifest in all clades simultaneously. It would be implausible to argue that biological factors intrinsic to the diversifying clades themselves would be sufficient to cause a simultaneous diversification, especially over such a brief interval.

The Cambrian event is therefore more a step function than an S-curve. The cell type description is falsified by the recalibration for similar reasons. In the case of both the logistic and cell type models, the main difficulty is, considering that animals *sensu strictu* existed before the Cambrian, how does one, in different lineages, time the lag-to-exponential (or attainment of 40-50 cell types, respectively) to coincide exactly with the base of the Tommotian? For this to occur, Early Cambrian animal taxa would have to be viewed as taxonomic diversification time bombs, with all clades bearing synchronized, silently ticking fuses waiting to go off at exactly 530 million years before present.

In spite of the metaphorical appeal of such a Cambrian event as an intrinsic (to clades or ontogenies, respectively) “Cambrian explosion,” such a notion begs the question of what synchronized the metaphorical evolutionary fuses. Rising levels of oxygen might be invoked to explain such a simultaneous change, but this explanation is insufficient considering that active and presumably aerobic burrowers, known by their trace fossils, lived tens of millions of years before the Cambrian. Therefore, one must reject the logistic and cell-type explanations because the evolutionary changes proposed by these hypotheses would have had to have occurred simultaneously in a variety of animal clades. This problem, serious before Bowring et al.’s (1993) recalibration, becomes insurmountable when the Tommotian-Atdabanian interval is shrunk to 5-6 million years.

The ecotone model passes the test of a short Tommotian-Atdabanian interval. Indeed, this model predicts a rapid Cambrian event, for ecological message delivery (of, in this case, threat of and the opportunities of macropredation) can as shown by the above calculations propagate through a large group of taxa with high speed. The diversity of the Cambrian still must be generated (evolved), of course, but the ecotone model comes equipped with a potent evolutionary forcing mechanism. This is not a mere displacement of the problems encountered by the logistic and cell type models—high diversification rates become directly linked to predation pressure (McMenamin 1988), a pressure that is applied in a rapid and pervasive fashion.

Another application of equation (26) will demonstrate the link between interval length and rate of message propagation. Bowring et al.'s (1993) estimate of 5 million years will be used for *t'*. At *V* = 1000:

$$\ddot{o} = \left(\frac{2}{5}\right)\left(\ln[999]\right) = 2.76 \qquad (29).$$

At *V* = 10,000, the rate increases only to:

$$\ddot{o} = \left(\frac{2}{5}\right)\left(\ln[9999]\right) = 3.68 \qquad (30).$$

For *V* = 100,000, *ö* rises only to 4.6 deliveries per million years. Thus, this model is quite robust to varying estimates of the numbers of individual taxa affected, and can model the spread of the required effect at a rate consistent with the latest geological data. In other words, assuming between 1,000 and 100,000 late Vendian metazoan taxa bearing the potential for transformation to predators, a message delivery rate of between 2.7 and 4.6 messages per million years is required to transform the fauna to one rich in predators. For the higher rate (4.6), this would mean on average one message delivery per predator species per 217,391 years. This rate does not appear unreasonable, and may even be conservative, especially in light of indications that the transition from filter feeder to predator (in a case apparently lacking the accelerating influence of a 'message-delivering' predator) can occur in as little as 7,000 years (Kelly-Borges 1995).

The arguments above demonstrate that the ecotone model is consistent with a very rapid Cambrian diversification. The logistic and cell type models are falsified by the short Tommotian-Atdabanian interval.

DISCUSSION

Several assumptions are required by the ecotone model. These must be examined in detail, for it would be folly to construct a mathematical model consistent with geological data but at a variance with paleobiological knowledge.

The first assumption is that the Vendian marine biota was largely free of megascopic predators, and was characterized instead by a variety of autotrophic animals. This hypothesis (McMenamin 1986, 1988, 1998) has gained support recently with the reports of the photosymbiotic fungiid coral *Leptoseris fragilis* photosynthesizing at 145 meters water depth (Schlichter and Fricke 1991) and by calculations showing that symbionts in coral fix three to four times more carbon than photosynthetic plankton in the upwelling regions of all the oceans (Hawksworth 1994). Micropredators were surely present in the Vendian, but the abundance of large, nonskeletogenous bodies (many with presumed autotrophic lifestyles) during this time argues forcefully against the presence of large, triploblastic animal predators. So the first assumption appears sound.

The second assumption of the ecotone model is that attainment of a predator or parasite lifestyle is a viable response, by prey species which themselves are triploblastic animals, to the onset of megapredation. This assumption has been challenged by Bengtson (1994, p. 425), who was unable to conceive “of any behavior pattern or selective advantage that would produce this effect.”

Unbeknownst to Bengtson (1994), the switch from prey to parasite or predator has occurred repeatedly in the history of life. Indeed, since all predators are evolutionarily derived, it necessarily follows that all predators are ultimately evolved from non-predators. Vermeij (1987) suggests that swallowing whole prey is perhaps the most common initial type of predation, considering that it may only be a small evolutionary step from trophic strategies of deposit feeding or particulate suspension feeding. Analogous change frequently occurs within the life of individual marine animals. Sebens and Koehl (1984) have documented the ontogenetic transformation of sea anemones from potential prey to predator.

It should be emphasized, however that this assumption (that predators can induce non predators to become predators themselves) is the most heterodox claim of the ecotone hypothesis. No modern examples of this process have been documented, although it is not difficult to imagine selective pressures and evolutionary constraints under which such a phenomenon might occur. Furthermore it seems possible that such a transformation could occur quickly, requiring only a few or even only one generation under the right circumstances.

A recent discovery sheds light on the possible evolution of trophic transformations. Vacelet and Boury-Esnault (1995) describe Mediterranean sponges belonging to genus *Asbestopluma* that have abandoned microphagous suspension feeding and evolved carnivory. These sponges capture crustaceans by means of filaments adorned with raised hook-shaped spicules.

The fact that the nearest relatives to the Mediterranean *Asbestopluma* specimens are deep water, open marine species raises questions about the origin of this shallow water sponge population. One possibility is that it originated from a sweepstakes colonization event from the North Sea, in which case the speciation event must have occurred rapidly, within the past 7,000 years (Kelly-Borges 1995).

A Cambrian example of a potential prey-to-predator switch involves trilobites. The proximal cause for trilobite skeletonization was likely to have been predatory pressure from such predators as *Anomalocaris* (McMenamin 1988, McMenamin and McMenamin 1990). Shortly afterward, trilobites used this same exoskeleton to prey on other organisms. The spiny gnathobases of the Cambrian trilobite *Olenoides serratus* were utilized to tear and shred prey organisms (Whittington 1985, p. 57).

It seems clear then that herbivorous and/or prey species can become predators. Virtually all undoubted heterotrophic Vendian animals, as known from their trace fossils, were bilateral grazers and deposit feeders, apparently generalized in their feeding preferences and with the potential to be transformed into predators without requiring a radical alteration of *baüplan.* The first macroscopic predator to appear with low prey specificity came upon a marine biosphere filled with unprotected or weakly defended prey species, and induced the predatory (or in some cases parasitic) lifestyle shift in numerous prey species, as battered and isolated survivor populations adjusted to the new conditions. Other prey changes such as skeletons and rapid escape also occurred, but among the strategies most favored by natural selection were those that allowed the endangered prey to respond in a few generations with a minimum of morphologic change.

The only hard parts expected to occur in a Vendian grazer or deposit feeder would have been in the oral area—radular teeth or analogous structures. These would be the first features co-opted by the organisms as defensive devices, and would therefore have had the highest potential, of any of the possible skeletal elaborations of the animal’s body, to lead quickly to new food sources.

In an observation that is further consistent with the new radiometric dates, the interval of message spread (ended by recipient saturation) would be expected to be short since the diversity of animals in the Vendian was not high relative to today. The predator-parasite transformation hypothesized here involved species of organisms already present in the marine biosphere, rather than relying on hard-to-test claims of genetic flexibility or on synchronization in unrelated lineages of either runaway diversification or attainment of a threshold cell number. Fossil evidence suggests that Vendian triploblasts all existed at a similar level of behavioral development, and one might reasonably expect almost evenly matched predator-prey exchanges during the onset of macropredation. Prey lineages that survived these exchanges would be “preadapted” to become predators themselves, and to rapidly propagate the ecological message among similar organisms with propensities to respond in the same way. Indeed, the behavior switch confers a double selective advantage; what was once a source of mortality leads, perhaps even before a single new species has been generated, to a new, relatively concentrated food resource. Such a “payoff,” along with other payoffs associated with switch in function of defensive morphological traits to feeding traits, were no doubt needed to sustain an event as far reaching and as sudden as the Cambrian diversification. More importantly, the ecotone transformation implies nearly simultaneous ecological change with potential to induce rapid evolutionary response in both the prey organisms and the predators themselves.

Certainly the predatory lifestyle, at least at a microbial scale, was present for hundreds of millions of years before the Cambrian. Probably also there were metazoan predators before the first shelly fossils, but these early predators were too small or otherwise incapable of either inducing skeletonization in their prey or triggering significant ecological or evolutionary changes. The third assumption underlying the calculation of *ö* above is that the ecotone transformation was initiated by a single, exceptional predator species.

A possible challenge to the ecotone model involves the Vendian shelly fossil *Cloudina*. Vermeij (1987, p. 361) inferred that this shelly organism was a herald of the predator-prey escalation that followed in the Cambrian. Vermeij’s inference received apparent support with the report of boreholes in cloudinid shells (Bengtson 1994), but the putative borings of cloudinid tubes have been reinterpreted as the results of microdolomite crystal formation with subsequent dissolution (Debrenne and Zhuravlev 1997). Even if the cloudinid holes had represented a Vendian event of macropredation, they would have little relevance to the Cambrian event, as it is known that this type of predation leads to evolutionary dead ends (Fursich and Jablonski 1984).

Viewed as an ecotone transformation, the Cambrian diversification involves a qualitative change in marine trophic relationships, and as such is unique. It must be set apart from all subsequent evolutionary radiations, which in the majority of cases (as, for instance, in the case of the Cenozoic radiation of Mammalia after extinction of the great archosaur groups) represent occupation of ecological vacancies in an already structured ecosystem.

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FIGURE CAPTION

Figure 1. Ecological message deliveries per unit time. This figure shows a family of curves for equation (21) with *ö* varying from one to ten. The ordinate represents the level of “message delivery”; the abcissa can be taken to represent millions of years.