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Middle Mississippian Blastoid Extinction Event

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The Middle Mississippian blastoid (Phylum Echinodermata) extinction event (about 340 million years ago) was a rapid, habitat-specific extinction. Blastoids became rare or absent in shallow-water environments after the extinction, and this change was probably synchronous worldwide. Onshore-offshore habitat shifts have been recognized as an important historical trend among marine benthos. Unlike trends exhibited by other groups, blastoids appear to have repopulated shallow-water habitats after a period of diminished diversity and abundance.

MAJOR EVOLUTIONARY PATTERNS have received considerable study in recent years, including rapid mass extinctions and longer duration onshore-offshore habitat shifts. Important questions concerning mass extinctions include, among others, timing of the extinctions, proximate causes, periodicity of events, and the environmental response of affected organisms. Many community types and specific clades apparently originated in nearshore habitats and migrated through time to deep-water habitats (*1*).

Discovery of an abundant and diverse blastoid fauna (Phylum Echinodermata) in relatively deep-water cratonic sediments of the Mississippian (Lower Carboniferous, about 360 to 320 million years ago) Fort Payne Formation of south-central Kentucky (*2*) and recent analysis of the stratigraphic distribution of European blastoids (*3*) allow us to interpret the ecologic fabric of a significant blastoid extinction event. Blastoids underwent a major shift in habitat preference, from shallow water to deep water, at the middle to late Osagean boundary (Chadian to Arundian, or conodont zone divisions Vla to Vlb) blastoid extinction event. This extinction and habitat restriction appear to have occurred synchronously (within limits of biostratigraphic resolution) in both North America and Western Europe (*4*). The shift to deeper water habitats is especially striking because blastoids were primarily shallow-water benthos throughout their existence from the Middle Ordovician to the Late Permian (Caradocian to Kazanian) (*5*).

In North America, Kinderhookian blastoids were never dominant faunal elements; however, they were successful in both shallow-water and deep-water cratonic sea carbonate settings. Examples include the Hampton Formation of central Iowa (two genera) and the McCraney Formation of northeastern Missouri (two genera). Blastoids were also common locally in deep-water settings associated with Kinderhookian Waulsortian mounds in the western United States. Five blastoid genera are recognized from these deep-water facies in the Lodgepole Limestone of central Montana (*7*).

During the early to middle Osagean, blastoids were still present in deep-water settings, but they became important faunal elements in shallow-water carbonate settings (Fig. 1). Deep-water occurrences include facies associated with Waulsortian mounds in the Lake Valley Formation (early to middle Osagean) of New Mexico (six genera) and sediment-starved cratonic basin conditions of the early Osagean New Providence Shale in western Tennessee (one genus). Shallow-water lower to middle Osagean carbonate platforms with blastoids include the Redwall Limestone of northern Arizona (five genera) (*8*) and the Burlington Limestone of Iowa, Illinois, and Missouri. Blastoids attained their maximum diversity in the Burlington seas, where crinoids and blastoids dominated the entire benthic community. Approximately 17 blastoid genera (20 percent of all described blastoids) are known from the Burlington Limestone (*5*, *9*). In addition to a high diversity, blastoids were relatively abundant in the Burlington.

A significant extinction and change in habitat preference among blastoids occurred after deposition of the Burlington. Although a regression and a transgression event have been proposed at this interval (*10*), carbonate sedimentation continued on the Burlington platform to yield the late Osagean Keokuk Limestone. In marked contrast to the abundance and diversity of Burlington blastoids, only three genera of blastoids are known from the Keokuk Limestone. Crinoids remained abundant and diverse during Keokuk deposition. Deeper water cratonic habitats in the late Osagean continued to support moderately diverse and abundant blastoid faunas (Fig. 1), such as from the prodeltaic sediments of the New Providence Shale in northern Kentucky and southern Indiana (five genera) (*11*), and the Fort Payne Formation of south-central Kentucky composed of Waulsortian buildups, crinoidal buildups, and several allochthonous facies (seven genera) (*2*). Blastoids in the Fort Payne are relatively common.

In Western Europe Late Tournaisian (Courceyan) blastoids are known from shallow carbonate settings, where they are relatively common and moderately diverse (Fig. 1). The best documented lower to middle Courceyan fauna is from Tournai, Belgium (five genera) (*12*). Lower to middle Courceyan faunas are also known in shallow-water carbonate facies in Ireland and Britain (*3*), such as the Hook Head Formation (County Wexford, Ireland) (four genera).

Upper Courceyan and Chadian (lower Visean) blastoids were commonly associated with the widespread, deep-water Waulsortian facies, particularly in the Craven Basin

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in Britain and the Dublin Basin in Ireland (*3, 13*). Examples from the Upper Chadian Clitheroe Limestone in Britain include the Salthill Quarry, Clitheroe, Lancashire, (four genera); Bellmanpark Quarry, Clitheroe, Lancashire (two genera); and the Calamine Mines of the Duke of Buccleugh, near Whitmore (four genera). An Irish example of blastoids associated with Chadian Waulsortian mounds is the Cover Mudstone from Feltrim Hill, County Dublin (three genera). No record of either shallow or nearshore facies with blastoids is preserved from the upper Courceyan or Chadian (Fig. 1) (*3*).

After the Chadian-Arundian extinction, blastoids were rare during the Arundian and Holkerian and were only known from Ireland. Fragments of a single blastoid are recorded from the deep-water, prodeltaic Bundoran Shale, County Donegal, Ireland (Arundian in age). Blastoids were not present in the shallow-water platform carbonates deposited throughout Ireland and Britain (*14*) during the Arundian and Holkerian.

Both in North America and Western Europe, significant blastoid extinctions accompanied the virtual elimination of blastoids from shallow-water habitats. Onshore to offshore habitat shifts accompanied by extinction have not been commonly cited, rather the documented offshore shifts have been gradual. A nearshore origin with progressive offshore expansion has been documented for various community types; for individual clades, isocrinid crinoids migrated into deeper water in the Mesozoic, and Paleozoic bivalves expanded from terrigenous to carbonate habitats (*1*).

This blastoid extinction suggests that a global reorganization of late Osagean stalked echinoderm communities must have occurred. Immediately after the extinction blastoids were common only in deeper water habitats. Few, if any, blastoid species present in the middle Osagean (Chadian) continued after the event, and many middle Osagean genera became extinct at this time.

The shift in blastoid habitat preference to deeper water settings lasted only a few million years. During the Meramecian (Asbian to Brigantian), blastoids reinvaded the full spectrum of shallow-water habitats to become common again in shallow water. Blastoids numerically dominated many Meramecian echinoderm communities in North America. The diversification of *Pentremites* was typical of the Meramecian blastoid expansion (*15*). North American shallow-water blastoid occurrences in the Meramecian include the Harrodsburg Limestone (three genera) and the Salem Limestone (five genera) in southern Indiana, among others.

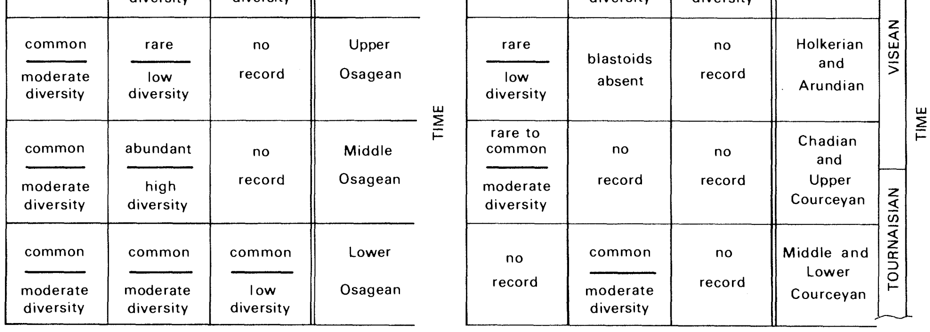
Asbian blastoids repopulated a wide variety of shallow-water and nearshore habitats in Western Europe. Monospecific but abundant blastoid faunas are associated with shallow-water reefs in the Dartry Limestone in northwestern Ireland (*5*). Blastoids are also known from a nearshore nodular clay in the Meenymore Formation at Cashel, County Fermanagh, Ireland (three genera) and at Slievemore, County Sligo, Ireland (four genera).

The cause or causes for the middle Mississippian extinction event and habitat shift remain unclear. However, a global cause is suggested by the nearly synchronous and widespread nature of this event.

One potential global, physical environmental cause is a change in sea level; and a small magnitude, short duration fall and rise of sea level has been suggested at the middle Osagean to late Osagean (Chadian to Arundian) boundary (*10*). However, the relation of a drop in sea level to blastoid extinctions is obscure. In North America, deposition of both the Burlington and Keokuk limestones, respectively, before and after this change in sea level, was on shallow-water carbonate platforms. Pelmatozoan echinoderms dominated in both the Burlington and Keokuk; but blastoids, abundant and diverse in the Burlington, are rare in the Keokuk. Physical environmental changes alone cannot explain the extinction event, as evidenced in the preserved stratigraphic record.

Rather it would appear that some intrinsic, biotic difference between crinoids and blastoids is responsible for their differential response to changing conditions during the Middle Mississippian. One potential explanation is that blastoids were simply outcompeted by crinoids in shallow-water platform habitats during migration associated with a change in sea level. It is also possible that intrinsic changes in blastoid extinction and origination rates during this interval brought about the elimination of shallow-water blastoids, irrespective of any environmental perturbation. Neither of these alternatives or other potential causes can be effectively tested at this time.

Regardless of the cause, the middle to late Osagean habitat-specific extinction event brought about the onshore-offshore habitat shift in blastoids. The extinction and habitat restriction occurred rapidly, but the onshore to offshore trend was reversed when blastoids later repopulated shallow-water habitats.



NORTH AMERICAN BLASTOIDS

ENVIRONMENT (Relative Water Depth)

Deep	Shallow	Nearshore	Relative Abundance Relative Diversity
no record	common moderate diversity	common moderate diversity	Meramecian
common moderate diversity	rare low diversity	no record	Upper Osagean
common moderate diversity	abundant high diversity	no record	Middle Osagean
common moderate diversity	common moderate diversity	common low diversity	Lower Osagean

WESTERN EUROPEAN BLASTOIDS

ENVIRONMENT (Relative Water Depth)

Deep	Shallow	Nearshore	Relative Abundance Relative Diversity
no record	abundant low diversity	common low diversity	Brigantian and Asbian
rare low diversity	blastoids absent	no record	Holkerian and Arundian
rare to common moderate diversity	no record	no record	Chadian and Upper Courceyan
no record	common moderate diversity	no record	Middle and Lower Courceyan

Fig. 1. Time-enrivonment diagram for Lower Mississippian Blastoidea, showing relative blastoid abundance and relative blastoid diversity (*6*). "Nearshore" refers to those habitats within fair weather wave base; "shallow" represents habitats below fair weather wave base but above storm wave base; and "deep" refers to habitats deeper than storm wave base. Only the time of extinction can be directly correlated between diagrams, which is the Middle Osagean–Upper Osagean boundary in North America and the Chadian-Arundian boundary in Western Europe. "No record" indicates that for a given time few examples of an environment are well documented, whereas "blastoids absent" indicates that no blastoids are known despite the fact that the habitat is well represented.

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Directional Selection and the Evolution of Breeding Date in Birds

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In many bird species, those pairs that breed earlier in the season have higher reproductive success than those that breed later. Since breeding date is known to be heritable, it is unclear why it does not evolve to an earlier time. Under assumptions outlined by Fisher, a model is developed that shows how breeding date may have considerable additive genetic variance, appear to be under directional selection, and yet not evolve. These results provide a general explanation for a persistent correlation of fitness with a variety of traits in natural populations.

IN BIRDS OF THE TEMPERATE ZONE clutch size and other measures of reproductive success typically decline as the breeding season progresses (*1–3*). This has led several workers to suggest that natural selection generally favors earlier breeding dates. If this is so, the unanswered question is why such selection has not caused the birds to evolve earlier breeding (*4–6*). One hypothesis is that the evolution of breeding date is constrained by lack of heritable variation (*2*), but this is not supported by several studies that have shown moderate to high heritabilities for breeding date in natural populations (*7*).

Fisher (*9*), in his elaboration of Darwin's theory of sexual selection in monogamous birds, provided an alternative hypothesis. Darwin had proposed that the health and vigor of females influences both the date at which they breed and their fecundity (*10*). Good health causes females to breed early and to raise more offspring, with the result that the earliest breeding individuals tend to be the most fecund. Fisher gave a numerical example in which there is an optimal intermediate breeding date, but in which the early breeding females nevertheless have highest fecundity. He showed that such a pattern could arise from nonheritable variation in female nutritional condition ("health" in Darwin's terminology) if good nutrition simultaneously causes higher fecundity and earlier breeding (*11*). Here we develop a quantitative-genetic model of Fisher's hypothesis which shows how early breeding females can be the most fecund even when the environment favors an intermediate breeding date and there is additive genetic variation for when females breed.

There is now strong empirical evidence that nutrition does affect both fecundity and date of breeding, as suggested by Darwin and Fisher. First, an association of high nutritional state with early breeding is clearly established (*12*). Supplemental feeding advanced breeding date in 12 of 15 studies of natural populations (*13, 14*), and protein reserves of females have been directly measured and correlated with time of breeding in two species (*15*). Second, females in good nutritional condition typically have higher reproductive success. This has been demonstrated by supplemental feeding experiments (*13, 14*), by direct measurements of protein reserves (*16, 17*), and by correlations between food abundance and several measures of reproductive success in natural populations (*16, 18*).

To show that a correlation between fecundity and breeding date is consistent with heritability for breeding date at an evolutionary equilibrium, we develop the following quantitative genetic model. We assume that a female's breeding date b is the sum of three factors: an additive-genetic component, x; a nonheritable component representing nutritional state, n; and a residual nonheritable component due to other environmental factors and nonadditive genetic effects, e. A female's breeding date can therefore be written

$$b = x - n + e \qquad (1)$$

where the sign of n is negative because a higher level of nutrition causes the female to breed earlier. Following the standard assumptions of quantitative genetics (*19*) the components x, n, and e are assumed to be independent and normally distributed, with means $\bar{b}$, 0, and 0, and variances σ_x^2, σ_n^2, and σ_e^2, respectively. We incorporate the positive effect of nutrition on fecundity with the exponential function $W_n(n) \propto \exp(\alpha n)$, where $W_n(n)$ is the fecundity of a female in nutritional state n, and α is a positive constant that scales the strength of the effect of nutrition on fecundity with respect to its effect on breeding date.

First consider the implications of variation in nutrition. From Eq. 1, the covariance between nutrition n and breeding date b is $-\sigma_n^2$. This negative phenotypic covariance implies that earlier breeding females have greater fecundity, since nutrition and fecundity are positively correlated. The covariance between n (nutrition) and x (the additive genetic component of breeding date) is zero, however, and so there is no genetic correlation between breeding date and reproductive fitness. Thus, in the absence of other evolutionary forces, breeding date will not evolve despite a persistent phenotypic correlation between breeding date and fitness. These conclusions can also be deduced from a path diagram (Fig. 1).

Now consider how breeding date will evolve if the environment favors some

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