

# Closing the Phosphatization Window: Testing for the Influence of Taphonomic Megabias on the Pattern of Small Shelly Fossil Decline

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*Small shelly fossils (SSFs) are a group of mostly problematic, small skeletal elements preserved primarily through secondary phosphatization. They dominate lower Cambrian diversity, but appear to suffer a sharp decline in the Botomian Stage or equivalent levels outside Siberia. This observed decline coincides with a significant reduction in phosphogenesis, suggesting that it may be attributable to the closure of a phosphatization taphonomic window. The influence of taphonomic bias on observed patterns of SSF extinction at the end of the Botomian was tested using a dataset consisting of 558 Cambrian skeletal genus occurrences compiled from 109 references. Analyses indicate that SSF preservation is significantly enhanced by, and for most taxa, restricted to, a phosphatization window. Independent proxies indicate that prevalence of secondary phosphatization declined from 74% and 64% of all preservational modes during Nemakit-Dal'dynian + Tommotian and Atadabanian + Botomian times, respectively, to 40% of all modes during Toyonian + middle Cambrian times, coincident with a severe reduction in observed SSF diversity. Subsampling methods that control for variations in the phosphatization window were used to test whether observed SSF diversity trajectories are biased. The corrected curve suggests that although the decline of SSFs was real, it may have been significantly exaggerated by the closure of a phosphatization window.*

## INTRODUCTION

Small shelly fossils (SSFs), millimeter-scale skeletal elements of largely problematic taxonomic affinity, dominate earliest Cambrian skeletal animal diversity. They appear to have suffered a severe reduction in diversity, however, during the late early Cambrian (Botomian Age), in what has been identified as the first major extinction of the Phanerozoic (the Botomian extinction; Palmer, 1982; Zhuravlev and Wood, 1996; Zhuravlev, 2001). Subsequent to the extinction event, the diversity of SSFs continued to decline, whereas constituents of the Cambrian fauna (*sensu* Sepkoski, 1992), a relatively minor component of pre-Botomian diversity, went on to dominate middle and late Cambrian (Furongian) diversity (Sepkoski, 1992; Zhuravlev and Wood, 1996).

While the response of other taxonomic groups (e.g., archaeocyathids and some trilobites) during the Botomian

event indicates that the extinction was real, the subsequent pattern of SSF taxonomic decline may have been affected by taphonomic megabias (cf., Kowalewski and Flessa, 1996; Behrensmeier et al., 2001). SSFs appear to be preserved primarily through secondary phosphatization (Qian and Bengtson, 1989; Bengtson et al., 1990; Brasier, 1990; Dzik 1994); in fact, it is possible that their preservation may rely on—or more certainly be enhanced by—a phosphatization taphonomic window (Brasier, 1990; Dzik, 1994), hereafter referred to as a phosphatization window. Their decline in the Botomian coincides with a significant reduction in phosphogenesis (Cook and McElhinny, 1979; Cook 1992), raising the possibility that it may be attributable at least in part to the closure of this phosphatization window. The recent discovery of SSF taxa, previously unknown from the middle Cambrian, in phosphatic limestones from the middle Cambrian Georgina Basin in Australia (Porter, 2000; in press) supports this contention and suggests that more SSFs may be found in middle Cambrian rocks if suitable taphonomic windows were explored (see also Butterfield and Nicholas, 1996; Van Iten et al., 2002).

This paper examines the role of taphonomic megabias in creating the pattern of SSF diversity decline by attempting to quantify three issues. First, how much is SSF preservation enhanced by secondary phosphatization? Second, how significant is the decline in phosphatization through early and middle Cambrian time? Finally, to what extent can the severe reduction in SSF diversity at the end of the Botomian Age be attributed to the closure of this phosphatization window?

## METHODS

### Dataset

To address the questions posed above, a dataset of 558 genus occurrences of SSFs and several proxy taxa was compiled from 109 references (see Appendices 1–3, reposted online at <http://www.ngdc.noaa.gov/mgg/sepm/archive/>). SSFs are taken here to be equivalent to the variety of short-ranging problematica identified in Sepkoski's (1992) factor analysis of early metazoan diversity as a major component of the Tommotian fauna. As such, SSF taxa are united not by any common biological features *per se*, but rather by their shared diversity history, and, as tested here, possibly by their taphonomic characteristics. Monoplacophoran mollusks, orthothecid hyoliths, and sabelliditids are also a part of this fauna, although they have not been included in this analysis. Although Sepkoski (1992) did not specify which groups were included under the designation, 'variety of short-ranging problematica,' reasonable estimates can be made using the same list of metazoan genera (Bengtson, 1992) that Sepkoski (1992) used for his analysis. The following taxa from Bengtson's list were assumed to be in this category: agmatans, cambroclaves, conulariids, coeloscleritophorans, mobergellans, *Microdictyon*, paracarinachitids, paiutiids, 'problematica' (a variety of shells, sclerites, tooth-shaped fossils, tubes, and cones with unknown higher taxonomic affinities), tommotiids, trilobozaans, utahphosphids, 'possible coeloscleritophorans,' 'possible trilobozaans,' 'possible brachiopods,' 'possible hyoliths,' and 'possible mollusks.'

Proxy taxa provide an independent proxy for the relative abundance of preservational conditions through early and middle Cambrian time; importantly, they do not show a decline in diversity across the early–middle Cambrian boundary (33 genera and 72 genus occurrences in the Atdabanian + Botomian interval versus 32 genera and 71 genus occurrences in the Toyonian + Middle Cambrian interval). They include hyolithomorph hyoliths, non-monoplacophoran molluscs, and phosphatic brachiopods (see discussion under Analyses below).

Bengtson's (1992) list included not only valid Cambrian skeletal taxa, but also their synonyms. This was used to correct for taxonomic synonymies, thereby minimizing artifacts associated with taxonomic oversplitting. Genera not on Bengtson's list (<1%) were omitted from the database. Taxonomic names erected since 1992 were accepted as given.

A 'genus occurrence' was counted as the presence of a particular genus in a particular lithologic unit: geologic members wherever possible, otherwise formations. Presence of a genus in the same member (or formation) at different localities was counted as a single occurrence. Taphonomic mode, member and formation name, locality, geographic region, and age were recorded for each genus occurrence. Genus occurrences for which there was no information about taphonomic mode were omitted unless reasonable estimates could be made. If a genus was preserved in more than one way in a single lithologic unit, each different taphonomic mode was counted separately. Eight taphonomic modes were identified: (1) molding by Fe and Mn oxides, (2) glauconitization (casts and molds), (3) "Burgess Shale type" preservation of compressions in shale, (4) phosphatization (casts and molds), (5) casting and molding by siliciclastics (sand and silt), (6) silicification (casts and molds), (7) pyritization (casts and molds), and (8) original shell material. The last category includes recrystallized shell material, and refers only to preservation of original shell material in the absence of other taphonomic modes that might enhance preservation and/or identification. Thus, calcareous shells preserved in phosphatic facies are considered phosphatized because their identification is (almost always) based on phosphatic internal molds. Similarly, originally phosphatic shells preserved under phosphatizing conditions—as judged by the presence of phosphatized calcareous taxa and/or the presence of a secondary phosphatic coating—were considered phosphatized, rather than original shell material. In the absence of phosphatizing conditions, such shells would be considered original shell material.

Early and middle Cambrian time was divided into three bins based on Siberian stratigraphic divisions (see Geyer and Shergold, 2000): (1) the Nemakit-Dal'dynian + Tommotian stages (NDT), (2) the Atdabanian + Botomian stages (AB), and (3) the Toyonian Stage + middle Cambrian (TM). Each of these covers roughly the same amount of time (~10–15 Myrs; Bowring and Erwin, 1998). The stratigraphic scheme recently published by Geyer and Shergold (2000) and Geyer et al. (2000) was used to correlate strata from different regions with the Siberian stages.

Many references on Cambrian fossils, most notably those from Siberia, supply no information on preservation and thus were not included in the dataset. The results of this study, therefore, must be viewed only as representa-

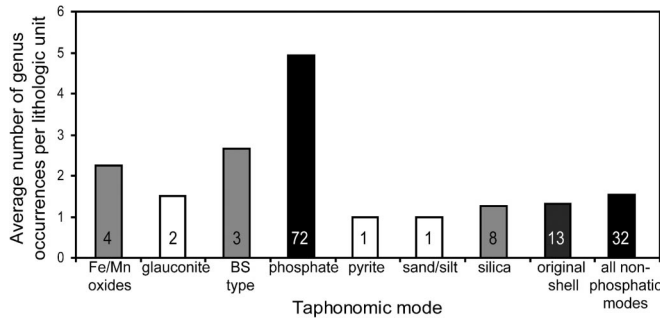
tive of the global pattern and should be tested with more thorough investigations.

### Analyses

To determine whether SSF preservation was enhanced by phosphatization, the number of SSF genus occurrences in each taphonomic mode was divided by the number of lithologic units in each mode (this controls for differences in the abundance of different taphonomic modes). The result can be thought of as the average number of genus occurrences per taphonomic mode unit.

To determine whether there was a significant decline in phosphatization from early to middle Cambrian time, the proportion of lithologic units in each time bin that preserves phosphatic fossils (casts and/or molds) was used as a proxy for the abundance of phosphatic facies through time. More detailed proxies for the abundance of taphonomic modes, incorporating, for example, outcrop area, could be employed in future analyses. Note that the relative number (i.e., the proportion) of lithologic units in each mode, rather than the absolute number of units in each mode, is used because of variation in the total number of lithologic units per time bin. Lithologic units with fossils preserved in more than one mode were counted more than once. Lithologic units that could not be well constrained stratigraphically were not counted. To avoid circularity, the capacity to preserve SSFs must be recognizable in the absence of SSFs; thus, non-SSF taxa, in addition to SSF taxa, were used to identify taphonomic mode units. These proxy taxa (hyolithomorph hyoliths, non-monoplacophoran molluscs, and phosphatic brachiopods) were chosen because they exhibit the same range of original skeletal composition found in SSFs and they are preserved in the same variety of taphonomic modes as SSFs, but, unlike SSFs, their diversity (Sepkoski, 1992; Zhuravlev and Wood, 1996; Zhuravlev, 2001) and number of genus occurrences (this dataset) remain stable through the early and middle Cambrian.

To determine the extent to which the severe reduction in SSF diversity from early to middle Cambrian time can be attributed to the closure of a phosphatization window, a subsampling analysis was employed (see Alroy et al., 2001). A list of phosphatized SSF genera from each phosphatic unit was compiled for NDT, AB, and TM time. Lists ranged from 47 SSF genera (representing the NDT Zhongyicun Member, Dengying Fm) to zero genera (those phosphatic units with no SSF genera represented; e.g., the AB Olenellus Limestone, Shropshire, England). Eleven lists—equal to the total number of phosphatic lithologic units for the middle Cambrian bin—were chosen randomly, without replacement, from each collection, and the diversity of this subsample was calculated (Shinozaki, 1963; equivalent to the lists unweighted method of Alroy et al., 2001). This method assumes that the lists are taphonomically comparable (Alroy, 2000), which, given that they have been chosen on the basis of their taphonomic mode, is valid. According to Alroy et al. (2001), problems with this method can arise if the modal number of specimens per list varies systematically through time, but there is no such variation apparent in this data set (mode = 1 for lists in each of all three time bins). Subsampling was repeated 100,000 times to create diversity distributions indicating



**FIGURE 1**—Average number of SSF genus occurrences per lithologic unit, calculated for each taphonomic mode, and used as a proxy for how well each taphonomic mode preserves SSFs. The number of lithologic units in each mode is indicated both numerically within each bar and by the shade of the bar (darker shades indicate more units and thus greater certainty). BS= “Burgess Shale.”

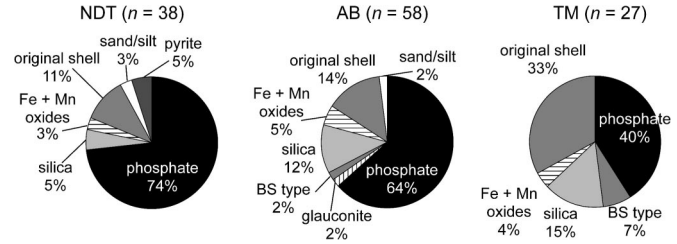
the likelihood of specific diversity levels given the presence of only eleven phosphatic units.

## RESULTS

### How Much is SSF Preservation Enhanced by Phosphatization?

Figure 1 shows the average number of genus occurrences per taphonomic-mode unit, with the number of lithologic units indicated both numerically within each bar and by each bar's shading. The data indicate that phosphatization preserves on average more SSF genera (4.9) than any other taphonomic mode: more than three times that for all nonphosphatic modes averaged together, and, with the exception of ‘Burgess Shale-type’ preservation—itsself a taphonomic window—significantly higher than the number for any other single taphonomic mode (Student's *t*-test,  $P < 0.05$ ). Indeed, most SSF taxa (88%) occur only in phosphatic facies.

This pattern could be explained in a number of ways. SSFs may have created the facies in which they are preserved (cf., Behrensmeier et al., 2001); the decline in phosphatization through the Cambrian could thus reflect real taxonomic or ecological/populational decline of this group. This is unlikely, however, because high accumulations of phosphate, such as those associated with most SSF assemblages, require an external source (Martill, 1988; Xiao and Knoll, 1999), which is consistent with explanations for Cambrian phosphogenesis (e.g., Cook and Shergold, 1984; Donnelly et al., 1990). A second possibility is that most SSF organisms lived only in environments that favored phosphatization; a decline in the prevalence of these environments would thus cause the extinction of SSF taxa. This possibility depends on a reasonable explanation for why SSF taxa in particular were restricted to such environments and other Cambrian taxa were not. A third possibility, favored here, is that the pattern reflects enhanced SSF preservation associated with secondary phosphatization. Phosphatization can enhance SSF diversity estimates in at least three ways. First, secondary phosphatization can occur very early in diagenesis (e.g., Briggs and Kear, 1993, 1994; Hof and Briggs, 1997; Xiao and Knoll, 1999) and thus preserve skeletal material that otherwise might be destroyed, for example, by dissolution. Second,



**FIGURE 2**—Relative abundances of taphonomic modes through time, represented by the proportional number of lithologic units in each taphonomic mode.  $n$  = total number of lithologic units in each time bin. Calculated percentages do not add to 100 due to rounding errors. Acronyms: NDT= Nemakit–Daldyn + Tommotian; AB= Atdabanian + Botomian; TM= Toyonian + middle Cambrian.

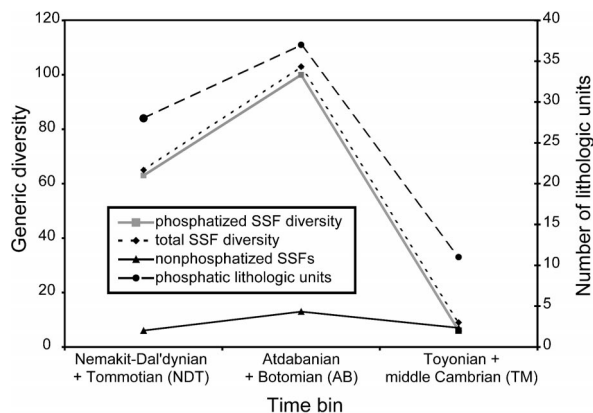
unlike most other taphonomic modes, secondary phosphatization is capable of preserving exceptionally fine detail (e.g., Runnegar, 1985; Bengtson et al., 1990), resulting in better taxonomic resolution and thus higher diversity estimates. Finally, phosphatized SSFs are unusually amenable to micropaleontological study. Unlike SSFs preserved as carbonate shells, phosphatized SSFs survive acid maceration, a technique that certainly enables better taxonomic resolution than thin sectioning. SSFs preserved in other taphonomic modes (e.g., Fe/Mn oxides, pyrite, silica) can survive maceration as well, but unlike phosphatized SSFs, they are almost always preserved as internal molds, precluding detailed identification.

### How Significant is the Decline in Phosphatization Through Early and Middle Cambrian Time?

Figure 2 shows the proportion of lithologic units of each taphonomic mode for each time bin. It indicates that the abundance of phosphatic facies declines through the early and middle Cambrian from a high of 74% in the NDT, through 64% in the AB, down to 40% in the TM. Note that the total number of lithologic units does not remain constant through this interval; the number drops from 58 in the AB to 27 in the TM, but this can be attributed almost entirely to the drop in phosphatic facies. Abundance of nonphosphatic facies through this interval remains approximately the same (21 for AB versus 16 for TM). Data on phosphate abundance through the lower and middle Cambrian, derived from proxy taxa alone, corroborate the pattern exhibited by the SSFs + proxies, except that they suggest an even more severe drop in the abundance of phosphatic facies across the early/middle Cambrian boundary (79% to 29%). Thus, the data indicate that the phosphatization window did close significantly from the early to the middle Cambrian.

### To What Extent Can the Severe Reduction in SSF Diversity at the End of the Botomian Stage be Attributed to the Closure of a Phosphatization Window?

Figure 3 shows observed generic diversity for total, phosphatized, and nonphosphatized SSFs, as well as the abundance of phosphatic facies through early and middle Cambrian time. There are three things to note in this graph. First, total diversity is nearly indistinguishable from phosphatized diversity, but quite different from non-



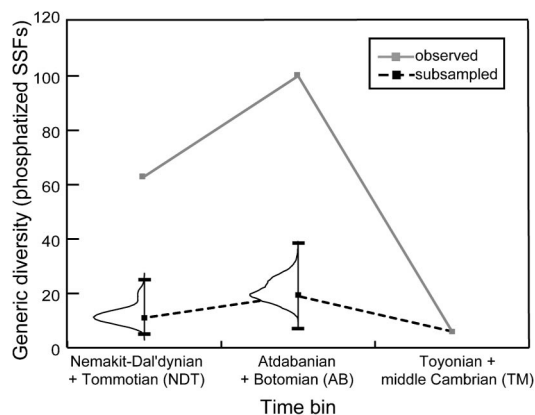
**FIGURE 3**—Observed generic diversity of total SSFs, phosphatized SSFs, and nonphosphatized SSFs, and abundance of phosphatic facies through Cambrian time.

phosphatized diversity, suggesting that total diversity is largely a reflection of phosphatized diversity. Thus, biases in phosphatized diversity estimates strongly affect total diversity estimates. Second, both total and phosphatized diversities decline sharply from the AB into the TM, closely mirroring a decline in the abundance of phosphatic facies, suggesting that prevalence of phosphatization may indeed control patterns of SSF diversity. Finally, SSFs preserved in nonphosphatic facies—notably those facies that do not vary appreciably through time (see previous section)—show only a slight decline in diversity from the AB into the TM.

Figure 4 illustrates the results of the subsampling analysis, which controls for variations in the abundance of phosphatic facies through time. If the decline in observed SSF diversity from the AB through the TM were entirely an artifact of the decline in phosphatic facies, observed TM SSF diversity would be comparable to subsampled AB diversity. Instead, it is still relatively low (falling just outside the 95% confidence interval for AB time), suggesting that there is less than a 5% chance that observed TM diversity is this low because of a taphonomic artifact. Indeed, it suggests that the extinction of SSF taxa was still quite severe—the TM diversity level is ~33 to 50% that of the AB level—although not as severe as a literal reading of the fossil record would suggest (~90% losses; Fig. 3). Thus, while the record of SSF mass extinction is not an artifact of taphonomic megabias, the apparent severity of that extinction may be. Interestingly, the subsampled diversity trajectory of phosphatized SSFs (Fig. 4) is similar to the *observed* diversity trajectory of non-phosphatized SSFs (Fig. 3). Because the abundance of nonphosphatic facies stays relatively constant across this boundary (see discussion above), diversity patterns observed through this non-phosphatized taphonomic window may be less affected by taphonomic megabias.

## DISCUSSION

Early Cambrian taxa were affected in different ways by the Botomian extinction event. Observed patterns of archaeocyathid diversity, which, notably, are independent of the phosphatization window, indicate that this group was decimated in the extinction (80 to 90% extinction at the ge-



**FIGURE 4**—Observed (gray line; from Fig. 3) and subsampled (black dashes) phosphatized SSF generic diversity through Cambrian time. Subsampled SSF diversity controls for variations in the abundance of phosphatic facies through time were calculated for Nemakit-Dal'dynian + Tommotian and Atdabanian + Botomian times by drawing at random, without replacement, 11 lists (as represented by lithologic units) and calculating this subsampled diversity. This was repeated 100,000 times to produce the diversity probability distributions, shown here in vertical orientation in each subsampled time bin. The mode of each distribution is represented by a black square, and the 95% confidence intervals by error bars. The Toyonian + Middle Cambrian datum represents observed diversity, based on 11 lithologic units.

neric level; Debrenne, 1991) and never recovered (Debrenne, 1991; Zhuravlev and Wood, 1996; Zhuravlev, 2001). In contrast, observed patterns of echinoderm and brachiopod diversity suggest these groups were little affected (Zhuravlev and Wood, 1996). Observed patterns of SSF diversity indicate a history similar to that of the archaeocyathids, but this study suggests a more moderate picture: SSFs do suffer a significant decline in diversity (~33–50% extinction at the generic level), but it may not have been as severe as a literal reading of the fossil record would suggest (~90%). Taphonomic megabias resulting from the closure of a phosphatization window exaggerated the apparent effects of the Botomian crisis on the Tommotian fauna.

This analysis was set up to determine whether the record of SSFs, as a group, suffers from taphonomic megabias. It is important to note, however, that SSFs are not a natural group in the sense that they do not necessarily share any biological or ecological characters—they are united only by a common diversity history. That the group as a whole suffers from taphonomic bias does not imply that every member does. Indeed, as noted previously, although most taxa are preserved only in phosphatic facies, several taxa (~12%) are preserved in a range of taphonomic modes, indicating that they, at least, do not depend on a phosphatization window. *Chancelloria*, for example, is preserved by Fe/Mn-oxide and glauconite mineralization, recrystallized calcite, and organic compressions, in addition to secondary phosphatization (most occurrences are, nevertheless, in phosphatic facies). What is interesting to note, however, is that survival patterns of these taxa actually strengthen the claims made here: of those taxa that are preserved in non-phosphatic modes in the early Cambrian, ~15% were found in middle Cambrian rocks, compared to less than 1% of those that are restricted to the phosphatic window. That is to say, preservation in a great-

er range of taphonomic modes is correlated with a greater chance of being preserved in middle Cambrian rocks. Of course, there could be a causal connection here—those taxa that have wider environmental ranges are both more likely to be preserved in a variety of taphonomic modes and more likely to survive extinction. However, the alternative cannot be ruled out: those taxa are more likely to be preserved in the middle Cambrian because they are not restricted to a single taphonomic mode.

One issue that is difficult to resolve is why some taxa are found only in phosphatic facies. The answer may be some combination of factors discussed above. Taxa found only in phosphatic facies may not be identifiable without the detailed preservation that phosphatization provides. These taxa also may be rare, and thus not usually found without picking through thousands of macerated specimens. They may consist of labile materials that require exceptional circumstances for their preservation, or they may have been environmentally restricted such that they did not occur in environments where other types of exceptional preservation occurred (e.g., Burgess Shale-type deposits).

A reliable, quantitative estimate of actual SSF diversity decline through the Cambrian will depend on better sampling of phosphatic facies from the middle and late Cambrian. Recent investigations of phosphatic limestones from the middle Cambrian Georgina Basin, Australia, corroborate the general pattern of SSF decline and increased dominance of the Cambrian fauna (*sensu* Sepkoski, 1992), but have also yielded a surprising abundance of SSF taxa previously unknown from this time, including at least two halkieriid species and possible sachtitids (Porter, 2000; in press). Such discoveries suggest that more complete sampling of phosphatic facies from post-Botomian times could substantially change current views of SSF diversity history.

### CONCLUSIONS

Phosphatization provides a valuable window on early skeletal animals. Without it, our knowledge of early animal diversification would be significantly reduced. Because this taphonomic mode greatly enhances preservation, however, variations in its abundance through time can bias observed diversity trajectories. This apparently is the case for the pattern of SSF diversity decline after the Botomian extinction: a significant decrease in the abundance of phosphatized facies may have caused the decline in SSF diversity to appear much more severe than it was in actuality. Accurate estimates of actual SSF diversity are severely limited by changing taphonomic conditions; focused sampling of middle and late Cambrian phosphatic facies will mitigate this problem.

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