

Strength in numbers: high phenotypic variance in early Cambrian trilobites and its evolutionary implications

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Summary

Analysis of the degree of intraspecific morphological polymorphism during the evolutionary history of trilobites using an informatic approach⁽¹⁾ provides striking evidence of a long-suspected but previously unsubstantiated pattern: degrees of polymorphism are markedly higher in phylogenetically basal, stratigraphically early species. This unequivocal pattern prompts further exploration of the relationship between microevolutionary variance and macroevolutionary history. It demonstrates that the ‘traditional’ fossil record of skeletonized organisms can provide unique insight into questions of major evolutionary interest. *BioEssays* 29:1081–1084, 2007. © 2007 Wiley Periodicals, Inc.

The delightful “exceptionally preserved” fossils that frequently grace the pages of the science weeklies are often spectacular but it is unclear whether such unusual-by-definition specimens are representative of the normal populations that they belong to. And in all the understandable excitement about ancient embryos and feathered dinosaurs, it is easy to overlook the power of the “traditional” fossil record of skeletonized remains for its great fidelity, continuity, and taxonomic and ontogenetic scope. Here, the problem is one of overabundance. For example, esoteric vocabulary embedded in a disparate literature describes the 15,000 known species of trilobite recovered over the last 200 years, and trilobite paleontology surely meets anyone’s definition of a specialist’s specialty. Such richness, however, can be turned to advantage through an informatics approach. An example is Mark Webster’s important paper⁽¹⁾ on reconstructed temporal trends in trilobite intraspecific variation published recently in *Science*. The trick for the trilobite specialist, of course, is to focus on questions of broad interest in evolutionary biology that the trilobite fossil record is best placed to answer.

Webster addressed an issue that is “lore” among trilobite specialists, who have long bemoaned the difficulty of construct-

ing species-level systematics for Cambrian trilobites. This is because, as Darwin recognized, species boundaries based on morphology are commonly indistinct. Indeed, it’s always a challenge to distinguish intraspecific from interspecific differences, and especially so in fossils. Terms such as “lineage crossing” “developmental flexibility” and “plasticity” have been bandied about in studies of Cambrian trilobites to donate the observed large morphological variances, while those working with geologically younger, more evolutionarily derived, trilobites have found species definition easier. This frustration in classification of the early trilobites hints that there was something different about the way in which these species varied phenotypically when compared to later ones, and prompts the question of why this might be so. Trilobites appeared in the fossil record some 20 million years after the base of the Cambrian Period. While it’s clear that the major differentiation both within and among animal phyla was already established by that time, it is still possible that patterns of variation in early Cambrian species might reflect a “warm afterglow” of the Cambrian radiation. If such a pattern could be demonstrated convincingly, we can ask whether early variability differs from that in later species because of “internal” reasons related to the way in which development was controlled in these species, or whether it was due to “external” influences associated with the selective environment in which these species lived.⁽²⁾ Furthermore, trilobites provide a striking example of the “bottom heavy” pattern of clade diversification, in which maximum morphological and taxonomic diversity was generated early in clade history. This pattern is commonly documented in the fossil record and not only in association with the Cambrian radiation, hinting at a pattern of even broader significance.

The first problem, and the one that Webster’s study addresses, is to assess whether the impression of early species variability and later reduced species variability is truly valid. Although detailed studies of individual Cambrian species have claimed to support the trend,⁽³⁾ such studies are subject to the general criticism of exceptionally preserved fossils: do such individual cases accurately reflect a general pattern? A similar problem applies to the classic trend from high to low variance in trunk segmentation specifically seen between early Cambrian and later trilobites:⁽⁴⁾ it is only one character

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complex (although, in my opinion, one of particularly rich potential insight⁽⁵⁾). Webster tackled these problems by compiling data from his own and from published phylogenetic analysis of trilobites for several character complexes. He conducted a meta-analysis of the degree of intraspecific polymorphism in 982 species. This straightforward approach yielded a clear and straightforward answer: earlier and phylogenetically more basal trilobites do indeed show significantly higher levels of intraspecific polymorphism than later, more derived ones. Reassuringly, given the nature of morphological species definition, this result applies to subsets of trilobite species of different geological ages conducted by the same individual scientist. This argues against a potential bias caused by different taxonomic approaches among workers specializing in trilobites of different geological age. Hence, apparently, there really was something different about how early trilobite species varied compared to later ones, particularly those alive between about 525 and 500 million years ago. This is an important result not only because it makes explicit to evolutionary biology what was previously implicit to trilobite specialists, but also because the trend is so remarkably clear.

Where to go from here? One temptation might be to dismiss the result as an overinterpretation of the fossil record, on the grounds that species recognition is untestable in fossils, but here Webster is on solid ground. The fossil record of skeletonized trilobites is surprisingly good, particularly for those groups well enough preserved to merit phylogenetic analysis at low taxonomic levels. Furthermore, recent studies of the well-preserved skeletonized record tend to support congruence between patterns of morphological variance in fossils and living taxa for several animal groups.⁽⁶⁾ (However, it is true that clear recognition of subspecies is more common in the post Cambrian). A more serious concern may be the way in which Webster relates phenotypic variation to evolutionary change. While intraspecific variation is, of course, necessary for evolution, the extent to which phenotypic plasticity promotes or directs evolution is debatable.⁽⁷⁾ But here again the fossil record is making important empirical contributions. Gene Hunt's recent work on patterns of phenotypic variance in living and recently fossilized ostracods suggests that evolutionary trends do indeed mimic patterns of intrapopulational variation. Indeed, studies such as Hunt's and Webster's may mark the return of paleontological data to current debates among evolutionary ecologists, and help span the shaky ground between paleontology and microevolutionary biology, still reverberating from the punctuated equilibrium debate.

It would be interesting to know if the degree of polymorphism among the Cambrian species in Webster's analysis markedly exceeds to that known among living taxa, which can show extremely high rates of intraspecific morphological evolution.⁽⁸⁾ That more than 70% of early and middle Cambrian

species were polymorphic in at least one character may not be an astonishingly high proportion—what of cryptic sexual dimorphism, for example? Hence the issue of punctuated equilibrium might be relevant to Webster's study in a different way. Niles Eldredge's study of morphological stasis concerned the derived Devonian trilobite species belonging to the genus now known as *Eldredgeops*.⁽⁹⁾ It remains to be seen whether the story here is more the extremely low intraspecific variance of derived species such as those Eldredge examined. For no matter whether patterns of intraspecific variation among multiple successive samples of derived trilobite species are described as static, random walks or directed trends, none published to date seem to be of a magnitude sufficient to fuel the evolutionary diversification of the clade as a whole: the evolutionary rates observed are far too slow.

How does Webster's fit with other comparative studies of Cambrian and later trilobites? Here, unsurprisingly, the answer is complex. Studies of trilobite evolutionary rates show faster species turnover in the Cambrian,⁽¹⁰⁾ but the rates are not outstandingly high for marine invertebrates at other times in the fossil record.⁽¹¹⁾ Nor is there strong evidence for a temporal change between the early Cambrian and later times in the degree of morphological transition associated with speciation.⁽¹²⁾ Furthermore, the extent to which the earlier Cambrian, in which Webster finds high intraspecific variance, shows morphological diversity at the level of the clade Trilobita, as a whole, depends on the characters examined. This interval, however, does appear to be the acme of variation in the overall number of trunk segments⁽¹³⁾ but, in the early Cambrian, aspects of head shape show markedly less morphological variety than at later times.⁽¹⁴⁾ It has long been argued that, while derived clades were dominated by peramorphic heterochrony,⁽¹⁵⁾ early trilobite evolution was characterised by the dominance of paedomorphosis,⁽¹⁶⁾ hinting at a difference in evolutionary mode among earlier trilobites and those clades that rose to dominance later, in the Ordovician and thereafter. Although the progressive development of trilobite segmentation invites heterochronic interpretation, recent studies have questioned whether such evolutionary transitions among trilobites are strictly heterochronic in origin.^(17–19) Nevertheless, here again the "lore" of earlier trilobite specialists, in this case originally proposed in support of Haeckelian recapitulation, may contain a kernel of truth: many of the characters that Cambrian trilobites experimented with, such as the number of trunk segments, were stable among post-Cambrian trilobites that were differentiated on the basis of novel characters or at least marked embellishments of structures evident in more basal forms.⁽¹³⁾ For these reasons, I was expecting Webster's result to show character-specific differences in the degree of polymorphism through time. But that was apparently not the case: decreasing polymorphism went across the board, influencing all characters, both the old and new. Hence although relatively high phenotypic variance

in thoracic segment number is matched by high variance in this character among early trilobites as a whole, suggesting a simple scaling between microevolutionary and macroevolutionary patterns, high phenotypic variance in aspects of head shape is apparently not matched by high head shape diversity in the clade as a whole. This suggests a Cambrian limit to diversification operative at the clade level but not at the species level. It will be interesting to examine the temporal, spatial and environmental distribution of these polymorphic character states for more clues to the sources of these differences. The data set also offers other tantalizing opportunities for exploring the relationship between morphological complexity and variation.

Webster's study does not address the question of whether the decrease of phenotypic variance was the result of the "internal" tightening of developmental regulation or "external" changes in selective environment. That question was at the core of Steve Gould's book *Wonderful Life*,⁽²⁰⁾ a commentary on the significance of the Cambrian soft-bodied fauna of the Burgess Shale. Gould favoured the former option. Although it has since been argued that the commonality of the developmental toolkit among metazoans effectively excludes that interpretation,⁽²¹⁾ that view now seems debatable. Changes involving regulatory tinkering in the relationships among long-established developmental kernels could still have significant phenotypic import. Nevertheless, a study of the temporal pattern of variability in trilobite trunk segmentation, and the reappearance of a Cambrian-esque pattern of variation in a phylogenetically derived Silurian trilobite mimicking a form common in the Cambrian favours the environmental interpretation.⁽²²⁾ Mature specimens of the Silurian trilobite *Aulacopleura konincki* varied by several trunk segments within a single population, as did some Cambrian homeomorphs, while all other trilobites of the same assemblage showed stable segment counts in maturity. Thus it seems that when this derived 435 million year old trilobite converged on a Cambrian *gestalt*, the same pattern of phenotypic variability emerged again, arguing against the irreversible tightening of developmental control. But things may not be as simple as they seemed at first. Additional studies of *A. konincki* show precise control of developmental decisions including those concerning the numbers of segments. Indeed, this trilobite provides the earliest example of targeted growth known in the fossil record.⁽²³⁾ Thus it is evident that the factors affecting morphological plasticity are diverse. Paleontologists need to move beyond simply equating phenotypic plasticity with sloppy developmental control. The obvious next step is to look at the control of segmentation in those phylogenetically basal Cambrian trilobites that share the same form as *A. konincki*. We may be in for more surprises before this saga reaches the limit of resolution possible in the fossil record, but these studies suggest that we can take this line of enquiry quite some distance when the record is good.

In addition to advertising the "exceptionally preserved", paleontology has also recently been marketing its relevance for understanding past episodes of global change, occasioned by dramatic improvements in the degree of temporal resolution possible in rocks millions of years old and our improved ability to read environmental signals in the ancient record. But data from the "traditional" fossil record can do more for us, particularly in the area of evolutionary developmental biology. Although we can never hope to gain equivalent insights into developmental regulation afforded by the study of extant organisms, if the pattern of rampant intraspecific polymorphism Webster documents was general to metazoan clades in the aftermath of the Cambrian radiation and unique to it, then we are only going to find such patterns by studying fossils. Fortunately, the outstandingly rich record of the temporal diversity of trilobite systematics and ontogeny offers a range of opportunities for immersing ourselves in the nitty-gritty of bridging the microevolutionary to macroevolutionary divide in the early evolution of derived metazoans. This challenge requires and justifies a host of specialized studies conducted at a range of taxonomic scales. Trilobite paleontology may be a specialist field, but it has special strengths. Webster's paper provides the first convincing demonstration of a long-suspected general pattern at the taxonomic levels, one at which we witness and make inferences about evolution. It will stimulate research into dissecting the fossil record for patterns of morphological change, through a combination of detailed studies of individual taxa and synoptic views at higher taxonomic levels, thus encompassing both microevolution and macroevolution.

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