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A Cambrian Peak in Morphological Variation Within Trilobite Species

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Morphological variation within species is a raw material subject to natural selection. However, temporal change in morphological diversity has usually been studied in terms of variation among rather than within species. The distribution of polymorphic traits in cladistic character-taxon matrices reveals that the frequency and extent of morphological variation in 982 trilobite species are greatest early in the evolution of the group: Stratigraphically old and/or phylogenetically basal taxa are significantly more variable than younger and/or more derived taxa. Through its influence on evolutionary tempo, high intraspecific variation may have played a major role in the pronounced Cambrian diversification of trilobites.

Many higher taxa show a markedly asymmetric diversification history, with rapid initial increase in morphological diversity among taxa (disparity) and subsequent decline in or cessation of evolutionary inventiveness (1–4). Rates of taxonomic diversity increase are also often higher during the early portion of clade evolutionary history (5, 6). Because the potential rate and magnitude of evolutionary change (evolvability) for a species must be to some extent a function of the degree of morphological variation exhibited by that species (7, 8), change in the frequency or nature of intraspecific variation within a clade could profoundly influence its evolutionary dynamics. To the extent that observed phenotypic variation reflects heritable variability (7) and therefore evolvability, a clade exhibiting a bottom-heavy diversification history would be predicted to show a temporally declining degree of intraspecific variation among its constituent

members, as has been claimed for some animal clades [“Rosa’s Rule” (9, 10)].

Here I investigate long-term trends in morphological variation in species using the 270-million-year history (Early Cambrian through Late Permian) of trilobites. Trilobites have a character-rich morphology, abundant fossil record, and high diversity. The diversification history of trilobites was bottom-heavy (fig. S1A): Origination and extinction rates of trilobite genera were generally higher in the Cambrian than later (fig. S1, B and C), although there was rapid diversification within some post-Cambrian clades (11). Maximal disparity was achieved during the Early Cambrian [based on among-species variation in thoracic segment number (12)] or the Ordovician [based on among-species variation in cranial outline (6, 13) and qualitative assessment of gross anatomy (14)]. Although it has been suggested that the net decline in evolutionary rate corresponded to a general decrease in morphological variability within trilobite species through time (15, 16), the few pertinent studies to date do not provide strong empirical support for unusual variation within

Cambrian trilobite species in any aspect of morphology other than number of thoracic segments at maturity [(12); see supporting online material (SOM)], and even that trait is variable within only very few species.

I explored temporal patterns in intraspecific variation as represented by character states coded as polymorphic within trilobite species in cladistic analyses. Species coded as polymorphic for a given character are assumed to have exhibited marked variation that spanned two or more states defined by the original authors. Aspects of organismal shape, counts of meristic features (including presence or absence of particular features), and locations and discrete types of particular anatomical structures can all form the basis for characters coded in cladistic analyses, thus maximizing morphological coverage (SOM).

I examined 68 trilobite character-taxon matrices for intraspecific polymorphisms (table S1), but application of stringent criteria to reduce the potential for among-study bias (17) resulted in exclusion of some entire matrices, and of particular characters and/or taxa from others (table S1). The final data set consisted of character-taxon matrices from 49 independent studies (tables S1 and S2). Character-state information for a total of 982 species was included (table S2), representing ~5% of all valid trilobite species (18). All eight orders of trilobites, plus the problematic burlingiids, were represented. I treated agnostids as trilobites (19–21), but my general conclusions are not dependent upon their inclusion. All orders were represented by more than 100 species in the analysis, with the exception of the Redlichiida (79 species), the Corynexochida (50 species), and the Asaphida (26 species). With the exception of the Permian, geologic periods were subdivided into two or three temporal bins (typically corresponding to epochs); the stratigraphic age at this finer level of resolution was known for 957

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of the species. The final data set included representatives from every temporal bin, spanning the entire geologic range of the Trilobita. Most temporal bins included data from 60 or more species (Fig. 1A), although the Late Cambrian, Late Silurian, Late Devonian, Carboniferous, and Permian were each represented by fewer than 40 species. Of the 25 species for which age was known only at the period level of resolution, all were post-Cambrian in age and 24 were coded with no polymorphisms (the polymorphic species being an Ordovician proetid): Their inclusion would therefore have strengthened the temporal trend detected by the present analysis. Some 40,957 positively coded character states, each with the potential for intraspecific polymorphism, were included [excluding missing, inapplicable, and redundant (the same species coded for the same character in multiple studies) characters].

More than 35% of the 982 included trilobite species were polymorphic in at least one positively coded character (table S2). However, these polymorphic species were neither evenly nor randomly distributed through time (Fig. 1, A and B). More than 70% of included Early and Middle Cambrian trilobite species were coded as polymorphic for at least one character. This proportion is significantly higher than in all later temporal bins, where fewer than 40% (and often fewer than 20%) of trilobite species were coded as polymorphic for at least one character. The proportion of species with at least one polymorphism drops sharply between the Middle Cambrian (75%) and Late Cambrian [8% (22)], then rises to 40% in the Early Ordovician (coincident with the first sampling of the diverse phacopid and proetid orders), after which there is a progressive decline through the Middle Devonian (1%), interrupted only by a particularly low value (0%) in the Late Silurian. Approximately 37% of included Late Devonian species were coded with at least one polymorphism (all heralding from study 43 in table S1). No polymorphism was recorded in character-state coding among the 23 post-Devonian species. It is unclear whether this pattern is better interpreted as a steplike drop from Early and Middle Cambrian high proportions (<70%) to post-Middle Cambrian low proportions (0 to 40%, averaging 13%), or as a progressive decline through the Paleozoic from the Early and Middle Cambrian (<70%) through the post-Devonian (0%) made noisy by intervals of poor sampling. The proportion of trilobite species polymorphic in at least one character was significantly higher in the Early and Middle Cambrian than in later times.

The most extreme degrees of intraspecific variation were also documented in Early and Middle Cambrian trilobites (Fig. 2, A and B, and fig. S2), when some species were polymorphic in more than 20% of their coded characters. None of the 588 post-Cambrian species exhibited polymorphism in more than 15% of their coded characters (Fig. 2C). The average propor-

tion of characters for which a species was coded as polymorphic falls from 3% in the Early and Middle Cambrian to 0% in post-Middle Cambrian bins.

The phylogenetic distribution of species exhibiting any degree of polymorphism in coded characters is also not uniform (Fig. 3, A and B). A significantly higher proportion of species belonging to the stratigraphically old and/or early diverging (19) clades Redlichiida (53%), Ptychopariida (79%), and Agnostida (88%) are polymorphic for at least one character compared to the younger and/or more derived (19) Corynexochida (10%), Proetida (17%), Phacopida (7%), Lichida (13%), Asaphida (4%), and Burlingiidae (0%). The temporal decline in intraspecific variation therefore results primarily from differences among trilobite orders. However, there is also support for declining frequency of polymorphic

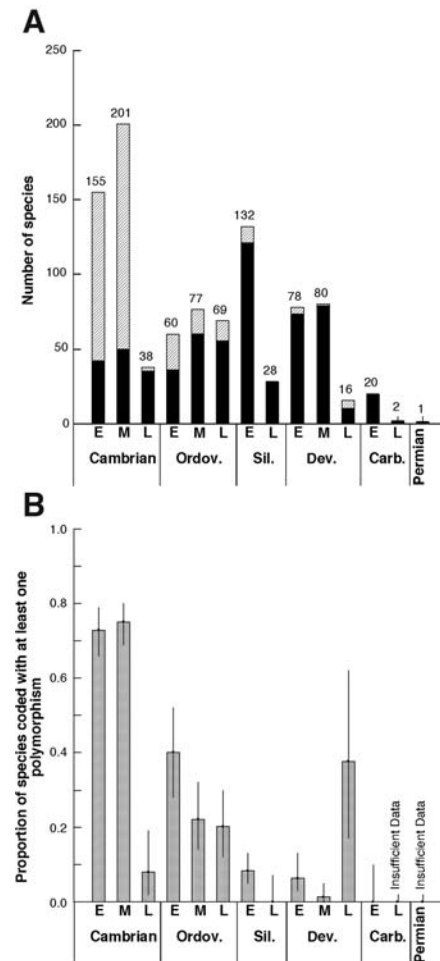


Fig. 1. Temporal pattern of the frequency (A) and relative proportion (B) of trilobite species coded as polymorphic in at least one character in cladistic analyses. Hatched and solid shading in (A) denotes polymorphic and nonpolymorphic species, respectively. Geologic period abbreviations: Ordov., Ordovician; Sil., Silurian; Dev., Devonian; Carb., Carboniferous; E, early; M, middle; L, late. Error bars indicate two-unit profile likelihood confidence intervals. Data are from table S2.

species through time within the long-ranging, well-sampled orders Proetida (Fig. 3, C and D) and Phacopida (Fig. 3, E and F), although the latter showed a return to high proportions in the Late Devonian (attributable to a single study; see above). Any sustained trends within other orders is unclear because of insufficient taxonomic or temporal sampling (figs. S3 and S4), although a significant drop in the proportion of species exhibiting polymorphism following an Early and/or Middle Cambrian peak was seen for the

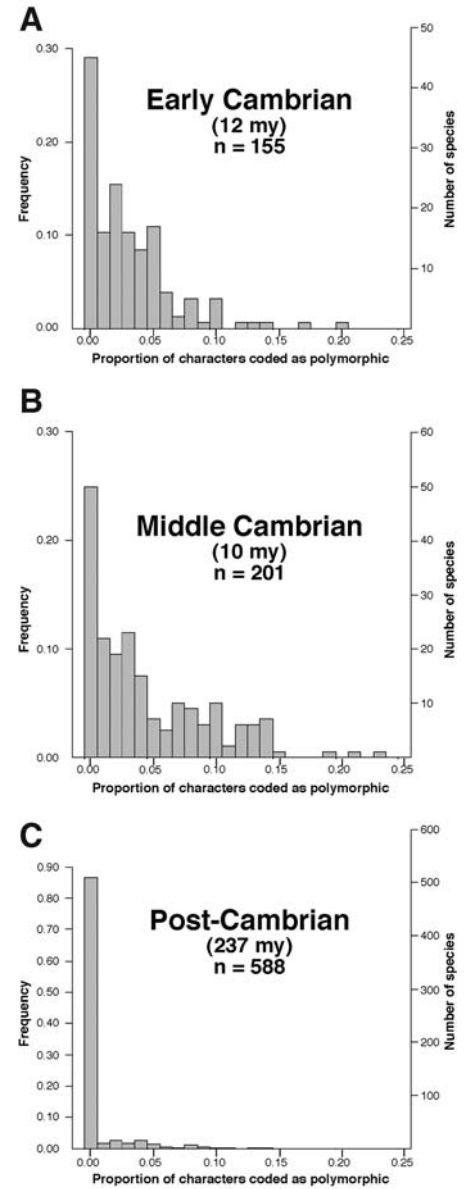


Fig. 2. Frequency distributions for the proportion of characters coded as polymorphic within trilobite species for the Early Cambrian (A, median = 2.8%), Middle Cambrian (B, median = 3.6%), and post-Cambrian (C, median = 0.0%). Approximate duration (in millions of years, my) of each temporal bin is shown; duration for Early Cambrian is based on trilobite-bearing portion only. Frequency distributions at higher temporal resolution are shown in fig. S2. Data are from table S2.

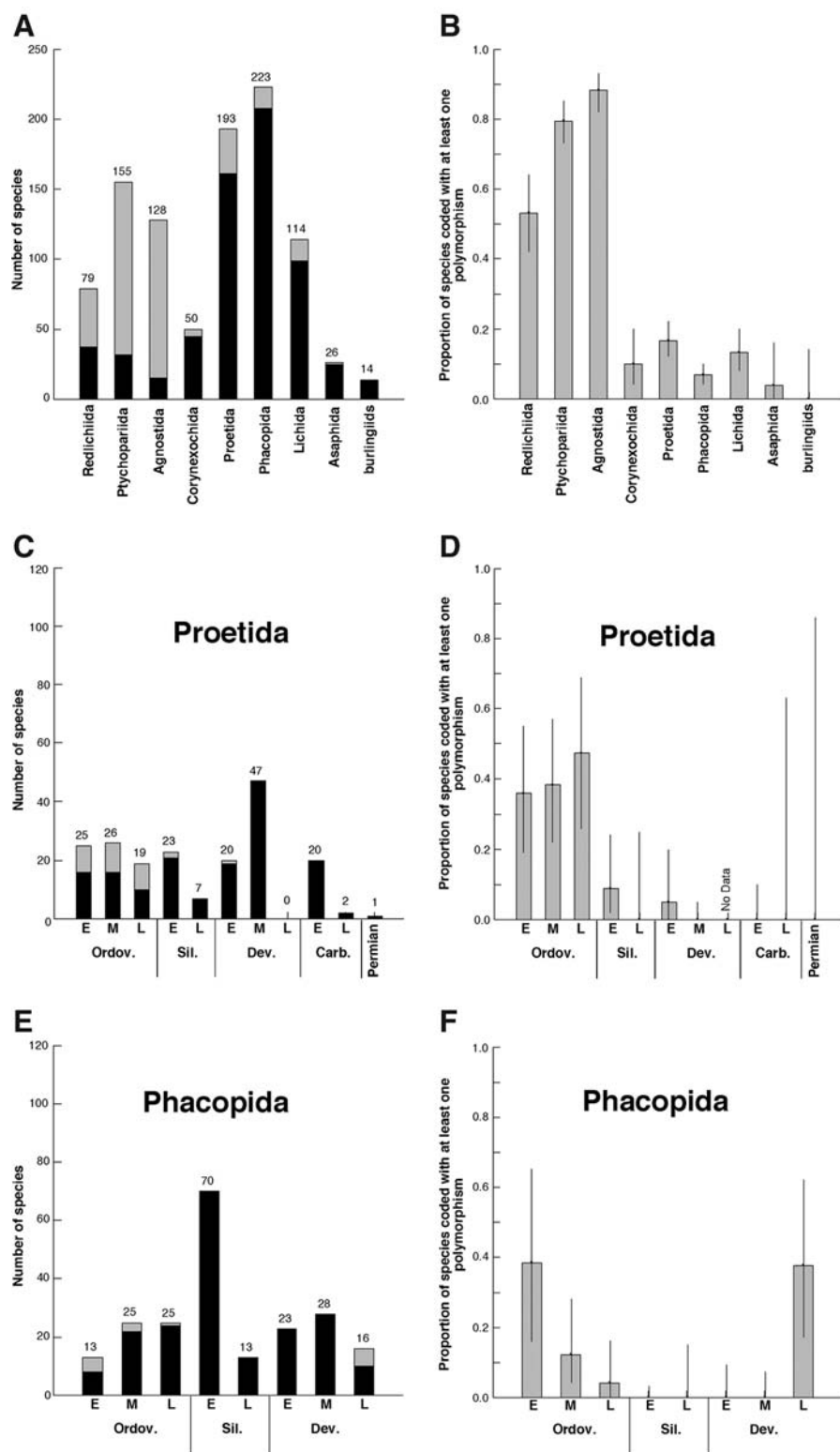


Fig. 3. (A and B) Differences among trilobite orders in the frequency (A) and relative proportion (B) of species coded as polymorphic in at least one character in cladistic analyses. (C and D) Temporal pattern of the frequency (C) and relative proportion (D) of proetid trilobite species coded as polymorphic in at least one character in cladistic analyses. (E and F) Temporal pattern of the frequency (E) and relative proportion (F) of phacopid trilobite species coded as polymorphic in at least one character in cladistic analyses. Hatched and solid shading in (A), (C), and (E) denote polymorphic and nonpolymorphic species, respectively. Error bars indicate two-unit profile likelihood confidence intervals. Data are from table S2. Abbreviations as for Fig. 1.

Ptychopariida [but see (22)] and Agnostida. Whether the higher frequency of polymorphic species early in clade history (here detected in the Trilobita as a whole, the Proetida, and arguably the Phacopida, Ptychopariida, and Agnostida) is indicative of a general phenomenon detectable at levels of lesser phylogenetic inclusivity is unknown. The second (Late Devonian) peak among phacopid species suggests that general trends in intraspecific variation are reversible [see also (23)].

The nonuniform phylogenetic and temporal distribution of intraspecific variation in trilobites is unlikely to result from a bias in morphological coverage (i.e., the range of characters examined) or in character-state definition, because similar temporal and phylogenetic patterns are detected when analysis is restricted to characters of unequivocal homology across clades and to characters with minimal potential for among-worker differences in coding (figs. S5 and S6). There are fewer trilobite species per genus on average in the Cambrian versus the post-Cambrian (18). If this reflects a worker-related bias of “Cambrian lumpers” versus “post-Cambrian splitters,” then a higher degree of apparent variation should be expected within Cambrian trilobite species and the results could be construed as artifact. However, similar temporal and phylogenetic patterns are detected based on the work of single researchers (figs. S7 and S8). The post-Cambrian increase in number of species per genus could result from a decline in generic extinction rate (fig. S1C): Genera originating in the Cambrian had shorter average durations than genera originating in the post-Cambrian (24), resulting in accrual of lower species-level diversity per genus. Any worker-related bias in generic concept would not affect the results, which involved only species-level data.

The nature of intraspecific variation can influence the rate and direction of adaptive response of a lineage to selective pressure (8, 25, 26). The high rates of trilobite generic origination in the Early and Middle Cambrian relative to the post-Cambrian (fig. S1B) are consistent with claims that intraspecific variation can also promote speciation and diversification (27). However, the Late Cambrian mismatch between high generic diversification rates and the marked decline in intraspecific variation is inconsistent with such claims, suggesting either that other factors play an important role in generic diversification rate or that intraspecific variation is grossly underrepresented in the Late Cambrian sample (22).

The nature of the relation between intraspecific variation and morphological diversification is complex because the components of trilobite anatomy were evolutionarily decoupled. Thus, whereas the maxima of intra- and interspecific variation in thoracic segment number coincide during the Early Cambrian (12), the Middle Ordovician maximal disparity in cranial shape was attained later than the Early/Middle Cambrian maximum in frequency of intraspecific variation in characters determining cranial

outline [fig. S9; although the rate of increase in disparity of cranial shape was highest in the Early Cambrian and slowed from the Middle Cambrian through Middle Ordovician (figure 5 in (6)]. The role of intraspecific variation in the generation of novelty and therefore of macroevolutionary trends in disparity is unclear: A hypothesis that intraspecific variation is the source of disparity increase predicts that a polymorphism should involve a derived feature, but the data relate only to whether or not a species is polymorphic for a given character, irrespective of whether the character states are derived, primitive, or convergent on another species.

The observed decline in intraspecific variation may have resulted from increasing developmental or ecological constraints. Developmental constraints may stem from increased integration among or regulation of developmental systems, resulting in decreased capacity to generate or accommodate change in those systems without negative effects on viability (4, 28–33). Ecological constraints may stem from progressive niche specialization associated with increased diversity and competition: In an ecospace dominated by incumbents, selection pressure could reduce fitness of variant phenotypes even though developmental regulation and integration may remain unchanged (29, 34). Constraint resulting from a decline in developmental flexibility, in success rate for ecological establishment, or in both (2, 4) could lead to loss of phenotypic variation within species and diminishing morphological innovation, which translates into slower response to selection and declining rate of morphological and taxonomic diversification. Further investigation is required to determine the causal mechanisms and whether the post-Middle Cambrian decline in the frequency and extent of intraspecific variation detected here was unique

to trilobites or to this time interval. Nevertheless, demonstration of this pattern and its potential correspondence to diversification rate in trilobites suggests that within-species variation may play an important role in shaping clade macroevolutionary history.

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Supporting Online Material

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Tables S1 and S2
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Four Climate Cycles of Recurring Deep and Surface Water Destabilizations on the Iberian Margin

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Centennial climate variability over the last ice age exhibits clear bipolar behavior. High-resolution analyses of marine sediment cores from the Iberian margin trace a number of associated changes simultaneously. Proxies of sea surface temperature and water mass distribution, as well as relative biomarker content, demonstrate that this typical north-south coupling was pervasive for the cold phases of climate during the past 420,000 years. Cold episodes after relatively warm and largely ice-free periods occurred when the predominance of deep water formation changed from northern to southern sources. These results reinforce the connection between rapid climate changes at Mediterranean latitudes and century-to-millennial variability in northern and southern polar regions.

The study of abrupt climate change has focused mainly on the last glacial period (1–13) and has provided important in-

sights about the dynamics of the climate system (14, 15). Synchronization of the $\delta^{18}\text{O}$ records from Greenland and Antarctic ice cores has

shown that the regions around Antarctica were warming during short-term cooling stages in Greenland (1). These high-latitude changes were paralleled by the fine-scale variability of sea surface temperatures (SST) from lower latitudes in their respective hemispheres (16, 17) and were directly linked on a regional scale to the extension and retreat of polar ice (3, 4) and the reorganization of atmospheric (5, 6) and oceanic circulation (7–13).

A number of paleoarchives have shown that century-to-millennial climate variability also was

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