Cambrian and Recent Morphological Disparity

We congratulate D. E. G. Briggs *et al.* for tackling the fascinating, difficult, and important issue of changes in the pattern of overall morphological disparity through geologic time (*1*). They conclude that modern disparity of arthropods is about equal to that in the Cambrian, thus controverting a widely held premise (*2*) that maximal disparity occurred early in the history of metazoan life and that disparity has subsequently decreased as many body plans became extinct while surviving designs stabilized through some form of genetic and developmental "locking" (often evolving great ecological diversity within surviving body plans—barnacles to lobsters among Crustacea, for example). We think, however, that a methodological error invalidates Briggs *et al.*'s conclusion and that the error's direction of bias affirms the opposite view that Cambrian disparity was greater. Moreoever, even if their conclusion were correct, it would support the idea of unusual speed and flexibility in Cambrian evolution followed by constraint upon fundamental anatomical change.

In historical sciences, tests and experiments cannot always be ideally controlled because one must work with the available organisms that happened to evolve and because one cannot always manipulate situations to yield an optimal experimental design. Therefore, any unavoidable bias should lie in a direction that would tend to disconfirm one's preferred hypothesis. Briggs *et al.* attempt to falsify the hypothesis of maximal Cambrian disparity by showing that modern disparity is just as great, but their methodology artificially inflates modern disparity. Their Cambrian arthropod sample consists of 25 taxa that "allow an adequate number of characters to be coded" (*1*), but the modern sample includes only one chosen representative from each "of the 21 main classes or subclasses of Recent arthropods" (*1*).

Well-fossilized Cambrian arthropods may not represent a truly random sample of those forms that swam and crawled in the Cambrian seas, but because complete sampling is not needed to measure disparity as average distance in morphospace (*3*, *4*), there is no obvious reason to suppose that the Cambrian sample is biased with regard to morphological disparity. Ironically, the sample of Recent arthropods in the study by Briggs *et al.* is biased. To a first approximation, the major classes and subclasses of arthropods represent a series of coherent morphological designs. Although it may seem that each of these designs should be included in a study of disparity, a random sample of Recent arthropods would likely include several representatives of some (sub)classes and no representatives of others. Thus, a random sample would have several points relatively close together in morphological space (representatives of the same design) and would likely exclude some of the morphologically more peripheral designs. Briggs *et al.*'s Recent sample, because it lacks multiple representatives from single arthropod subgroups and because it must include a member of each major subgroup, has higher apparent disparity (fewer short distances and greater total range) than would a random sample.

If a modern sample so biased to overdispersion still falls somewhat short (although not statistically so) of Cambrian disparity, then we can conclude that comparable samples would probably yield higher Cambrian disparity. Moreover, Briggs *et al.*'s own data support maximal Cambrian disparity in two ways.

1) Even with the inherent biases, and as shown in figure 2A of the report by Briggs *et al.*, 9 of the 11 points most distant from the joint centroid represent Cambrian taxa. The only modern arthropods in this group of maximally "unaverage" forms are the millipede *Julus* and the horseshoe crab *Limulus*; the latter, at least, represents a taxon of minimal size that might not have been included at all under a sampling scheme comparable to that used for the Cambrian taxa. The hypothesis of Cambrian maximal disparity does not argue that all peripheries of morphospace should be occupied by Cambrian taxa, but only that decimation and stabilization reduced the number of post-Cambrian designs to fewer potential positions.

2) Briggs *et al.* include a cladistic analysis to supplement their phenetic study with the argument that "the number of character transitions involved in the acquisition of a particular morphology from an ancestral form provides a measure of disparity" (*1*). Although we question this argument (*5*), we note that, as Briggs *et al.* allow, Cambrian taxa are more disparate by their own criterion of greater average cladistic distance from the basal node of the cladogram (*1*). This situation arises, as Briggs *et al.* (*1*) state, because many modern (and few Cambrian) forms are uniramian, and uniramians (as a major arthropod subgroup) branch off low on the cladogram. This branching pattern supports the idea of maximal Cambrian disparity because most of the highly derived subgroups had already originated within the Cambrian [figure 3 in (*1*)]. Later extinctions removed many of these derived groups, thus reducing disparity. Contrary to the implication of Briggs *et al.* [(*1*), pp. 1672 and 1673], the idea of maximal Cambrian disparity (*2*) does not rest on the *number* of extinct "phyla" or problematica, but on the perceived *magnitude* of differences among Cambrian animals.

The fact that morphological disparity has not increased dramatically since the Cambrian agrees with a claim made by one of us that arthropod evolution does not represent a "cone of increasing diversity" (*2*), that is, a concordant increase in taxonomic diversity and morphological disparity. Yet such a pattern would be expected if the magnitude of morphological constraints and transitions did not change greatly over geologic time (*4*, *6*). The fact that 500 million years of post-Cambrian arthropod evolution has not produced a greater variety of form than a few million years of Cambrian evolution argues for an increase in constraint on morphological evolution after the Cambrian. What combination of evolutionary and ecological mechanisms have produced this change in constraint remains an open question.

Mike Foote
Museum of Paleontology,
University of Michigan,
Ann Arbor, MI 48109
Stephen Jay Gould
Museum of Comparative Zoology,
Harvard University,
Cambridge, MA 02138

REFERENCES AND NOTES

1. D. E. G. Briggs, R. A. Fortey, M. A. Wills, *Science* **256**, 1670 (1992).
2. S. J. Gould, *Wonderful Life: The Burgess Shale and the Nature of History* (Norton, New York, 1989).
3. M. Foote, *Palaeontology (London)* **34**, 461 (1991); *Univ. Mich. Mus. Paleontol. Contrib.* **28**, 101 (1991).
4. ______, *Proc. Natl. Acad. Sci. U.S.A.* **89**, 7325 (1992).
5. S. J. Gould, *Paleobiology* **17**, 411 (1991).
6. J. W. Valentine and D. H. Erwin, in *Development as an Evolutionary Process*, R. A. Raff and E. C. Raff, Eds. (Liss, New York, 1987), pp. 71–107.
7. We thank D. E. G. Briggs, R. A. Fortey, and D. W. McShea for discussion.

21 July 1992; 9 September 1992

Briggs *et al.* (*1*) demonstrate that the proliferation of higher taxa during the Cambrian "explosion" is largely a taxonomic artifact and that morphological diversity among Cambrian arthropods was no greater than among extant forms. However, those with the view that morphological diversity was greater in the Cambrian (*2*) can still argue that the analysis performed by Briggs *et al.* was biased in that it considered only "good" arthropods, while the Cambrian "oddballs," those with the most bizarre body plans, were excluded from the study.

Science

Cambrian and Recent Morphological Disparity

Mike Foote and Stephen Jay Gould

Science **258** (5089), 1816.
DOI: 10.1126/science.258.5089.1816

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. The title *Science* is a registered trademark of AAAS.