

This criticism can be countered only by repeating the analysis on a much wider cross section of organisms (from different phyla)—a rather intractable proposition that would involve attempting to quantify morphological differences between animals as dissimilar as a cockroach and an earthworm.

A more intriguing result of Briggs *et al.* concerns their phylograms. The validity of performing a cladistic analysis on such a limited, heterogeneous selection of arthropods (some Cambrian and Recent species, with no taxa from the intervening period) is questionable, even if the arthropods are accepted as monophyletic. Analyses (of tetrapod relationships) that considered a similarly limited number of taxa (3) have been shown to yield spurious results (4). Nevertheless, if one assumes that the phylograms of Briggs *et al.* are approximately correct, it follows that, on average, the Cambrian organisms have accumulated 32.4 character state changes from the reconstructed ancestor at the base of the tree, while recent organisms have accumulated only 27.2 changes. Yet Cambrian organisms were separated from this ancestor by a few million years, while Recent organisms are separated from it by an interval of nearly 600 million years. In other words, these results imply that Cambrian arthropods underwent as many evolutionary changes during the Cambrian as extant organisms have undergone during the whole of the Phanerozoic. The analysis by Briggs *et al.* includes an "exhaustive" list of morphological characters, including (cladistically uninformative) unique derived traits; hence it cannot be argued that recent taxa are actually more highly derived than Cambrian taxa, but that many changes in the former, being autapomorphies, were not considered in the cladistic analysis.

Only two other explanations remain. One is that morphological change has effectively ceased since the Cambrian, which is obviously not true. The other is that only a limited number of changes are possible in the arthropod *bauplan*, that all these possibilities were exhausted by the end of the Cambrian, and that since then arthropod evolution has involved nothing but convergences and reversals. During the Cambrian most changes were divergent, but by the end of the period the limits to divergence had been reached and changes were largely homoplastic. This interpretation is supported by the low consistency index (0.268) of the cladistic analysis performed by Briggs *et al.* and by their conclusion that the morphospace occupied by Recent arthropods is approximately the same as that occupied by Cambrian arthropods. In other words, morphological change has continued, and Recent taxa have accumulated far more

changes from the ancestral state than had their Cambrian counterparts. However, because post-Cambrian changes have largely involved loss and reacquisition of traits that had already appeared during the Cambrian, these extra steps could not be detected on the most parsimonious phylograms (for example, a gain and subsequent loss of a trait would have mapped onto the phylogram as no change at all). Hence extant taxa, when compared with their hypothetical ancestor on the phylograms, do not appear to be any more derived than their Cambrian counterparts. The lack of further divergence of arthropods since the Cambrian suggests the existence of rigid evolutionary constraints and is a finding that cannot be ignored.

Michael S. Y. Lee
Museum of Zoology,
Downing Street,
Cambridge CB2 3EJ, United Kingdom

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Response: Foote and Gould generously applaud our attempt to address the difficult issue of disparity among Cambrian animals independent of a restrictive taxonomic framework. Gould's account of the Burgess Shale (1), an enormous stimulus to research on the pattern of evolution during the Cambrian radiation, drew the important distinction between taxonomic diversity and morphological disparity. Noting the large number of taxa with unusual morphologies that appear to negate the possibility of relationship to any modern group, he concluded that "[t]he Burgess Shale includes a range of disparity in anatomical design never again equaled, and not matched today by all the creatures in all the world's oceans" (1, p. 208). The arthropods (most diverse in the Cambrian, as today) appeared to support this view on the basis of a comparison of the totality of design in the Cambrian and in Recent times: "group after group of orphaned arthropods spoke of Burgess anatomy far beyond the range of any later time" (1, p. 167). Our study (2) was an attempt to test this view by quantifying disparity and allowing the amount of morphological evolution during the Cambrian

radiation to be assessed. Of course we do not deny that the Cambrian radiation took place—the evidence to support it is overwhelming—we merely caution that it may not have been as dramatic as previously supposed.

Foote and Gould argue that our selection of Recent taxa biased the study and that we should have used a random sample for comparison with the Cambrian taxa. Because more than 90% of modern arthropods are insects, the chances of a random sample including much else are small; such a sample, however, tells us more about the diversity of hexapods than about disparity among modern arthropods. The selection of Cambrian taxa also was not random; it is biased in favor of benthic muddy substrate dwellers. A random sample of known Cambrian arthropods would have been no more satisfactory because it would have been dominated by trilobites as a result of their favorable preservation potential. It should be obvious that we cannot obtain a modern sample truly comparable to the Burgess sample. Thus we compared *known* disparity in the Cambrian with that in the Recent sample and demonstrated that earlier studies (1) have exaggerated our impression of the former in the light of the number of problematic taxa (those that could not be readily assigned to living groups). Our Recent sample provided a reasonable way of including the range of modern arthropod morphology, although much more disparate forms could have been selected. Because the Cambrian arthropods fall into the same major clades (2, 3), the range of morphology they display is limited by the same phylogenetic constraints.

Foote and Gould argue that the lack of multiple representatives from single arthropod subgroups results in an apparent higher disparity in the Recent sample. Higher taxa are not necessarily equivalent in morphological separation—six of the living uniramians lie in a much tighter cluster than the three Cambrian trilobites, for example. Multiple sampling would result only in a slight rotation of the cloud of taxa to align it with the more densely clustered points; furthermore, one of our metrics (range) is not directly affected by such clustering. To discuss disparity in terms of exactly which taxon is most distant from the centroid runs the risk of overestimating the precision of the approach and the significance of individual morphologies. Distances incorporate no directional information, and we have no measure of the significance of slight variations in the values. Hence our conclusions were couched in more general terms. On the cladogram, the average distance of the Cambrian arthropods from the basal node exceeds that of the Recent arthropods but, as we empha-

sized (2), this reflects branching order. The distances, however, like those from the centroid, are interspersed, and not significantly different (according to the Mann-Whitney test). The majority of the Cambrian arthropods can be plotted either as members of a large crustacean-crustacean-morph clade or within the sister-group arachnomorphs. The trilobites and Recent chelicerates are subsidiary themes within the arachnomorphs; they appear to be widely separate groups only if the evidence of the other Cambrian arthropods is not taken into account. New discoveries of exceptional Cambrian faunas will, no doubt, prompt a reconsideration of arthropod disparity some time in the future, but the issue can only be satisfactorily resolved by comparing a wider range of taxa (which would be an even more difficult task). Evolution during the Cambrian may have been peculiar only to the extent that metazoans were radiating into largely unoccupied biospace. With new and more sophisticated attempts to quantify the results, we can move to a more complete understanding of its nature

and significance.

Lee questions whether a cladistic analysis that is confined to Cambrian and Recent taxa, and that omits temporal intermediates, can provide a valid means of assessing phylogeny. The majority of post-Cambrian arthropod fossils can, however, be accommodated readily in existing taxonomies and mostly fall comfortably within accepted orders. Moreover, ongoing investigations of a wider range of arthropod taxa, including some of the more unusual Devonian forms, reveal a cladogram with identical high-level topology, although details at lower levels vary. Arthropod evolution since the Cambrian has no doubt involved numerous losses and re-acquisitions of characters. These contributed to arthropod "derivedness" and to large apparent patristic distances from the root of the phylogram, but did not increase the morphological disparity of the group. These reversals did not significantly affect those characters that define the major modern groups. Artificial randomized data sets (4) produce a distribution of tree lengths that are significantly longer ($PTP <$

0.01) than that from the original data, which indicates that significant information that is phylogenetically useful remains despite much homoplasy.

Derek E. G. Briggs

*Department of Geology,
University of Bristol,*

*Wills Memorial Building, Queen's Road,
Bristol BS8 1TR, United Kingdom*

Richard A. Fortey

*Department of Palaeontology,
Natural History Museum,
Cromwell Road,*

London SW7 5BD, United Kingdom

Matthew A. Wills

*Department of Geology,
University of Bristol*

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Response

Derek E. G. Briggs, Richard A. Fortey and Matthew A. Wills

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