Analysis of the Burgess Shale

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Gould (1989, 1991) has argued that the animals of the Burgess Shale show more than average morphological disparity, and in his 1989 book he recurrently mentioned their diversity at high taxonomic levels in his argument. Several critics pointed out that ancestral faunas inevitably show relatively high diversity at high taxonomic levels if the characters used to define modern higher categories are applied retrospectively. Gould (1991) offered an embryological argument as a “rebuttal of the charge that claims for early disparity rest upon a retrospective fallacy.” He suggested that the Burgess animals developed in a relatively unstable manner. His main evidence was the purportedly low value of the consistency index (C) in Briggs and Fortey’s (1989) cladogram.

The purpose of this note is to suggest some further tests for the peculiarity of the animals of the Burgess Shale—tests that may prove more persuasive, to skeptics, than those offered so far—and to point out that all the available evidence is consistent with a null evolutionary model, in which the properties of zoology show no general change over time.

The Value of C in Briggs and Fortey’s Cladogram is not Low.—Briggs and Fortey (1989) found $C = 0.384$ for 28 taxa and described it as “rather low.” A number of compilations of consistency indexes have been published (Brooks et al. 1986; Archie 1989; Sanderson and Donoghue 1989). For Archie’s data set, the graph (Archie 1989: fig. 3) reveals that a consistency index of 0.38 is almost exactly what we should expect for a sample of 28 average taxa; the prediction from Sanderson and Donoghue’s data set is slightly higher, about 0.45, but 0.38 is still well within the scatter of consistency indexes for sample sizes in the region of 28. Thus, Briggs and Fortey’s study provides no evidence that the Burgess arthropods are exceptionally difficult to classify cladistically. Briggs et al. (1992) subsequently published a cladogram containing arthropods from both the Burgess and modern faunas. The sample size was increased to 46 taxa and C duly decreased to 0.268. The value again falls within the expected range for the number of taxa. There is a large literature on the relevant properties of C (Archie 1989, 1990; Farris 1989a,b, 1991; Klassen et al. 1991; Goloboff 1991a,b; Meier et al. 1991).

If C Had Been Low, it Could Have Been for Artifactual Reasons.—A lower than average C for the Burgess Shale could result if the taxonomy of the animals were more preliminary than average or, as Gould (1991: p. 215–216) suggested, because “most of the 46 characters [in Briggs and Fortey’s 1989 study] are defined as losses or reductions of parts or segments (“loss of labrum,” “loss of oublure,” “loss of cephalic gnathobases”), changes notoriously subject to homoplasy.” Both factors could operate, if those “losses or reductions” are the sorts of characters a pioneering taxonomist would pick.

Both explanations are testable. Taxonomists could be presented with several arrays of species, of various degrees of familiarity, and asked to classify them. The degree of developmental stabilization should be controlled for (perhaps by using the same sets of species with different experts, some trained in one set, others in another). If the first artifactual explanation is correct, the cladistic trees for more familiar forms should have higher C; if Gould’s is, C should be correlated...
with the proportion of “loss” characters in different studies. The relation between C and the proportion of loss characters could also be tested in the compilations cited above. It should also be possible to test whether the proportion of loss characters decreases in successive cladistic investigations of a taxon.

A Low C Does Not Demonstrate Unstable Development.—If C were low (and not for artifactual reasons), it could be because the taxon had unstable development; but it could also be due to natural selection. If natural selection were relatively changeable in the Burgess conditions, a low C would have resulted. Natural selection and constraint, here as elsewhere, are both theoretically valid hypotheses to explain morphological patterns, and natural selection has to be ruled out before a low C can be used to support the embryological hypothesis.

Morphological and Cladistic Evidence Could Be Collected for the Embryological Hypothesis.—Measurements of fluctuating asymmetry might reveal whether the animals of the Burgess Shale had relatively erratic embryology. Fluctuating asymmetry is widely used to measure developmental homeostasis (Van Valen 1962; Kieser and Groeneveld 1991).

A cladistic test of whether a taxon had evolved historically from a less to a more stable mode of development might be possible (though, as for low C, the evidence would be open to an alternative selective interpretation). Gould (1991) hypothesized that a small sample of species survived from a large fauna of species with unstable development, and those survivors subsequently proliferated and evolved more stable development. As time passes, the older ancestral species of a clade fade up to the higher Linnaean branches and the more recently evolved species form subgroups within those higher taxa. Therefore, the pattern Gould suggests should result in a low C at all taxonomic levels in the Burgess fauna, but the low values of C should retreat to the higher Linnaean levels as time passes. For Recent taxa, C will be low for the top branches of the cladogram, but higher for the species that have evolved in the later, tamer mode. There is the statistical problem that in a null model (one in which there is no evolutionary change in embryology) C will be higher for the older branches simply because more time has passed: we should have to test whether the differences in C up and down the cladogram exceeded the null prediction, but that is not an intractable problem.

Characters used to Define Groups are Tautologically Constant within Those Groups.—The constancy of characters within a group, if they have been used to define the group, is not evidence of relative developmental stability. It could (again) be due to selection, but even on a null evolutionary model, in which all characters had stochastically equal developmental stability, characters would be taxonomically distributed in various patterns. Taxonomists would pick characters that were constant across groups to define groups. Gould (1991) suggests it is “fair to assume” that taxonomically defining characters are developmentally stable, but his evidence is the characters’ taxonomic constancy, and his arguments (though logical enough) are speculative. He also notes (1991: p. 417-418) that taxonomic characters may be constant in fossil as well as modern animals; but that fact only shows how well the taxonomists have done their job: it is not evidence of developmental stability. Embryological hypotheses have to be tested embryologically; taxonomic distributions can be influenced by many other factors, including chance. Evidence from fluctuating asymmetry might again be useful: it could be used to test whether taxonomically defining characters are embryologically more stable than nondefining characters, and whether characters used to define higher groups are more stable than those used to define lower groups.

Phenetic Measurement Has Not Yet Been Shown to Test Morphological Variability in a Principled Way.—The “obvious” test of whether the Burgess animals are abnormally variable would be a multivariate phenetic measuring job. Gould (1991) argued that such a test should be developed. Briggs et al. (1992) made the first attempt. They measured 134 characters in 21 modern and 25 Cambrian arthropod species, and factored the measurements by principal components analysis. They found that the “disparity among living arthropods is similar to that in Cambrian arthropods.” The result is interesting, but not definitive.
Any such test runs into the standard problems of phenetic taxonomy: there are many ways of measuring phenetic patterns; they can give different answers; no higher principle is available to choose among them (see Ridley 1986 and references therein). Thus, if principal components analysis gives one result, another cluster statistic could give another. Gould (1981: p. 243–255) explained the same abstract problem in relation to the factor of general intelligence (g). (Indeed, devising a phenetic test of relative morphological variability would require us to solve problems very like those posed by g.) Gould (1991) gives no argument to justify a particular measure, and none are available in the literature. The problem might be soluble if we moved away from the idea of general morphology and tried instead to test a specific hypothesis, such as Gould’s embryological hypothesis: the hypothesis itself might suggest a particular phenetic procedure. But until a particular phenetic procedure is justified, two decades of phenetic taxonomic research provide good reason to doubt whether this proposed line of inquiry will yield the promised fruits.

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