Response: Bretscher's defense of the retrograde lipid flow (RLF) model is admirable, but misplaced. He states that our findings (*1*) do not allow a distinction to be made between the current models of cell locomotion. This critique of the interpretation of our results fails on several counts.

The RLF model proposes that dorsal and ventral cell membranes flow rearward with respect to the front edge of the cell. Bretscher introduces a new concept, termed "slippage," in reference to stationary cells whose locomotory mechanism remains active. He explains that in these cells (which are "slipping badly") a point on the cell surface would move rearward with respect to the substrate, but that, in moving cells (where no "slippage" occurs) a "particle just behind the leading lamella would be expected to remain stationary with respect to the substrate." It is important to realize, however, that in both these cases a point on the cell surface would be moving rearward with respect to the leading edge, and the distance between the bleached line and cell edge would increase. Our results were obtained by initially measuring the movement of the bleached line and cell edge with respect to the substrate [(*1*), figure 4A]. These values were then used to calculate the normalized relative velocity (R), which is a measure of the difference between the bleached-line and cell-edge velocities. Each different model of locomotion is characterized by a different R value (*1*). According to the RLF model, a line bleached on the surface of a locomoting PMN would be expected to move rearward with respect to the cell edge. Consequently the distance between the bleached line and cell edge would increase. We did not observe this beyond the limits of experimental variation. Instead we found that the bleached line moved in concert with the leading cell edge, $R = 0$, in stark contrast to the RLF model. Nor was Bretscher's new prediction that rearward lipid flow with respect to the substratum (and cell edge) should be seen in the stationary cells demonstrated. One of our control experiments (*1*, p. 1230) was to photobleach stationary cells. In those cases no line movement with respect to the substratum (or to cell edge) occurred. In cells 1 and 15 [(*1*), figures 4 and 5], *forward* motion of the bleached line was accompanied by only a small extension of the cell. These cells were presumably "slipping badly," yet rearward motion of the line with respect to the substratum (or cell edge) was not seen.

Bretscher states that we would not be able to distinguish between an R value of 0 and one of 0.5 and therefore we cannot reject the RLF model. This conclusion appears to be based on a miscalculation of an R value. If one assumes that rearward lipid flow in the region of the bleached line is half the speed of cell extension, then $R = (V_c - V_f)/V_c = (1 - (-0.5))/1 = 1.5$, not 0.5. It may be difficult to distinguish between R values of 0 and 0.5, but we can easily distinguish between 0 and 1.5. The issue of scatter is therefore not relevant, as we would be able to detect a rearward lipid flow of one quarter our original estimate ($V_f = -2$).

Finally, Bretscher cites two atypical cases (our experiments 1 and 15) in which considerable forward movement of the bleached line was accompanied by little cell extension. He is correct that in these cases the R values would be very large. These large values would be mainly due to the discontinuous mode of PMN locomotion and the small time interval between the first and the second post-bleach images. In some cases, cell extension can slow to an undetectable rate during this interval (V_c is very small), but with significant movement having occurred by the time the final image is acquired. Therefore, when one calculates R the denominator will be very small. These cases remain in contradiction with the RLF model.

In an earlier comment Bretscher (*2*) implied that particular models for cell locomotion can only be tested by comparison to "rather remote observation" on how cells move. Our recent work demonstrates that this is not so. Furthermore, complementary experiments, some also directly testing predictions of his hypothesis regarding capping (*3*), have not supported his model but have instead provided evidence for a cytoskeletal mechanism in this process (*4*).

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Bryozoan Morphological and Genetic Correspondence: What Does It Prove?

J. B. C. Jackson and A. H. Cheetham (*1*) demonstrate that morphologically distinct Bryozoa ("morphospecies") can be identified by allozyme difference as biological species, which is said to support punctuated equilibrium in the evolution of cheilostome Bryozoa (*2*). The study responds to criticisms, including mine (*3, 4*), that fossil species and morphological variation cannot be distinguished sufficiently to test the punctuated equilibrium hypothesis. In my book (*4*), I cite Cheetham's study of Bryozoa as the only one that supports the punctuation pattern. It fits a persistence criterion (*5*), whereby a budded off species arises, diverges morphologically, and then persists with long-term stasis, surviving with its progenitor species.

The issue is not whether one can identify co-existing species by their morphology. I can tell gray squirrels from red squirrels, and I expect that they can be proved to be genetically distinct. Similarly, no one is too surprised that co-existing forms in the fossil record, proved to be morphologically distinct, will often turn out to be different species. The real question (*4*, p. 352) is whether one can identify different species as they are splitting, or recently after they have split. Co-existing morphospecies can be distinguished often, and they may well be biospecies. But these results only say that species are morphologically distinct, not that all morphological distinctions mark species. The time resolution of Cheetham's study (*2*) is no better than 160,000 years. Were the initial divergences polymorphisms? Morphological plasticity? Speciation events? We will not know. There are many cases where distinct intraspecific morphological polymorphisms would surely be mistaken as separate species, genera, and even families (*4, 6*). Surveys of morphological and genetic distance do not support any particular theory relating morphological evolution to speciation rate. In desert pupfish, considerable local morphological differentiation occurred in the absence of species-level allozymic differentiation (*7*).

The distances reported for species in the genera *Steginoporella* and *Stylopoma* (mean = 1.2, SD = 0.53) cannot be distinguished from distances between fairly distantly related nonsibling species. For the genus *Paras-*

mittina, the one interspecific distance reported is infinity, meaning that the two species have no alleles in common. If other species comparisons are any gauge, the species are distantly related and arose from a common ancestor millions of years ago (*8*). In none of the cases reported do the distance data demonstrate that ancestry was close enough to be relevant to the punctuated equilibrium hypothesis. We know nothing of the relatedness of the bryozoan species, either from fossils or from a cladistic analysis.

The results of Jackson and Cheetham are not surprising. Morphologically distinct species are expected to be genetically distinct, but this has been shown in hundreds of studies (*8*), including one of *Parasmittina* (*9*). Cheetham's results are convincing enough to support a punctuated equilibrium pattern, but they do not resolve what really happened at the crucial stage of splitting. They do, however, counter the legion of other studies that show extensive morphological change within fossil lineages lacking cladogenesis (*4*). Punctuated equilibrium still has not been shown to be a dominant or a necessary mechanism for the generation of morphological diversity.

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Response: Levinton's confidence in the biologic validity of morphospecies is a welcome change. In his recent book (*1*), Levinton indeed discussed evolutionary stasis in *Metrarabdotos* (*2*) as supporting the punctuation pattern. But he also questions the heritability of the characters used for species discrimination and states that "one cannot rule out the possibility that speciation is rampant, but morphological evolution only occurs occasionally" under particular conditions. Moreover, a section of his book is titled, "Can fossil species be identified?" with the implication that they often cannot. How then can he conclude that our results showing excellent correspondence between morphologic and biologic species "are not surprising"?

Levinton raises the specter of species with extreme intraspecific polymorphisms, such as those of many social insects. He suggests that our results show only that morphologic species are genetically distinct, but not that morphologic differences necessarily mark species. However, in our study [note 12 in (*3*)], colonies were not preassigned to species. Instead, the numbers of species and their morphologic limits were developed empirically from the morphometric data. No other biologic information was employed. This procedure resulted in the discrimination of three species of *Stylopoma* where only one had been recognized previously—a separation subsequently validated by both genetic analysis and breeding experiments. Extreme polymorphism may be a potential taxonomic problem in other groups, but apparently not for cheilostome Bryozoa.

The correspondence between morphology, genetics, and phylogenetic relationship is complex, and much essential information is lacking. This is why we did not address these issues in our paper. The genetic distances measured between congeneric species in our study were large, which might suggest considerable time since divergence (*4*). However, the morphologic distances between many of these species overlap substantially those measured by Cheetham for inferred sister species of *Metrarabdotos* at their point of first appearance in the fossil record. Furthermore, the morphologic distances between sister species of *Metrarabdotos* persisted relatively unchanged throughout their history, which suggests that morphologic distance should be a poor predictor of how recently sister species have split. There is also no statistically significant relationship between the degree of morphologic and genetic distance among the congeneric species pairs examined ($R^2 = 0.23$, $n = 7$, $P > 0.3$), and the most similar species morphologically (*Parasmittina* species 1 and 6) showed the greatest genetic differences. What all this means phylogenetically is difficult to say without adequate fossil data. The only close correspondence between morphologic and genetic variation in these bryozoans is at the level of consistent discrimination between species.

The original theory of punctuated equilibrium states that species originate fully differentiated morphologically after relatively brief periods of cladogenesis and persist unchanged for millions of years (*5*). The pattern of *Metrarabdotos* evolution is consistent with this statement, pending the issue of the biologic validity of cheilostome morphospecies [which was a matter of some debate before our study (*6*)]. Levinton appears to have redefined the theory of punctuated equilibrium to focus on mechanisms of speciation "at the crucial stage of splitting," but this was not the subject of our paper.

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