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Response: We agree with the major theme of the comment by Gary and Keihm that, because of the importance of monitoring global temperature by satellite microwave methods, all aspects of satellite data processing and interpretation should be critically evaluated.

It is true that, in a statistical sense, the larger the year-to-year variability in globally averaged tropospheric temperatures, the more uncertain is any calculated trend over 10 years. However, Gary and Keihm's statement that the slope uncertainty "could actually be much greater" than the standard error they have calculated for our 10 years of data (0.07°C) seems to have no statistical basis. Even if we had observed a large upward trend during our 10-year period of analysis, the last 100 years of thermometer data suggest that a 10-year trend is probably not useful for predicting what might happen in the coming decades.

Gary and Keihm also address the importance of our satellite intercalibration procedure. As our original paper pointed out, overlaps between successive satellites resulted in agreement of 0.01°C per month for all five periods. Such agreement improves with the length of the overlap. On the basis of small levels of uncertainty of the intercalibrations, we estimate a cumulative uncertainty of 0.02°C for the 10-year period. The lack of any trend in the difference between anomalies from different MSUs is itself evidence against any significant drift in frequency of the instrument channels. As discussed in our more recent paper (1), weather balloon comparisons over 5 years have shown no change in the NOAA-6 MSU response to the statistical noise level of those comparisons (0.01°C). The differences in response of about 0.5°C between instruments is irrelevant to the study, since we were concerned only with temperature anomalies about the mean for a given instrument.

The small effect of the MSU weighting function being partly in the stratosphere (which is predicted to cool if the troposphere warms) will need to be taken into account if future MSU channel 2 brightness temperature trends are to be accurately interpreted as thermometric temperature

trends of the troposphere only.

Gary and Keihm's final point regarding the small effects due to other geophysical signals (water vapor, cloudiness, and soil moisture variations) in the data has also been addressed in detail in our recent paper (1).

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Lipid Flow in Locomoting Cells

J. Lee *et al.* conclude (1) that the "retrograde lipid flow (RLF) hypothesis is no longer tenable as a general model for cell locomotion." In their experiments, they marked a line in the plasma membrane lipids of a moving polymorphonuclear leukocyte (PMN) that is parallel to the advancing edge of the cell. They then observed how this line moved with respect to the advancing edge as the cell moved forward. The membrane flow hypothesis [reference (2), itself a refinement of the lipid flow scheme (3)] predicts it would move backward. In 9 out of 16 cases this is what they actually found. However, is the observed rate of rearward movement that which is predicted by my hypothesis? They state that the membrane flow hypothesis demands a rearward line migration that moves two times as fast as the leading edge advances—all measured with respect to the substratum [note 21 in (1)]. This is incorrect. In a commentary (4) on an earlier paper from this group (5), I explained that the membrane flow hypothesis predicts that a particle on the dorsal surface of a cell (or in this case, a line drawn in the cell surface) will migrate rearward with respect to the leading edge. How fast it should do so depends on a variety of factors, including how fast the cell is potentially moving and where on the cell surface the particle is. I say "potentially moving," because the advancing edge, in the process of extending, may or may not actually attach to the substratum. Whether it does or does not attach to the substratum makes no difference to the *mechanism* of the motor, but does affect the rate of locomotion. In other words, the cell may move forward if the front attaches, or "slippage" may occur if it does not. [An example of a cell in a purely slipping mode is one on the edge of a stationary colony of spread epithelial cells: the advancing edge can no longer advance and so slips, the slippage often being seen as ruffling of the advancing edge (6).] A particle just behind the leading lamella would be expected to remain stationary with respect to the substrate if no slippage occurred, and to move backward with

respect to the substrate if the cell were slipping. In assuming a rearward line migration with respect to the substrate, Lee *et al.* assume their PMNs are slipping badly: given the rate at which they move on glass this seems improbable.

Lee *et al.* (1) draw the line in the cell's plasma membrane near the middle of the cell; the predicted rearward membrane flow there would be one-half that at the front (7) (assuming these cells are flat sheets, which surely they are not). Their marker line might therefore be expected to move rearward with respect to the leading edge at half the speed that the leading edge advances over the substrate. In their terminology, this would give an *R* factor of 0.5, not the 3 they state. The scatter observed in their data (in their figure 4) is such that one cannot distinguish between an *R* of 0 or 0.5

In figure 4 of the paper by Lee *et al.*, it is stated that two cells (1 and 15) have *R* values of 0 and about -0.6. Following their method of calculation, I find these figures should be about -20 and -40; if these experimental measurements are actually correct, they suggest that none of the models considered by Lee *et al.* can be valid.

In conclusion, the report by Lee *et al.* sheds little light on whether the membrane flow model (2) applies to PMNs or not.

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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-*