stages fundamental to any model of intrademic spatial variation. The biological justification of the model has been discussed elsewhere (*2*).

As a hypothetical example, consider the earthworm, which improves plant growth through a variety of pathways (*8*). Because plants form the foundation of any biological community, the effects of the earthworm (both direct and indirect) on almost every member of its community are positive. However, the reverse is unlikely to be true; the effects of the community on the earthworm are variable. The success with which the earthworm operates depends to a large extent on the community that surrounds it. Plant litter may or may not be of a shape or texture that is easy to ingest. Secondary compounds leached into the soil may stimulate or inhibit.

Consider two plant species (A and B) that benefit equally from earthworm activity but differ in their effect on the earthworm (E). Let per capita fitnesses equal

$$\frac{N(\mathrm{A})_{t+1}}{N(\mathrm{A})_t} = \frac{N(\mathrm{B})_{t+1}}{N(\mathrm{B})_t} = 1 + m_{A,B}\left\{\left[\frac{N(\mathrm{E})_t}{L+N(\mathrm{E})_t}\right]K_{A,B} - N(\mathrm{A})_t - N(\mathrm{B})_t\right\} \quad (5)$$

$$\frac{N(\mathrm{E})_{t+1}}{N(\mathrm{E})_t} = 1 + m_E\left\{\left[\frac{N(\mathrm{A})_t}{N(\mathrm{A})_t + N(\mathrm{B})_t}\right]K_E - N(\mathrm{E})_t\right\} \quad (6)$$

These are modifications of the logistic equation in which the carrying capacity of each of the plants depends asymptotically on worm activity, while the carrying capacity of the worm depends on the relative proportions of A and B. The constants m and K represent the rate of increase and the maximum carrying capacity, respectively. The constant L governs the rate at which carrying capacities of the plants become asymptotic (*9*).

Simulation results for communities with and without variation are presented in Fig. 1. In traditional models (without variation) A and B retain their starting proportions. Natural selection cannot discriminate between them because, although they vary in their effects on the earthworm, these effects provide feedback to both plant species equally. However, given variation in community composition, each plant species differentially feels its own effect, A is selected for, and such selection eventually causes the extinction of B. The opposite would have occurred if the worm had a negative effect on the plants. In this case the worm and plant A would have been driven to extinction. If the equations are reconstructed such that an optimal density of worms exists as far as the plants are concerned, the proper ratio of A and B automatically results to produce it. Finally, if the worm varies in its effects on the plants, it will evolve to maximize plant fitness (and therefore its own, through indirect effects). The variance was equal to the mean densities in the simulation trials presented here, but the qualitative results occur whenever the variance in species composition is greater than zero.

In this example the earthworm's existence depends on the function it performs in its community. However, this does not violate the principle of individual selection, for per capita fitness is at all times the criterion of selection used in these models. Given sufficient control of the community over its component species, the concepts of individual and community adaptation become synonymous.

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4. Matrices imply linear equations; they are used for illustrative purposes but are not necessary for the basic model.
5. Evolution involves a change in the relative proportions of competing "types;" for the purposes of this discussion, it does not matter whether these types are alleles, genotypes, or species. Thus, while evolutionary arguments are usually cast in terms of intraspecific genetic changes (competition between genotypes), interspecific changes in community composition can be the result of the same process (competition between species). The words "species" and "genotype" can be used interchangeably throughout this argument.
6. For a rigorous treatment of the concept, see R. Levins, in *Ecology and Evolution of Communities*, M. L. Cody and J. M. Diamond, Eds. (Harvard Univ. Press, Cambridge, Mass., 1975), pp. 16–50. Two exceptions to this rule are acceptable to traditional models: (i) symbiosis involves a one-to-one interaction between individuals, in which case indirect effects are automatically funneled back to the individual that caused them. In terms of the structured deme model, this corresponds to a trait-group size of one; (ii) if individual recognition is possible, indirect effects can be behaviorally redirected to the individuals that cause them.
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8. For a traditional view on earthworms, see G. C. Williams, *Adaptation* and *Natural Selection* (Princeton Univ. Press, Princeton, N.J., 1966).
9. In this model the plants depend completely on the earthworm and the earthworm depends completely upon plant *A* (K = 0 without the essential species). This is an unrealistic assumption. However, aside from being useful as an illustrative tool it has one other justification. Multispecies communities probably do have total or near total control over most of their members. The only way to simulate this dependency of a species on its community in a simple model is to increase the amount of control per species.
10. I thank A. B. Clark, T. W. Schoener, C. A. Istock, L. Van Valen, and M. E. Gilpin. Supported by NSF grant BMS 75-17663.

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Evaluation and Publication of Scanning Electron Micrographs

When applied appropriately and critically to biological materials, scanning electron microscopy (SEM) may reveal important, unanticipated morphological details and relationships. It is particularly well suited to the study of large specimens at high resolution and requires relatively short processing times. The rapid proliferation of published micrographs obtained by this relatively new technique has apparently not been accompanied by the establishment of widely accepted criteria for assessment of their scientific merit. It is our purpose to draw attention to some of the major interpretative pitfalls and to suggest practical guidelines for review and publication.

Initially, our attention was drawn to this problem by a difference of opinion concerning the normal configuration of the arterial endothelial surface. Smith *et al.* (*1*), describing the appearance of the arterial endothelial surface as revealed by SEM, identified luminal projections arising from the lining of canine pulmonary arteries as normal structures of endothelium. Wolinsky (*2*), in a subsequent technical comment, suggested that the projections might have been produced by retraction of the vessel wall before or during fixation and proposed that such structures might be absent if vessels were examined in the physiologic (that is, distended) state. Since that exchange, SEM descriptions of the luminal surface of undistended arteries have continued to appear, but the controversy regarding the appearance of the normal endothelial surface has remained unsettled. Quite recently, for example, Fujimoto *et al.* (*3*) considered endothelial microvilli in their own undistended vessels to be normally occurring structures. They cited the findings of Smith *et al.* in confirmation but ignored Wolinsky's challenge. In an attempt to resolve this problem we undertook a detailed study of the intimal surface appearance of arteries fixed in situ by perfusion at various controlled pressures. We found, as Wolinsky predicted (*2*), that most of the surface projections were absent when intraluminal pressures were maintained at physiologic levels during fixation. In addition, other endothelial projections and surface details, such as bridges and undulations,

were found to be artifacts of sampling, preparation, processing, or viewing technique. These findings are reported in detail and discussed (*4*) and are in agreement with those of Davies and Bowyer (*5*).

Similar technical problems exist with regard to interpretation of SEM findings in other biological materials. For example, otherwise informative photographs of high technical and scientific quality, published recently in *Science*, contain incompletely verified or unidentified incidental structures that could mislead the reader. An important study of the mouse supraependymal cell (*6*) presented SEM photographs of cell surface projections as evidence that subependymal cells had phagocytosed latex spheres; similar structures on another micrograph were called "platelets." Corresponding transmission electron micrographs were neither furnished nor mentioned in support of these assertions. In addition, a recent cover illustration showed a scanning photograph of a sperm cell possibly entrapped by a "leukocyte" (*7*). Although the accompanying legend explained that surface changes in the otherwise unidentified leukocyte corresponded to its interaction with the sperm cell, all of the leukocytes in the picture had bizarre projections of several types. No mention of SEM was to be found in the text of the related report. The picture was suggestive, but neither substantiated nor detracted from the content of the report. We cite these instances by way of illustration—it is not our intent to take the otherwise sound work of these investigators to task. Nevertheless, the quality of illustrative material published in *Science* is justifiably assumed to be of high standard by readers in a wide range of scientific disciplines, and we consider it appropriate to make an urgent cautionary statement about the pitfalls of examining and interpreting surface structures in biological materials.

Scanning electron microscopy is an important adjunct to investigations of blood vessel structure, but its true value became apparent only as we learned to control avoidable artifacts and recognize the range of effects produced by different processing and preparation techniques. Artifacts that appear regularly and could be mistaken for normal structures can be grouped into three principal categories.

1) *Accretion of extraneous materials.* These include crystals derived from solutes in fixatives and buffers, particles of mounting glue, precipitated serum protein occurring as thin, homogeneous coatings or as discrete clumps, and incompletely expunged vapor bubbles of various sizes and shapes trapped beneath the metal coating. Glycerol is a particularly tenacious contaminant that is not removable by critical point drying or by mild vacuum.

2) *Distortion of real cell and tissue surface details during processing.* This is caused by variations in fixative osmolality, by shrinkage during critical point drying, by excessive physical manipulation, and by partial or total removal or disruption of underlying intracellular structures during solvent exchange procedures. Specific artifacts caused by failure to restore arteries and other mechanically functional tissues to physiological dimensions are also included here.

3) *Distortion during viewing.* Exposure to the scanning electron beam pits specimens, but it also causes cells and other tissue components to curl at their edges or to split. Other specimens become warped and attenuated when exposed excessively. A deceptive range of changes, interpretable as normal variants or transitions, can be produced in the same or successive specimens. "Charging" artifacts are, of course, well known.

On the basis of our own extensive experience with the arterial wall, we suggest that investigators who decide to embark on SEM studies of biological material resort to at least two principal means for identifying distortions and artifacts peculiar to their particular preparations. (i) The nature of configurations and projections should be established or verified by locating, examining, and measuring these structures by transmission electron microscopy, preferably using the specimen already viewed by SEM. (ii) Procedural options in specimen handling, preparation, and viewing should be varied in order to discover artifacts and gauge the relation of technique to the appearance of real surface structures.

The prevalence of published artifacts and their misinterpretation by authors as well as by readers could be greatly reduced if the following steps were taken.

1) Scanning electron micrographs of structures not previously identified by suitable verification should be accompanied by photographs of the same specimen prepared by conventional transmission techniques—light or electron microscopic, or both. Such verifying illustrations should be provided at equivalent magnifications.

2) The publication of scanning photomicrographs that do not present data necessary to the argument of the paper should be discouraged. Such micrographs, though esthetically pleasing and novel, may not be subjected to sufficient critical scrutiny by reviewers and are often inadequately described in either text or legend. They often bear unidentified artifacts that a reader may take for real structures.

3) Incidental artifacts, which authors fully realize are artifacts, on otherwise valuable micrographs, should be identified as such in text or legend.

4) A detailed description, or a reference to a detailed description, of all sampling and preparation techniques employed should be included whenever SEM observations are published. The current use of many different techniques may otherwise render comparison and reproducibility of results extremely difficult, if not impossible.

The value of SEM as a research tool is likely to increase as it is applied to a wider range of biological materials and as differential histochemical techniques become available. Investigators will need to consider carefully the extent to which SEM examination of their material will actually provide data not otherwise available by more economical, accurate, and standardized means. It would seem that the time has arrived to develop a consistent critical approach to the evaluation and publication of SEM pictures, in order that suitable standards for review may be established. Otherwise, indiscriminate publication for novelty's sake and an uncritical approach to technical details and unidentified artifacts will tend, unjustly, to discredit a potentially powerful morphologic tool.

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