
CONTROVERSY

A Scientific Scandal?

David Berlinski & Critics

DAN-E. NILSSON:

I appreciate the opportunity to respond to David Berlinski's essay on the 1994 paper I authored with Susanne Pelger called "A Pessimistic Estimate of the Time Required for an Eye to Evolve" ["A Scientific Scandal," April]. Because it gives them credibility, I generally do not debate pseudo-scientists, but I have decided to make an exception here.

Apart from a mix-up in chronology and some other minor peculiarities, the only major flaw in Mr. Berlinski's description of our paper is his misunderstanding of the response variable R, which he calls a measure of "visual acuity." It is not, and the original paper does not say so. This is his first serious mistake—and it gets worse.

Mr. Berlinski's next move is to list the important information he claims is missing in our paper. (At regular intervals he repeats the phrase: "they do not say.") But all the necessary information is there. I cannot reply individually to every point here, but two examples will do. Mr. Berlinski claims that there is no unit for morphological change and that

we do not explain how we arrive at a sum of 1,829 steps of 1 percent, but explanations for both are given on page 56 of our paper. He further claims that we fail to explain how morphological change relates to improvements in visual acuity, though pages 54 through 56 (together with the graphs and legends in figures 1 and 3) deal with exactly that, and in great detail.

For the rest of his essay Mr. Berlinski focuses on issues where he believes he has detected logical flaws. He is not right in a single case, and instead reveals an insufficient background in visual optics, sampling theory, basic evolutionary theory, and more. Nor does he seem to have read key references such as Warrant & McIntyre (1993), Falconer (1989), or Futuyma (1986). Without such knowledge it would be hard to grasp the details of our paper, but it is standard scientific practice not to repeat lengthy reasoning when a short reference can be given.

But there is more. Mr. Berlinski has a problem with definitions. "Morphological change" becomes "biological change." "Spatial reso-

lution" (visual acuity) becomes "sensitivity of vision." He does not distinguish between selection and intensity of selection. He is obviously confused by the difference between the 1-percent steps that we use as a unit of measure for morphological change and the 0.005-percent change per generation that is our conservative estimate of evolutionary rate.

Mr. Berlinski attempts a peculiar probability argument involving the random substitution into the word "at" of letters "fished from an urn," but he does not realize that his example implies a single individual in the population, in which case there can of course be no selection at all. Again, he badly needs to read Falconer's standard work.

Contrary to Mr. Berlinski's claim, we calculate the spatial resolution (visual acuity) for all parts of our eye-evolution sequence, and the results are displayed in figure 1 of our paper. The underlying theory is explained in the main text, including the important equation 1 and a reference to Warrant & McIntyre (1993), where this theory is derived. Yet Mr. Berlinski insists that "Nils-

son and Pelger do *not* calculate the visual acuity of any structure." It would be much simpler for Mr. Berlinski if he went just a tiny step farther and denied the existence of our paper altogether.

Had these and other points been unfortunate misunderstandings, I would have been only too happy to help, but I have the distinct impression that they are deliberate attempts to eliminate uncomfortable scientific results. Why does Mr. Berlinski not read up on the necessary scientific background? Why does he so blatantly misquote our paper? Why has he never asked me for the details of the calculation he claims to want so badly? It is simply impossible to take Mr. Berlinski seriously.

Mr. Berlinski is right on one point only: the paper I wrote with Pelger has been incorrectly cited as containing a computer simulation of eye evolution. I have not considered this to be a very serious problem, because a simulation would be a mere automation of the logic in our paper. A complete simulation is thus of moderate scientific interest, although it would be useful from an educational point of view.

Our paper remains scientifically sound, and has not been challenged in any peer-reviewed scientific journal. I do not intend to take any further part in a meaningless debate with David Berlinski.

*Lund University
Lund, Sweden*

PAUL R. GROSS:

"A Scientific Scandal" is itself a scientific scandal: the continued publication, in a political-cultural opinion journal, of David Berlinski's uninformed bellyaching about evolutionary biology. COMMENTARY is not the place for quasi-technical arguments against Darwinism, or for reprinting the scientific papers or textbook chapters that disprove them.

Mr. Berlinski has several times found fault with me. The method is characteristic, and it is salient in this

latest article. I had written earlier that his disparagements of Darwinism are old and naive, refuted in the literature. Responding in the March issue ("Darwinism versus Intelligent Design"), he dismissed this airily as an unanswerable gripe. But it is not a gripe. Nor was it meant to be answered in COMMENTARY. It is just a fact about the scientific literature. Any reader can check for himself. Examples include: Mark Ridley, *Evolution*, 2nd Edition (1996); John Gerhart and Marc Kirschner, *Cells, Embryos, and Evolution* (1997); Rudolf A. Raff, *The Shape of Life* (1996).

Only once, in the eleven years since the start of their anti-evolution PR-blitz, have any arguments of Mr. Berlinski's colleagues at the Discovery Institute's Center for Science and Culture appeared in the primary literature. That was an early philosophical monograph by the Christian apologist William Dembski. Mr. Berlinski (in "Has Darwin Met His Match?," December 2002) now rejects that argument as applied to biology, although he gave Dembski's book a glowing blurb. The rest of their anti-evolution kvetching has been in trade books mainly from religious publishers, in nonscientific journals, testimony to legislators, interviews, speeches, and rallies for the faithful. For this, Mr. Berlinski offered the crank excuse: scientific prejudice. And as *coup de main*, he quoted lines from a 1986 essay of mine. But the burden of that essay is precisely the opposite of Mr. Berlinski's reason for quoting it. It was about a distinguished regular contributor to the scientific literature.

The obvious purpose of "A Scientific Scandal," like Mr. Berlinski's other adventures in evolutionary thought, is to belittle Darwinism. He cites Darwin himself, who worried a little that his theory might not be able to account for the eye. Mr. Berlinski's real case is that Darwin's fears were justified: evolutionary theory cannot explain the eye, and there has been a cover-up.

But Darwin's fears are ancient history: Darwin was still haunted by Paley's 1802 version of the argument from design. A century and a half have passed.

In the 21st century there is no question that eyes, endlessly varied in structure and quality, have evolved. Most of the intermediates between a primitive patch of photosensitive cells and the camera eye of a fish or a mammal exist. Many more have existed in the past, during the 540 million years since there have been eyes.

So what is the fuss about? In their 1994 theoretical paper, Nilsson and Pelger modeled one possible evolutionary pathway to the geometry of a fish-like eye from a patch of photoreactive cells. There were already such cells on Earth a billion years before there were eyes. Nilsson and Pelger used pessimistic estimates of such relevant parameters as the intensity of selection for their number-crunching. The point was to determine how many plausible, populational micro-steps of variation would be needed for very weak selection to yield a fish-like eye—and then under reasonable assumptions to convert micro-steps into generations and years. The answer was about 350,000—a geological blink of the eye. This answer is just one of many to the failed 19th-century complaint of insufficient time for evolution to have taken place.

Mr. Berlinski misunderstands or misinterprets critical elements of the paper. Then he quibbles ponderously about terms and assumptions—and about a popular gloss of the paper by Richard Dawkins. He accuses some of his critics of fraud for having failed to denounce Dawkins's use in a trade book of certain of those terms. Mr. Berlinski's arguments are quibbles.

But these quibbles are beside the real point, which is that we lack grounds for believing that eyes evolved. That is false. Eyes, like anything else, could have been invented at a stroke by a supernatural

designer. But there is no evidence of it. Neither can it ever be disproved. The only *explanation*, however, that we have for the structure of eyes—as solid as any explanation in science—is Darwinian evolution.

Like the intelligent-design group as a whole, Mr. Berlinski seems unable or unwilling to understand the newest branch of biology: evolutionary *developmental* biology. There, with the discovery of the developmental regulatory genes, we have learned how subtle, how versatile, and yet how simple the mechanisms can be for transforming one biological structure to another. (A professional but accessible account can be found in *From DNA to Diversity: Molecular Genetics and the Evolution of Animal Design* [2001] by Sean B. Carroll, Jennifer K. Grenier, and Scott D. Weatherbee. A popular but sound insight is available in: “Which Came First, the Feather or the Bird?” by Richard O. Prum and Alan H. Brush, *Scientific American*, March 2003.) A reader whose view of science comes only from Mr. Berlinski will never know of such things.

Jamaica Plain, Massachusetts

MATT YOUNG:

Creationists often claim, without presenting evidence, that there has not been enough time for a complex organ such as the eye to have evolved. To examine that claim empirically, Nilsson and Pelger devised a scenario in which an eye could have evolved through stages that are known to exist in the animal kingdom. I described their scenario in my last letter to *COMMENTARY* (March), and David Berlinski has it almost right in “A Scientific Scandal.”

Briefly, Nilsson and Pelger formed an eye by changing various parameters, such as aperture diameter, in 1-percent increments, until no improvement could be made. One percent is an arbitrary number (any small increment will suffice) and does not represent the change in a single generation. Using what they and Richard Dawkins describe as conservative

numbers, Nilsson and Pelger calculated an average change of 0.005 percent per generation. The relative change in n generations is therefore $(1.00005)^n$, which they set equal to the overall change of morphology in their simulation ($1.01^{1,829}$, where 1,829 is the number of 1-percent steps required to form an eye). The number 1.00005 is not, contrary to Mr. Berlinski, a percentage; it is the relative change of a given parameter in a single generation. Nilsson and Pelger concluded that an eye could have evolved in approximately 350,000 years.

Does anyone claim that an eye evolved precisely as Nilsson and Pelger’s simulation suggests? No. But I stand by my statement that they have given the lie to the creationists’ claim and firmly made the case that an eye could have evolved within a geologically short time.

Mr. Berlinski argues, for example, that morphological changes of the skull might slow the process. Never mind that only vertebrates have skulls, and Nilsson and Pelger’s eye is, again contrary to Mr. Berlinski, an invertebrate eye. The development of an eye will require not only morphological changes but also advancements to the nervous system and the brain. Will these requirements bring evolution to a halt? Georges Cuvier asked the same question in 1812, and the answer is, “no.” We now know that evolution progresses in a modular way, with different systems evolving in parallel and nearly independently. If Mr. Berlinski thinks that various modules could not have co-evolved, he needs to support his argument quantitatively, not just proclaim it. Nilsson and Pelger have shown precisely what they set out to show: that an eye could have evolved in a geologically short time and that the eye itself is not a limiting factor. Mr. Berlinski holds against them that they did not perform the full-fledged simulation he wants them to have done and seems to think that their calculation is therefore somehow faulty.

I will not respond to Mr. Berlinski’s disdainful tone, nor to the cheap shots directed at me personally. Nor will I continue the pointless distraction of whether Nilsson and Pelger performed a simulation or a calculation. I am, however, concerned with Mr. Berlinski’s contention that reputable scientists have conspired to support a technical paper that he finds “unfounded”; charging specific individuals with “fraud” is not to be taken lightly. The paper has survived peer review, and has not been shown to be unfounded in any peer-reviewed journal. If Mr. Berlinski thinks the paper is unfounded, let him submit a paper of his own to a peer-reviewed journal and find out what the scientific community thinks of his ideas. It is unlikely that scientific journals, which have occasionally published papers on homeopathic medicine and the Bible codes, would reject Mr. Berlinski’s paper out of sheer prejudice.

Colorado School of Mines
Golden, Colorado

MARK PERAKH:

It is funny that *COMMENTARY*—by no measure a scientific publication—has allocated so much space to recent articles by David Berlinski. With no record of scientific research, either in biology or in computer science, he sets out to pronounce judgment on topics within these two fields.

But contrary to Mr. Berlinski’s rhetoric, any scandal related to Nilsson and Pelger’s paper occurred only in Mr. Berlinski’s imagination. Nilsson and Pelger estimate the time necessary for the development of an eye, a calculation that entails certain assumptions but which is viewed by many scientists as sufficiently sound. (According to the *Science Citation Index*, Nilsson and Pelger’s article has been positively referenced in at least 25 peer-reviewed scientific publications.)

But Mr. Berlinski, unlike all these scientists, does not like Nilsson and

Pelger's conclusion, and obfuscates the issue by discussing the distinctions among computer simulations, models, and calculations. These semantic exercises are inconsequential to the real question: whether an eye could have developed in a geologically short time via a Darwinian mechanism, as Nilsson and Pelger and scores of biologists familiar with their work think.

A reader cannot fail to notice an especially appalling feature of Mr. Berlinski's escapade: he accuses ten respected scientists of "scientific fraud." The reason for that preposterous accusation is that they did not repudiate Nilsson and Pelger's work. Mr. Berlinski apparently cannot imagine that these scientists, among them professional biologists and physicists with records of substantial achievement, can have an opinion of Nilsson and Pelger's work different from his own. His accusation sounds even odder coming from a man who provided rave blurbs for books by William Dembski and Michael Behe even though, as is clear from his article in the December 2002 *COMMENTARY*, he is actually in disagreement with them regarding essential parts of their assertions. Maybe by his standards this is a manifestation of integrity, but to me it looks more like an expediency whose roots are not exactly in the search for scientific truth.

Bonsall, California

JASON ROSENHOUSE:

Connoisseurs of pseudoscience will recognize in David Berlinski's latest essay the standard tropes of the crank's playbook: the smug sarcastic tone, the barrage of bullet-point criticisms to create the illusion that something truly rotten is being exposed (criticisms he knows will be answered by nothing more formidable than a few indignant letters), the crude baiting of scholars of vastly greater accomplishment than he, and the presentation of minor errors as tantamount to fraud.

Mr. Berlinski has no interest in

bringing clarity to difficult scientific issues. If he did, he would not have made so many misrepresentations in describing Nilsson and Pelger's work. Two examples: Mr. Berlinski's claim that their model eyes were simply "flogged up an adaptive peak" ignores the fact that establishing the existence of such a peak was one of the primary accomplishments of the paper. That there is a smooth gradient of increasing visual acuity linking a light-sensitive spot to a lens-bearing eye is a discovery that they made, not a foregone conclusion. And his claim that "in their paper there is no mention whatsoever of randomly occurring changes" falls flat, since the need for such changes is explicitly mentioned in the discussion section of the paper, and is plainly implied throughout.

In addition, Mr. Berlinski would not have unloaded so many spurious criticisms. For example, his query—"why is selection pressure held constant over the course of 300,000 years"—is easily answered by noting that it was held constant at a value that was ludicrously low for almost any environment.

Once we have swept the field of Mr. Berlinski's distortions we are left with a few simple facts. (1) Several decades of research on the evolution of eyes has not only made it plain that eyes have evolved, but has also revealed the major steps through which they did so. (2) Nilsson and Pelger's paper provides an elegant capstone for this research, by providing a convincing calculation for an upper limit on the time required for an eye to evolve. (3) Minor errors in popular treatments of Nilsson and Pelger's paper do nothing to change facts (1) and (2). (4) Finally, David Berlinski is not a reliable source for scientific information.

Kansas State University
Manhattan, Kansas

NICK MATZKE:

David Berlinski should be congratulated for pointing out Richard Dawkins's inaccurate description of

Nilsson and Pelger's paper as a stochastic computer simulation of the evolution of the eye (it was actually a mathematical model). But Mr. Berlinski should remove the plank from his own (discussion of the) eye. He asserts that one of the problems that Nilsson and Pelger did not consider was how the skull would be "reconstructed" to include eye sockets. But as any decent student of even high-school biology would know, eyes evolved before bones. Cephalochordates, the closest invertebrate relatives of vertebrates, have primitive eyes but no bones. In fact, based on genetic evidence, many biologists now think that vertebrate eyes share a common ancestral eyespot with insect eyes.

To envision the evolution of the eye as occurring on some kind of mythical eyeless fish with a fully formed skull and brain is a typical creationist straw man. Biologists know that all manner of gradations of eye complexity exist in extant organisms, from creatures with a single photoreceptor cell, through the various stages that Nilsson and Pelger depict, to the advanced camera-eyes of mammals and cephalopods. Sometimes the whole sequence from eyespot to advanced eye with lens can be seen in a single group (e.g., snails), yet another thing Mr. Berlinski would have known had he followed Nilsson and Pelger's reference to the classic work on eye evolution, a 56-page article by Salvini-Plawen and Mayr in *Evolutionary Biology* (vol. 10, 1977) called "On the Evolution of Photoreceptors and Eyes." That paper answers many of the questions that Mr. Berlinski asserts are unanswered or unanswerable.

If Mr. Berlinski is going to declare as bunk the central organizing theory of biology, he should take the matter up with biologists in the professional literature rather than in forums like *COMMENTARY*, wherein elementary questions like "which came first, skulls or eyes?" can be botched and yet still be published.

Goleta, California

DAVID SAFIR:

Once again, David Berlinski has shown how a truly scientific inquiry can expose academic and intellectual fraud by evolutionists. As a physician, I have always been made uneasy by the assertions offered by proponents of evolution to explain complex biological life. Mr. Berlinski shows exactly how the process works: start with the belief that no other possible explanation for the diversity of life on earth could exist other than what we think we know about evolution; demonstrate utter contempt for other ideas (ad-hominem attacks are often employed here); then simply invent a pathway describing how it might have been possible to get from point A to point B—from a light-sensitive spot, say, to a complex eye. Where I come from this is called nonsense.

I would feel better about a theorist like Richard Dawkins if he did not pontificate about how gloriously perfect his explanations are. I cast my fate instead with scientists like Mr. Berlinski who keep an open mind. The jury is still out, after all, and will be for a very long time.

Los Gatos, California

NORMAN P. GENTIEU:

As a retired science writer, I appreciated David Berlinski's superb analysis refuting Nilsson and Pelger's simplistic scenario of the evolution of the mammalian eye. To account for the perfection of that incredibly complex organ by means of formulaic fumblings is nothing less than preposterous. I wonder if Nilsson and Pelger might some day use this iffy method to explain the development of stereoscopic color vision.

"A Scientific Scandal" is an apt name for the docile acceptance of a dubious theory. What has happened to vetting? Back in the 1950's, the science establishment did not hesitate to zap Immanuel Velikovsky and his *Worlds in Collision*.

Philadelphia, Pennsylvania

David Berlinski

In "A Scientific Scandal," I observed that Dan-E. Nilsson and Susanne Pelger's paper, "A Pessimistic Estimate of the Time Required for an Eye to Evolve," was a critic's smorgasbord. There are so many things wrong with it that even the finickiest of eaters could leave the table well-satisfied and ready for a round of Alka-Seltzer. But, in itself, there is nothing here that suggests a scandal. Dan-E. Nilsson is a distinguished scientist. Witness his discovery that the mysid shrimp, *Dioptromyysis pauciponisa*, is an organism whose eyes are at once simple and compound (D. Nilsson, R.F. Modlin, "A Mysid Shrimp Carrying a Pair of Binoculars," *Journal of Experimental Biology*, Vol. 189, pp. 213-236, 1994), or his precise work on the optical system of the butterfly (D. Nilsson, M.F. Land, J. Howard, "Optics of the Butterfly Eye," *Journal of Comparative Physiology*, A 162, 341-366, 1988). Together with Susanne Pelger, he has simply written a silly paper. It happens. And in the literature of evolutionary biology, it happens very often.

No, the scientific scandal lies elsewhere. Nilsson and Pelger's paper has gained currency in both the popular and the scientific press because it has been misrepresented as a computer simulation, most notably by Richard Dawkins. Word spread from Dawkins's mouth to any number of eagerly cupped but woefully gullible ears. Subsequent references to Nilsson and Pelger's work have ignored what they actually wrote in favor of that missing computer simulation, in a nice example of a virtual form of virtual reality finally displacing the real thing altogether. This misrepresentation of scientific work is a species of fraud, no different in kind from plagiarism in journalism or the fabrication of data in experimental physics. It is the indifference to this fraud that I denounced as scandalous.

Recognizing so many fond familiar faces among my critics—Paul

Gross, Jason Rosenhouse, Matt Young, and Mark Perakh have replied to previous essays of mine in COMMENTARY—I hoped that self-interest, if nothing else, might have prompted a moment of critical self-reflection. No very delicate moral sense is involved in determining that fraud is fraud. If Richard Dawkins is one of their own, all the more reason to apply to him the moral standards that Messrs. Gross, Rosenhouse, Young, and Perakh are accustomed to applying to their intellectual enemies.

Reading their letters, I realize that they had no intention of saying boo. What could I have been thinking?

DAN-E. NILSSON is persuaded that I wrote my essay because I am moved to reject "uncomfortable scientific results." He is mistaken. The length of time required to form an eye is a matter of perfect indifference to me; had he and Susanne Pelger been able to demonstrate that the eye was in fact formed over the course of a long weekend in the Hamptons, I would have warmly congratulated them. As I have many times remarked, I have no creationist agenda whatsoever and, beyond respecting the injunction to have a good time all the time, no religious principles, either. Evolution long, evolution short—it is all the same to me. I criticized their work not because its conclusions are unwelcome but because they are absurd.

The vertebrate eye, Nilsson and Pelger claim, emerged from a patch of light-sensitive cells. Climbing up evolution's greasy pole, or adaptive peak, those cells got to where they were going by invagination, aperture constriction, and lens formation. In explaining the evolution of the eye in terms of such global geometrical processes, Nilsson and Pelger rather resemble an art historian prepared to explain the emergence of the *Mona Lisa* in terms of preparing the wood, mixing the paint, and filling in the details. The

conclusion—that Leonardo completed his masterpiece in more than a minute and less than a lifetime—while based squarely on the facts, seems rather less than a contribution to understanding.

It is hardly surprising, then, that while theoretical optics serves *qualitatively* to justify the overall connection Nilsson and Pelger draw between morphology and visual acuity, nothing in their paper and nothing in their references justifies the *quantitative* relationships they employ to reach their quantitative conclusion. To be sure, Mr. Nilsson denies that this is so. “Contrary to Mr. Berlinski’s claim,” he writes,

we calculate the spatial resolution (visual acuity) for all parts of our eye-evolution sequence, and the results are displayed in figure 1 of our paper. The underlying theory is explained in the main text, including the important equation 1 and a reference to Warrant & McIntyre (1993), where this theory is derived.

In fact, no underlying theory whatsoever is explained in Nilsson and Pelger’s main text, or in the legend to figure 1; and while they do assert that calculations were made, they do not say where they were made or how they were carried out. The burden of Mr. Nilsson’s denials is conveyed entirely by equation 1 and by his references.

Let us start with equation 1, and with figure 1b that this equation is said to control. It is in figure 1b that aperture constriction takes over from invagination in getting an imaginary eye to see better. The graph juxtaposes aperture size against detectable spatial resolution. Having dimpled itself in figure 1a, Nilsson and Pelger’s blob is now busy puckering its topmost surface to form a pinhole in figure 1b.* In a general way, the curve they present is unremarkable. No one doubts that spatial resolution is improved in an eye when its aperture is constricted. But why is it im-

proved in just the way that Nilsson and Pelger’s graph indicates?

Equation 1 is of scant help in this regard, despite Nilsson’s insistence that it is important. Drawing a connection among visual acuity, focal length, light intensity, and noise, the equation specifies the local maximum of a curve, the place where it stops rising. In other words, it specifies a point; and it does nothing more. “We can now use this relationship,” Nilsson and Pelger nevertheless declare, “to plot resolution against aperture diameter.” They can do nothing of the sort, at least not in *my* calculus class. Knowing that a man has reached the summit of Mt. Everest, we still know nothing about the route he has taken to get there. What is needed if Nilsson and Pelger are to justify their graph is the equation from which equation 1 has been derived by differentiation. It is not there, just where I said it would not be.

Similarly with Nilsson and Pelger’s references, which do nothing to support their argument. Quite the contrary. Three papers are at issue: (1) A.W. Snyder, S. Laughlin, and D. Stavenga, “Information Capacity of the Eyes” (*Vision Research*, vol. 17, 1163-1175, 1977); (2) A.W. Snyder, “Physics of Vision in Compound Eyes” (in *Vision in Invertebrates*, Handbook of Sensory Physiology, edited by H. Autrum, vol. VII/6A, pp. 225-313, 1979); and (3) E.J. Warrant & P.D. McIntyre, “Arthropod Eye Design and the Physical Limits to Spatial Resolving Power” (*Progress in Neurobiology*, vol. 40, pp. 413-461, 1993). Of these papers, the first is recapitulated (and corrected) in the second, and the second is summarized in the third. In what follows, references to Snyder are always to the Snyder of his second paper.

As their titles might suggest, both “Physics of Vision in Compound Eyes” and “Arthropod Eye Design and the Physical Limits to Spatial Resolving Power” deal with *compound invertebrate* eyes. Nilsson and

Pelger’s work is devoted to the evolution of the *camera* eye characteristic of fish and cephalopods. Theoretical considerations that apply to bugs do not necessarily apply to fish or octopuses, the more so since their eyes are structurally different, as are their evolutionary histories. Writing about the compound eye, Nilsson himself has remarked that “it is only a small exaggeration to say that evolution seems to be fighting a desperate battle to improve a basically disastrous design” (Dan-E. Nilsson, “Optics and Evolution of the Compound Eye,” in *Facets of Vision*, edited by D.G. Stavenga & R.C. Hardie, p. 3075, 1989). Whatever the desperate battle going on among the arthropods, there is no battle at all taking place among the vertebrates or the cephalopods. Nilsson and Pelger’s eye moves from triumph to triumph with serene and remarkable celerity.

If the papers by Snyder and Warrant & McIntyre say nothing about fish or octopuses, neither do they say anything about evolution. No mention there of Darwin’s theory, no discussion of morphology, not a word about invagination, aperture constriction, or lens formation, and *nothing* about the time required to form an eye, whether simple, compound, or camera-like.

The purpose of these three papers is otherwise. No less than any other system of communication, the eye represents a balance struck between signal and noise. There is the object out there in the real world—whether a point source like a star, or an extended source like a grating of light and dark lines—and there is its image trembling on the tips of the retina’s budded nerve cells. Slippage arises between what the object is and how it is seen. Noise occurs in the visual system as the result of the random nature of photon emission, and it also occurs as the result of inherent imperfections in the eye’s op-

* Three curves are given in figure 1b, representing three different levels of light intensity, but this plays no role in what follows.

tical system. The theoretical optician abbreviates these limitations in one mathematical instrument.

Imagine one of Nilsson and Pelger's plucky light-sensitive cells, and then extend two flanking lines from the cell up past the constricted aperture and out into space, so that the cell and those two flanking lines form a cone with a flat top. In the center of the cone, where a cherry would sit atop the ice cream, there is a light source. The cherry moves to the sides of the cone in angular steps; the cell dutifully responds. The correlation between moving cherry and twitching cell constitutes the optician's "angular-sensitivity function."

Equation B15 (p. 238) in Snyder's "Physics of Vision in Compound Eyes" defines the signal-to-noise ratio of a hypothetical eye in terms of noise, modulation contrast (the difference in intensity between black and white stripes in a grating), and the modulation-transfer function, which is simply a mathematical transformation of the eye's angular-sensitivity function (its Fourier transform). Lumbering in Snyder's footsteps, Warrant & McIntyre split his equation into two of their own (equations 10 and 11 in Warrant & McIntyre, p. 430), the one describing the signal, the other the noise in a hypothetical visual system. They observe what is in any case obvious: whatever the parameters affecting visual acuity, signal and noise will always reach a point where the first is drowned out by the second and the system fails, a point evident enough to anyone trying to see in the dark.

These equations lead by primogeniture to Nilsson and Pelger's equation 1, which, as it happens, does not appear anywhere in their sources in the form in which they express it. But neither Snyder's original equation nor Warrant & McIntyre's bright bursting clones in any way suggest that the tipping point between signal and noise is unique. The ratio of signal to noise in an

optical system depends on a host of factors, including head size and eye movement, most of which Nilsson and Pelger ignore. Nor, for that matter, do these equations taken in isolation justify any particular quantitative conclusions. Until the angular-sensitivity function is specified, whether theoretically or experimentally, its role is ceremonial.

Such specification is no easy busi-

ness. Determining the shape of the angular-sensitivity function is a little like trying to guess an astronaut's weight in space. Scales are not likely to be of use. In an early paper dealing with this subject and devoted experimentally to flies, K.G. Götz noted that the angular-sensitivity function in *Drosophila* seemed to follow what is known mathematically as a Gaussian probability dis-

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tribution (K.G. Götz, "Die optischen Übertragungseigenschaften der Komplexaugen von *Drosophila*," *Kybernetik*, 2, pp. 215-221, 1965). It was an interesting idea, but one that led to very considerable computational difficulties.

Looking Götz-ward, and understandably recoiling, Snyder adopted a different strategy. In assessing the weight of an astronaut in space, it is simpler to count the calories he consumes and the exercise he undergoes than to try to measure his weight directly. His weight, although unmeasured, follows inferentially. In just the same way, Snyder thought to consider the angular-sensitivity function indirectly by considering the structures that determined its shape. These, he assumed, were the eye's retinal receptive field—the area of the retina responding to signals—and its optical "blur spot"—the smeared image represented on the retina corresponding to the sharp object being seen. Let them both, he declared, be identically Gaussian. Why not? Both parameters had simple mathematical natures. The retinal receptive field is given as the ratio of the rhabdom's diameter to its posterior nodal distance, the optical blur as the ratio of the wavelength of stimulating light to the eye's aperture. From this the shape of the angular-sensitivity function followed.

The result is known as the Snyder model. "*The great beauty of this model,*" Warrant & McIntyre remark (in words that they have italicized), "*is that if one knows some very simple anatomical information about the eye*"—i.e., the nature of its optical blur spot and retinal receptive field—"one has the ability to predict . . . the approximate shape of the angular-sensitivity function" (p. 434). In referring to Warrant & McIntyre, Nilsson and Pelger are, in fact, appealing to Snyder, the *maitre* behind their masters—for, like Snyder, they, too, assume that retinal receptive fields and optical blur spots are identically Gaussian (p. 54).

But theory is one thing, and living flesh another. Staking their all on Snyder's model, Nilsson and Pelger must live with its consequences. "Having considered the physical limitations to resolving power," Snyder wrote, "in addition to the absolute sensitivity of eyes, we now apply our concepts to real compound eyes." This is something that Nilsson and Pelger never do. And no wonder. For Snyder then added the rather important caveat that bringing theory to bear on life "requires *precise* knowledge [of various optical parameters] in the various regions of the eye" (Snyder, p. 276, emphasis in the original).

If precise knowledge is needed in applying Snyder's model, precise detail is what is lacking in Nilsson and Pelger's paper. Precise detail? *Any* detail whatsoever.

And for obvious reasons. When tested, Snyder's model turns out to be *false* across a wide range of arthropods. As Warrant & McIntyre note glumly, "The model, on the whole, works best for those eyes for which it was originally formulated—apposition compound eyes functioning according to geometrical optics—but recent careful and sensitive measurements of angular sensitivity reveal that even in these types of eye, the model often performs poorly." Readers may consult figure 34 (p. 441) of Warrant & McIntyre's paper to see how poorly the Snyder model does. In studies of the locust *Locusta*, real and predicted angular-sensitivity functions do not even share the same qualitative shape.

Responding to my observation that no quantitative argument supports their quantitative conclusions—no argument at all, in fact—Mr. Nilsson has thus (1) offered a mathematically incoherent appeal to his only equation; (2) cited references that make no mention of any morphological or evolutionary process; (3) defended a theory intended to describe the evolution of vertebrate camera eyes by referring to

a theory describing the theoretical optics of compound invertebrate eyes; (4) failed to explain why his own work has neglected to specify any relevant biological parameter precisely; and (5) championed his results by means of assumptions that his own sources indicate are false across a wide range of organisms.

In acknowledgments to their paper, Nilsson & Pelger thank E. J. Warrant for help with their computations; in the acknowledgments to *their* paper, Warrant & McIntyre thank Mr. Nilsson for critically reading what they have written.

Schnapps all around, I am sure.

I TURN next to the morphological units that are missing from Nilsson and Pelger's paper. It makes no sense to say of a ruler that it is one long. One what? When the "what" has been specified, a physical unit has been indicated: one inch, say, in the case of length, one pound in the case of weight. If one inch and one pound are units, length and weight are their dimensions. Only an origin in zero remains to be specified to complete the picture.

In my essay, I observed that Nilsson and Pelger had not specified their unit of morphological change. Nilsson now asks me to consider again their remarks on p. 56 of their paper. There, he is certain, I will find the missing unit carefully explained. Here is what they write, and it is *all* that they write: "Our principles have been to use whole-length measurements of straight structures, arc lengths of curved structures, and height and width of voluminous structures."

Very well. These are the fundamental units. They are none too clearly explained—try estimating the volume of a donut by looking at its height and width—but I know roughly what Nilsson and Pelger are getting at. What they do not say is *how* these three separate fundamental units are combined in a single overall derived unit of change.

A homely example may make this

more vivid. Except for the fact that it cannot see, a Swedish meatball is rather like an eye. And plainly it makes no sense to ask of two Swedish meatballs, one of them twice as greasy but half as wide as the other, which of them is bigger—at least not until units of grease and length have been *combined*. But this is, in general, no easy task, not even when shape alone is under consideration. “It is important to keep in mind,” C.P. Klingenberg and L.J. Leamy write (“Quantitative Genetics of Geometric Shape in the Mouse Mandible,” *Evolution*, 55(11), pp. 2342–2352, 2001), “that shape is a multivariate feature and cannot be easily divided into scalar traits without imposing arbitrary constraints on the results of the analysis.” To see how difficult a conceptual problem Nilsson and Pelger have set themselves, readers may follow the trail of Klingenberg & Leamy’s references to the badlands of current work on geometric morphometrics.

Operating perhaps on the principle that a difficulty disclosed is a difficulty denied, Nilsson and Pelger do mention this very point, citing an example of their own on p. 56 to show just how arbitrary can be the business of calculating combined or derived units. In then justifying their own procedure, which is never explained, they remark: “As we are going to relate our measure of morphological change only to general estimates of phenotypic variation” in visual acuity, “we will be safe as long we avoid unorthodox and strange ways of comparing origin and product.”

Origin and product? I am sure they meant origin and unit. No matter. The remark speaks for itself.

THERE IS next the matter of random variation: the heart of the matter so far as I am concerned. Nilsson and Pelger’s paper is not an exercise in theoretical optics. It is intended to serve polemical purposes. Thus, they write: “In this context it is ob-

vious that the eye was never a real threat to Darwin’s theory of evolution” (p. 58). By “this context,” they mean one in which only “eye geometry” and “optical structures” are up for grabs. But whether in this context or any other, it is as a defense of Darwin’s theory that Nilsson and Pelger’s theory fails most obviously.

Let me review the chief steps in their argument. There is morphological change on the one hand, visual acuity on the other. As their population of light-sensitive cells alters its geometry—by means never specified—visual acuity perks up. In all, they assert, 1,829 steps are involved in tracing a path from their first patch to their final “product.”

Just how do Nilsson and Pelger’s light-sensitive cells move from one step on that path to the next? I am not asking for the details, but for the odds. There are two possibilities. Having reached the first step on the path, the probability that they will reach the second (and so on to the last) is either one or less than one. If one, their theory cannot be Darwinian—there are no random changes. If less than one, it cannot be right—there is no way to cover 1,829 steps in roughly 300,000 generations if each step must be discounted by the probability of its occurrence.

Demonstrating the existence of a path between two points in the history of life is in general not hard. What is hard is determining how the path was *discovered*. (This was the point of the linguistic example I offered in my essay.) If one assumes, as Nilsson and Pelger do, that probabilities need not be taken into account because all transitions occur with a probability of one, there is no problem to be discussed—but nothing of any conceivable interest, either. In responding to this obvious point by generously suggesting that I need to spend more time by the lamp with D.S. Falconer’s *Principles of Quantitative Genetics*, Mr. Nilsson has covered an embarrassment by addressing an irrelevance. Neither

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population size nor natural selection is at issue.

A few minor matters. Falconer's response variable R is a measure, all right: a measure of the extent to which the mean of some quantitative phenotypic character—snout length, crop yield, scab color, or scrotum size (examples from the literature, I am afraid)—rises or falls as the result of natural selection. Just what I said, just as I explained. Although I offered no definitions in my essay, the paraphrases I employed were harmless. Why not say "sensitivity to vision" instead of "visual acuity," just to vary pace and prose? But in one respect, Mr. Nilsson is right: I did not distinguish between selection and intensity of selection. Neither does he. Neither does Falconer's response statistic, which contains only one selectional parameter, and that one measuring the intensity of selection. Neither does anyone else in this context.

His paper with Susanne Pelger, Mr. Nilsson writes, has never been criticized in the peer-reviewed literature. I am certain that this is so.

PAUL R. GROSS takes the occasion of his current letter to assure readers that what he meant in his last letter he did not say and what he said he did not mean. Like golf, Mr. Gross suggested in the 1986 essay from which I uncharitably quoted in the March COMMENTARY, science is rather a clubby affair, and just as a great many men prefer to cover the links sedately in the company of men like themselves—tassels on their shoes, alligators on their polo shirts—so scientists prefer to keep company with their own, men and women who share their tastes, point of view, outlook on life.

These are sentiments so candid that I was surprised to find Mr. Gross expressing them. But he is now prepared to disown what he said. The club is just fine, and just look at those splendid greens! The admissions board is to be faulted only when, by accident or inadver-

tence, it excludes one of its own, a scientist who like L.V. Heilbrunn has *published in the literature*. Such men are entitled to wear the gold cufflinks with the crossed golf clubs; keeping *them* out would be irresponsible. But keeping out the others is not only good science but good sense. *Ipse dixit.*

A few other points deserve comment. In offering Nilsson and Pelger the oil of his approval, Mr. Gross affirms that I have misunderstood or misinterpreted critical elements of their paper. In keeping with his longstanding policy of never documenting his discontent, he does not say which elements. As I keep reminding him, this is not sporting. Still, it is inconceivably droll to see Mr. Gross excusing Richard Dawkins's misrepresentation of Nilsson and Pelger's work by appealing to the fact that Dawkins expressed his views in a *trade book*. Mr. Gross apparently believes that outside the country club, a man can say anything he wants, a policy that he would not dream of applying to critics of Darwin's theory.

A few of Mr. Gross's remarks suggest a need for remedial reading. I have never argued that "evolutionary theory cannot explain the eye." How on earth would I know *that*? And explain what in particular? Its emergence, its structure, its physiology, its biochemistry? What I contended specifically is that Nilsson and Pelger's paper is just nuts. Conspiracies and cover-ups are, in any case, not in my line, and I never suggested or supposed that evolutionary biologists who failed to criticize Richard Dawkins for misrepresenting Nilsson and Pelger did so as part of a conspiracy. Like *droshky* horses, they were only doing what comes naturally: turning a blind eye.

If the burden of Nilsson and Pelger's paper was to demonstrate the existence of "one possible evolutionary pathway to the geometry of a fish-like eye from a patch of photoresponsive cells," as Mr. Gross

writes, they have surely wasted their time. The existence of such a path is hardly in doubt. Every normal human being creates an eye from a patch of photoresponsive cells in nine months.

I certainly agree that the "only explanation we have for the structure of the eye . . . is Darwinian evolution." But neither an orchestra nor an explanation becomes good by being the only game in town.

On the other hand, I disagree that Darwin's theory is as "solid as any explanation in science." Disagree? I regard the claim as preposterous. Quantum electrodynamics is accurate to thirteen or so decimal places; so, too, general relativity. A leaf trembling in the wrong way would suffice to shatter either theory. What can Darwinian theory offer in comparison?

Finally, I would hardly dispute Mr. Gross's claim that "with the discovery of the developmental regulatory genes, we have learned how subtle, how versatile, and yet how simple the mechanism can be for transforming one biological structure to another." If he were to re-read the correspondence (COMMENTARY, September 1996) following the publication of my "The Deniable Darwin" (June 1996), he could not fail to be struck by my reply to his own letter, in which I specifically called attention to work on regulatory genes and eye formation—the very work that he now suggests I am keeping from my readers. Subtle and versatile, those genes? Yes, indeed. Absolutely astonishing? That, too. But hardly a triumph of Darwin's theory. For one thing, no Darwinian theorist had predicted the existence of these genes; for another, no Darwinian theorist has explained their emergence. The facts are simply far more fascinating than anything that poor drab Darwin, endlessly sifting time and chance, could possibly have imagined.

CITING THOSE ever useful but eternally anonymous "creationists,"

Matt Young argues yet again, as he did in our earlier exchange, that Nilsson and Pelger have given the lie to creationist claims. If it was their computer simulation that originally lent ardor to his asseverations, now it is their paper itself. Mr. Young is a man plainly prepared to rely on an endless series of fallback positions. In the end, he may have to argue that his refutation is its own best friend, and that Nilsson and Pelger's paper is itself superfluous.

No one doubts that the eye has evolved. Not me, in any event. Fish have eyes; rocks do not. Those eyes came from somewhere—right?—and if coming from somewhere counts as evolution, count me among its champions. No one doubts, furthermore, that the “eye could have evolved in 350,000 generations.” As I remarked earlier, the eye could have evolved in a weekend. The issue is whether it could have evolved in 350,000 generations *given the constraints of random variation and natural selection*.

I have absolutely no idea. Neither do Nilsson and Pelger. And neither does Matt Young.

Arguing now from the last trench before the bunker, Mr. Young writes that Nilsson and Pelger's paper deals with the development of *invertebrate* eyes, and triumphantly chides me for overlooking this point. On p. 56 of their paper, Nilsson and Pelger write: “After constriction of the aperture and the gradual formation of a lens, the final product becomes a focused camera-type eye with the geometry typical for aquatic animals (e.g. fish and cephalopods).” Fish are, of course, vertebrates, as anyone who has picked the flesh from a flounder knows. Perhaps I will be forgiven if I refer to this exchange as shooting fish in a barrel.

Making the point that the emergence of even the most modest eye will require simultaneous and parallel evolutionary development, Mr. Young asks that I defend my claim that this process could not have tak-

en place by quantitative steps. In the first place, I made no such claim, if only because its truth struck me as obvious. But were I to make such a claim I would observe, as Richard Dawkins does, that to the extent that simultaneous and parallel changes are required to form a complex organ, to that extent does the hypothesis of random variation and natural selection become implausible. It is one thing to find a single needle in a haystack, quite another to find a dozen needles in a dozen haystacks at precisely the same time. Surely the burden of proof in such matters is not mine. I am not obliged to defend such mathematical trivialities as the proposition that as independent events are multiplied in number, their joint probability of occurrence plummets.

I have no idea what Mr. Young means when he writes that the number 1.00005 is not a percentage. Every number can be expressed as a percent, and every percent is a pure number. But he gets half credit for spotting a slip: the figure of 1.00005 between parentheses on p. 33 in my text should have been .005. Mr. Nilsson, who also spotted the slip, gets the other half. Me? I blame my editors.

Finally, I did not fault the scientific community for failing to criticize Nilsson and Pelger's work. I did the job of criticism myself. I faulted the Darwinian community—Mr. Young included—for failing to denounce scientific fraud, specifically the misrepresentation of Nilsson and Pelger's work by Richard Dawkins. Now I see that Mr. Young feels I have manhandled him in these exchanges. Too bad. COMMENTARY is not some academic mouse hole.

MARK PERAKH, a *sensei* of the “not-ed scientists say” school of self-defense, is right in one respect: the computer simulation missing from Nilsson and Pelger's paper has no bearing on what they actually said and claimed. And right in a second respect: “The real question [is]

whether an eye could have developed in a geologically short time *via a Darwinian mechanism*” (emphasis added). But then, although quite confident that I am wrong in my criticisms, he offers nothing by way of rebuttal. Like so many of these martial-arts types, he is too busy preparing himself to run from the field with honor to bother doing battle.

Contrary to what Mr. Perakh asserts, not only can I imagine, I do not doubt, that “distinguished scientists,” many with a record of “substantial achievement,” can have an opinion different from my own. It happens all the time. I would not dream of accusing ten respected scientists of fraud simply because they passed on the opportunity to have a go at Nilsson and Pilger. The men and women I criticized earned my contempt the hard and dirty way, by saying nothing about scientific misconduct when it was right under their noses.

LIKE MR. PERAKH and Paul R. Gross, Jason Rosenhouse regards Richard Dawkins's misrepresentation of Nilsson and Pelger's work as a “minor error.” Some minor, some error. What, may I ask, is the difference between inventing data out of whole cloth and inventing a computer simulation out of whole cloth? Should not evolutionary biologists be held to the same standards as physicists? Or even journalists? What part of the declaration that fraud is fraud does he fail to endorse? These are not semantic issues. If I claimed in print that Mr. Rosenhouse has four eyes, his denials would not turn on what I meant. Two eyes, I am sure he would say, are not there. Two eyes, and one computer simulation.

Mr. Rosenhouse believes that Nilsson and Pelger made an important discovery: namely, “that there is a smooth gradient of increasing visual acuity linking a light-sensitive spot to a lens-bearing eye.” This is not their discovery, it is a restate-

ment of their chief assumption. "The model sequence is made," they write, "such that every part of it, no matter how small, results in an increase of the spatial information the eye can detect" (p. 53). Note: *made*, not discovered.

To repeat, the flaw in Nilsson and Pelger's work to which I attach the greatest importance is that, as a defense of Darwinian theory, it makes no mention of Darwinian principles. Those principles demand that biological change be driven first by random variation and then by natural selection. There are no random variations in Nilsson and Pelger's theory. Whatever else their light-sensitive cells may be doing, they are not throwing down dice or flipping coins to figure out where they are going next.

Mr. Rosenhouse's conviction that the randomly occurring changes required by Darwin's theory are nevertheless "plainly implied" throughout Nilsson and Pelger's paper owes nothing to the facts and little to common sense. If changes in their model were really random, their temporal estimates would be apt to change by orders of magnitude, a point I made in my essay and again in my reply to Dan-E. Nilsson above. In my essay I also questioned Nilsson and Pelger's decision to hold selection pressure constant over time. In this, I found myself echoing John Gillespie (*The Causes of Molecular Evolution*, 1991, p. 294). "[W]e must be concerned," Gillespie writes, "with models of selection in variable environments. How could it be otherwise? Natural selection is a force adapting species to their environments. Environments are in a constant state of flux; selection coefficients must be in a constant state of flux as well." What is good enough for Gillespie is good enough for me.

In approving of the value chosen by Nilsson and Pelger for selection pressure, Mr. Rosenhouse writes

that it is "ludicrously low for almost any environment." Is it indeed? The figure that Mr. Rosenhouse calls ludicrous, Nilsson and Pelger term pessimistic, and Mr. Gross reasonable. The correct term is arbitrary—as in, it is anyone's guess what the variance among a bunch of fish might have been a couple of million years ago. Studies of variance and heredity typically deal with tiny populations and small periods of time. Studying the collared flycatcher, *Ficedula albicollis*, Merilla, Kruuk, and Sheldon collected eighteen years of data for 17,171 nestlings in order to reach some quite modest quantitative conclusions (J. Merilla, L.E.B. Kruuk, and B.C. Sheldon, "Natural Selection on the Genetic Component of Variance in Body Condition in a Wild Bird Population," *Journal of Evolutionary Biology* 14, pp. 918-921, 2001). Nilsson and Pelger's imaginary population ranges over space and time in a way that could not possibly be disciplined by the data.

NICK MATZKE believes that Nilsson and Pelger provide a mathematical model for the development of the eye. Let us be honest: beyond a few finger-counting exercises, there is no mathematics in their model, and while their references do contain some legitimate mathematics (nothing beyond second-semester calculus, but also nothing to sneeze at), their references, as I have shown in patient detail, do not support their theory. The task of modeling the eye's complicated geometry from light-sensitive cell to fully functioning eye is utterly and completely beyond our powers, as a glance at any textbook dealing with embryology would show.

Mr. Matzke devotes the greater part of his otherwise interesting letter to doing battle with various "creationist straw men." It is useful work, I am sure, the more so since the creationists are never named.

But whoever they are, I am not among them. Quite the contrary, I am as eager to do right by the snails as he is: why should he think otherwise? It is only when he passes to matters of fact that we part company.

Nilsson and Pelger's theory is intended to encompass the evolution of the eye in fish and cephalopods. Fish indisputably have bones, an attractive skull, and for the most part two staring eyes. The cephalochordate *Branchiostoma* (*Amphioxus* in a now out-of-date system of nomenclature) is widely taken by paleontologists to be a very plausible ancestral model to the vertebrates. It has certain vertebrate features while lacking others. These others include bones, a skull, a brain, and *paired sensory organs*: in other words, it has no eyes. Mr. Matzke's very confident assertion that cephalochordates have "primitive eyes" is simply untrue.

Now that I have swept away a few straw men of my own, let us see what is left to clean up. In my essay I wrote that Nilsson and Pelger made no attempt to discuss the cost-benefit payoffs associated with an improvement in visual acuity. My aim in discussing the reconstruction of the fish skull was not to argue that eyes came first *or* that bones did. Paired sensory organs *and* bones are characteristics of the vertebrates. Plainly they evolved together. Plainly, too, one function of the bony skull in vertebrates is to provide protection for the paired sensory organs located on their heads. The protection racket, as every Mafia boss is aware, does not come cheap; but Nilsson and Pelger, in adding up the benefits of visual acuity, did not ever bother to consider the vigorish. This is such an unobjectionable point that I cannot imagine why Mr. Matzke found it fishy.

I very much appreciate the letters from David Safir and Norman Gentieu.