Living in a physical world

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The diversity of life on earth dazzles all of us – the rich profusion of its designs, the wide size range of its organisms, the complexities of its hierarchical levels, and so forth. Undaunted, we life scientists seek broadly applicable rules, common patterns of organizations, and order beneath the perceptual chaos; we look for alternatives to the easy answers of revealed truth.

Biology, no less than the physical sciences, treads this bumpy path – indeed the overt diversity of life puts especially bad bumps in its way. Perhaps its special difficulty underlies the gradual estrangement of biology from the more obviously successful physics of the post-Newtonian era and its awkward reintegration into the larger world of science in the twentieth century. That process remains incomplete; blame, if leveled, rests on the untidiness and distinctiveness of the subject. The tidy formulas of Newtonian physics work even less well for us than they do for, say, practicing engineers. Life directs its chemistry with sets of governing molecules and carries it out with the aid of catalysts of breathtaking specificity. And biology enjoys a strange organizing principle, evolution by natural selection, barely hinted at elsewhere in science.

No aspect of this reintegration has been (and continues to be) more successful than what we have come to call molecular biology – a statement at once fashionable and incontrovertible, one with which I have no grounds to take issue. What matters here, indeed the entire justification for the essays that begin with the one here, comes down to the following. The very success of this chemically-reductionist biology too easily diverts us from other conjunctions of physical science and biology.

This series will explore aspects of biology that reflect the physical world in which organisms find themselves. Evolution can do wonders, but it cannot escape its earthy context – a certain temperature range, a particular gravitational acceleration, the physical properties of air and water, and so forth. Nor can it tamper with mathematics. The baseline they provide both imposes constraints and affords opportunities. I mean to explore both.

And I will take what other biologists might find an unfamiliar approach – one, by the way, that I have found productive enough to recommend. Instead of asking about the physical science behind a specific biological system, I will consider aspects of the physical world and ask what organisms, any organisms, make of each, both how they might capitalize on them and be in some fashion limited by them. In effect, this will be a search for commonalities and patterns, the only unusual feature being the physical rather than biochemical or phylogenetic bases. If this approach to science were a dart game, I would be thrown out – for throwing darts at a wall first and only subsequently painting targets around the points of impact.

The series will concern itself mainly (but not exclusively) with organisms rather than ecosystems or organelles. It will follow the author's bias and personal experience toward mechanical matters, doing less than equal justice to radiations and electrical phenomena. It will be speculative, opinionated, and idiosyncratic, aiming to stimulate thought and perhaps even investigation, to open doors rather than just describing them.

When I began to do science, over forty years ago, I wondered first whether and then where I would get ideas worth pursuing. Now, on the cusp of retirement, I wonder what I am going to do with my accumulated head- and notebooks-full of questions. Maybe we need something like a patent expiration date – if one does nothing with a hypothesis for some number of years, it should somehow revert to the public domain. I am not an unequivocal advocate of a strict rule, inasmuch as I have, on occasion, resurrected one of my old ideas, applying some additional insight or new tool in my experimental armamentarium – or just responding to a renewed interest. Still, these essays should, if nothing else, provide an opportunity to air untested ideas with some hope that others might care to pursue them.

Living in a physical world I. Two ways to move material

"No man is an island, entire of itself," said the English poet John Donne. Nor is any other organism, cell, tissue, or organ. We are open systems, continuously exchanging material with our surroundings as do our parts with their surroundings. In all of these exchanges, one physical process inevitably participates. That process, diffusion, represents the net movements of molecules in response to thermal agitation and place-to-place concentration differences. On any biologically-relevant scale, it can be described by exceedingly precise statistical statements, formulas that take advantage of the enormous numbers of individual entities moving around. And it requires no metabolic expenditure, so it is at once dependable and free.

But except over microscopic distances diffusion proceeds at a glacial pace. For most relevant geometries, a doubling of distance drops the rate of transport per unit time by a factor, not of two, but of four. Diffusive transport that would take a millisecond to cover a micrometer would require no less than a thousand seconds (17 min) to cover a millimeter and all of a thousand million seconds (3 y) for a meter. Diffusion coefficients, the analogs of conventional speeds, have dimensions of length squared per time rather than length per time.

Organisms that rely exclusively on diffusion for internal transport and exchange with their surroundings, not surprisingly, are either very small or very thin or (as in many coelenterates and trees) bulked up with metabolically inert cores. Those living in air (as with many arthropods) can get somewhat larger since diffusion coefficients in air run about 10,000 times higher than in water, which translates into a hundred-fold distance advantage. Beyond such evasions, macroscopic organisms inevitably augment diffusion with an additional physical agency, convection, the mass flow of fluids. Circulatory systems as conventionally recognized represent only one version of a ubiquitous scheme.

One might expect that good design balances the two physical processes. Excessive reliance on diffusion would limit size, slow the pace of life, or require excessively surface-rich geometries. Excessive reliance on flow would impose an unnecessary cost of pumping or require an unnecessarily large fraction of body volume for pipes, pumps, and fluid. A ratio of convective transport to diffusive transport ought, in other words, to have values around one for proper biological systems. Such a ratio represents nothing novel; one has long been used by chemical engineers. This so-called Péclet number, *Pe*, is a straightforward dimensionless expression:

$$Pe = \frac{vl}{D} \, , \qquad (1)$$

where *v* is flow speed, *l* is transport distance, and *D* is the diffusion coefficient. (Confusingly, a heat-transfer version of the Péclet number may be more common than this mass-transport form; it puts thermal diffusivity rather than molecular diffusion coefficient in its denominator.)

Calculating values of the Péclet number can do more than just give a way to check the performance of the evolutionary process. In particular, it can provide a test for our hypotheses about the primary function of various features of organisms. I think that justification can be put best as a series of examples, which will follow after a few words about the origin of this simple ratio.

One can view the ratio as a simple numerator, *mv*, for bulk flow, with a denominator representing a simplified form of Fick's first law for transport (mass times distance divided by time) for diffusion, *DSm/V*, where *S* is cross section and *V* is volume. Using l^2 for area and l^3 for volume, one gets expression (1). Of course, the way we have swept aside all geometrical details puts severe limits on what we can reasonably expect of values of *Pe*. Only for comparisons among geometrically similar systems can we have real confidence in specific numbers. Still, living systems vary so widely in size that even order-of-magnitude values ought to be instructive.

From a slightly different viewpoint, the Péclet number represents the product of the Reynolds number (*Re*) and the Schmidt number (*Sc*). The first,

$$Re = \frac{rlv}{m} \, , \qquad (2)$$

where *r* and *m* are fluid density and viscosity respectively, gives the ratio of inertial to viscous forces in a flow. At high values bits of fluid retain a lot of individuality, milling turbulently as in a disorderly crowd; at low values bits of fluid have common aspirations and tend to march in lock-step formation. In short, it characterizes the flow. The second,

$$Sc = \frac{m}{rD} \, , \qquad (3)$$

is the ratio of the fluid's kinematic viscosity (viscosity over density) to the diffusion coefficient of the material diffusing through it. It gives the relative magnitudes of the diffusivities of bulk momentum and molecular mass. In short, it characterizes the material combination, solute with solvent, that does the flowing.

A few cases where calculating a Péclet number might prove instructive.

(i) *The sizes of our capillaries and kidney tubules*

Consider our own circulatory systems, in particular the size of the vessels, capillaries, where function depends on both diffusion and flow. Do we make capillaries of pro-

per size? After all, we devote about 6·5% of our body volume to blood and expend about 11% of our resting metabolic power pushing it around – so it ought to be important. And it appears that we do size them properly. For a capillary radius of 3 μm, a flow of 0·7 mm s^{-1}, and a diffusion coefficient (assuming oxygen matters most) of 18×10^{-10} m^2 s^{-1}, the Péclet number comes to 1·2. If anything, the value turns out a bit better than one expects, given the approximations behind it (Middleman 1972).

Of course nature might pick different combinations of radius and flow speed without offending Péclet. (We ignore the side issue of fit of red blood cells, tacitly assuming that their size is evolutionarily negotiable.) Smaller vessels would permit faster flow and lower blood volume, but the combination would, following the Hagen-Poiseuille equation, greatly increase pumping cost. Larger vessels require greater blood volume, the latter already fairly high, and slower flow, which would make the system less responsive to changes in demand. One suspects something other than coincidence for the similar blood volume (5·8%) in an octopus (Martin *et al* 1958).

Quite likely this choice of capillary size, based on Péclet number and some compromise of volume versus cost, sets the sizes of much of the rest of our circulatory systems in an effective cascade of consequences. According to Murray's law (LaBarbera 1990) the costs of construction and operation set the relative diameters of all vessels; thus if something sets diameter at one level in their hierarchy, it ends up determining the diameters of all the rest. The rule is a simple one – branching conserves the cubes of the radii of vessels, so the cube of the radius of a given vessel equals the sum of the cubes of the vessels at some finer level of branching that connect with it.

What about the reabsorptive tubules of our kidneys, in particular those just downstream from the glomerular ultrafiltration apparatus? Again, the system represents a far-from-insignificant aspect of our physiology; 20 to 25% of the output of the heart passes through this one pair of organs. About 20% of the plasma volume squeezes out of the blood in the process, in absolute terms around 60 ml min^{-1} per kidney. Each kidney consists of about 2,000,000 individual units, the nephrons. Thus each glomerulus sends on for selective reabsorption about $0·5 \times 10^{-12}$ m^3 s^{-1}.

The sites of the initial phase of reabsorption are the proximal tubules, each about 40 micrometers in inside diameter. Combined with the earlier figure for volume flow, that means a flow speed of 0·40 mm s^{-1}. So we have speed and size. Diffusion coefficient can be assigned no single number, since the tubules reabsorb molecules spanning a wide size range, from small organic molecules and ions to small proteins with molecular weights of around 40,000. So coefficients most likely range from about $0·75 \times 10^{-10}$ to 40×10^{-10} m^2 s^{-1}. That produces Péclet numbers from 2 to 100. At first glance these seem a bit high, but the

story has an additional aspect. Those tubules reabsorb at least 80% of the volume of the filtrate, so by the time fluid leaves them, its speed has dropped by at least a factor of 5. That gives exit Péclet numbers a range of 0·4 to 20, with an average number in between – quite reasonable values, indicative (to be presumptuous) of good design. Flow in the tubules comes at a relatively low cost, at least relative to the power requirements of filtration and the kidney's chemical activities. So one might speculate that the system contrives to bias its Péclet numbers so for most molecules over most of the length of the tubule values exceed one, albeit not by much.

(ii) *The size of plant cells*

One can argue that the boundary between the cellular and the super- (or multi-) cellular world reflects the upper size limit of practical, diffusion-based systems, that getting above cell size takes some form of convective augmentation of transport. I like that view, which tickles my particular biases. But I have to admit that the notion cannot apply to plant cells. On average, the cells of vascular plants run about ten times the size of animal cells, with "size" taken as typical length. They are of the order of 100 μm in length but somewhat less in width; 25 μm should be typical of the distance from membrane to center. That increased size might have devastating consequences for transport were it not for the internal convection common to such cells. Put another way, the size scale at which convective transport comes in does not correspond to the size of plant cells.

That bulk flow system within plant cells goes by the name "cyclosis." We know quite a lot – but far from all – about how microfilaments of actin (a key component of muscle) power it; only its speed matters here. That speed is around 5 μm s^{-1} (Vallee 1998). Focusing on oxygen penetration and using a penetration distance of 25 μm gives a Péclet number of 0·07. That tells us that the system remains diffusion dominated, that cyclosis does not reach a significant speed. Looking at carbon dioxide penetration, with a diffusion coefficient of 0·14 m^2 s^{-1}, raises that number too little to change the conclusion.

Perhaps we should take a different view. Size, speed, and a presumptive Péclet number around one permit calculating a diffusion coefficient, which comes to $1·25 \times 10^{-10}$ m^2 s^{-1}. That corresponds to a non-ionized molecule with a molecular weight of about 6000. Thus the system appears convection-dominated for proteins and other macromolecules and diffusion dominated for dissolved gases, amino acids, sugars, and the like.

(iii) *Sinking speeds of phytoplankton*

Diatoms plus some other kinds of small algae account for nearly all the photosynthetic activity of open oceans.

Paradoxically for light-dependent organisms, most of the time most of these phytoplankters are negatively buoyant. Not that they sink rapidly; 4 μm s^{-1} (a foot a day, in the antediluvian units used where I live) is typical. According to one commonly cited view, that sinking improves access to carbon dioxide by minimizing the depletion around a cell caused by its own photosynthetic activity. In effect, the cell walks away from its personal environmental degradation. Still better, it walks away with no cost of locomotion. Of course it (or its progeny) may eventually suffer, as the sinking brings it down to depths at which net photosynthesis cannot be achieved. Somehow (and wave-induced water mixing comes into the picture) the cost-benefit analysis favours this slight negative buoyancy.

Calculating a Péclet number casts serious doubt on this view, doubt first raised (with an equivalent argument) by Munk and Riley (1952). For a diatom about 10 μm in diameter, that sinking rate of 4 μm s^{-1}, and the diffusion coefficient of CO_2, 14×10^{-10} m^2 s^{-1}, we get a value of 0·03. Diffusion, in short, rules; convection, here due to sinking, will not significantly improve access to carbon dioxide. We might have chosen a slightly larger distance over which CO_2 had to be transported to be available at adequate concentration, but even if a distance ten times longer were chosen, the conclusion would not be altered.

Why, then, should a phytoplankter sink at all? The calculation tacitly assumed uniform concentration of dissolved gas except where affected by the organism's activity, so it might be seeking regions of greater concentration, lowering sinking rate wherever life went better. In a world mixed by the action of waves that seems unlikely, even if (as appears the case) buoyancy does vary with the physiological state of a cell. Perhaps phytoplankters bias their buoyancy toward sinking so they are not likely to rise in the water column and get trapped by surface tension at the surface. If perfect neutrality can not be assured, then sinking may be preferable, as long as the speed of sinking can be kept quite low. Surface tension may be a minor matter for us, but it looms large for the small. In the millimeter to centimeter range a creature can walk on it – the Bond number, the ratio of gravitational force to surface tension force is low. Below that a creature may not be able to get loose once gripped by it – the Weber number, the ratio of inertial force to surface tension force drops too far (Vogel 1994). But that argument presumes that diatoms have hydrophobic surfaces, which, I am told, may not be the case. So another hypothesis would be handy.

(iv) *Swimming by microorganisms and growing roots*

More often we think of movement by active swimming than by passive sinking. Some years ago, the physicist Edward Purcell (1977) wrote a stimulating essay about the physical world of the small and the slow, looking in particular at bacteria. Among other things, he asked whether swimming, by, say, *Escherichia coli*, would improve access to nutrients. By his calculation, a bacterium one μm long, swimming at 20 μm s^{-1} (see Berg 1993), would only negligibly increase its food supply, assumed to be sugar. To augment its supply by a mere 10%, it would have to go fully 700 μm s^{-1}. Purcell's answer to why swim at all turned on the heterogeneity of ordinary environments and the advantage of seeking the bacterial equivalent of greener pastures, as suggested above for diatoms. Otherwise the bacterium resembles a cow that eats the surrounding grass and then finds it most efficient to stand and wait for the grass to grow again.

The Péclet number permits us to cast the issue in more general terms. Sucrose has a diffusion coefficient of $5·2 \times 10^{-10}$ m^2 s^{-1}; together with the data above we get a Péclet number of about 0·04. Swimming, as Purcell found, should make no significant difference. But the conclusion should not be general for microorganisms. Consider a ciliated protozoan, say *Tetrahymena*, which is 40 μm long and can swim at 450 μm s^{-1}. If oxygen access is at issue, the Péclet number comes to 10, indicating that swimming helps a lot. Indeed it might just be going unnecessarily fast, prompting the thought that getting enough of some larger molecule might underlie its frantic pace. Or it might swim for yet another reason.

Growing roots provide a case as counterintuitive as the result for swimming bacteria but in just the opposite direction (Kim *et al* 1999). A root can affect nutrient uptake by altering local soil pH. Root elongation speed runs around 0·5 μm s^{-1}, slower than the most sluggish tortoise. But it turns out to constitute a significant velocity, enough so that (at least in sandy soil) the Péclet number gets well above one. Values for the rapidly diffusing H$^+$ ions for typical growing roots may exceed 30, using root diameter as length. That means motion affects the pH distribution in the so-called rhizosphere more than does diffusion.

(v) *Flow over sessile organisms*

For sinking diatoms and swimming microorganisms we evaluated hypotheses about why creatures did what they did. In some loosely analogous situations we can test claims about their physical situations, in particular about flows. How fast must air or water flow over an organism to affect exchange processes significantly? To put the matter in sharper terms, can the Péclet number help us evaluate a claim that extremely slow flow matters? After all, neither producing nor measuring very low speed flows is the most commonplace of experimental procedures.

For instance, consider the claim that a flow of 0·2 to 0·3 mm s^{-1}, around a meter per hour, significantly increases

photosynthesis in an aquatic dicot, *Ranunculus pseudo-fluitans* (Westlake 1977). The finely dissected, almost filamentous leaves are about 0·5 mm across. Inserting the diffusion coefficient of CO_2 gives a Péclet number around 100, which certainly gives credibility to the report. One guesses that even slower flows should be significant.

Another paper (Schumacher and Whitford 1965) reports that a flow of 10 mm s^{-1} significantly increases photosynthesis in a green alga, *Spirogyra*, made up of filaments about 50 μm in diameter. A Péclet number of about 300 provides emphatic support, again suggesting that far slower flows should also matter. Conversely, it prompts one to ask whether so-called still water, the control in such comparisons, was still enough so flow was truly negligible. My own experience suggests that thermal convection and persistence of filling currents can complicate attempts to prevent water from flowing – still water does not just happen.

A third paper (Booth and Feder 1991) looked at the influence of water flow on the partial pressure of oxygen at the skin of a salamander, *Desmognathus*. It found that currents as low as 5 mm s^{-1} increased that partial pressure, facilitating cutaneous respiration. With a diameter of 20 mm, that flow produces a Péclet number of 50,000. A sessile *Desmognathus* may need flow, but it does not need much. Again, the quality of any still-water control becomes important.

(vi) *Two functions for gills*

Most swimming animals use gills to extract oxygen from the surrounding water. Whatever their particulars, gills have lots of surface areas relative to their sizes. Many aquatic animals suspension feed, extracting tiny edible particles from the surrounding water. Whatever their particulars, such suspension feeding structures have lots of surface areas relative to their sizes. While most suspension-feeding appendages look nothing like gills, some not only look like gills but share both name and functions. No easy argument implies that such dual function gills should balance those two functions. Quick calculations of Péclet number can tell us which function dominates their design and help us to distinguish respiratory gills from dual-function gills.

Consider a limpet, *Diodora aspera*, a gastropod that uses its gills for respiration. With gill filaments about 10 μm apart, a flow rate of 0·3 mm s^{-1} (J Voltzow, personal communication), and the diffusion coefficient for oxygen, the Péclet number comes to about 2. A bivalve mollusk, the mussel *Mytilus edulis*, with dual function gills presents a sharp contrast. The effective distance here is about 200 μm and the speed about 2 mm s^{-1} (Nielsen *et al* 1993). That gives a Péclet number around 100 for oxygen access.

Clearly the system pumps far more water than necessary were respiration the design-limiting function.

One can do analogous calculations for fish, where a few kinds use gills for suspension feeding as well as respiration. A typical teleost fish has sieving units 20 μm apart (Stevens and Lightfoot 1986) with a flow between their lamellae of about 1 mm s^{-1} (calculated from data of Hughes 1966). For oxygen transport, the resulting Péclet number is 5·5, not an unreasonable value for an oxygenating organ. One gets quite a different result for a fish that uses its gills for suspension feeding. A somewhat higher 80 μm separates adjacent filtering elements. but the main difference is in flow speeds. These run around 0·15 m s^{-1} for passive ("ram") ventilators (Cheer *et al* 2001), and 0·55 m s^{-1} for pumped ventilators (Sanderson *et al* 1991). The resulting Péclet numbers, 6,500 and 20,000 (again using oxygen diffusion) exceed anything reasonable for a respiratory organ.

(vii) *Air movement and stomatal exchange*

All of the previous examples involve diffusion and convection in liquids. The same reasoning ought to apply to gaseous systems as well – fluids are fluids, and diffusion and convection occur in all.

Leaves lose, or "transpire," water as vapour diffuses out though their stomata and disperses in the external air. Transpiration rates depend on a host of variables, among them wind speed and stomatal aperture, the latter under physiological control. Immediately adjacent to a leaf's surface, the process depends, as does any diffusive process, on concentration gradient, from the saturated air at the stomata to whatever might be the environmental humidity. The stronger the wind, the steeper the concentration gradient as the so-called boundary layer gets thinner.

Consider a bit of leaf 20 mm downstream from the leaf's edge, with downstream indicating the local wind direction. And assume a wind about as low as air appears to move for appreciable lengths of time, as a guess, 0·1 m s^{-1}. The effective thickness of the velocity gradient outward from the leaf's surface can be calculated (Vogel 1994) as

$$d = 3 \cdot 5 \sqrt{\frac{x\boldsymbol{m}}{v\boldsymbol{r}}} \quad , \tag{4}$$

where x is the distance downstream, and $\boldsymbol{m}$ and $\boldsymbol{r}$ are the air's viscosity and density, respectively, 18×10^{-6} Pa s and 1·2 kg m^{-3}. The thickness comes to 6 mm. (This must be regarded as a very crude approximation; among other things, the formula assumes a thickness that is much less than the distance downstream.) With that thickness, that wind speed, and the diffusion coefficient of water vapour in air, $0 \cdot 24 \times 10^{-4}$ m^2 s^{-1}, the Péclet number is 25. So even

that low speed suffices to produce a convection-dominated system.

What might that tell us? It implies, for one thing, that changes in wind speed should have little or no direct effect on water loss by transpiration. If water loss does vary with wind speed, one should look for something other than a direct physical effect, something such as changes in stomatal aperture. For another thing, it implies that a leaf in nature would not have adjacent to its surface very much of a layer of higher-than-ambient humidity. So-called "vapour caps" are not likely to mean much with even the most minimal of environmental winds.

(viii) *The sizes of morphogenetic fields and synaptic clefts*

A variant of the Péclet number may give some insight into such things as the development of animals. Much of pattern formation depends on the diffusion of substances, morphogens, whose concentration gradients establish embryonic fields. Establishing larger fields not only means lower gradients (or higher concentrations of morphogens) but would take more time, a non-negligible resource in a competitive world. Breaking up velocity into length over time we get:

$$\frac{l^2}{Dt} \, . \tag{5}$$

(The reciprocal of this expression is sometimes called the mass transfer Fourier number.)

To get a situation in which diffusion is not relied on excessively, we might assume a value of one. A typical morphogen has a molecular weight of 1000; its diffusion coefficient when moving through cells (a little lower than in water) ought to be around 1×10^{-10} m^2 s^{-1}. A reasonable time for embryonic processes should be a few hours, say 10^4 s. The numbers and the equation imply embryonic fields of around 1 mm, about what one does indeed find. The argument for the size of embryonic fields (put somewhat differently) was first made by Crick (1970).

In effect, the calculation produces what we might consider a characteristic time for a diffusive process. Consider ordinary synaptic transmission in a nervous system. The most common transmitter substance, acetylcholine, has a molecular weight of 146 and a diffusion coefficient around 7×10^{-10} m^2 s^{-1}. With a 20 nm synaptic cleft, the corresponding time comes to 0·6 ms. That value is at most slightly below most cited values for overall synaptic delay, which run between about 0·5 and 2·0 ms, implying that much or most of the delay can be attributed to transmitter diffusion.

Where else might calculations of Péclet numbers provide useful insight? We have not considered, for instance, olfactory systems, either aerial or aquatic. Are the dimensions and flow speeds appropriate in general; are they appropriate for the specific kinds of molecules of interest to particular animals? What of the speeds and distances of movement of auxins and other plant hormones? Might we learn anything from comparing systems in which oxygen diffuses within a moving gas with ones in which it diffuses in a flowing liquid, systems such as, on the one hand, the tubular lungs of birds and the pumped tracheal pipes of insects and, on the other, the gills of fish, crustaceans, and the like?

In fields such as fluid mechanics and chemical engineering, dimensionless numbers pervade have amply proven their utility. I argue here, as I did on a previous occasion (Vogel 1998) that they can help us see the relevance of physical phenomena to biological systems. Péclet number may be an especially underappreciated one, but (as I hope to illustrate in further pieces) far from the only one worth our consideration.

Who, incidentally, was this person Péclet? One does not normally name a number after oneself. Someone may propose a dimensionless index and then the next person who finds it useful names it after the first. Or the first to use one may name it for some notable scientist who worked in the same general area. Péclet number is a case of the latter. Jean Claude Eugène Péclet (1793–1857) was part of the flowering of French science just after the revolution. He was a student of the physical chemists (as we would now call them) Gay-Lussac and Dulong – names yet remembered for their laws – and a teacher of physical science. He did noteworthy experimental work on thermal problems and wrote an influential book, *Treatise on Heat and its Applications to Crafts and Industries* (Paris 1829).

Putting his name on a dimensionless number was done a century later, by Heinrich Gröber, in 1921, in another important book, *Fundamental Laws of Heat Conduction and Heat Transfer*. That thermal version of the Péclet number antedates the mass-transfer version used here. The latter, as far as I can determine, first appears in a paper on flow and diffusion through packed solid particles, by Bernard and Wilhelm, in 1950. They note its similarity to the dimensionless number used in heat-transfer work and call their version a "modified Peclet group, symbolized Pe' ". They shift, confusingly and deplorably, from an acute accent in "Péclet" to a prime ('), now usually omitted, at the end. Analogous indices for thermal and material processes is not unusual, but ordinarily the two carry different names – such as Prandtl number and (as earlier) Schmidt number. Amusingly, most sources mention one of the versions of the Péclet number with no acknowledgement that there is any other.

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