Series

Living in a physical world
X.
Pumping fluids through conduits

STEVEN VOGEL
Department of Biology, Duke University, Durham, NC 27708-0338, USA
(Fax, 919-660-7293; Email, svogel@duke.edu)

1. Introduction

The first of these essays argued that, because diffusion is ineffective over all but minute distances, an organism larger than a typical cell must move fluid to move material (Vogel 2004). By whatever name, internal bulk fluid movement absorbs energy, if nothing else as a consequence of that universal fluid property, viscosity. Supplying that energy requires provision of some manner of pump. Such a pump may also accelerate fluid or lift it against gravity, but neither of these rise to quite the same level of inevitabi-lity. Not that pumping must incur metabolic cost – sometimes an external agency can be co-opted to do the requisite work.

The diversity of circumstances under which organisms pump fluids, the phylogenetic diversity of the organisms, and the structural diversity of the pumps themselves all militate against treating biological pumps as a single class of functional devices. Separate books, or at least separate chapters, deal with the ascent of sap in a tree, the suction of blood by a mosquito, and the suspension feeding of a clam. Here I want to explore generalizations that might emerge from considering pumps in all of that functional, phylogenetic and structural diversity.

As well, pumps have been ubiquitous components of human technology since the first fields were irrigated with water that gravity alone could not supply, that is, since water was first hoisted from lake, river, or well. A remarkably wide range of simply-constructed yet effective devices remain in use where industrial products have yet to reach agrarian cultures. Among our machines, only electric motors may exceed them in range of sizes, applications, and designs. Engineers, designing pumps for diverse applications, have worried about variation in operating conditions, efficiency, and other parameters. In analysing and classifying nature's pumps, we biologists thus come late to the game, and we ought to take full advantage of all that earlier attention.

[In part, this essay extends the general reasoning of a predecessor (Vogel 1995), one that a reviewer of its manuscript rightly noted did not turn out quite as satisfactorily as the author had hoped. I will, of course, have to reiterate some of the points of that paper.]

2. The relevant variables

An insect, most famously an ant, can lift many times its own body weight – but it cannot lift it far. Similarly, a tree can draw sap upwards with pressures of tens of atmospheres, millions of pascals – but it does so very slowly. We may be overly impressed by the spectacularly high forces and pressures that organisms can produce and insufficiently mindful of constraints on distances and volume flows. Processes such as lifting weights or forcing fluids through pipes involve three variables, and these may operate in a wide range of combinations. Force, distance, and power define a lifting task, with power just the product of force and rate of change of distance. Similarly, pressure, volume flow, and power define the task of a pump, with the last again the product of the first two. A bivalve mollusk can pump its own volume of water in, across its gills, and out again every few seconds, but it does so against only a few pascals of pressure – a volume flow no less impressive than the pressure generated by a sap-lifting tree.

A particular graphic representation of pump performance has enjoyed long usage in engineering and is shown, without specific data, in figure 1. With only a slight modification (incorporated here, as will be noted shortly) it should work as well for biological pumps, even if we usually cannot

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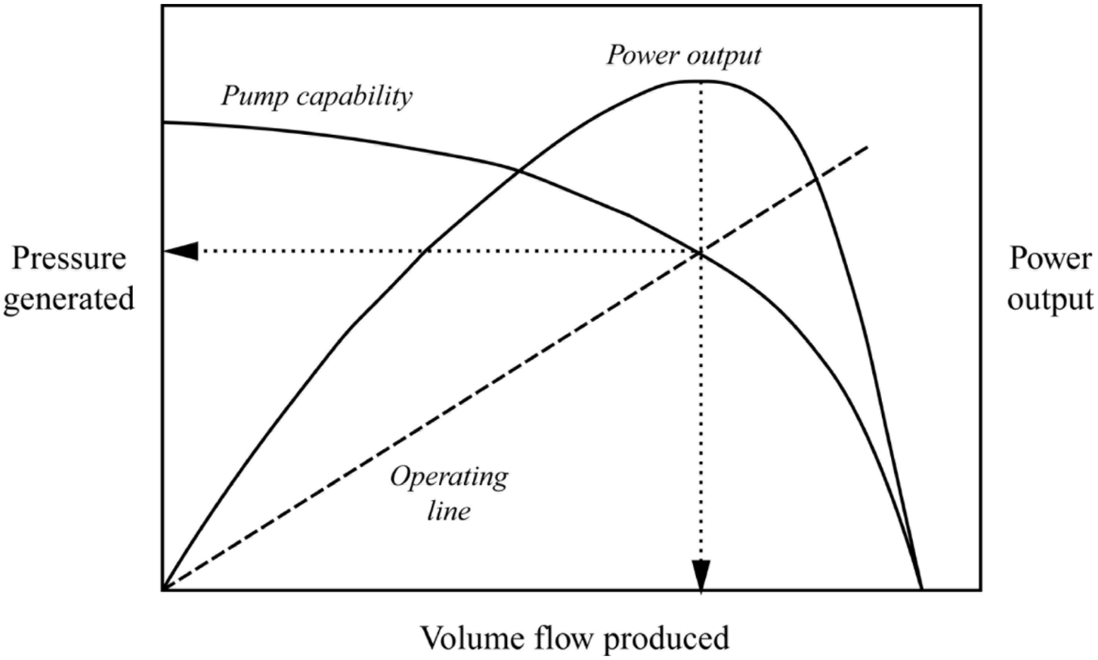

Figure 1. A pump performance graph. Most pumps yield plots similar to this one; they differ mainly in the scaling of the axes. The axis-to-axis outer curve ("pump capability") marks the limits of the pump under any operating condition. The dashed line corresponds to the operating condition set by the particular load imposed on this pump, while the dotted lines give the pressure and volume flow maxima for that particular load. This example shows an optimally efficient combination of pump and application–the intersection of operating and pump capability lines lies just beneath the point of maximum power output.

measure pump performance quite as far from normal operating conditions and must extrapolate to get the end points of their basic operating lines.

The maximum pressures most pumps can produce occur under conditions of zero volume flow, while their maximal volume flows happen when the opposing pressure or pressure they produce is zero. So a curved line from one axis to the other, the "pump capability" line, along with the axes themselves, defines a potential area of operation – possible combinations of pressure (Δp) and volume flow (Q). In a actual application, operating conditions are constrained by the resistance of the load, defined by how much volume flow corresponded to each value of pumping pressure. For most technological pumps, the pressure needed varies with the square of the volume flow it has to produce. Thus the "operating line" forms a parabolic curve extending upward from the origin. For virtually all biological pumps, Δp will vary almost directly with Q, so the line from the origin will be straight rather than parabolic. In either case, the intersection of this operating line with the pump capability line marks the maximum output of the particular pump in a particular application.

Size underlies that difference between technological and biological pumps. For the relatively small sizes and low speeds of the latter, most flows will be laminar. Thus the Hagen-Poiseuille equation or something analogous applies; it defines a resistance ($\Delta p/Q$) that is ohmically constant over the range of pressures and flows.

The power (P) a pump puts out equals the product of its volume flow and the pressure increase of the fluid passing through it – $Q\Delta p$. In practice, the graph indicates power on a second ordinate. Its curve begins and ends at the abscissa since zero values of either pressure increase or volume flow mean zero power output.

For an ideal match of pump to task, the peak of the power output curve should lie just above (or below, since the ordinates have different scales) the point of intersection of the operating line and the pump capability line. The graph thus gives a valuable view of that coupling. If peak power output occurs well to the left of the intersection, the pump is one designed more as a pressure producer and less as a volume impeller than would be best. Its peak power output will not be reached, wherever on the operating line it works. If, conversely, peak power output occurs to the right of that intersection, the pump produces too much volume flow and too little pressure; again its maximum power output will not be realized. This second mismatch can have a particularly serious consequence if, as when lifting from a well or from ground to top of tree, producing any useful output demands some minimum (here gravitationally-determined) pressure – that is, a pressure threshold must be exceeded to get any flow.

In short, specifying the power output of a pump, even power output plus energy conversion efficiency, may not indicate whether a particular pump will give proper service when harnessed to a particular task. Pumps vary widely in the mixes of pressures and volume flows they can produce – in the specific shapes and positions of their operating lines. While all graphs of the kind shown in figure 1 may look similar, the scales on their axes will be anything but.

3. A functional classification of pumps

The literature on pumps for technological uses (for instance, Karassik *et al* 2000) recognizes two general categories, with diverse implementations of each. Only a few devices fail to fit comfortably into one class or the other. (The specific names of each, though, differ somewhat from source to source, leading to occasional awkwardness for on-line searching or using indices.) A few words about the devices in each category might stimulate recognition of biological equivalents beyond ones long obvious.

Those in one category are most often called "displacement" or "positive displacement" pumps. In many of these, fluid is drawn into a chamber and then persuaded (as by reducing the chamber's size) to leave by a different route. Most familiar are ones with pistons that move back and forth in chambers, plus valves to ensure unidirectional, if pulsatile, flow – for instance the ones with which we hand-inflate pneumatic tires. A less common version, diaphragm pumps, change chamber volume with periodic pushes against a flexible element that forms one of the chamber's walls; it exchanges the problem of a closely fitted piston for that of a non-rigid element. Other displacement pumps work by translocating the functional chamber itself. In the commonest versions – gear, screw, vane and lobe pumps – multiple moving components carry fluid along as they themselves move. In another displacement pump, the so-called air-lift (or gas-lift) pump, bubbles of gas rising through a narrow vertical tube of liquid carry liquid upward in the moving chambers of liquid formed between each pair of bubbles. Similar to these latter two types, and of especial biological relevance, is the peristaltic pump, with its traveling constrictions of flexible tubes. It eliminates contact between fluid and pump housing and tolerates flows of variable viscosity and fluids with suspended solids. But the technological versions perform inefficiently and are not particularly reliable, so they have remained uncommon. The flows produced by displacement pumps range from nearly steady to severely pulsatile unless paired with some external buffer.

Those in the other category are called "dynamic," "fluid dynamic" or "rotodynamic" pumps, with this last name recognizing their ordinarily rotational operation. All depend on fluid dynamics rather than fluid statics. The commonest types drive fluids with axial or centrifugal fans; most familiar are ones driving air with either propellers or squirrel-cage blowers. Another type is the jet pump, in which one liquid is squirted into a channel or duct of another liquid through a jetting orifice or "eductor." While typically lower in efficiency than are rotary pumps, jet pumps need no moving solid parts. The vacuum pumps that we attach to tap water outlets are the most familiar examples. Related to jet pumps are other devices in which one flow induces another – old-fashioned carburetors drew in gasoline this way, and a variety of buildings, old and new, achieve ventilation by using ambient wind to draw air through themselves.

The present focus on the distinction between the two categories grows out of one particular generalization. Displacement pumps work best at higher operating pressures than do dynamic pumps – and, of course, vice versa. No sharp value of pressure marks the transition, though, with the simplicity of displacement pumps making them preferable for some low-pressure applications and the smooth operation of dynamic pumps lying behind their use, often with multiple stages, to produce fairly high pressures. Precisely this same distinction applies to the pumps found in organisms. Despite the imperfect dichotomization, the mechanical and operational distinctions between the categories help us understand the particular distribution of pump types we observe in nature. Thus the distinction provides an analytic and functional categorization nicely complementary to our traditional phylogenetic viewpoint.

We will begin with a brief look at the way past and present agrarian societies pump water, taking their simple devices as illustrative of pump types, before dealing with the greater complexity and diversity of biological pumps. In engineering textbooks, fluid statics precedes fluid dynamics because of its (at least superficially) relative simplicity. Similarly, displacement pumps have preceded dynamic pumps in adoption by humans, and they remain more common among less industrialized technologies. Still, they have long been a diverse lot. One gets a good view of the different types in recent and present use from the collection of pictures collected by Thorkild Schiφler and posted on the website of the Experimentarium, of Hellerup, Denmark (*www.experimentarium.dk/uk/naturvidenskab_og_teknik/schiolers/*); additional material can be downloaded from *www.timsmills.info/URL-S/Animal%20Powered%20Systems.pdf*.

Devices immediately recognizable as displacement pumps range from simple buckets and scoops to more complex pot chains, dragon-bone chains, swinging canoes (dhoons), shadufs, saquiyas (or saqias, etc.), and hoists (delous). One that, unusual for displacement pumps, avoids pulsatile or intermittent operation is the Archimedean screw (figure 2), a helical screw either turning in a tube or fixed within a cylindrical housing that turns. A Roman fresco at

Pompeii shows an Archimedean screw pump operated as a treadmill by a person on the outside; in modern versions the operator typically turns a crank at one end. (Cranks, at least in Europe, are medieval and later). The shallow incline of the tube allows pockets of water to form; turning then raises the pockets. They still find occasional and even large-scale use at air-water interfaces – if fully submerged, pockets do not form, so they then become inefficient viscosity-dependent dynamic pumps.

The only fluid dynamic pump apparently at all common in preindustrial societies is the noria (figure 2), and it relies on displacement as well as dynamics. A flowing stream turns an undershot waterwheel (the dynamic part); water-holders attached to the periphery of the same wheel fill from the same stream and raise water to an elevated spillway (the displacement part). As we will see – and one reason to start with old human technology – nature seems to face the same (or at least an analogous) difficulty in devising

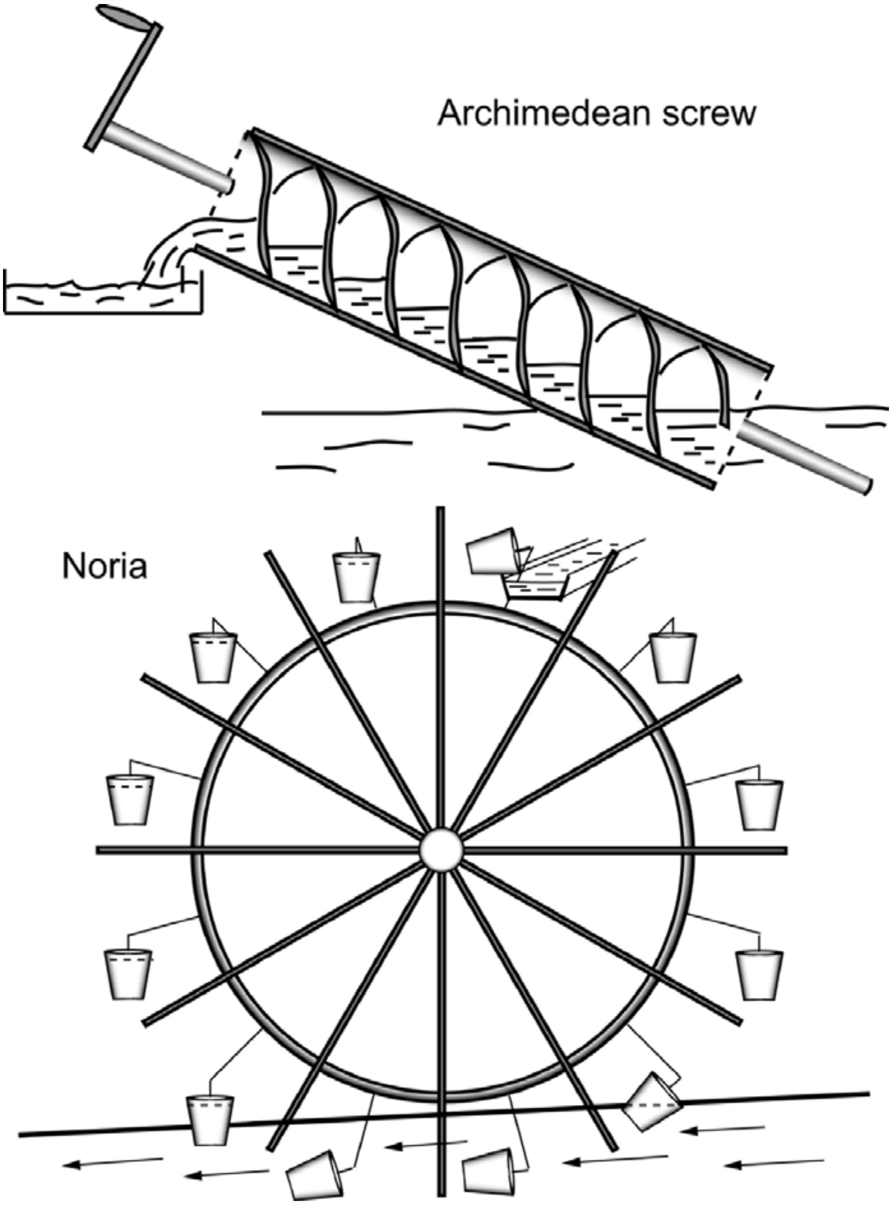

Figure 2. Two ancient devices for lifting water, an Archimedean screw and a noria; both are at least in part dynamic pumps. We still use a large-scale, modern version of the Archimedean screw for some low-lift, high volume applications. But the noria has become anachronistic, most directly replaced by the hydraulic ram, which became practical in the 19th century with the advent of inexpensive metallic components of decent precision.

dynamic pumps. Indeed, judging from our technological versions, nature may face an additional obstacle. All but a few dynamic pumps (such as jet pumps) employ rotating elements – hence the common name “rotodynamic.” Such continuously rotating wheel-and-axle devices, of course, do not occur in eucaryotic organisms.

In looking at the pumps organisms employ, we will limit our purview to those that move liquids, that is, water plus aqueous solutions and suspensions. As a less obvious circumscription, we will for the most part exclude devices where the objective is movement of pumper rather than pumped – despite the artificiality of a line between, say, paddle-based locomotion and paddle pumps.

4. Living displacement pumps

The displacement pumps of organisms range from ones with close technological analogs to others that, although not fundamentally novel, have limited appeal for humans – either we have more attractive alternatives or they work in ways awkward for our materials, machines, and applications.

(i) *Valve-and-chamber pumps*: A single chamber whose volume can be changed, together with a pair of valves, satisfies the minimal requirements for such a pump. Our hearts, paradigmatic examples, have four chambers and six valves and operate as a pair of pumps, each with a two-stage pressure booster. Additional valve-and-chamber pumps return both blood from the veins of our legs and lymph from our tissues to our hearts – routine contractions of our skeletal muscles squeeze the chambers, these no more than the lengths of vessel between adjacent valves.

Valve-and-chamber hearts are widespread among the metazoa, particularly among vertebrates and mollusks. The requisite machinery demands only ordinary additions – just valves and muscle – to a flexible tubular element. Even single chambers can produce pressures of over 20,000 Pa, as do the left ventricles of tall mammals. The lymph hearts of fishes, amphibians and reptiles consist of contractile vessels with valves (Prosser 1973, Ottaviani and Tazzi 1977), and so do the lateral hearts of the giant earthworm, *Glossoscolex* (Johansen and Martin 1965). Some insect hearts may also operate as valve-and-chamber hearts (Jones 1977). Nor do all such pumps occur in circulatory systems. Valves on the inputs to the mantle chambers of jet-propelled cephalopods together with self-valving output funnels amount to the same kind of chamber-plus-paired-valves. Jetting scallops use their mantles as valves in an analogous manner. Similarly, the mouth, oral and branchial chambers, and opercula of fishes that pump water over their gills operate in this fashion (Lauder 1980).

(ii) *Valveless chamber and piston pumps:* Where pumps need produce only single pulses of fluid or reciprocating flows, valves become superfluous. That happens in many systems and appears in so many guises that the underlying commonality can easily escape notice. Our urethral pumps (see Glemain *et al* 1990) work this way. Most jet propulsors, from those of jellyfish (DeMont and Gosline 1988) to the anal jets of dragonfly nymphs, are valveless chamber pumps. Anal jets can produce both single jet pulses (Hughes 1958) and repetitive respiratory flows (Pickard and Mill 1974), with the same equipment serving both functions. Similarly, most injectors make use of valveless chambers, including the venom injectors and squirters of rattlesnakes and cobras (Kardong and Lavin-Murcio 1993, Young *et al* 2003, 2004), of the toxic snail, *Conus*, (Schulz *et al* 2004), and of spiders (Yigit *et al* 2004). So does the branchial chamber of jetting fishes, another system that can alternatively serve for respiration (Brainerd *et al* 1997).

And valveless chambers underlie most suckers, including both blood- and nectar-sucking insects (Kingsolver and Daniel 1995). Even aphids, which can use the considerable hydrostatic pressures of plant phloem to drive fluids in through their stylets, retain the capacity to generate suction in this way (Kingsolver and Daniel 1995). Most often sucking chambers depend on expansion tied to the elastic recoil of some muscularly-stressed material. The pressures sucking insects produce can be well below ambient, even, in the bug *Rhodnius*, subzero (Bennet-Clark 1963).

Less common than valveless chambers are piston pumps, perhaps because the physical arrangement represents something unusual in nature – however ordinary it might be in human technology. Several kinds of infaunal marine worms have been described as irrigating their burrows by acting as piston pumps, in particular the clam worm *Nereis,* and the parchment worm *Chaetopterus*. In both cases that may oversimplify the well-coordinated movements of appendages as well as body walls (Riisgård and Larsen 1995).

(iii) *Valveless moving chamber (peristaltic) pumps:* These typically produce pressures lower than the preceding two types, and they are likely to be lower in energetic efficiency; like them they should be easy to evolve from a basic muscle-enclosed tube. Our intestines and our esophagi, of course, depend on peristalsis, as do the hearts of most annelids, holothurians (sea cucumbers) and arthropods (Martin 1974). Burrow irrigation in *Nereis*, noted above, seems to involve some peristaltic body wall movement as well as piston action. Inasmuch as earthworms locomote in an essentially peristaltic mode, we might expect similar peristaltic pumping among burrow-dwelling aquatic oligochaete as well as polychaete annelids.

Besides their undoubted ease of evolution, peristaltic pumps have functional advantages. Pumping liquids of high viscosity or with a lot of suspended solids presents no great problem. Peristaltic action provides mixing as well as lateral transport, offsetting the laminarity of low-speed flows in small pipes. That should be of some consequence (as in intestines) where absorption or exchange across pipe walls accompanies lengthwise transport – if not in, say, ureters. And pumping direction can be reversed with nothing more than a minor shift in neuromuscular coordination. Both intestines and esophagi can go either way. Cud-chewing bovids routinely reverse their esophageal pumping, and insect hearts often switch directions (Jones 1977).

(iv) *Osmotic pumps:* These uniquely (but not necessarily) biological devices operate not by decreasing the size of a compartment but by increasing the volume of what the compartment must contain. Organisms rarely engage in active transport of water; instead they move ions or small molecules, with water following by passive osmosis. Thus the driving force for osmotic pumps comes indirectly from such transport or else from local increase in osmotic strength as a result of dimer, oligomer, or polymer hydrolysis.

Most osmotic pumps are small; indeed these are the predominant pumps that drive bulk fluid flow in unicellular systems. They may move low volumes, but they can develop high pressures, fortuitously complementary with the peculiar ability of small systems to resist great pressure differences. A mere molar difference in solute concentration (assuming a non-electrolyte) across a membrane produces about 2.2 MPa of pressure. To cite a specific case, the fungus *Gibberella* (Trail *et al* 2005), about which more below, produces a peak pressure of about 1.5 MPa. Nonetheless, these pumps suffer from several drawbacks. For one thing, they act at surfaces, so scaling up three-dimensionally takes a disproportionate increase in surface area, either with folds or villi or by proliferation of the basic units. For another, pumping ordinarily consumes the osmolyte, not as fuel, but by simple dilution – a water-pump that works by hydrolyzing starch into osmotically active mono- or disaccharide will find that those products have been diluted and then carried away in the flow it produces. So resynthesis may require more than mere metabolic reversal. While countercurrent or other such devices may help, the basic problem cannot be entirely evaded.

Osmotic pumps figure in at least two of the schemes for throwing fungal projectiles that were described in the third essay (Vogel 2005), those of *Pilobolus* and *Gibberella*. In both, osmotic engines power hydraulic ejection both by providing hyphae with liquid and by stretching their elastic walls; *Gibberella* does so by transporting potassium, with chloride coming along as counterion. Another osmotically charged hydraulic engine closes the Venus flytrap (Forterre *et al* 2005). One can point as well to the excretory organs of animals, varying from partially osmotic to fully osmotic ones such as the aglomerular kidneys of some marine teleost fishes. (Our own kidneys capitalize on arterial blood pressure and thus on our hearts to drive their initial glomerular ultrafilter.)

The protonephridia of some acoelomate invertebrates, the best known being the flame cells of planaria, are a peculiar case – or perhaps one should say possible case. Ducts opening to the exterior remove excess water, as required by these fresh-water creatures. Presumably water transport follows some osmolyte secretion that gets reabsorbed. One wonders about the role of the one cilium (in solenocytes) or the tuft of cilia (in flame cells) at the blind ends of these ducts (Schmidt-Nielsen 1997). Osmotic pumps work at high pressures and low flow rates, while ciliary pumps, as fluid dynamic devices, do best when called on for the opposite service. I have seen no suggestion about what good – perhaps a bit of stirring – one or a few cilia can do under such circumstances. Our own renal tubules may have cilia, but no analogy can be drawn. Ours lack central microtubules and cannot propel fluid; instead they appear to work in the opposite mode, as generators, more specifically as flow sensors (Yokoyama 2004).

Osmotic pumps play major parts in two large-scale fluid transport systems, although in both instances the details of their mechanisms have yet to be fully elucidated. If you cut the top off a well-watered herbaceous plant, sap oozes out from specific places, the xylem elements, on the cut surface. Water is absorbed from the soil and then pumped up the stem by so-called root pressure. Herbaceous stems may provide the obvious expression of the phenomenon, but it occurs in some large, woody plants as well. Pickard (2003a, b) provides a good view of the present knowns and unknowns surrounding root pressure.

While flow in xylem depends mainly on evaporative pull from the top, osmotic pumping seems mainly responsible for driving flow in the complementary tissue, phloem. Again, the details have given trouble. The classic Munch hypothesis from the 1930s invokes osmotic forces, and that they play some role has not been contentious. But once again the details still confuse us; here one encounters a daunting diversity of structures, flow pathways, and chemistry. A look at, for instance, van Bel (1993) or Thompson and Holbrook (2003) will give some sense of the problems involved.

An osmotic pump should be designed to get as much passive water movement for a given amount of osmolyte transport as possible. That underlies a feature common among such pumps. Instead of secreting osmolyte into some large external (or extracellular) spaces, they discharge it into restricted areas, isolated to some extent from those larger volumes. Thus its concentration is (and, for a time remains) higher. Depending on the system, osmolyte may be ultimately lost downstream or actively reabsorbed for reuse. The loops of Henle of mammalian kidneys play a particularly fancy version of this game, with a countercurrent multiplier isolating a region of high osmolarity. The basic arrangement seems to have been first recognized by Curran (1960) in rat intestines and by Curran and MacIntosh (1962) as a general phenomenon. It was later demonstrated in the water-ejecting invaginations of gall bladder cells by Diamond and Bossert (1967), who gave it the nicely descriptive name, "standing gradient osmotic flow." As noted by Tyree and Zimmermann (2002) (and at least tacitly by Nobel 2005), in higher plants such standing gradient osmotic devices serve crucial roles in generating root pressure and in loading and propelling flow in phloem.

(v) *Evaporative pumps:* In one sense evaporative pumps work in the opposite manner from osmotic pumps. Instead of generating positive pressure by transport of osmolytes and wate into a compartment, they generate negative pressure by removing liquid from a compartment. Like osmotic pumping, evaporative pumping requires no macroscopic moving machinery, preadapting it for use by plants. Osmotic pumping depends on differentially permeable membranes, biologically ubiquitous; evaporative pumping requires an air-water interface, limiting its applications to terrestrial or semiterrestrial organisms. So evaporative pumps should be less widely distributed. They should be limited, as well, by a peculiar asymmetry between positive and negative pressures. At least in physical models, pressures can be increased without intrinsic limit, while pressures cannot easily be decreased much below zero. Thus one might expect pressure drops to be limited to whatever amounts offset ambient pressures. Another possible constraint is that evaporation must occur across a surface that can, at the same time, tolerate the pressure difference that the pump generates.

Despite both evident and possible limitations, evaporative pumping probably moves more liquid through organisms than do all other macroscopic pumps combined. It does, one might say, the heavy lifting in drawing water from soil and raising it to the photosynthetic structures of terrestrial plants, which in some sense pay with such water loss to obtain rare and precious atmospheric CO_2. These plants manage to evade the zero pressure limit, not trivially but monumentally, generating tensions in water as low as – 120 atmospheres (12 MPa), far below zero. They manage to create interfaces that withstand such pressure differences without either collapsing or restricting evaporation; they do so by taking advantage of the fine-scale cellulose meshwork of their cell walls and the high surface tension of water in contact with air. The seventh essay (Vogel 2006) described this remarkable scheme; let me just note here that the evaporative pumps of terrestrial plants generate the most extreme pressures of any biological pumps, and that such pumps are rare elsewhere in either natural or human technology.

5. Nature's dynamic pumps

For these perhaps we should retain the additionally qualified name one sometimes sees, *fluid dynamic pumps*, since another group of biological pumps depends on the dynamics of solid materials. Compared to the analogous devices in our technology, the fluid dynamic pumps of organisms appear both less diverse and more distant in appearance. That greater distance emerges from two basic differences between the two technologies – not only nature's inability to make macroscopic rotational machinery, but also our lack of anything much like cilia or ciliated and thus wall-pumping tubes.

(i) *Drag-based paddles:* In our quest for efficient propulsion, propellers, which move blades normal to flow, have largely replaced paddles, which move them parallel to flow. One must go back to the noria to find a fluid dynamic pump based on the drag of broad blades in flow. Similarly, nature makes only limited use of pumps based on paddling. Foster-Smith (1978) recognized such a pump in the amphipod crustacean, *Corophium volutator*, which burrows in mud and propels water by beating its pleopods. I suspect that members of the infaunal shrimp genera *Upogebia* and *Callianassa* do likewise. But they could do so only occasionally, since they normally live in blind pockets branching off their U-shaped burrows, and since they seem to depend on flow induced by asymmetry of the burrow apertures. Foster-Smith found that *Corophium* could achieve pressures only about 4% as high as those made by the piston pumpers *Nereis* and *Arenicola*, although for its size it could drive considerably greater volume flows.

(ii) *Lift-based propellers:* My search for liquid-propelling pumps, *sensu strictu*, that use propellers has come up nearly dry. Some fishes do ventilate egg masses by tail beating while stationary, but I found no specific performance data. In air, at least, one can point to the hive-ventilation system used by honeybees. One or a series of honeybees beat their wings while standing just beyond the entrance to their hive. Hertel (1966) points out that a line of bees constitutes a multi-stage axial compressor analogous to that used in the jet engines of aircraft; one should be aware that the photograph he provides has been inappropriately retouched. Southwick and Moritz (1987) claim that hives "breathe" as the bees alternately pump it out and allow it to inhale elastically. The present discussion of pumps suggests otherwise – even a line of bees should form a high-volume, low-pressure pump, and beehives do not feel as if they have the required low elastic modulus and high resiliency.

(iii) *Ciliated surfaces and chambers:* By contrast with both the previous fluid dynamic pumps, these abound in nature. Muscle must be persuaded to move fluid with some form of transducing equipment; cilia do so as their basic *modus operandi*. Cilia may be far slower in operation than muscle, but a collecting manifold with a decreasing aggregate cross-sectional area can raise the output velocity of a ciliary or flagellar pump. For instance, with their flagellar pumps, sponges eject water at about 0.2 m s^{-1}, a far higher speed than any flagellum can generate directly. Ciliary pumps find wide use for low pressure, high volume applications such as suspension feeding.

But they have several drawbacks. Cilia are microscopic and work at that scale. So scaling up a pipe with ciliated walls encounters the problem of a pumped cross section that increases faster than the pumping circumference. In addition, the cilia-lined pipe cannot have the gently parabolic velocity gradient of a remotely pumped pipe. The entire gradient from the mandatory zero speed at the wall to the peak speed of the pipe cannot span as much as the length of a cilium, so it becomes severe even at modest maximum flow speeds. Since viscous energy loss depends on the steepness of that velocity gradient, ciliary pumping suffers from an intrinsically low efficiency in all but the narrowest pipes and channels. Still, for surfaces across which organisms exchange material or heat, that steep velocity gradient can be advantageous. Thus ciliated surfaces serve admirably for organs such as gills – as on the gills of most gastropod mollusks, where they pump water for respiration, and on those of bivalve mollusks, where they play a central role in suspension feeding (Vogel 2004).

One wonders whether this inauspicious scaling explains their absence on the gills of fish and whether the gills of aquatic arthropods would find them useful were motile cilia known to that phylum. Less puzzling is their absence as pumps in our capillaries. Velocity presents no problem, since blood in our capillaries flows at speeds that cilia can produce. But effective operation is precluded by the relatively high resistances of circulatory systems – the steep slopes of lines from the origin on graphs such as that of figure 1 – together with the low positions of ciliary pump capability lines on the *y*- or pressure axes. We might wish for circulatory systems in which well-disseminated ciliated capillaries make our fallible hearts unnecessary. But the low pressure-generating capability of ciliary pumps rules them out, at least where blood volumes remain under 10% of body volumes, as in both vertebrates and cephalopods. (LaBarbera and Vogel 1982 failed to consider the need to match pump performance to system resistance and mistakenly attributed the choice between ciliary and muscular pumping solely to ancestry.) For the same reason, and as noted earlier, one suspects that pumping cannot be the primary function of the cilia of flame cells and solenocytes.

(iv) *Capillary (surface-tension) pumps:* Inasmuch as it lifts water against gravity, the capillary rise of water in a narrow hydrophilic tube constitutes a proper pump. As does evaporative pumping, such surface-tension pumping works only with an air-water interface; so, similarly, it lies solely in the domain of terrestrial and semi-aquatic organisms. Even with a considerably greater range of cases than evaporative pumping, its role remains by comparison a modest one.

From time to time one runs across statements (by non-biologists) asserting that sap rises in trees as a result of capillarity – simply by the ascent of an aqueous fluid in a hydrophilic tube. That cannot be the case, as repeatedly pointed out (see, for instance, Nobel 2005), because the conduits are just too wide. The capillary rise of water in a circular vertical tube, *h*, is

$$h = \frac{2\gamma\cos\theta}{\rho g r}, \tag{1}$$

where γ is its surface tension, 0.073 N m^{-1}; ρ is its density, 1000 kg m^{-3}; θ is the contact angle (0° for perfect wetting); g is gravitational acceleration; and r is tube radius. Even under ideal circumstances, water will rise only 1.5 m in a small tracheid, one 20 μm in diameter. In a xylem vessel of 200 μm, as in an oak, the rise will be ten times less. Even with perfect wetting, sustaining a 50 m column of water by capillarity would require a tube less than 0.6 μm across.

Capillarity does matter in a few cases, for the most part situations involving narrow tubes of no great length. Rehydration of dry stems and leaves of the resurrection plant *Myrothamnus* depends on it, but conduit diameters are of the order of 2 μm (Schneider *et al* 2000, Tyree 2001). Some insects, most notably orchid bees, draw in nectar through their probosci at least in part by capillarity (Kingsolver and Daniel 1995, Borrell 2003). At least two kinds of birds use the mechanism, hummingbirds to draw in nectar (Kingsolver and Daniel 1983) and phalaropes to raise small quantities of water with edible plankton up a vertical bill whose tip has been dipped in a body of water (Rubega and Obst 1993).

Capillarity, in the guise of wicking, can move liquid upward on the outside of sufficiently wettable surfaces. A few cases have been described, not surprisingly, in amphibians. Lungless plethodontid salamanders (at least the genus *Desmognathus*) breathe through wet skin and can stay wet by wicking water upward as well as by exuding body water through their exceptionally permeable skin (Lillywhite 2006). Toads (genus *Bufo*), which lack skin mucus, can stay moist by wicking as well (Licht and Lillywhite 1974).

(iv) *Flow inducers:* These may be more common in nature than in modern human technology. While our jet pumps have little in the way of immediate natural analogs, nature capitalizes on both the elevated pressure of oncoming flows and the reduced pressure due to flow over an orifice opening normal to flow. The low pressures they produce impose the main limitation on flow inducing pumps. Pressure cannot deviate either upward or downward from ambient by significantly more than the dynamic pressure difference, Δp, defined by Bernoulli's principle,

$$\Delta p = \frac{\rho v^2}{2}, \tag{2}$$

where v is the speed of flow. (For small-scale and thus low Reynolds number flows, pressures will be still lower.) A fish swimming steadily at 0.5 m s^{-1} can generate only about 125 Pa, or 1/800th atm. A suspension-feeder working at 0.1 m s^{-1} has available a mere 5 Pa, or 1/20,000th atm. Still, a baleen whale swimming with open mouth at 3 m s^{-1} can take advantage of a more substantial 4500 Pa, or 1/22nd atm. I gave considerable space to flow inducing schemes earlier (Vogel 1994) and will do little more than mention representative cases here.

Ram ventilation in fishes is the best-known case of pressure elevation at an orifice facing into a flow. Its use varies fish to fish, with a trivial role for it in some, a role only at high swimming speeds (where respiratory needs are greatest, of course) in others, and a total dependence on it in some large, fast fish that consequently must either swim or asphyxiate (Steffensen 1985). Analogous pumps with upstream-facing inputs drive the suspension feeding systems of some ascidians and caddisfly larvae; they probably drive fluid through the olfactory passages of many fish as well.

Still lower pressures are available for drawing fluid out of an elevated orifice. The arrangement, though, finds use by keyhole limpets and abalones to draw water across their gills for respiration, by some sand dollars to draw food-laden water from underlying sediments up past their oral surfaces and through their slots, and perhaps by the shrimp genera mentioned earlier to irrigate their U-shaped burrows. Sponges take advantage of both elevated pressures on their upstream facing (and indirectly on their other) ostia and the reduced pressures at the oscula through which they discharge water.

(v) *Temperature gradient pumps:* Flows can be induced in several ways by spatial variations in temperature. Some of these were noted in essay 4 (Vogel 2005b); most such pumps move air rather than water. Free convection, the most obvious, drives the internal circulation of some giant African termite mounds (Turner 2000) as well as providing some cooling currents around sunlit trees during periods of unusually low wind. Evaporative pumps, especially sap lifters, were considered earlier as displacement devices. A related arrangement, evaporation in one place and condensation in another – as in heat pipes – might better be regarded as a dynamic pump. But at this point its use by organisms is no more than a suspicion. Finally (and more clearly dynamic) is Marangoni pumping, flow driven by surface tension gradients that follow temperature gradients – again, it remains something to be kept in mind as a distinct possibility for organisms. All of these pumps develop very low pressures.

6. An index for pump performance

Figure 3 gathers data for pressure boost and volume flow for 53 pumps, 37 displacement and 16 dynamic. They were chosen for their diversity in function and the range of values of the two variables they represented; they include sap lifters, hearts, blood suckers, jets, projectile ejectors, gill irrigators, and suspension feeders. The graph appears to confirm the generalization that in nature as in human technology displacement pumps for the most part work at higher pressures and dynamic pumps at lower pressures; a *t*-test of the data gives a significance level for that distinction of about $P = 0.05$. The data support considerably less well the notion that displacement pumps work at lower volume flows, either by inspection of the graph or by another *t*-test.

Can we contrive a single parameter that encapsulates our picture of how biological pumps sort out? One might calculate a ratio of the two variables, $\Delta p/Q$, for each of the pumps on the graph – or for any others. But, like the data for volume flow, the distinction between our two general pump types fails statistical test by a clear margin ($P > 0.2$), even though the mean $\Delta p/Q$ of the displacement pumps comes out higher than that of the dynamic pumps. On that score alone, the ratio has little if any value for biological pumps. One suspects trouble from the huge size range of these pumps together with the intrinsic size- and speed-sensitivity of the ratio. Thus dimensional manipulation of the ratio gives $\rho v/S$, where S is conduit cross section. Assuming consistent density, faster flowing systems will be biased higher values, while larger systems tend toward lower values. A dimensionless ratio might be more informative, assuming one can be found with unambiguously defined and easily determined variables.

One possible ratio is the pressure coefficient, C_p, long used in fluid mechanics to describe pressure distributions around bodies in flow. It divides pressure by dynamic pressure, the pressure that would be generated were the moving fluid to be suddenly halted, as described by Bernoulli's principle. Specifically,

$$C_p = \frac{2\Delta p}{\rho v^2}, \tag{3}$$

in effect a dimensionless form of eq (2). v represents the highest speed in the system, most often at the output of the pump. Pressure change appears, as we would like, in the numerator, while flow speed stands in for volume flow in the denominator.

In practice, though, the pressure coefficient does almost as poor a job sorting out pump types as a pressure-volume flow ratio. Applying it to the 39 of the previous 53 pumps for which I found adequate data yields a distinctly odd ranking. For instance, both the lymph hearts of toads and our own lymphatic vessels, which we mainly pump with our skeletal muscles, have values up with the xylem of trees, a bias attributable to their very low speeds. And the sporangium of the fungus, *Pilobolus*, an osmotic engine, gives the lowest value of all; its very high speed overcompensates

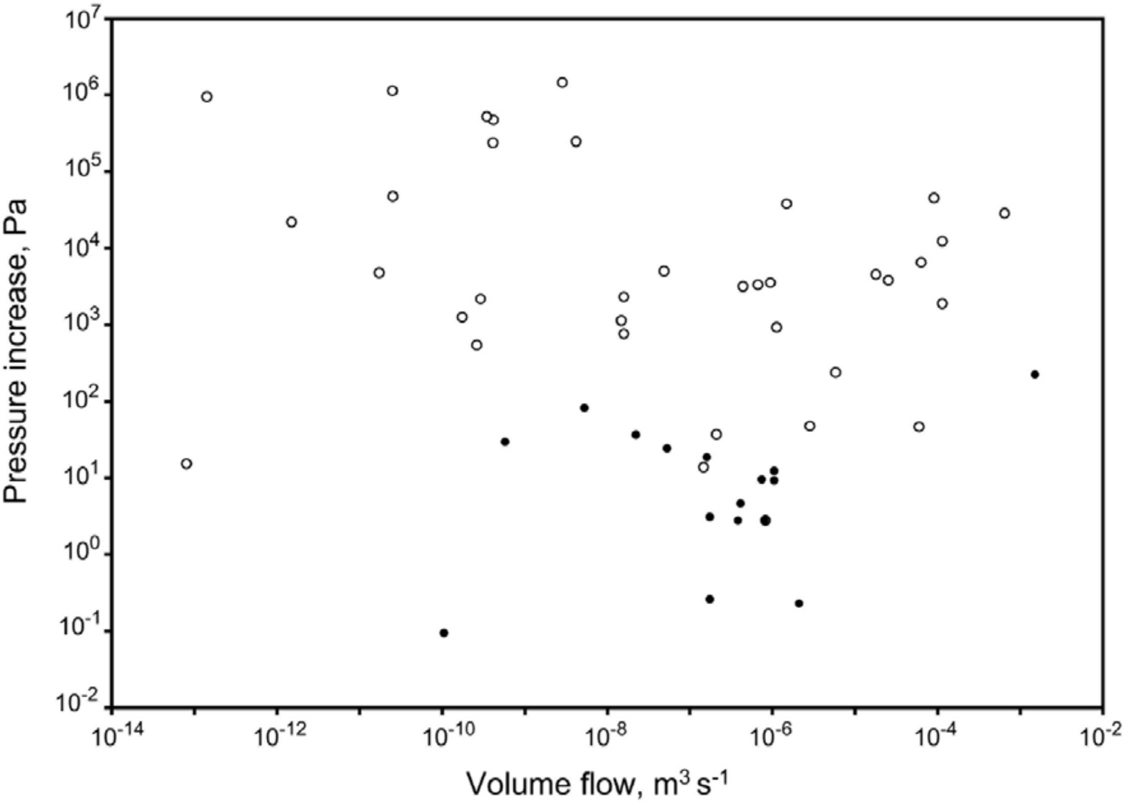

Figure 3. Pressure produced versus the resulting volume flow for a collection of different pumps; all of those described in figure 4 are included, as well as some additional examples (of the same general types) for which I found no data for either radius or flow speed.

for its substantial pressure. At least the ratio puts the very high pressure, low flow xylem of pine, oak, and the vine *Entadopsis* near the top. Its oddities most likely result from the tacit presumption in the formula of flow at high Reynolds numbers – relatively large, fast, and turbulent – rather than at biologically appropriate low Reynolds numbers and laminar flows. (And so one might add a t for "turbulent" and designate this pressure coefficient C_{pt}.) Put another way, its denominator reflects an inertial energy loss rather than a more relevant viscous loss.

In my earlier look at pumps (Vogel 1995) the coefficient was for just this reason replaced by one that presumed viscous rather than inertial pressure loss,

$$I = \frac{\Delta pt}{\mu}, \tag{4}$$

where t is time and μ is viscosity. Density has deferred to viscosity, as usually happens in low-Reynolds-number formulas. Among a set of pumps more limited than the present one, xylem and hearts came out at the top, as we think they should. But two displacement pumps produced the lowest indices, the jet of the jellyfish *Polyorchis* and the blood sucker of the bug *Rhodnius*. This last generates the greatest pressure difference known in any animal. The index has a practical problem as well, the interpretation of t, a kind of length-less inverse velocity. Without great conviction, I took it as the transit time for a bit of fluid to pass the part of the system with the greatest resistance. Not only does it take more guesswork than one would prefer but it cannot escape ambiguity for the tapering pipes so common among organisms.

A dozen years later, I offer an alternative dimensionless ratio. This one divides the pressure force, pressure times cross section, by viscous resistive force. The latter, the product of viscosity, flow speed, and vessel radius, comes either from Stokes's law for the drag of a sphere or from an equation (eq 13.17 in Vogel 1994) for the pressure drop of flow through a circular orifice. We might call it the "pressure coefficient for laminar flow" to draw an analogy with the well-established (turbulent) pressure coefficient of eq (3). Specifically,

$$C_{pl} = \frac{\Delta pr}{\mu v}, \tag{5}$$

To get the ratio from the most appropriate source, the Hagen-Poiseuille equation for laminar flow through a circular pipe, one has to assume an isometry in which pipe length can be replaced by pipe radius. As we'll see, that assumption occasionally generates peculiar values, and it must be borne in mind when drawing inferences from values of the ratio.

Figure 4 gives values for the 39 pumps previously mentioned, 30 displacement and 9 dynamic. What can we make of these numbers?

While the overall range of values varies 2.5-million-fold, functionally homogeneous groups cluster satisfyingly. The xylem pumps, the jets, and the blood suckers each span ranges of about 10-fold, while the hearts (including both

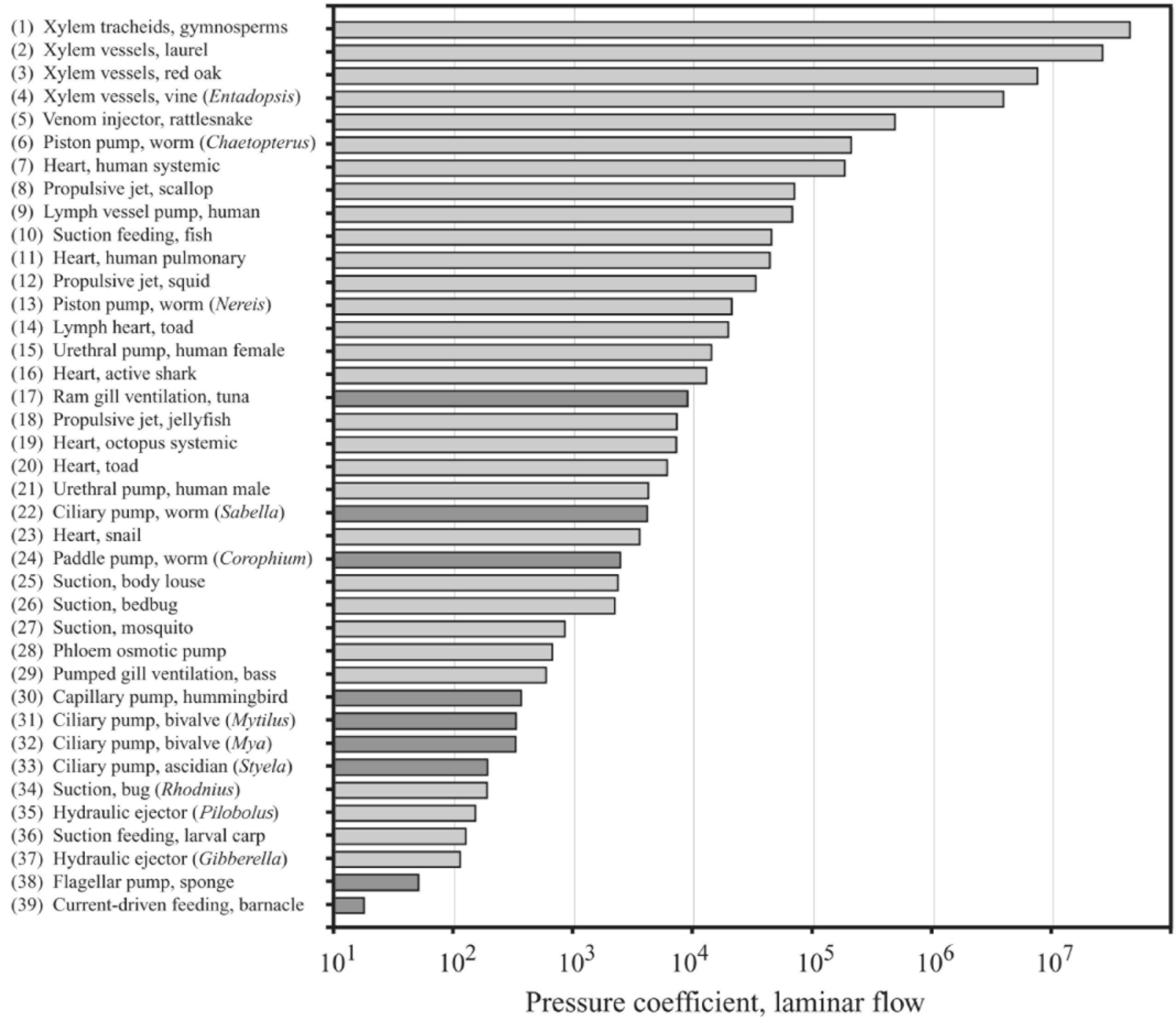

Figure 4. Values of an index of pump performance, a pressure coefficient that applies to laminar flows. Darker bars mark the dynamic pumps. [Sources: (1) Cermák *et al* 1992, Pittermann and Sperry 2003, (2) Cermák *et al* 1992, (3) Kramer 1959, Zimmermann 1971, (4) Fichtner and Schulze 1990, (5) Kardong and Levin-Murcio 1993, Young *et al* 2003, (6, 13, 22, 31, 32, 33) Riisgård and Larson 1995, (7, 11) textbook values, (8) Cheng *et al* 1996, (9) Milnor 1990, (10) Alexander 1969, (12) Shadwick 1994, (14) Müller 1833, Jones *et al* 1992, (15, 21) Glemain *et al* 1990, (16) Lai *et al* 1990, (17) Stevens and Lightfoot 1986, (18) DeMont and Gosline 1988, (19) Wells 1987, Agnisola 1990, (20) Gibbons and Shadwick 1991, (23) Jones 1983, (24) Foster-Smith 1978, (25, 26, 27) Daniel and Kingsolver 1983, (28) Nobel 2005, (29) Lauder 1984, (30) Kingsolver and Daniel 1983, (34) Bennet-Clark 1963, (35) Vogel 2005a, (36) Drost *et al* 1988, (37) Trail *et al* 2005, (38) Bidder 1923, Vogel 1978, (39) Trager *et al* 2000.]

single and dual-stage pumps) vary less than 50-fold. Ciliary and flagellar pumps vary about 6.6-fold, with the flagellar one of a sponge not unexpectedly the lowest. Thus the ratio provides expectations for pumps not yet analyzed – it appears to have predictive value.

The evaporative pumps of xylem come out at the top, with the highest value for the narrower tracheids of gymnosperms – they generate comparable pressures but get less flow from them than the wider vessels of broad-leafed trees. A vine, with (as is typical) the widest vessels, gives the lowest value in the group. r may be larger than for other vessels, but v increases by a greater factor.

Flows over the gills of fish span a wider range, 360-fold, but the distribution of cases within that range looks quite reasonable. Suction feeding, with its necessity for rapid, impulsive flow, yields the highest value. The ram-ventilating tuna also has a high ratio, the highest for any dynamic pump. But it swims exceptionally fast, and so has access to the greatest driving pressure. We also note a low value for pumped gill ventilation, whose respiratory function demands continuous, low cost flow, and suspect that the low value preadapts the system to take advantage of ram ventilation during faster swimming.

Two dynamic pumps, both of suspension-feeders, give values that look anomalously high, the paddle pump of the amphipod *Corophium* and the ciliary pump of the polychaete *Sabella*. But we may be miscategorizing the infaunal *Corophium* as a dynamic pump. Since the paddles operate within its tube they make what is more like a set of moving compartments, as in the human-powered "dragon-bone" pumps in China that move water from one rice paddy to another – and less like the serial paddles on say, a rowed trireme or galley. *Sabella*'s ratio may draw attention to the limitation of the ratio alluded to earlier. It erects a fan of ciliated tentacles normal to flow, in effect a huge number of ciliary pumps operating in parallel. That parallel array may not increase pressure at all or velocity all that much, but it makes use of the radius of the entire array, as done here, at least questionable. Using the distance between individual ciliated elements reduces the value down to the level of the other ciliary pumps, those of two bivalves and an ascidian. I have not altered either the categorization of *Corophium* or the value for *Sabella*, in part to preserve them as illustrative examples and in part to avoid such conscience-troubling *post hoc* adjustments.

A look at refilling in a sea anemone points up the predictive value of the ratio. When disturbed, *Metridium* can contract its body wall musculature and collapse down to form an inconspicuous flat blob, largely by expelling almost all the water in its central gastrovascular cavity through its mouth (Batham and Pantin 1950). It then slowly reinflates, according to textbook accounts, by pumping water back in through ciliated tubes, the siphonoglyphs, while it keeps its mouth closed. Batham and Pantin (1950) measured reinflation pressures around 25 Pa. Using the dimensions of their animals and an estimate (from various sources and personal observations) of an hour for the process, I calculate a pressure coefficient for laminar flow of 1.0×10^5. The value lies between those of our systemic hearts and of the jets of scallops, about 250 times higher than even the exceptionally high value for the ciliary pump of *Sabella*. Perhaps the usual accounts incorrectly assume that pumping by the ciliated tube does most of the work. One need not look far for another player. The viscoelasticity of the body wall of *Metridium* has about the right elastic modulus and temporal behavior for the task, judging from the measurements of Alexander (1969), Gosline (1971) and Koehl (1977).

Several final notes on this measure of pump performance. Notice that the ratio contains the product of pressure and radius. Since for a given material the tolerable pressure varies inversely with the radius of the pipe, this nicely offsets any scaling relationship that relationship might impose. The ratio does less well in correcting for the effects of collecting or expanding manifolds – constricting a flow will increase its speed, both lowering the numerator and raising the denominator.

Unexpectedly, perhaps, whether or not the pumping activity is sustained makes little difference. Venom injection by rattlesnakes and spore ejection by fungi are the quickest of mechanical processes, but their widely different values span almost the entire range of long-acting pumps. And while some blood suckers (like *Rhodnius* and lice) remain painlessly attached to their hosts for long periods, others (like mosquitoes) get the job done quickly lest they be swatted; nonetheless, their ratios differ little. Such indifferences suggest that efficiency, energy and power play, at most, secondary roles in determining the match of pump type to application. That parallels what I noted for the scaling of ballistics, where force (there in the guise of stress) appeared more critical than work or efficiency (Vogel 2005a).

7. Yet another kind of pump

A brief comment earlier noted the imperfection of the dichotomy between displacement and dynamic pumps in human technology. We saw a case of that same imperfection in nature's pumps when categorizing the pump of an amphipod, which used paddles, ordinarily dynamic, to form moving compartments, as in some displacement pumps. Using the two categories to distinguish among the pumps of organisms may run into a more general difficulty, the exclusion of other categories of devices. Perhaps we should bear in mind that biomechanics usually recognizes functional devices in nature by their similarities to devices in human technology. Clearly not everything in our technology devices has a natural equivalent. Less obviously, devices in nature may lack technological analogs – less obviously because that lack makes them easier to overlook.

One of the differences between the two technologies is their relative reliances on rigid versus flexible structural materials. Thus we speak of artifacts that change shape under load as "deformed" – a word whose pejorative sense reflects our preference for rigidity. Think back – only two of the technological pumps mentioned make significant use of flexible materials. Peristaltic pumps squeeze tubing; while inefficient, they avoid possible contamination of fluid with pump parts. Diaphragm pumps pulse a (periodically replaced) rubber or neoprene membrane to change the volume of a compartment; they have some advantage when, as in sewage systems, pumping slurries of suspended solids. But in nature, flexibility appears to be the default condition, with rigid materials used only where functionally mandatory. Can we recognize ones other than peristaltic pumps that depend on flexible materials?

When visiting the laboratory of Mory Gharib a few years ago, I was shown a more refined version of the device pictured in figure 5, one in which a very flexible element completes a circuit of otherwise inflexible conduits. Repeatedly compressing the flexible tubing near one of its ends produces an impressively strong unidirectional flow with the aid of neither check-valves nor peristalsis. Thus this valveless pump can be run in either direction, depending on where the flexible tubing is compressed. How it works seems clear enough – compressing the tube forces fluid in both directions, but one responds by expansion of the flexible tubing rather than by sending the fluid on through the rest of the circuit. Crude models tolerate a wide range of sizes, tube flexibilities, and circuit resistances.

The hearts of ascidians may work the same way as do these models. These hearts have long been known to reverse periodically, which they do by changing the end at which a pacemaker triggers constriction (Martin 1974). They seem not to work by reversible peristalsis but to depend on some other direction-determining arrangement. By cardiac standards, ascidian hearts produce only modest pressures, about 300 Pa in a large one (Goddard 1972), implying only modest resistance levels in their circulations. While insect hearts, also valveless low-pressure devices, commonly reverse, they have usually been described as peristaltic (Sláma 2003). Still, given the great diversity of the arthropods, this kind of valve-less, non-peristaltic, reversing pump might well occur somewhere among them.

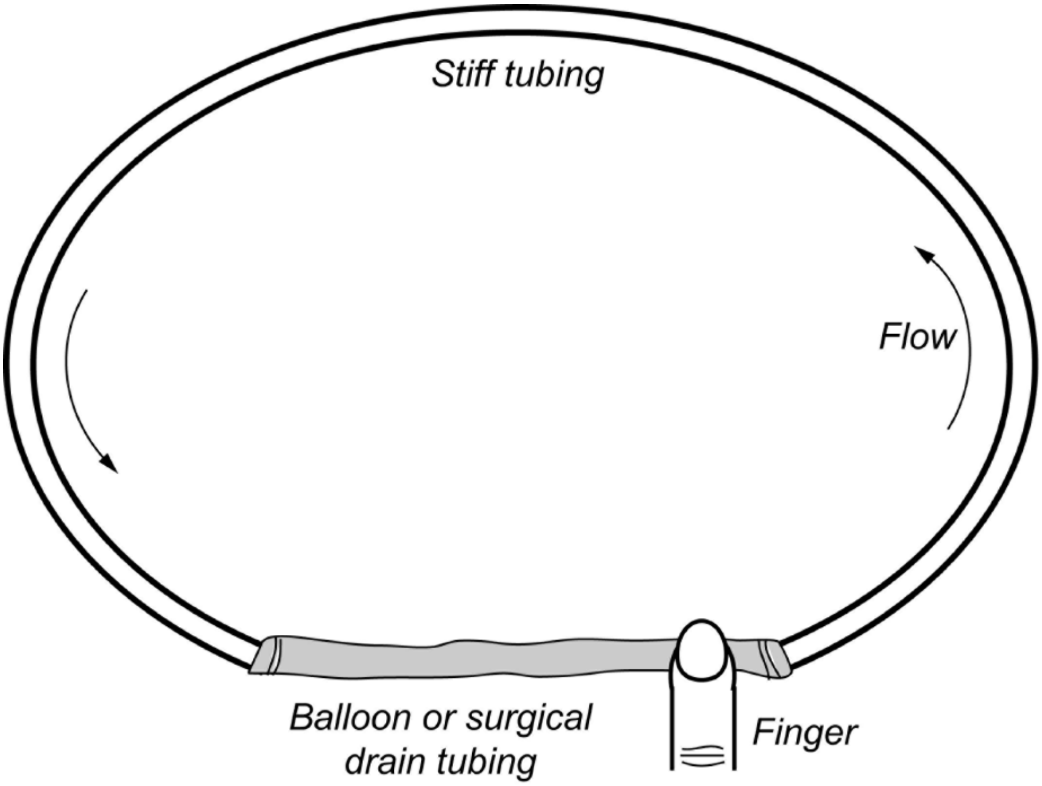

Figure 5. Perhaps the simplest possible solid dynamic liquid pump. Pressing repeatedly near the right end of the flexible tube, as here, drives the fluid counterclockwise around the circuit–as one can see with either a few trapped bubbles or some suspended matter. The pump tolerates addition of a substantial resistive element in the stiff tubing, and even a very crude one can generate 2500 Pa.

Forouhar *et al* (2006) have recently described something analogous to this valveless pump, one also not likely to be limited to a small group of organisms. As they point out, an embryonic vertebrate heart begins pumping well before it develops valves. Working with zebrafish embryos, they showed that such a tubular heart need not depend on peristalsis. Instead, they propose that pumping results from the suction generated by propagation of an elastic wave in the wall of the heart.

Perhaps we should entertain the idea that a third general category of pumps occurs among organisms, one that might be called "solid-dynamic pumps," together with explicit use of the qualifier "fluid" for the dynamic pumps described in earlier sections here. Such solid-dynamic pumps would likely be associated with quite specific tunings of the multi-dimensional properties of flexible biological materials. We vertebrates and cephalopods certainly come close to using such a pump as we buffer the radical pressure fluctuations of our hearts with flexible arterial walls whose stress-strain curves match the requirements set by our various blood pressures.

8. Perspectives and speculations

Two final items. First, what we see here are curious and varied combinations of functional and phylogenetic constraints. Higher plants must do with pumps that need no moving, macroscopic solid parts, which largely limits their options to evaporative and osmotic pumps. Both such displacement pumps can generate impressively high pressures but neither does well when volume flow is the measure. Induction by external flows remains an option, but in terrestrial systems it will move air rather than water. A few kinds of animals such as sponges can make no macroscopic pumping machinery either, but at least cilia and flagella give them reasonable low-pressure, high-flow options. Arthropods know nothing of motile cilia, relying mainly on the movements of rake-like appendages for suspension feeding and on peristaltic and hydraulic pumping for internal bulk transport. Yes, the pumps of nature appear well-chosen for their assigned tasks, but, no, no creature has anything approaching a free choice from a comprehensive catalog.

Second, whether analysing locomotion, photosynthesis or foraging, we biologists have given considerable attention to energetic efficiency as an index of performance. This essay, for instance, implied early on that a maximal product of pressure generated and volume moved per unit time, power output, marked a pump as well matched to its task. Most often, energetic efficiency can be unambiguously defined, and it accords well with prejudices from our physics courses, the physical devices in our lives, and our fuel bills.

But I am skeptical about whether efficiency provides a unique or even a particularly good comparative measure of devices of such disparate function as the pumps that move aqueous liquids through organisms. For one thing, all too often quantity of water moved may not adequately represent useful output. A suspension feeder may prefer to move less water if by doing so it can increase the fraction of edible material it extracts. Similarly the cost relative to oxygen extracted by a gill may be minimized at a different flow rate than one that minimizes cost relative to the volume of water pumped.

For another, pressure ordinarily represents what we might call an unavoidable evil. It may be something with which a system finds itself stuck from first principles, as with the gravitational loss of sap ascent. Or it may reflect some trade-off, with as circulatory vessel size versus the effectiveness of transmural diffusive exchange, or blood volume versus speed of flow. Only in hydraulic systems such as the fungal projectile ejectors does pressure matter as much as flow.

Finally, for many pumps metabolic cost must be the least immediate of considerations – what fraction of its overall output does a rattlesnake devote to squirting venom? Should a mosquito suck more slowly to minimize the cost of getting its dinner? We might assert (admitting the rare exception) that energetic efficiency will matter, if at all, for pumps that operate steadily rather than for those that give an occasional pulse.

Nor, for that matter, need pumping incur any metabolic cost at all. Somewhat paradoxically, the only initial construction and maintenance impose any cost on both the highest and the lowest pressure pumps – solar energy powers the evaporative pump that lifts sap while the energy of fluid moving with respect to a surface powers both ram ventilation and the variously-employed current-induced flows.

In short, a look at pumps may inject some valuable doubt about whether we can find in the living world a straightforward measure of utility comparable to power or energy in mechanical technology, information in telecommunications and computing, or money in economics.

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Mory Gharib started me thinking about valveless peristaltic hearts, Ron Grunwald brought up capillarity on the skin of plethodontid salamanders, Fred Nijhout straightened me out on insect hearts, Tim Pedley pointed out the insufficiency of my first index for pump performance, Amy Zanne headed me in the right direction on flow in the xylem of trees, and Melvin Tyree drew my attention to the diversity of instances of standing gradient osmotic flows

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