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Form and Function in Organisms[1]

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SYNOPSIS. While form and function are always together in organisms, the studies of morphology and physiology often take place in different places by different people. In the 20th century some zoologists have re-united the two into a point of view called "functional morpholgy." The concepts a student should know in order to set about a study in functional morphology include: (1) the scales of size and time, (2) structural hierarchy, (3) permission and constraint of function, (4) properties as descriptors of structure and function, (5) analogy and homology. The structural phenomena that a student will see in any organism include: (1) pattern, especially polarity and symmetry, (2) dimensions that signify the size scale, (3) heterogeneity, which includes the concepts: (4) composite materials and (5) anisotropy resulting from the preferred orientation of fibers and crystals. Rather than being a discipline, functional morphology is the combination of structural and physiological thinking that invites other points of view, especially those of development and evolution, to be added.

Structure without function is a corpse; function without structure is a ghost (Vogel and Wainwright, 1969).

In the real world that we all study—the living organism—form and function are never separate. No form exists other than as a result of function. No form exists without a function, and no function exists without a formal cause and context.

Our minds separate form and function as an analytical exercise: in our reductionist world, we take things apart to see how they work. Our written and spoken explanations are linear, and it is convenient to treat one component at a time. Perhaps too often we leave the parts lying around to gather dust or get lost like the parts of a clock we took apart, intending to fix and reassemble it. Our final understanding of organisms must be as wholes that are components of the evolving biosphere. Form and function of organisms can only be rejoined in our minds by the application of effort, skill, and a good notion of the intact organism. If this is so, then students might want to learn how to perform analyses of form and function. I will address my remarks to learners—by which I mean students and teachers.

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To begin, I will offer some definitions. Form is shape. It is the external surface of a body. It is part of a larger category, the structure which is the form and the substructure of the body. Substructure (often refered to as structure) is the list of components, their geometric description, their connections, and their angular array in three dimensions. These definitions tell us that structure can be observed by eye, and its dimensions can be measured with a meter stick or its derivative. Structure is studied by observation.

Morphology is derived from Greek roots and refers to the study of form. Since the major way we learn about things in nature is through our eye-and-mind, we might also say that morphology is the creation of structural images. This is useful because it focuses on the abstractions our minds make as we study things. What we see through a microscope are images created by the optical refraction, dispersion, and reassembly of the light entering the microscope: we do *not* see the specimen on the slide. As scientists, we create prose, poetry, and graphic or 3-dimensional images of structure and function from the information our senses and minds select from their exposure to the specimen. Structure and function that we report in journals and books are, after all, abstractions, hypotheses, models, paradigms, conceits, and images. Each of these treats one or a few aspects of structure. As such, each tells us what is drawing our attention. A central concern for all students of functional morphology is "What are we paying attention to?" This necessarily puts the equally important question "What are we ignoring?" into bright relief. This pair of questions is important for all branches of science—and for the humanities, the arts, and engineering.

Function is changing structure (Picken, 1960). It follows physical laws of gravity, motion, diffusion, optics, and electromagnetism. It requires us to perceive and measure time (duration, rate). Most biochemical and physiological studies of a *function* seek to reveal its mechanism. Function is studied by experimentation. In an experiment, one observes a structure, perturbs the system, and then observes the change in structure that has occurred. This is as true in metabolic studies, where most of the structures are molecular, as it is in studies of locomotion where the changing structure is visible, photographable, and often tangible. Physiological, developmental, and evolutionary studies reveal the organism as a process. Because structures change, they have function and history.

Put together, we might call the subject of structure and function biology, but that would alarm more than it would instruct. In the first half of this century, the great organismic biologist Sir Maurice Yonge called it functional morphology. He was reacting to the zoological literature of the time much of which was blatantly either only structural or only functional. It may be recalled that Sir James Gray formed the Society for Experimental Biology and created the *Journal for Experimental Biology*. His reason for doing this was that his papers on animal locomotion were being rejected by the existing zoological journals because his studies were experimental.

Functional morphology is a point of view, a way of looking at phenomena in nature and human design. It connects structure with the physiological point of view. As it is used in zoology today, its scales of size and time include those of the organism: it can employ information that is visible, audible, tangible, tasty, and fragrant. Because we can use all these sources of information in functional morphology, it is intuitively comfortable for us to learn, and therefore easy to teach, especially to folks who have not already mastered the complicated language and tools of modern science. DNA, group selection, and neutrinos are wonderful, but did you ever see one? Or hold it, wriggling, in your hand?

The organism is the teacher's prime tool: it joins the classroom, the laboratory, the library, the museum, the art studio, the coffee clatch, and especially the field trip in the lessons of life that can be instantly understood and long remembered. The *structure and function of the organism* give context and perspective for the cellular and molecular approaches to the study of life.

Every structural feature of every organism has three equally important biological contexts: functional, developmental, and evolutionary. Of each structural feature we must ask "What is its function and the mechanism by which it functions?", "What were the steps and causal mechanisms in its development?", "What were the steps and causal mechanisms in its evolution?" Since the processes of function, development, and evolution are qualitatively different, answers to them reflect the magnificent complexity of living things. To discuss only functional aspects of structure is to ignore the other two major contexts for biological structure.

What to Know

I will give short answers to two questions that have guided me in teaching functional morphology. The first question is "What do I have to know to do a project in functional morphology?" A surprisingly short list of concepts can launch an exercise, a master's thesis, or a career in the study of structure and function.

Scales of size and time

One must recognize that biological structures exist from the invisibly small to the invisibly gigantic and that molecular changes in structure occur faster than we can see them, while our heartbeat can be seen, heard, and felt. Still slower changes include those of development and metamorphosis, and the slowest changes of all are the evolutionary ones that take place over generations.

The physical rules of function differ for structures of molecular and elephantine size. Molecules get bumped around by Brownian movement and even small insects can skate on the surface tension of a pond. As for larger bodies, gravity doesn't begin to threaten structural integrity of a body that takes a 10 m fall unless the body is about the size of a puppy or larger (Went, 1968). Cheer and Koehl (1987) and Kingsolver and Koehl (1985) show how function of similar structures changes qualitatively with change in size in the feeding and flying appendages of arthropods. Good books abound on the importance of scale to organisms: Alexander (1971), Morrison *et al.* (1982), McMahon and Bonner (1983), Calder (1984), Schmidt-Nielsen (1984).

Hierarchy

In a first approximation we divide the structures of the universe into levels in a hierarchical scale of increasing structural complexity. The familiar hierarchy builds upward from atoms, to molecules, to organelles, to cells, to tissues, to organs, to systems, to organisms, to populations, to communities, to ecosystems, to the biosphere. We notice that biological research concentrated on organisms up through the first third of the 20th Century. Then questions of cells took over for a third, and now in the final third, we are in an era where most of the resources for biological research are being spent to answer molecular questions.

Are questions at one level fundamentally different than those at another? Certainly the tools used in analysis differ at different levels. We can watch gorillas with the naked eye, but we use light microscopes to see cells and electron microscopes to study the substructure of mitochondria and chromosomes. The reasoning of chemistry and thermodynamics dominates molecular biology, that of Newtonian physics dominates physiology, ecology, and behavior.

We frequently stand at one level and look down the scale a step or two as we search for an explanation of function. For example, we define muscle cell function by saying that it shortens forcefully. We analyze muscle cell shortening by describing the sliding motion of actin and myosin filaments past one another within the cell.

But the "function" or role of muscle at higher levels is not of the same quality. Some muscles allow us to move arms and legs, some cause the extension of the tongue or the expansion of the heart wall, while others move breakfast through the gut. Is it right to say that the function of muscle in the larynx that converts expired air into song is the same function of muscle that flaps a butterfly's wing? Surely not. These are muscles whose underlying structural and functional properties are qualitatively different. No amount of studying only the lower levels of structure and function would allow us to know the higher level "function." Substructural differences are important to the substructural levels, but the value and usage of the different substructures is controlled by the higher level "function."

I put the word in quotes because it is the wrong word. We need another word for this kind of function. "Purpose" would do, but in today's usage, at least in America, it carries the unacceptable connotation of conscious intent. Perhaps the German word *Zwecke* is the right word: purpose or goal, not necessarily with conscious intent. If we can use the word *Gestalt* without translation, we should also use *Zwecke* to mean the role of a structure at higher levels in the structural hierarchy (Riedl, 1975, 1981).

Permission and constraint

It is necessary to include this obvious, truistic pair of concepts because of the current popularity of the word "constraint." No one reading this, I think, needs to be told about the usefulness of the concept of constraint. It shows us functional boundaries: where functions start and stop; where species can live and where they can't. It pertains to the limits of function and allows us to study natural selection, among other worthy things. The discovery and description of the mechanism of each limit to each function are the major subjects in much, perhaps most, functional research today.

But realize this: function is *permitted* by the structure that is appropriate for the conditions where the function occurs. In embryogenesis, a function is absent until the structure has developed to the appropriate extent to allow the function. For example, the eye of a chick cannot form a focused image on the retina until enough water is removed from the cornea to allow its fibrous structure to transmit light with minimum scattering (Coulombre and Coulombre, 1961). Similarly, a particular function does not occur in individuals of a species until a structural mutation arises to permit the function. For example, Kingsolver and Koehl (1985) have shown that insects couldn't glide or fly until cuticular extensions, that could have first functioned effectively in temperature control, became large enough to permit aerodynamic function. Concerning the organisms we see, we might well care to learn what they are permitted to do before we consider their constraints. The concept of the onset and permission of function is as fertile a substrate for thought and research as is constraint. It is a fundamental concept. It represents a positive point of view. Try it!

By the way, the biggest source of permission in biology is the physics of the surface of Earth. Life as we know it seems scarce indeed on other heavenly bodies in our universe. On Earth, we are aware of where our own life is permitted. It is constraints that make it hurt when we find ourselves in the wrong physical situation—deep in the ocean, high in the atmosphere. Our comfort and normal function are permitted through our bodily structure by physics. The physical concepts we use to study organismic structure and function are typified by Newton's 17th Century laws of optics, gravitation, and motion. Our concepts of biological function have not yet caught up in any major way with Einstein's kind of functional physics. Happily, Newtonian physics is simple, and intuitively easy to grasp by students.

Properties

Properties are wonderful! They allow us to connect specific structural features of organisms with their functions. Properties allow us to reconnect structure and function, one piece at a time, in our scientific synthesis of organisms from the results of our analyses. For example, the strength of a tendon is the force it takes to break it (function) divided by the cross sectional area (structure). The contraction rate of a muscle is the distance it shortens (structure) per second (function: changing structure with time). The permeability of a membrane is the volume of material passing through (function) per unit thickness and area (structure) of the material. And so on.

It is especially important that any property being estimated is the one that most precisely fits the biological function being studied. For example, strength of bones is useful when the limits of function are being studied, but stiffness is more important for studies of normal use. Often toughness or the amount of work (energy) that must be put into a bone to fracture it is even more relevant to functional studies than either strength or stiffness (Currey, 1984). The student of functional morphology should also realize that properties are invented by workers to help them solve problems. Therefore, anyone can invent a property if the ones already in use are inappropriate. There is a lot of room here for creativity based on physical and biological insight.

Consideration of properties of components of a system brings us to think about the whole system. Systems have properties too, and all the properties of a system must be compatible. Furthermore, the properties of systems are different in kind from properties of components. This is of great interest and it represents a challenge to the functional morphologist to understand how the properties of systems and components are in fact related to each other.

It is not enough for a hip joint to have the ball and socket form, covered by slick, shock-absorbing articular cartilages. There are nerves, blood vessels, and muscles traversing the joint that must not be crushed by compression on the inner side or stretched and broken on the outer side when the joint is bent. Peripheral to that, the skin has to stretch and compress the right amount. It wouldn't do to spend a lot of energy stretching skin and nerves at every step: nerves and skin accommodate stresses and permit function. There is compatibility of materials across the joint. Referring back to the structural hierarchy, a higher level word for this is harmony, a term for which we have no operational definition that allows us to estimate it quantitatively. I hope our ability to deal with structural complexity will soon lead to the scientific definition and study of harmony in biological organization. Perhaps developmental biologists will be the first to speak informatively on this subject. Workmanship is another such higher level property that bears study. Murdock and Currey (1978) have done a case study illustrating the importance of workmanship in the shells of two species of barnacle to their life style and survival as species. And Best (1988) has made a thorough analysis of the higher level concept performance in her study of the sea pen as a filter feeder.

Analogy and Homology

If structures in animals of different taxa are similar in function only, they are analogous. If they have common ancestry, they are homologous. The use of these terms is based on the interdependence of functional and evolutionary causes. Analogy is concerned only with mechanism of function; homology recogizes that evolution, the unique historical process in biology, is a factor in the similarity of structure. For example, we say that the streamlined body forms of cetaceans and fishes are homologous. We would not bother with this distinction if there were an unbroken lineage of streamlined amphibians, reptiles, and mammals from fish to cetaceans. The discussion of these terms keeps us thinking about the causes of similarity. Remane (1952) gave us the first useful set of criteria for the identification of homologues; Riedl (1975, 1981) and Roth (1984, 1988), among others, have discussed their meaning.

This list of ideas is not an exhaustive one, but it is more than enough to inject a student into the study of form and function.

WHAT TO LOOK FOR

The second question to be answered is "When I look at an organism, what kinds of things will I see that will help me study its functional morphology?" Another pleasantly short list of features of all organisms will prepare one for most situations.

Pattern: Polarity and symmetry

The arrangement of the gross anatomical components will be simple and describable, and one of the basic features is the symmetry of their distribution about the body's longitudinal axis. It can be observed that multicellular animals (and plants) are cylindrical in shape or are clusters of cylindrical components (Wainwright, 1988). This provides for a longitudinal axis. It is also to be observed that cylindrical organisms are different on each end—they are polarized into a sensitive end that meets the environment first and another end that follows. Branches of many corals and spines of sea urchins are distributed around bodies in radial symmetry, while the distributions of antlers and legs show bilateral symmetry. Radial symmetry allows organisms to face the environment with the same competence from any radial direction. Bilateral symmetry is the result of structural development that gives a cylindrical body a head end that meets the environment first, plus a preference for having one side next to a substrate or a response to gravity that gives a preference for having one side up. In the design of a system, the choice of symmetry is a very early one indeed. It is noteworthy that each of these morphological features (cylindrical shape, polarity, radial and bilateral symmetry) permits enormous functional elaboration. Neville (1976) has written a simple and stimulating booklet on the subject.

Dimensions

This is obvious and easy, and it sets the size scale for the study. As noted above, the size scale is causally connected with the time scale.

Geneity

The structure of materials is said to be either homogeneous if all the subunits are similar and are similarly arranged or heterogeneous if more than one distributional rhythm is involved. While this is useful as a first approximation, homogeneous structures usually turn out to be heterogeneous when seen at higher magnification. So this distinction is often a matter of how closely you are looking—once again, what are you paying attention to? The particular details of heterogeneity do much to permit, control, and limit the physical properties of biomaterials. The optical properties of the cornea and lens, the piezoelectrical and mechanical properties of bone, wood, and shell and many soft connective tissues all rely on the specific mixture of polymer, mineral crystals, and fluid components. The major structural features of mixtures that control properties are the size, shape, orientation, and volume fraction of the discontinuous components such as crystals, fibers, and voids (Wainwright *et al.*, 1976), and the hydration and charge density of the continuous, amorphous polymeric phase (Myers and Mow, 1983). Kinds of heterogeneity that are important for functional analysis are given in the following two sections.

Composites: Aggregates and interfaces

In the mechanical function of structural materials, certain heterogeneous aggregates have come to be called composites. For example, the elastic properties of bone are a function of both the stiffness of its mineral and the stretchiness of the polymeric matrix between mineral crystals. Mineral crystals alone are very stiff but too brittle to be useful, while collagen alone is too compliant but provides for elastic deformability that makes bone a very tough material. Materials scientists have created a rich theory of composites that is useful in the functional analysis of structural biomaterials. It is satisfying to see that their theories are now being stretched by their increased awareness of the magnificent hierarchical complexity of biological materials.

In a similar way but to very different functional ends, the body is a composite. It is an aggregate of organs; an organ is an aggregate of tissues; a tissue is an aggregate of cells; and so on. A shell is an aggregate of polymers and mineral crystals in which the crystals are in layered aggregates. Aggregates are functionally interesting because they provide as many avenues to their analysis as there are kinds of components. The properties of materials and the behavior of bodies are compromises resulting from the particular cluster of components. Whether the components are attached rigidly, loosely, or not at all is fundamental to the integrity of the body and the specific functions of its parts.

In addition, the functional properties of any of these aggregates depends on the properties of the interfaces where components meet. This general condition has been most eloquently analyzed by the metallurgist C. S. Smith (1982) who shows how the properties of maleable metals depend as much on the weak interfaces between crystal grains (aggregates of crystals) as they do on the properties of the pure, continuous metal. His treatment of the importance of interfaces sweeps from the *mille feuille* structure of croissants and ancient Japanese sword blades to the glazes of ceramics and froths of bubbles. He applies the idea to the structure of culture: we exist in aggregates, and whether a larger aggregate functions smoothly depends on the "friction" and the nature of the connection at the interfaces between the components.

The strength and stiffness of a bone are high because the mineral crystals and collagen that comprise the bone are strong and stiff. But when bone is permanently bent or broken, the crack that causes the failure travels, for the most part, along the interfaces between the units. The interfaces are the weakest part of bone structure, but the orientation of these interfaces at high angles to potential cracks makes the cracks travel much farther, thus requiring much more energy to achieve a break (Currey, 1984). Similarly the functions of active clusters of molecules in a cell membrane function according to their interconnection and the ionic balance of the ambient fluid. It is revealing to study the cross section of any whole animal (earthworm, mouse) and ask whether tissues that touch one another are firmly attached or if they can slide past one another. This simple exercise tells about the functional connections for circulation, neural communication, and transmission of forces throughout the body. It is a simple but powerful tool for functional morphology.

Orientation and anisotropy

The units of every aggregate are oriented. The orientation may be perfectly parallel, preferred (not quite perfectly parallel), radial, or random. With respect to some cylindrical element, such as a blood vessel or a feather shaft, the orientation may be tangential or radial, and if it is tangential it may be circumferential, helical, or longitudinal. Optical, electrical, and mechanical properties vary with the degree of orientation of structures at all levels from molecules to appendages. Even the rate of permeability of the fish's swim bladder to gases depends on the orientation of guanine crystals in the bladder wall (Lapennas and Schmidt-Nielsen, 1977).

Solid materials are isotropic if the value of each property is the same in all directions through the material. While this is common in cement, steel, and glass, most biological materials are anisotropic. The most common cause of anisotropy (the unequal values of properties in different directions) in biological materials is the preferred orientation of molecules. At gross anatomical level, the nearly parallel array of major nerves, blood vessels, muscles, skeletal elements, and the longitudinal axis of the body or appendage is an important clue to many functional considerations.

Once again, this list is just a starter, but next time you hold a beetle, a buttercup, a gallstone, or a fossil in your hand, review these features and appreciate how much of the function of the creature you may be able to infer. If this interests you, you will be rewarded by reading Hickman (1980), Raup (1987), and Raup and Stanley (1971) on the functional interpretation of fossil structure.

It is good for scientists to gather to discuss the connections of any two such important subjects as structure and function. I am really glad we are all here doing this. At the same time, we must be aware that by focussing on these two, we are ignoring all the other aspects of organisms. In the atmosphere of the late 20th Century, it seems that not to discuss structure and function with respect to developmental and evolutionary considerations is a little like trying to play the game without the ball.

Why, after all this, should we care about structure and function? It seems to me that it is all in aid of understanding the evolution of organisms. By this I mean both the actual series of forms that succeeded one another over the past zillion years, and the mechanisms by which such changes in structure have been caused (permitted), have persisted, and disappeared. Surely evolution is the single most important and inclusive concept in biology and everything we learn about organisms must contribute to our understanding of evolution. If we learn things that cannot be fit into our idea of evolution, perhaps another idea will be found to displace evolution. If that happens, functional morphology will serve that idea, too. Functional morphology is not a subject unto itself. It is just a point of view, like all the other points of view (ecological, biochemical, behavioral, mathematical, etc.). It is a tool that can help us come to understand the origin, history, and continuation of life on Earth.

THE LONELINESS OF MORPHOLOGY

Recently I found myself writing a book on functional morphology and I thought I would first define morphology and physiology in terms that would tell students what the fields were about. I wanted to state the principles of both fields and look to see how they might be zipped together. Physiology was relatively easy: physical and chemical principles can indeed be applied to biological systems. And principles of biological function are also to be gleaned and used.

Morphology was just the study of form. I found no stated, useful principles of morphology! The only principles of form I found were in the field of topology, and I am frankly not interested in that degree of abstraction. There is no textbook of pure morphology. Books abound in atomic and molecular morphology, animal morphology, plant morphology, and geomorphology. But there is no text on the general study of form. Whyte (1968) mentioned a unique course in morphology that was given in Israel in the early 1950s. Has one been offered anywhere since then?

I became involved with Rupert Riedl in discussions that he said were about "classical morphology." I felt cheated that morphology was a field in central Europe, but that in the West we had only the more specialized subjects—functional and evolutionary morphology. Then I realized that their classical morphology equals evolutionary morphology. Their evolution is phylogenetic more than it is mechanistic.

Conclusion: No one studies just morphology. Structure is only interesting when it is studied in conjunction with something else—function, development, evolution.

The Origin of our Interest in Form and Function

What is the necessary connection between structure and function? Is it or might it be a causal connection? Why do we single out these two features of living systems to celebrate?

What are the features of biological systems that have been perceived for the longest time, say, by our anthropoid ancestors? Of the biological things in the habitat of early humans, most of the things that demanded attention, thought, and behavior were organisms. Senses of sight, touch, hearing, smell, and taste told our ancestors immediate things about other humans and other species. Other "feelings" and "senses" told them about spiritual, aesthetic, moral, economic, and political aspects of each other and of other species. Today we proclaim these latter aspects as scientifically irrelevant because of our inability to define them operationally and to agree on how to measure and interpret them. If we believe that function is change in structure, then we can *see* function with our eyes. But for us to recognize an observed structural change as a function, we must have some model in our mind that defines the function and makes the connection. Structural information comes to our retina as primary data; function must be inferred and calculated.

In days past, if our ancestors didn't connect the scent of a cave bear upwind with knowledge of its form and predaceous habit, they might well not have made the appropriate avoidance behavior. So human cognitive senses were naturally selected to be adept at making these correlations. No wonder we still make them!

We also evolved abilities to correlate organisms (structures) with spiritual and other less easily measurable features. Scientific revolutions have kept these features out of the mainstream of science for over a hundred years. They are now affecting the mainstream in some cultures in the form of conservation and animal rights. In this country today, marine mammals are achieving godlike status: they are so thoroughly protected that they may only be studied from afar by folks with binoculars. We may not seek to learn about their physiology.

The Biology of Physics

When I was was an impressionable youth, I was told by a physiologist that it didn't matter whether motion was caused by cilia, smooth muscle, or striated muscle. All that mattered was the movement's cost and efficiency. I descended into the blue funk of physics envy. Why couldn't I know such glaring truths and state them with such clarity and conviction? Why did I feel I had to *see* corals on a reef in order to study their symbiosis with algae and their ability to build skeletons big enough to be seen from satellites in orbit? I was a mere natural historian, a stamp collector, a cub scout among the sophisticated soldiers who studied energy and efficiency.

So I ascended into biomechanics—the application of mechanical physics to the analysis of organismic function. I learned that efficiency is the output energy divided by the input energy. Energy or work is force times distance: there is no structure there. The real world was just little packets of energy buzzing around. Even atomic physicists didn't help me: so-called particles have become less and less solid and tangible.

They are the ultimate packets of energy. The only thing that lightened my load was the observation that physicists couldn't measure the position of a particle and its velocity at the same time. Served 'em right.

Even Newton made more pronouncements about function (gravity, motion, refraction of light) than he did about structure. Except for what you can get from the concept of structure of elementary particles, physics is all about function. In the definition of force, it is a mass that is accelerated. It requires a mental leap, a stroke of pure imagination, to go from mass to structure. It doesn't matter to a physicist whether the mass is a proton, a galaxy, or an eye of newt. Science is important and physics is science: energy is what counts. Never mind that you cannot see, hear, feel, smell, or taste it. It lives in the mind—that uniquely human feature.

Then I learned that technology is also important for cultural reasons beyond those that tell us why physics is important. What do engineers do? They take the physicists' equations and convert them to deal with real structures. Engineering produces tangible products (structures with functions). Science produces ideas. Physics is the pure science. Does that make biology an impure science?

Biology has physics in it, but it also has chemistry, geology, astronomy, engineering, anthropology, and a lot else. Acceptable errors in biology are greater than they are in physics, but complex systems like buttercups represent enormous compromises: they appeal to our uniquely human contemplativeness and our desire and ability to see, correlate, and understand many aspects of complex systems. Most biomechanics is the application of mechanical engineering, not raw physics, to the analysis of systems such as cells and organisms. These systems have structure. Biologists also conceive of even more complex and abstract systems such as genera, guilds, and ecosystems whose functional units are organisms (structures).

Our primitive drive to make structures meaningful to us so we can perform selectively advantageous behavior still exists, and other ancient values that lead towards a more thorough understanding are also still with us. Science is as big as we make it. It can include structure as well as function. Perhaps Nirvana or salvation is achieved quickest through the recognition and contemplation of energy alone. But if I can't munch the carrot, watch the hawk, and smell the frangipani along the way, my fitness, in several senses of the word, is insignificant.

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