"Elegance: A Brief, Perfectly Balanced Instant of Complete Possession of Forms"

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Who would have thought that the humble nematode worm *C. elegans*, short for *Caenorhabditis elegans*, an organism smaller than the head of a pin, would become the focus of so much basic research in the study of animal cell biology and development? The reason is that a simple, primitive animal had to be selected that nonetheless would share many of the essential characteristics pertaining to central problems of human biology, including how genes determine processes such as development, precise body symmetry, nerve function, behavior, and aging. *C. elegans* was the perfect candidate to provide the biologist with the ideal compromise between complexity and ease of handling, and the first multicellular organism whose total genome was completely sequenced as of December 1998.[1]

What has this one-millimeter-long worm, who in nature lives among decaying vegetation, and in the laboratory spends its entire two- or three-week life span in a small petri dish feeding on bacteria, to do with Elegance as its name suggests? Elegance, a term evoked for "refinement, grace and beauty, precision, neatness, simplicity, or restrained beauty of style";[2] isn't this what the little worm represents in all its essence? Anyone who has seen a nematode move with undulating grace under the microscope and has marveled at its perfect body symmetry will readily understand. How appropriate that the particular epithet, *elegans*—that so well reflects and represents precision, simplicity, and neatness of biological structure—characterizes a species that is the prime model for the determination of most of the fundamental mysteries of modern biology.

Elegance in a biological context is especially equated with universal simplicity at the subcellular level;[3] simplicity, in that in nearly all living creatures, complex macromolecules that make up our DNA or genes are assembled from only a few basic building blocks, and likewise tens of thousands of proteins form the combination of just twenty subunits called amino acids. Simple and affordable technologies that are easily adapted for everyday use in the molecular biologist's laboratory have certainly changed the speed of scientific progress; a great example is the polymerase-chain reaction (PCR) technology that allows for rapid amplification of a gene product. The simple elegance of the PCR concept has quickly evolved to the point where PCR machines are standard laboratory equipment, without which many molecular experiments would be immensely time-consuming or simply not possible.

Another elegant biological tool is the manipulation of the green-fluorescent protein, GFP, which is responsible for the stunning blue and green bioluminescence of the Pacific Northwest jellyfish, *Aequorea victoria*.[4] Upon shining with ultraviolet light—but undetectable by human eyes—GFP will also produce a green light. This fluorescent property makes the cloning of the GFP gene so powerful because it may allow for *in vivo* tracking of proteins, monitoring of gene expression, following of cell populations, or the study of infections in a series of organisms, from yeast and plant cells, to the fruit fly and vertebrates, including humans. Again, it is the universality of a simple tool with wide-ranging applications that here evokes the concept of elegance.

What attracted me to become a biologist was the wonder I experienced as a child when observing beautiful shapes and forms in a drop of pond water under a rudimentary microscope, or collecting fossil ferns in the rich carboniferous deposits not far from my childhood home. Perhaps as a child I wouldn't have referred to these forms as being elegant *per se*, but today I can fully embrace such term for the overall body plan and internal structures of my former treasures.

To me, this elegance has reached its climax in the group of organisms called the red algae, a bias shared with many other marine botanists! Open any book of seaweeds, and you will find species with names such as *Gymnothamnion elegans*, a very delicate and feather-like alga reported from places such as South Africa, Brazil, Hawaii, or Australia. The name *elegans* encompasses

[1] See http://elegans.swmed.edu (July 2000). [2] *Merriam-Webster's Collegiate Dictionary* [on-line] (July 2000). [3] A. Rich, "DNA Comes in Many Forms," *Gene*, *135* (1993), 99-109. [4] See http://faculty.washington.edu/cemills/Aequorea.html (July 2000).

both simple-looking taxa such as *Griffithsia elegans* from Australia, and more complex ones, such as *Chondracanthus elegans* from Brazil or *Delisea elegans* from New Zealand and Australia, to cite just a few red algal species from around the world. Which criteria did the taxonomists have in mind when they described and provided such a name for their new species? What made them evoke the concept of Elegance? Was it elegance based on beauty of external form or internal anatomy that made these species different and stand out from other related species? Was it based on form superbly linked to structure, function, life-style, and life history? It was most probably a combination of all of the above.

My field of study is the systematics of such marine red algae, a field concerned with detecting patterns of evolutionary relationships among the species under study. Most red algae are characterized by bizarre life histories and a smorgasbord of fruiting body types. Their sheer elegance derives from the fact that, while being only a simple bunch of filaments, red algae have evolved a multitude of cytological and morphological modifications (*figure 1*) despite major developmental constraints; in other words, they can do so much with so little! A filamentous organization makes it possible to resolve all vegetative and reproductive structures into exact developmental components. Cells within filaments are linked by pit connections formed between cells after incomplete cell division; these are thus elegant morphological markers making it possible to follow each filament cell by cell with light microscopy.[5]

Red algal classification is predominantly based on the comparative morphology of the female reproductive system leading to the fruiting body, which is the result of fertilization and grows parasitically on the mother plant. It is an intriguing detective story to try to reconstruct the development of the entire fruiting body, for one has only a piece of the puzzle at any one time in any one section, with additional sections revealing the succession and differentiation of the various stages (*figure 1*). Although the red algae have produced some of the most beautiful and perfect, yes elegant, forms among all living organisms, true tissues are never produced, such as those formed in the worm *C. elegans*, or in green plants, or in some brown algae, and their 'complexity' hides a most remarkable 'simplicity'.

What does attract one person to the field of red algal systematics, and another to unravel structure at a more fundamental and universal level across the Tree of Life, and how do these biological pursuits relate to Elegance?

One of the world's great botanists and electron microscopists, Professor Irene Manton from Leeds University in England, was establishing techniques half a century ago for studying reproductive cells of mosses and ferns with the newly developed electron microscope.[6] Her interest quickly spread to the flagella of motile gametes in general, such as those of the larger brown algae. She discovered that all plant flagella broke up into 11 strands when dried, two being different from the others and central. This was exactly like the cilia of *Paramecium* and the sperm tail of the domestic fowl that were published around the same time elsewhere. Manton published these first findings in the journal *Nature* in 1950 and in the following years published a series of articles describing the flagella of algae, mosses, the bracken fern, and fungi, and transmitting to the reader the thrill she felt by discovering, to her great surprise, that all eukaryotes had basically the same type of flagellar structure, what became known as the 9 + 2, a universal feature prominently illustrated in every general biology textbook.

Manton explained that when she arrived at the University of Leeds in 1946, she found the town and the department so grey and dull that she filled the walls with her personal works of art to make the existence there bearable.[7] What impresses me most is that she alternated her electron micrographs with prints of abstract art.[8] She might thus have hung a photograph of a moss sperm next to a Mondriaan print, which was placed next to a micrograph of a rockweed flagellum, which in turn hung next to perhaps a Malevich print, more or less alternately for the sake of artistic effect (*figure 2*). To Manton, abstract art was very real, as real as the previously unknown ultrastructural patterns revealed from her plant sections. The patterns could be either free flowing or geometrical, or contain no recognizable shape, but all had structure that was very real, very captivating. She saw the same universal representation of patterns of Form converging upon nature and on the canvas through the mind of the artist, a direct reference to a common reality. This perceived reality may be unattainable to people who can't or won't try to experience or appreciate different realities that become one.

The term 'Abstract Art' generally refers to "images that have been abstracted or derived from nature but which, in the process, have been considerably altered or have been simplified to their basic geometric or biomorphic forms."[9] Isn't this what elegance is all about? Abstraction exists at different levels, like reality

[5] M. H. Hommersand and S. Fredericq, "Sexual Reproduction and Cystocarp Development," in *Biology of the Red Algae*, ed. K. M. Cole and R. G. Sheath (Cambridge, 1990), pp. 305-45. [6] I. Manton, "III. Plant Cilia and Associated Organelles," in *Cellular Mechanism in Differentiation and Growth*, ed. D. Rudnick (Princeton, 1956), pp. 61-71. [7] Ø. Moestrup, "Irene Manton (1904-1988)," in *Prominent Phycologists of the 20th Century*, ed. D. J. Garbary and M. J. Wynne (Hansport, 1996), pp. 345-53. [8] Max Hommersand, personal communication. [9] *Funk & Wagnalls Multimedia Encyclopedia* [on-line] (July 2000).

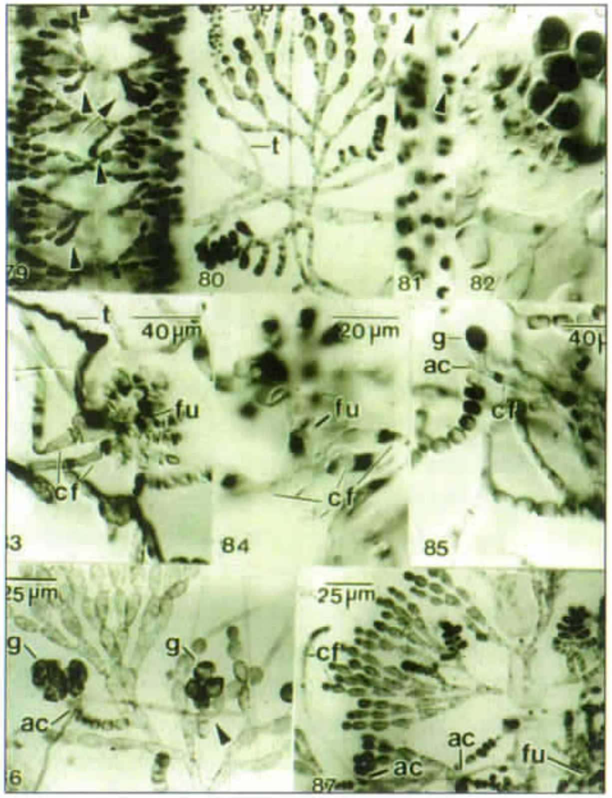

FIGURE 1

Female reproductive development of *Acrosymphton caribaeum* from Florida, stained with Wittmann hematoxylin, reprinted from M.H. Hommersand and S. Fredericq, "Sexual Reproduction and Cystocarp Development," in *Biology of the Red Algae*, ed. K.M. Cole & R.G. Sheath (Cambridge, 1990), figs 13.79-13.87, p. 326

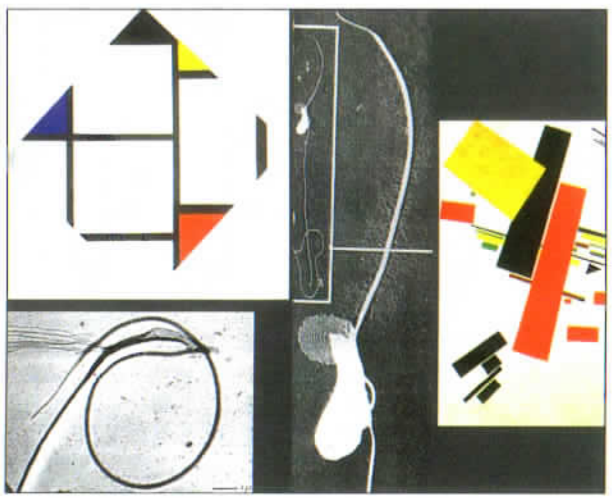

FIGURE 2

Top left: Piet Mondriaan, "Diamond Painting in Red, Yellow and Blue", *ca* 1921/25, National Gallery of Art, Washington, DC

Top right: Kasimir Malevich, "Dynamic Suprematism," Museum Ludwig, Cologne.

Bottom left: Spermatozoid of *Sphagnum acutifolium*, x5000, reprinted from I. Manton and B. Clarke, "An Electron Microscope Study of the Spermatozoid of *Sphagnum*," *Journal of Experimental Botany, 3* (1952), 265-75, pl. III., p. 274.

Center: Spermatozoid of *Fucus serratus* x3,200 and x16,000, reprinted from I. Manton and B. Clarke, "Electron Microscope Observations on the Spermatozoid of *Fucus*," *Nature, 166* (1950), 973-4.

exists at different levels: Perhaps a Piet Mondriaan diamond in all its reduced simplicity could be equated with the simplicity of the smallest biological or atomic particle, whereas a Paul Klee or a Eugene Martin *(figure 3)* bring out another level of reality, shown with both structure and free-flowing forms that include the next level of interactions, those highlighting the wonder of nature. Look at a Calder mobile that graces the cover of the latest books on molecular biology or a Kandinsky print on the cover of a treatise of population genetics.[10] The essence of abstract art and fundamental microbiological processes and structure become one; Irene Manton understood it so well.

Abstract art also brings to mind the theory of "forms" or ideas of Plato. In his theory of forms, Plato regarded the objects of the real world as being merely shadows of eternal forms or ideas. This is famously illustrated by the myth of the cave in which people are chained deep within the recesses of a cave and cannot see one another.[11] The only thing visible is the cave's wall, upon which appear shadows cast by models or statues of animals and objects that are passed before a brightly burning fire. One of the chained people, breaking free, escapes from the cave into the light of day and, with the aid of the sun, sees for the first time the real world and returns to the cave with the message that the only things seen up until then are merely shadows and appearances, and that the real world awaits if people are willing to struggle free of their bonds. So, as with art, what is real, what is abstract?

The Platonic forms are not material objects, nor are they concepts in our heads—they are abstract entities that exist on their own terms, apart from the physical universe, eternal and unchangeable. Physical objects are what they are by virtue of their *participation* in certain forms, reflecting these forms imperfectly in the material world. Plato believed that the forms were necessary to explain the physical world around him, as to him the only reason the physical universe is intelligible at all is that different things take on the same form. The material world we perceive through the senses seems always to be changing, while the world that we perceive through the mind, through reason, seems to be permanent and unchanging.[12]

One of the most beautiful, thought-provoking, and original passages ever written on form and abstraction was provided by the Belgian writer Suzanne Lilar in the evocation of the fossil: the fossil as the symbol of Form but also of the dignity of Matter *(figure 4)*. She writes:

> If the ammonite that lived two or 300 millions years ago only left behind an abstract pattern upon which it was moulded, matter again had to

[10] R. D. M. Page and E. C. Holmes, *Molecular Evolution: A Phylogenetic Approach* (Oxford, 1998); H. Caswell, *Matrix Population Levels: Construction, Analysis and Interpretation* (Sunderland, 2000). [11] See http://crystallinks.com/plato.html (July 2000). [12] See http://ucsub.colorado.edu/~camerorj/an.phil.tenten/lct.forms1010.html (July 2000).

support this form to come to our consciousness and allow us to see and touch it. All that had morphologically characterized the life of the fossil became reproduced in detail in stone; yet, besides the calcium carbonate and phosphate of the shell that finally became digested and replaced, as had organic matter before that, the ammonite that lived in the Devonian and today's fossil only have in common a sort of pattern upon which were shaped a set of proportions, of relationships, in other words, of Form in its pure abstraction, alone triumphant over time, alone representing the truth.[13]

The participation of matter and form: For Lilar, herein lies precisely the role and dignity of matter, namely to provide inseparable support to the mind, and for both always somehow to remain associated. The fossil represented for Lilar the concrete expression of the Platonic daydreaming of form, in that the truth didn't lie solely in the mind, nor solely in matter, but in their relationship; it confirmed to her that blending is proper to our condition and that there is purification only at the level of thought. For Lilar, this notion was reminiscent of the Aeidos of Plato, and of preference in Plato's Parmenides, in that by introducing the notion of participation, he made the Eleatic and Socratic doctrine of form less rigid.

Another way of appreciating the elegance of form was shown in the thirteenth century by Fibonacci in the universality of the so-called Fibonacci numbers, illustrated by the Nautilus shell spiral *(figure 5)*. A Fibonacci Spiral results when a spiral is drawn by putting together quarter circles, one in each new square, which increases in size by a factor of Phi (Ø = 1.618) in a quarter of a turn.[14] Elegance can thus be expressed simultaneously in both the geometrical and static state, and in the repeating free-flowing motion that culminates in the organic shape of the shell as we see it. The same can be said in art, where we can go from one level, shown by the hard-edged geometric structures, to another level, shown by the soft-edged, free-flowing shapes found in nature, and see that both states intrinsically relate to and complement one another, even though the forms may look abstract *(figure 6)*. But, as the artist Eugene Martin says, "If you seek just a little truth, as most, you should not ignore abstract forms, the basis from which all short-lived experiences we call reality spring."[15]

An elegant mental exercise we may be confronted with is that of making analogies, or experiencing similarities between apparently unrelated objects or ideas. Using a biological terminology, 'Analogy' refers to similarity of

FIGURE 3
Eugene J. Martin, untitled, 1996, acrylic on canvas, private collection

FIGURE 4
Devonian ammonite, private collection.

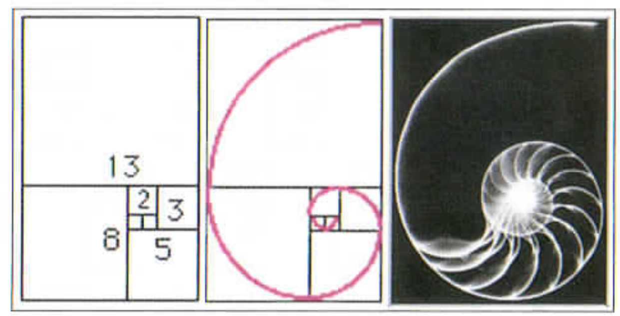

FIGURE 5
Nautilus shell and illustration of the Fibonacci numbers (0, 1, 1, 2, 3, 5, 8, 13, and add the last two to get the next), see http://www.mcs.survey.ac.uk/Personal/R.Knott/ Fibonacci/fibnat.html#spiral (July 2000).

[13] S. Lilar, *A propos de Sartre de de l'amour* (Paris, 1967), p. 43. [14] See http://www.mcs.surfvey.ac.uk/Personal/R.Knott/Fibonacci/fibnat.html#spiral (July 2000). [15] Eugene J. Martin, personal communication.

FIGURE 6
Eugene J. Martin, untitled, 1998, acrylic on canvas, private collection.

FIGURE 7
Left and bottom right: detail of St Lucie by Grünewald, *and top right:* *Cassis tuberosa*, reprinted from S. Lilar, *Journal de l'analogiste* (Paris, 1979), pl. V, p. 179.

FIGURE 8
Left: Eugene J. Martin, untitled, 1982, pen and ink on paper, private collection. *Right:* *Crouania attenuata*, collected by SCUBA from 30 m depth at East Flower Garden Banks Marine Sanctuary, Texas, October 2000.

structure between two species that are not closely related and attributable to convergent evolution, whereas 'homology' is similarity of features resulting from shared ancestry. A remarkable treatment that reflects on analogies is the *Journal de l'analogiste* by Suzanne Lilar, published in 1979.[16] To Lilar, the dress of St Lucie painted by Grünewald is strikingly reminiscent of the form of a shell, in particular that of *Cassis tuberosa*; the dress had taken on the form of the shell's valve, and the folds in the cloth followed the same precision and sequence of ridges, nodules, tubercles, and axis of the shell *(figure 7)*. This unexpected analogy was surely unintended by the painter, and for Lilar, it is exactly the experience of such analogies that attains the highest universal level of poety. Isn't the poetic experience what elegance should strive to fulfill?

If we remain open-minded and curious about the world surrounding us, we may see analogies on a regular basis, as I keep seeing in the evocation of the banding pattern in *Crouania*, a small red alga, and in the thorax of an extraordinary bird *(figure 8)*. We can also see an analogy of movement, in that the spiral of the ammonite fossil is reinforced by a similarly free-flowing curve expressed in the painting behind it *(figure 4)*. What we all love is the pleasure we experience when we suddenly become confronted with unexpected analogies, but as good systematists, it is homology of structure we study and strive to comprehend evolutionarily.

A wonderful little book, first published in 1943 by the great and influential French art historian Henri Focillon, entitled *The Life of Forms in Art*, points to the great universal moments throughout the evolution in art styles, which he often relates to forms in nature. For Focillon, and I think for all great art historians,

> a work of art is an attempt to express something that is unique; it is an affirmation of something that is whole, complete, absolute. But it is likewise an integral part of a system of highly complex relationships. A work of art is both matter and mind, both form and content. It is immersed in the whirlpool of time; and it belongs to eternity. A work of art is specific, local, individual; and it is our brightest token of universality.

We could easily substitute the word "species" for a "work of art", and the quotation would likewise be just as elegant. The title of my paper comes from Focillon's definition of Classicism, the ideal or doctrine whose enlightment and quest for scientific precision, balance, and harmony derived from the study of the golden ages of the ancient Greeks and Romans. To Focillon,

[16] S. Lilar, *Journal de l'analogiste* (Paris, 1979).

> Classicism is stability, security, following upon experimental unrest. "*Classicism: a brief, perfectly balanced instant of complete possession of forms*; not a slow and monotonous application of 'rules', but a pure, quick delight, like the akme of the Greeks". It is for this reason that the classic state differs radically from the academic state, which is merely a lifeless reflection, a kind of inert image.[17]

Focillon's Classicism is thus the state when everything comes together, everything makes sense: it represents the perfect moment. It isn't the theater and the wonderful exuberance of the Baroque, it isn't the lyrical of the Romanticism; it doesn't agitate too much; it is not too calm; it is pure perfection. As such, we can equate Focillon's definition of Classicism with Elegance, and then apply it to everything relevant that may surround us: a Greek temple, a suite by Bach, the perfect symmetry of the ammonite, or a painting representing a fusion of classical concern for elegance of form with a contemporary concern for balance, harmony, and rhythm (*figure 9*), or, in other words, "*a brief, perfectly balanced instant of complete possession of forms.*"

My remarks certainly would have been very different were it not for the three people who influenced me the most in making me see art—and elegance—in biological structure and process: the art historian Marie Fredericq-Lilar, my mother, who instilled in me a love of art and aesthetics, the writer Suzanne Lilar, my grandmother, who instilled in me a love of intellectual pursuit, and the painter Eugene Martin, my husband, who crystallized in me the combination of both.

FIGURE 9
Eugene J. Martin, untitled, 1995,
pen and ink on paper, private collection

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[17] H. Focillon, *The Life of Forms in Art*, trans Charles Beecher Hogan and S. Lane Faison (New York, 1948), pp. 1-2, 11-12.