Distrust That Particular Intuition: Resilient Essentialisms and Empirical Challenges in the History of Biological Individuality

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Abstract

There seem to be three intuitions about biological individuality that are held in western culture. This paper calls these intuitions about essences anatomical essentialism, physiological essentialism, and developmental essentialism. These intuitions reinforce one another. They work to a certain extent, and any explanation using one of the essentialisms tends to be accepted by an audience more easily. Yet when held unreflectively such intuitions lead to an impoverished understanding of individuality. These intuitions are highly resilient – histories of biology show how they have been challenged both analytically and empirically, yet they still persist to this day. I suggest this is because they both depend on and reinforce notions of purity, stability, indivisibility and autonomy.

Keywords: biological individuality; essentialism; Darwin; intuitions; parasitism; chimerism; levels of individuality; holobiont

Each living creature must be looked at as a microcosm - a little universe, formed of a host of self-propagating organisms, inconceivably minute and as numerous as the stars in heaven. (Darwin, 1868, p. II.404)

Stop focusing on biological individuals as entities and start seeing biological individuals as systems or relationships! Such points have been insisted upon since the 1930s or 1940s, by Ludwig von Bertalanffy or Georges Canguilhem (Gayon 1998, 308), or even the 1870s by Herbert Spencer (Gissis, this volume). All well and good, and many of the papers here are written in support. But the history of biology shows that such a habit is a difficult one to break. Despite repeated empirical demonstrations that biological individuals are not always tidy physical entities, this view is one to which people continuously return. I suggest this is because we intuitively individuate by imaginary essences.

"Essences" and "essentialism" are fraught terms in biology, especially in discussions about species and implications for natural kinds (Rieppel 2010; Wilson et al. 2007; Winsor 2006). They are used here reluctantly because only "essence" seems to convey the ontological intuitions I want to describe, and because only "essentialism" can capture the epistemological intuitions. The truly uncomfortable reader might use "intuitive pattern" in their place. Such difficulties reflexively illustrate how words can come to fail us when we try to articulate ourselves about biological individuality.

I suggest one intuitively individuates by using three kinds of essences in biology. The first is a spatial/anatomical/formal essence that takes the guise of a particular shape, which when physically divided ends the unity of the biological individual. The second is a physiological/energetic essence which behaves as a particular optimal state, such as health,
and anything detracting from that state can be seen as "foreign" to the biological individual. The third is a developmental/genetic essence, a specific pattern persisting over time, which when altered fundamentally changes the individual. For brevity I will refer to these individuating intuitions respectively as anatomical essentialism, physiological essentialism, and developmental essentialism.

Anatomical, physiological and developmental essentialism have been repeatedly challenged empirically as new discoveries have undermined our intuitions about biological individuality. Hence anatomical essentialism was challenged in the early 1740s by the discovery that the freshwater polyp Hydra viridis could regenerate after sectioning. Physiological essentialism has recently been challenged by findings that human physiological functions are assisted by various commensal and mutualistic microorganisms, not simply hindered by parasitic or pathological microbes. Developmental essentialism was challenged by the discovery in the early 1840s that certain jellyfish and parasites alternated between two distinct morphological forms during development. Yet these essentialisms live on. Why?

One reason is because each of the three essentialisms is strengthened by associations with purity and pollution, one way in which we filter our perceptions of the world (Douglas 1966, 36-37). Consider the popular contemporary intuition that each individual's genome is unchanging and unique - a form of developmental essentialism. We know this to be false, not only because genomes do change over time, but because of rare but major exceptions such as genetic chimerism, in which a single person develops out of a fusion of two separate cell lineages that otherwise would have been fraternal twins. Sometimes such people end up questioning whether this chimerism renders their selves multiple (Martin 2007, 221). Even renowned philosophers and bioethicists are guided by intuitions about individuality too. For instance, Jürgen Habermas's views on the advisability of different forms of medical genetic engineering – between good "repair" and bad "enhancement" - pivot upon developmental essentialism (Habermas 2003), although he should know better (see critique in Barnes and Dupré 2008, 232). Meanwhile governments and courts since the 1980s have used the assumption that individual people have unchanging genomic identities to make rulings. (Martin 2007, 206-7, 212).

Yet these three individuating intuitions also live on because they are often useful. They are not always incorrect, and nicely describe the world to a certain extent. For instance, physiological essentialism may be a reason why the germ theory strikes such a chord with the general public: not only does it work, but it nicely chimes with our intuitions about purity and pollution. The same point might be raised for the hypothesis of the "genetic bottleneck" as an explanation for unicellularity, to be discussed below: it appeals to an intuition of developmental essentialism. Any model or image or metaphor must oversimplify if it is to coordinate action between different people – how else could people communicate with one another if not by abstraction?

A third reason for the resilience of these essentialisms is because they fit with the cherished Western belief that each one of us is a unique being possessing agency and autonomy. This is partly fostered by beliefs in individual rights and responsibilities (Martin 2007, 222). But it also seems to emerge from a tendency most recently pointed out by Barry Barnes and John Dupré – the Durkheimian insight that rather than see agency and autonomy emerging out of a set of relationships that a person has with other people, these properties tend to be situated within the individual herself (Barnes and Dupré, 2008).¹ I expand upon this point in more detail below.

My task as historical commentator is to put these papers into some sort of larger historical pattern. What follows has two sides. On the one hand the story is something classically and unfashionably progressive. It is a tale of a "Copernican shift": a series of discoveries which gradually undermined our easy intuitions about biological individuality,
making individuality relativistic, dependent upon the researcher's perspective. Compare modern-day informatic perspectives on individuality with ancient depictions of a "soul" to see just how much change has occurred. It is a long way from incorporeal essences to defining an individual as a set of coordinated processes minimally necessary for that set to remain autonomous (Krakauer et al., this volume). The story of progress is not simply a tale of a move towards a greater array of explanations and perspectives: towards pluralism. It is also a shift towards a less-intuitively appealing world - if such a move can be called a progressive one.

Yet on the other hand there seems to be something more fragile. There is a constant danger of a person reverting back to intuitive conceptions of individuality, even when that person should know better. This danger of reversion is partly because the three essentialisms are easy to think with, and partly because audiences sometimes only seem to listen to points that appeal to intuitive individual essences. If there is an implicit tragedy here, it is that appeals to individual essences will always find large audiences, even if those appeals are oversimplifications. By way of an analogy, consider the many histories of science showing how science is a social process (simply because science happens to be done by groups of people)...consistently overshadowed in popular culture by biographies about lone scientific geniuses.2 The problem is not that there are many brilliant people in science, as there clearly are -- it is that this kind of science history is an impoverished view of how science works. The same holds true for thinking about biological individuality: our intuitions are insufficient for a complete understanding of it.

Intuitions of biological individuality: three essentialisms

There may be cognitive reasons for individuating by essence. Observing cross-cultural similarities, the anthropologist Scott Atran argued that intuitively perceiving living kinds may belong to our ability as humans to "fast-map" the world, an ability we share with other metazoa. When classifying animals, people in widely different cultures usually focus on vertebrates, placing them in different major groups; most invertebrates fall into residual ones by default. Carolus Linnaeus's class Vermes and the "puchi" of the Hill Pandaram culture of South India were both residual categories containing everything from insects to crustaceans. Such organisms tend to be lumped together because they lack "phenomenal resolution," usually being small and tending to hide or live in alien environments (Atran 1990, 65, 32-33). Atran's point about classification matters because vertebrates do not tend to challenge intuitions about biological individuality. Members of the puchi and Vermes do - but usually it is harder to notice them.

Atran also points out that humans tend to furnish the standard against which animals are compared and classified (Atran 1990, 32-33). One reason why this is relevant to biological individuality is because we associate our own individuality with autonomy. From the very beginning of its life each organism capable of awareness is the center of its own solipsistic universe. Every thought, every feeling, every action taken occurs at the very center of one's sensorium. In humans, each one of us is utterly accustomed to being at this centre. We also associate individuality with agency: we believe we can change many things in our sensorium. Indeed the issue of command and control ought to make biological individuality a key topic in the neurosciences as well, and the neurosciences a key resource for thinking about biological individuality. Is an organism controlled top-down, by a nervous centre that firmly controls the rest of the body, or does its apparent unity of action result from the bottom up, emerging out of the harmonious interaction of its various body parts? Nineteenth century neuroscientists differed wildly over the answers (Elwick 2003, 39; Elwick 2007).3
Emerging from our taken-for-granted sense of agency and autonomy are intuitions about three kinds of biological essences which constitute individuality. I will use seemingly "common-sense" examples to convey this intuitionism. They have a strange dual quality of obviousness and falsity. On the surface the intuitions verge on being plaitudes; with further reflection or the mustering of empirical cases, however, they are open to analytical and empirical challenge.

One intuition is that a biological individual is spatially or anatomically indivisible. If at a cabin in the woods I lose my hand, then the hand is no longer a part of me as an individual. It is no longer physically connected to my body; and I certainly have no further control over that hand. Such an intuition can be called anatomical essentialism.

Another intuition is that a biological individual constitutes a persistent yet unique set of functions which yield energy. Its body possesses functions such as metabolism which in combination lead to health. Something interfering with this set of functions can be identified as not belonging to the biological individual. If I am unfortunate enough to get a tapeworm, then I have become a host to a parasite. Such an intuition can be called physiological essentialism.

A third intuition is that a biological individual maintains a persistent and unique temporal pattern over its lifetime. This can be anything from an Aristotelian formal cause such as a soul, to genealogical thoughts about "bloodlines", to some modern neo-Darwinian thoughts about genes. My genome is necessary for my particular phenotypic traits to be expressed. If some sort of change is engineered in my underlying genome, then I am changed in fundamental ways as an individual. Such an intuition can be called developmental essentialism.

Several associated points follow from these intuitions about essences. For one thing, it's difficult to disentangle these three intuitive individual essences from each other. A developmental essence must somehow be linked with an anatomical essence since it dictates what form that organism will take, or the space it will take up. This is another reason why these individuating intuitions, while shallow, are hard to abandon: the three essences seem to be mutually reinforcing.

Furthermore, each of the essences seems necessary for there to be an individual. Remove one and there seems to be no biological individual. Thus if a body is somehow divided into two, intuitively these entities no longer seem to be a single individual. As a corollary, and to develop a point made by philosopher Ellen Clarke, the more of each of the three essences displayed by an entity, the easier it is to individuate. Thus a puppy is easier to see as an individual than a Portuguese man o' war or a grove of aspens (Clarke 2010, 322-323). These essences also seem to affect beliefs about higher and lower organisms: the more of the three essences displayed, the "higher" an organism seems to be.

In a related vein, purity seems to be important for an intuition about an essence, either by maintaining a boundary separating the essence from the outside, or through some kind of endogenous power this essence holds. Individuation is marked by degree of purity of essence. Individuation-by-purity also facilitates the reception of certain explanations. To repeat, non-life scientists see as reasonable the explanation that the microscopic entities known as "germs" cause diseases by "invading" or "contaminating" a body's purity. One reason for this belief in purity may again be anthropological: its opposite, "pollution," is the byproduct of our systematic ordering and classification of matter, something that does not fit into our cultural classifications. To paraphrase the anthropologist Mary Douglas, if dirt is "matter out of place" (Douglas 1966, 34-40) then something which challenges intuitive essences of individuality - such as a "germ" or apparent genetic "contamination" - constitutes a form of pollution. The resilience of our intuitions about individual essences is strengthened by a belief in a constant disorder held at bay by these essences.
However, our thinking about biological individuality has taken a Copernican route as we learned that our intuitions may not be entirely correct. Various challenges have forced us to consider alternatives to these essentialisms. What about plant cuttings? Does a genetic chimera get to vote twice? What does the discovery of hundreds of different bacterial species living inside each person – the "holobiont" (Gilbert et al. 2012; Gilbert, this volume) imply for the germ theory of disease?

Notice how each case depends on empirical examples. Indeed the entire point of the paper by Scott Gilbert, Jan Sapp and Alfred Tauber is to provide various instances which undermine simple intuitions about biological individuality. To paraphrase them – indeed they are themselves quoting Lynn Margulis - whether convenient to our beliefs or not, one has to note these examples because they're there (Gilbert et al. 2012, 336; Dawkins and Margulis 2009).

But such empirical refutations are made possible only by successive discoveries. It was simply not possible to discuss genomic chimerism in 1911, for instance. This is why the history of biology matters to thinking about biological individuality – because it furnishes examples that undermine our intuitions. Often these examples qualified as discoveries because they undermined our intuitions. Yet such an assertion is not necessarily progressivist if these discoveries keep getting forgotten - especially by historians of biology. It is to these discoveries that we now turn.

**Anatomical essentialism**

Anatomical essentialism, to repeat, is an intuition that a biological individual has a spatially or anatomically indivisible essence. This builds on what Olivier Rieppel discusses at the very beginning of his careful chapter. Indeed Cicero introduced the term *individuum* into Latin to describe not a living being, but instead Democritus's indivisible atom (Lecourt 1998, 218), and presumably it is from Latin that the current meaning of "individual" has derived. Accompanying that belief is that this anatomical essence is protected or bounded by some sort of envelope: the presence of other bodies within that spatial envelope may undermine biological individuality. Indivisibility will be addressed first, then purity.

Empirically, the intuition that an anatomical essence consists of its "indivisibility" is easily undermined. For one thing it's zoocentric: plants such as willow trees can be easily propagated through cuttings. Even in animals it has been known at least since Aristotle that certain animals can live after sectioning. Thus in his treatise *Measure of the Soul*, written around 388CE, St. Augustine of Hippo observed how after being cut into three, each of the separated parts of a millipede seemed to act as individuals (Trembley 1744, 299).

In retrospect this makes Abraham Trembley's discovery of the regenerative abilities of *Hydra viridis* seem unsurprising, though it became a scientific sensation in its day. In 1740 he gathered *Hydra* polyps from ditches in Sorgvliet, near the Hague, and put them in glass vessels. He then cut them into sections, and observed each section regenerate back into a complete *Hydra*. Trembley's research was partly oriented to one simmering dispute at the time – whether polyps, known as "zoophytes," were more properly described as animals (because they moved, somewhat like inchworms) or as plants (because they could form new *Hydra* from cuttings) (Lenhoff et al. 1986, 180-182).

Because *Hydra*’s apparent animality made it closer to humans, discussions about its individuality centered upon anatomical and developmental essences. Trembley's correspondent R.A.F. Réaumur wondered what happened to the polyp's "soul" when it was cut into pieces (Roger 1997, 122); one provocative answer, from J.O. de la Mettrie, was that its soul was material (Hankins 1985, 133; Spary 1996, 181-184). Why did the separated pieces become themselves new and complete *Hydra*? Such questions led to disputes over
whether the form of an individual pre-existed in ova or sperm (preformationism), or whether it gradually emerged from less-organized material (epigenesis) (Roe 1981, 12). All seem to have agreed that there was some sort of essence necessary for the Hydra to be considered an individual: thus John Turberville Needham and the Comte de Buffon argued that all organisms consisted of "organic molecules" circulating in and out of us, but only when attached to an interior mould dictating the organism's form (Roger 1997, 128-129).

The belief that the Hydra was also plant-like reveals the long concern of botanists with biological individuality. Plants not only reproduce from cuttings; they also seem to repeat their parts, with leaves, sepals and petals of flowers all being somewhat alike. Although often described as beginning with Goethe and the Romantic biologists, this claim of part-repetition was made as long ago as Theophrastus in 300BCE (Nyhart and Lidgard 2011, 380-381). This long concern with individuality helps us situate the cell theory of Matthias Schleiden and Theodor Schwann when they proclaimed that larger organisms were composed of repetitive "elementary particles" called cells, which also acted as "elementary individuals" (Schwann 1847, 167). Relevant here is the word "elementary", which seems to be derived from contemporary chemistry, where Antoine Lavoisier defined an element as any chemical that could not be further subdivided. Thus a cell could not be further subdivided without losing its anatomical and physiological essence. It was only in later instantiations of the cell theory that cells changed from anatomically indivisible units that emerged in a medium outside or within each cell ("exogeny" and "endogeny" respectively) into units that reproduced by division (Baker 1948; Mendelsohn 2003, 16). If depicted in terms of essences one might depict such a shift in cell theory as a move from anatomical essentialism to developmental essentialism.

The botanist Schleiden, following predecessors like Leibniz and Goethe, articulated a relativistic approach towards biological individuality: individuals could exist at different physical scales.

Now the individual is no conception, but the mere subjective comprehension of an actual object, presented to us under some given specific conception, and on this latter it alone depends whether the object is or is not an individual. Under the specific conception of the solar system, ours is an individual: in relation to the specific conception of a planetary body, it is an aggregate of many individuals. (Schleiden 1849, 127)

By "subjective comprehension" Schleiden seems to have meant the observer's frame of reference – even an entity as large as the solar system could be seen as an individual, if the background was large enough. What counted as an individual depended upon one's perspective.

Alongside such relativistic views about individuality was the notion of orders of individuality: a matryoshka-like picture of individuals made out of smaller individuals made out of still smaller individuals. Thus it was not simply cells or indivisible epidermis-covered entities that could be seen as individuals; if seen from a certain perspective, a cluster of them could be seen as an individual too. Schleiden's view influenced two very important evolutionists who also thought a great deal about individuality, Ernst Haeckel and Herbert Spencer.

Haeckel was Schleiden's student and in his 1866 Generelle Morphologie Haeckel discussed orders of individuality: what he called "tectology." He proposed six, from the simplest "first order" (such as cells), to the most complex "sixth order" (colonial organisms like a Portuguese man o'war). Higher order individuals were built up of simpler order ones (Haeckel 1866, 269-331, 332-363; Richards 2008). Such a conception was relativistic: an individual in one context became an organ in another. In Nyhart's words, for Haeckel "'Individual' and 'organ' were not absolute concepts but relative ones." (Nyhart 1995, 136). At
the same time as Haeckel, Herbert Spencer wrote about biological "compositions" of first, second, third and fourth order, in which more complex aggregations were built up from simpler units. We know Spencer was also influenced by Schleiden because Spencer – not fond of acknowledging his intellectual debts - actually used the Schleiden quote above in his Principles of Biology (Spencer 1864-1867, II:4-5, I:202-203). Indeed, in 1868 Haeckel wrote to Spencer and noted they shared the "same ideas", calling particular attention to his own sections in the Generelle Morphologie on individuality (Haeckel 1868).

Ultimately it is unimportant to determine who first enunciated the principle of levels of organization and orders of individuality. What is important is that by the late 19th century there had appeared a number of different systems of levels of organization. In 1911 the entomologist William Morton Wheeler pointed out not only Spencer's and Haeckel's systems, but also drew attention to August Weismann's. He also noted physicist-philosopher Gustav Fechner's very expansive system, one depicting the entire universe as a single individual organism composed of smaller ones (Wheeler 1911, 308-9). Ultimately such systems made it easier to depict individuals relative to a particular background or environment. Orders of individuality made it possible to see biological individuality relativistically, while at the same time retaining the spatial unity necessary for any anatomically essentialist view of an individual.

Developmental essentialism

Developmental essentialism is the intuition that a biological individual consists of an essence remaining stable over time. In 1819 Adelbert von Chamisso asserted that many marine polyps took on one form, then a completely different form, then returned to the first form; it was also suspected that certain parasites such as trematode worms also did this. In 1842 the Danish naturalist J.J. Steenstrup confirmed the suspicion, and claimed that this "alternation of generations" was a common pattern in plants and animals. Nyhart and Lidgard (this volume) discuss how over the next decade the discovery excited many European naturalists, forcing them to think and re-think how they designated relationships between parts and whole.

One reason why the claim of alternation of generations was controversial and exciting was because it challenged the intuition that an individual should be spatially indivisible: anatomical essentialism. How to solve this? One famous response was made by T.H. Huxley, who simply redefined the phenomenon using developmental essentialism. Huxley presented his solution as a way to cut through overly complex details. The individual could be defined as everything emerging from a sexually fertilized ovum. From "phytoid" in botany Huxley created the word "zoöid," using it to denote any entity emerging from an act of sexual fertilization that seemed to simulate an individual (Elwick 2007, 133).

Moving ahead forty years to 1892, not only can Weismann's proposed "germ plasm" be depicted as a persistent and pure developmental essence; its favorable reception owed much to its appeal to popular intuitions about that essence. Weismann proposed a complete separation between the "germ plasm" of the chromosomes and the rest of the body ("soma"): it was the germ plasm that determined the form that the body was to take. The standard account is that in so doing Weismann undermined contemporary "Lamarckian" claims to soft inheritance (Mayr 1982, 699-700). But Weismannism can also be seen as holding a commitment to a temporally persistent essence of biological individuality. That is, the germ-plasm was able to persist over time by remaining upstream from any somatic changes: it was powerful because it was kept separate and thus kept pure. Some interesting contemporary challenges - the most famous being Spencer's question of why worker ant larvae could develop into a queen in her absence – were dismissed not only with the "crucial experiment" of five generations of mice tails forcibly removed (Weismann et al. 1891), but also by
appealing to an intuitively pure developmental essence. Yet upon reflection, of course the germ changes over time, over generations: this is the only way Darwinian evolution can occur. The germ line cannot be completely stable - Weismann's intuition is useful, but only to a point.

It is telling that challenges to developmental essences are characterized as "contamination." A fairly recent example of this can be found in the case of Wolbachia. The latest version of developmental essentialism is that each individual, and each species, possesses a distinct and unchanging genome. Wolbachia is an intracellular bacterium most famous for its prevalence in arthropods, where it affects their development. But Wolbachia is also mutualistic in nematodes: its removal, by antibiotic, often kills or stunts the development of its wormy host. The implication is that Wolbachia's presence is actually necessary for nematodes to develop properly. Yet such mutualism is difficult to recognize by the developmental essentialist: in 1999 researchers studying nematode genomes complained of "bacterial sequences contaminating their filarial isolates", apparently ignorant of Wolbachia's presence (Kozek and Rao 2007, 11). That notion of contamination – implying a pure genomic essence – blinded the researchers to the fact that the Wolbachia-nematode relationship is a case of a "multi-genome ecosystem" (Bettan 2013).

Besides "contamination," another way to describe violations of pure developmental essence is to describe the result as mongrelism or chimerism. Consider human genomic "chimeras" who possess two genetically distinct cell lines. Known specifically as "tetragametic chimerism", this phenomenon occurs when two fertilized eggs fuse. A 2003 report in New Scientist describes one such chimera - a person known only as "Karen" - as "a mixture of two different people". It continues to use the language of developmentalist essentialism when claiming that "far from being pure-bred individuals composed of a single genetic cell line, our bodies are cellular mongrels" containing cells from our mothers as well as grandparents and siblings. The reporter obviously sees the subject as an individual, but it is significant that she uses the word "mongrelism" to explain the phenomenon to a general audience (Ainsworth 2003; Barnes and Dupré 2008). The sociologist of biomedicine Aryn Martin notes the ways in which popular culture defended individual personhood against threats such as Karen: from a Discovery Network documentary entitled "I am my own Twin" to "Bloodlines," the 2004 season finale of Crime Scene Investigation (CSI). In that CSI episode the chimeric villain is not initially charged with sexual assault because his semen and blood do not seem to genetically match, though eventually he confesses to the crime (Martin 2007, 215).

That said, although the effects of genomic chimerism are sometimes barely noticeable, they can often be quite harmful. The possible impairment caused by chimerism has been used to explain just why so many organisms in their life cycles go through a unicellular phase (a single pair of gametes), despite the inherent vulnerability of such an adaptation. The unicellular phase has been described as a "reproductive bottleneck" which ensures that only a single genome is present; it is a beneficial adaptation because the benefits of passing through a single-cell stage outweigh the costs (Grosberg and Strathmann 1998). Intuitively such an explanation seems reasonable because we automatically recognize the function of the reproductive bottleneck: as a filter to purify the developmental essence.

One problem with such intuitions is that they may lead us to prematurely close off alternatives – to overlook alternative forms of development that do not involve differentiation from a single cell. This would seem to be a point of Beckett Sterner's paper – that most work on the benefits and costs of multicellularity assume cases in which multicellularity emerges from the division of a single cell. But this is to ignore alternative states of how multicellularity arises, such as by aggregation of cells from the same organism or even from different species, as with biofilms (Sterner, this volume). Consider how slime molds develop:

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rather than differentiate from a single fertilized cell, *Dictyostelium discoideum* goes through a life cycle which starts as a mass of spores, each of which divides into an amoeba; these amoebae then divide into free-swimming independent daughter cells, which then aggregate toward a central point to form a migrating and seemingly unitary "slug", which then turns into a stalk that forms a mass of spores (Sunderland 2011, 510-511). Are there other forms of development which are being overlooked because of our intuitions?

**Physiological essentialism**

Physiological essentialism is the intuition that a biological individual often consists of a set of functions producing a unique yet persistent pattern of energy transformation. Metabolism can be seen in this way: converting the different physiological essence of another organism into one's own essence. As Claude Bernard said, the dog "does not get fat on mutton fat, it makes dog fat" (Bernard in Landecker, this volume). Hannah Landecker points out that not only was homeostasis the action of maintaining an internal system that was autonomous from the outer environment; the very activity of metabolism was a form of "transubstantiation" from one substance into another. Indeed it is telling that where Huxley saw in protoplasm the unity of all living substance from cells to microbes to plants and humans, making it interchangeable, a critic saw infinite difference and uniqueness (Landecker, this volume) – infinite different essences, perhaps.

What happens when other physiological essences within our bodies become rivals, ingesting the food we need to maintain our own energy and health? Michael Osborne's paper discusses a historical moment in which the meaning of parasitism changed from something relatively innocuous – organisms eating together as "messmates" – to something pathological. I suggest that parasitism became pathological when scrutinized by the light of physiological essentialism: the purity of the host's energy pattern (as homeostasis, health, or simple well-being) contaminated by outsiders. In this sense health became defined as freedom from interference by outsiders – fitting our preference for autonomy. We ought instead to prefer definitions of health such as Canguilhem's – the "margin of tolerance with respect to the environment's betrayals" (Canguilhem 1989, 199, 156; Gayon 1998, 313; Lecourt 1998, 221), but such a conception is more complex than a simple intuition of physiological purity.

Interestingly, physiological essentialism seems to mesh well with the definition of individuality as the aligned "fitness interests" of different bodily components. Body parts or functions that prosper at the expense of other components are depicted as "cheating" – hence cancer cells are highly fit as cell lineages, but their spread ends up harming or destroying the body in which they live (Folse III and Roughgarden 2010, 448). This seems to be one point of Matthew Herron's chapter – how organisms such as the volvocine algae manage to prevent such "within-organism conflicts". At the same time, however, Herron eschews physiological essentialism by pointing out that there are intermediate degrees of individuality also (Herron, this volume).

To discuss pathologies caused by internal disharmony also brings us to developments such as the germ theory. It would seem that the germ theory is not only instrumentally successful at preventing disease – it is also easy to think with. As noted above, its immense success is helped by capitalizing on our intuitions about our own internal purity and the threat of invasion or contamination. Yet intuitions about purity can only take us so far: the germ theory oversimplifies the role of foreign microbes, depicting them all as pathological. What about "good bacteria?" Gilbert, Sapp and Tauber (2012) note that certain diseases are actually prevented by the presence of some of our symbiont microbes, sometimes going even so far as to suppress harmful immune responses which lead to conditions like inflammatory bowel disease.
Indeed current research on the microbiome challenges physiological essentialism. It is generally agreed that there are about 10 times the number of microbial (protists, bacteria, fungi) cells relative to "human" cells. While the numbers differ considerably, this ratio stays relatively stable. Thus one 2010 paper in *Nature* estimated 100 trillion to 10 trillion. More importantly, this paper estimated that among these microbial cells, there were at least 160 different bacterial species in each individual human body surveyed, and sometimes far more (Qin et al. 2010, 64). Many of these bacteria fit the popular definition of being "good", since they contribute in different ways to the health of their human host, such as converting (fermenting) sugars to fatty acids and contributing vitamins. Gilbert, Sapp and Tauber trumpet this paper as part of a larger shift in how we perceive not only human health but also biological individuality. The existence of a microbiome – a microbial ecosystem – inside the human body would seem to strengthen the claim of their paper's title that "we have never been individuals."

But what Gilbert, Sapp and Tauber do not note is a reaction appearing almost exactly a year later, also in *Nature*. Another group of scientists claimed that despite this enormous variety of bacteria, there could be found only three stable types across humanity, regardless of national origin. These stable groups the authors call "enterotypes", and suggest these types imply a finite set of well-balanced symbiotic states between microbes and host (Arumugam et al. 2011). The philosopher John Huss is skeptical of this typology, and describes it as part of an emerging dispute over whether the "metagenome" is a genomic unit or a system (Huss 2013). In the context of this paper, the attempt at "enterotyping" might be seen a way to set out unique yet persistent patterns of energy transformation: a claim there are ultimately only several physiological essences. The concern is not whether this particular typology is useful, or even whether it oversimplifies (which it must do in order to coordinate action between people) – it is that people come to think that there are no alternatives.

**Conclusion: interfaces, not individuals**

How does one avoid essentialism when it comes to biological individuality? One route is to change perspective, boldly challenging the assumption that perspectives on structure and perspectives on function are antagonistic (Brigandt, this volume). Another strategy is to focus on relationships among biological individuals, whatever those individuals happen to be. To be sure, all the chapters in this volume – and biologists for that matter – do discuss relationships of some sort. Indeed it is probably not possible to be a pure essentialist in biology. Even the most staid descriptive anatomist must discuss how one body part is linked with others, for instance.

Olivier Rieppel's discussion of the enkaptic hierarchies of Martin Heidenhain (Rieppel, this volume) not only talks about nested hierarchical sets and the entities within each set, but also the links between these entities – what is variously called their integration, or the part-whole relation, or the new properties emerging when a set of parts at one level are integrated enough to compose a new whole. Andrew Reynolds focuses not on cells by themselves, or as parts making up greater wholes, but characterizes them as "gregarious social organisms in constant communication with one another by chemical and physical signals" (Reynolds, this volume, XXX). Snait Gissis insists that what characterized Herbert Spencer's thought was a focus on the interface between an "individual" at whatever level of organization and its environment: this interface was a "progressing equilibration" (Gissis, this volume). Evolution was a dialectical change resulting from that interaction. "Everywhere the differentiation of outside from inside comes first", he said, such as the simplest cell-wall distinguishing the cell contents from their environment (Spencer 1864-1867, II:378). Indeed it is odd that Spencer has become known to history as the key Victorian "individualist." I
suspect what is over-simplistically described as Spencer's "Lamarckism" is derived from our intuition that evolution must occur in individuals. But such an intuition impoverishes our view of Spencer's biology and indeed his social theory too.

The same intuition also oversimplifies our understanding of other evolutionists. This chapter began with an epigraph by Charles Darwin stating how each living creature ought to be seen as a microcosm. Although Darwin is well studied, his concerns about biological individuality have rarely been discussed. An interesting alternative history of Darwinism along these lines has periodically been suggested but never brought to fruition. One might move from his early Beagle experiments in which he bisected planarian flatworms (*P. tasmaniana*) and watched how in 25 days they formed "two perfect individuals" (Darwin 1844, 244), or how in his notebooks he described trees as "great compound animals" (Darwin 1987, 529). Jonathan Hodge described how in the late 1830s Darwin saw larger entities ("species" or "trees of life") as analogous to individuals while also depicting smaller ones (buds, cells, gemmules, living atoms, monads) as individuals too (Hodge 1985, 209). Philip Sloan noted how colonial invertebrates allowed Darwin to draw analogies between the species and the individual - (Sloan 1986, 421) – in other words, to see the individual relativistically.

Such a history would describe how the particles that Darwin called "pangenes" weren't hypothesized simply to explain heredity, as they tend to be explained today (cf Bowler and Morus 2005, 195). Darwin also proposed the mechanism of pangenes to solve problems noted above, such as why "lower animals reproduce so many perfect individuals." After all, Darwin saw sexual and asexual generation as fundamentally the same process: he did not see processes such as parthenogenesis as odd. Rather, "the wonder is that it should not oftener occur" (Darwin 1868, II:358). Such a history would enrich our view of Darwinism, which is generally explained using intuitive biological individuals. This bad habit was begun by Darwin himself, who in the *Origin* tended to use examples of dogs and birds to explain natural selection and descent with modification. Modern-day Darwinists and nature documentaries tend to do the same – as far as I am aware there are no breathless descriptions by David Attenborough of slime mold development. While using obvious biological individuals as examples facilitates explanations of the neo-Darwinian synthesis and the biological species concept, it is to rely on an impoverished range.

There is no reason for historians of biology - particularly those involved in the "Darwin industry" - to be stuck in this rut. For by taking up past questions about biological individuality we can revisit topics which have been so extensively discussed it seems that there is nothing left to say. That alternative history of Darwinism and biological individuality, in addition to taking up pangenes and compound animals, might be able to say new things about contemporary scientific opposition to Darwin's proposals. Consider the zoologist Louis Agassiz, now popularly known for his "creationism" or his threefold parallelism. Agassiz levelled a now-forgotten challenge to Darwinism which took up the matter of biological individuality and what he saw as Darwin's simplistic reading of it.

Would the supporters of the fanciful theories lately propounded, only extend their studies a little beyond the range of domesticated animals, - would they investigate the alternate generations of the Acalephs [cnidarians, commonly jellyfish], the extraordinary modes of development of the Helminths [flatworms], the reproduction of the Salpae [pelagic colonial tunicates], etc., etc., - they would soon learn that there are in the world far more astonishing phenomena, strictly circumscribed between the natural limits of unvarying species, than the slight differences produced by men, among domesticated animals; and, perhaps, cease to be so confident, as they seem to be, that these differences are trustworthy indications of the variability of species. For my own part, I must emphatically declare that I do not know a single fact tending to
show that species do vary in any way, while it is true that the individuals of one and the same species are more or less polymorphous. (Agassiz 1857-1862, III:98-99)

Ironically, Agassiz could not have realized that Darwin was just as privately intrigued about biological individuality as he himself was, since the Origin used only "domesticated animals" for its examples rather than, say, members of the puchi group. And to someone unaware that biological individuality was a highly contested issue in mid-19th century biology (Nyhart and Lidgard 2011, 374-5, Elwick 2004), Agassiz's own criticism seems confused – how can an individual be polymorphous? Lacking alternative terms, Agassiz had no choice but to use the word "individual," and that term seems to betray him.

An alternative history of Darwinism would take up what was the real mystery of mysteries – just what was a biological individual – but would not use the very word whose definition it was probing. What sort of term might it use? One possibility is to follow biologists such as T.H. Huxley and Ernst Haeckel and shift the conceptual ground by coining new words. For instance "holobiont" is favored by Scott Gilbert (this volume; Gilbert et al. 2012) to denote the complex interacting system of organisms and symbionts.

But would such names be favored in the wider culture, or even among scientists? There will likely be resistance because such words challenge our everyday experience as seemingly autonomous agents, and because scientific explanations that appeal to our own intuitions about essences tend to be more popular. I mentioned that this chapter was partly a story about a "Copernican shift" from an easy intuitive view of biological individuals to one that was more relativistic. But even in astronomy the change was not entirely smooth; our old intuitions die hard. Almost 500 years after Copernicus undermined the view that the sun went around the earth by suggesting that the earth instead went around the sun, astronomers still use the words "sunrise" and "sunset." Our own intuitions about individuality will probably be just as difficult to dislodge.

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1 Indeed, much of this commentary and its focus on essences is deeply indebted to the powerful meditations on essentialism in the final two chapters of (Barnes and Dupré, 2008).

2 There is even a rueful name for this phenomenon: the "Sobel Effect." (Miller, 2002)

3 At various points during our conferences it was asked why biological individuality is currently a 'hot' topic – one answer might be because issues of authority and control by agencies whose legitimacy used to be unproblematic are now hotly questioned, and new ways of conceiving how systems can be ordered and governed are emerging.

4 Spencer credits Schleiden, but does not give the actual source.

5 There is also a possibility that the concept of "emergent" properties originated from all of this levelling. It may be a coincidence, but Wheeler credited Spencer's closest friend, G.H. Lewes, with being the first to use the word "emergence" to denote how properties emerge at higher levels (Wheeler, 1928, p. 15).

6 The subject of the New Scientist article only discovered she was a tetragametic chimera when she needed a kidney transplant and so underwent blood tests to discover suitable donors.

7 Which is doubly strange – a foreign intervention to prevent the body's overreaction to what it perceives as a foreign intervention, all in the effort to maintain internal "purity."

8 This was his pre-1859 discussion about the apparent correspondence of paleontological sequence, embryological development, and "relative standing" of a species in the animal kingdom. Agassiz 1962 [1857], 29, 84.