THE EMERGENCE OF SEX

by Ursula Goodenough

Abstract. Biological traits, the foci of natural selection, are by definition emergent from the genes, proteins, and other "nothing-buts" that constitute them. Moreover, and with the exception of recently emergent "spandrels," each can be accorded a teleological dimension—each is "for" some purpose conducive to an organism's continuation. Sex, which is "for" the generation of recombinant genomes, may be one of the most ancient and ubiquitous traits in biology. In the course of its evolution, many additional traits, such as gender and nurture, have emerged. Patterns of sexual exchange are the basis for patterns of biological evolution and are central to the process of eukaryotic speciation. Human sexuality is central to our selves.

Keywords: death; evolution; gender; recombination; sex; sexuality; speciation

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How does a biologist make emergence interesting? It has been my experience that once the dynamics of emergence are explained, as wonderfully executed by Jeremy Sherman and Terrence W. Deacon (2007; see pp. 873–901 in this issue), and the basic emergence concept—"something else from nothing but"—is grasped, there's a way that ennui starts to creep in. This emerged from that, and that emerged from that, and. . . .

I therefore have elected to stack the deck by describing the emergence of sex, the hope being that the subject is of sufficient inherent interest that the narrative of its emergence as a central feature of our lives will at least give ennui a run for its money.

That said, sex, like all biological traits, has its narrative lows; it is likely that countless students have been driven away from biology by their struggles to understand what meiosis is all about. But there are narrative highs as

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[*Zygon*, vol. 42, no. 4 (December 2007)]
 ISSN 0591-2385

well. Since I have been studying the molecular mechanisms and evolution of sex in the laboratory for some thirty-five years, I am closer than most to its astonishing elegance, some of which I try to convey here. And, because I am writing for *Zygon*, I include some ruminations on the unique features of human sexuality. For the most part, however, I consider sex as a biological trait. Like all biological traits, sex is an emergent phenomenon. We can reduce it to its collection of nothing-buts—gender-determination and differentiation, mating and sexual selection, fertilization, meiosis—and reduce these to their nothing-buts—hormones, gametes, chromosomes, DNA—and then put them all back together and marvel that there emerges a unitary phenomenon—sex—that permeates the planet.

Formally, biological sex refers to activities leading to the production of recombinant genomes, where *genome* refers to the genetic information that specifies the construction and activities of an organism and *recombinant* refers to a genome that has acquired genetic information from another individual. Prokaryotes—bacteria and archea—engage in minimalist versions of sex that I describe first. Eukaryotes—organisms with true nuclei (karyons)—generate not only recombinant genomes but also recombinant offspring, and their sexual interactions entail far more complex and hence interesting events than prokaryotic versions.

Biodiversity

The story of sex needs to begin with an overview of evolutionary history. Figure 1 summarizes our current understanding of the evolutionary generation of biodiversity. The common ancestor of all modern life, at the hub of the diagram, is a hypothetical entity deduced from the fact that all modern life shares many complex features—for example, DNA-based genomes, triplet genetic code, ribosome-based protein synthesis, metabolic pathways—and hence must have evolved from an ancestor that also possessed these complex features.

Starting from the common ancestor, evolution followed three major routes, generating the three domains of life depicted in Figure 1: the Archaea, the Eukaryotes, and the Bacteria. Within each domain, further branching occurred to generate major subgroupings, and each subgroup, in turn, contains numerous sub-subgroups, not to mention the countless variants that went extinct along the way. To get a sense of how minimalist the Figure 1 diagram is, the reader is encouraged to find Animals—to the left in the Eukaryote "bubble" in the sub-grouping called opisthokonts—and realize what the diagram would look like if an attempt were made to depict the full animal radiation, including the human. To be legible, the diagram would need to be enlarged by several orders of magnitude. The figure is equally minimalist with respect to the prokaryotes—the bacteria and archaea—which were the only kinds of organisms on the planet for at least

the first half of life's history and which are estimated to represent some two-thirds of life's biodiversity.

Prokaryotic Sex

Sex in modern bacteria is widely distributed, and perhaps universal, and hence is likely to have been a trait that evolved early in prokaryotic evolutionary history. Prokaryotic sex is thought to occur infrequently, but given the vast sizes of prokaryotic populations, "infrequent" translates into "often" on a global scale.

Here and in subsequent sections, I often consider sex-related traits from two perspectives. I first reduce the trait, lifting up its key nothing-but parameters deduced via scientific inquiry (recognizing, of course, that these nothing-buts are themselves emergent from more basal nothing-buts). I then consider the emergent properties that flow from these relationships.

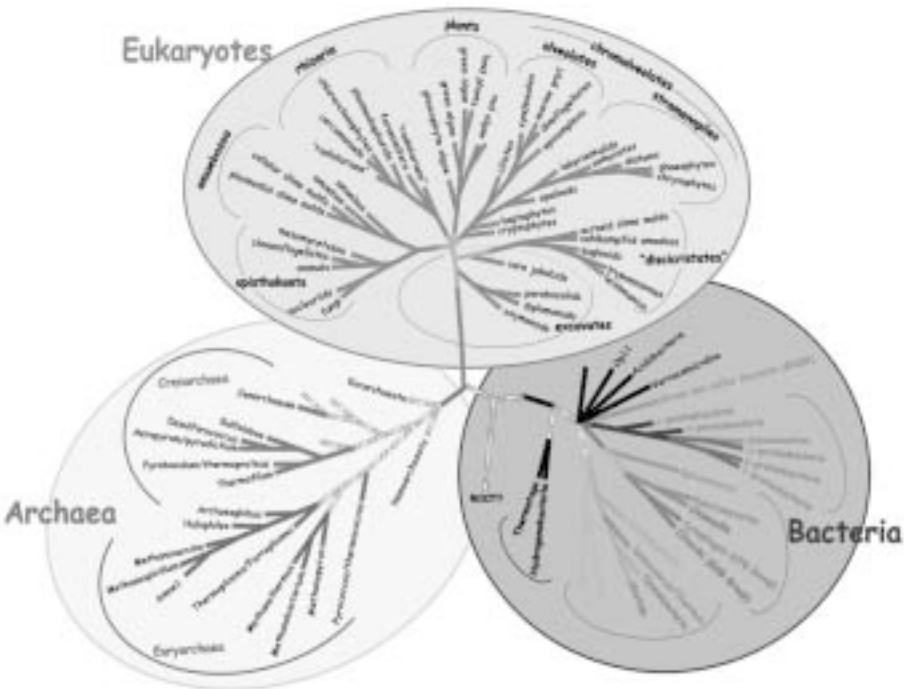

Fig. 1. Molecular phylogeny of the three domains of life (adapted from Baldauf et al. 2004), where the named groups are all modern organisms. The lengths of the lines connecting the various groups represent degrees of biological relatedness and not evolutionary time. Hatched lines indicate relationships that are still highly speculative. See *http://www-users.york.ac.uk/~slb14/labpage.html*.

Reduction: Prokaryotic sex entails taking naked DNA from exogenous (external) sources and incorporating it into genomes. In some cases (conjugation), DNA transfer is mediated by instructions encoded in DNA elements called plasmids; in other cases (transduction), the new DNA is introduced via viral infection; in other cases (transformation), naked DNA is simply pulled into the cell; in the archaea, where sexual exchange has only recently been discovered (Papke et al. 2004), additional mechanisms may well be operant. Once the exogenous DNA has entered the recipient organism by whatever means, enzymes are used to splice the incorporated DNA into the organism's genome by a process aptly termed "cut-and-paste," somewhat like editing a movie tape where original sectors are cut out and replacement sectors are spliced in.

Prokaryotic recombination is often *homologous*, meaning that when the introduced DNA includes sequences similar to sequences carried in the genome of the recipient, the donor DNA lines up with the recipient DNA and, via cutting-and-pasting enzymes, the donor information replaces the recipient information (like taking out a film scene and replacing it with another version of the same scene). But a hallmark of bacterial (and probably archaeal) sex is that the exchange can also be *promiscuous*: a bacterium may take up DNA from a bacterium of a very different lineage and splice nonsimilar (heterologous) sequences into its genome (the equivalent of splicing into a movie a scene from a different film). In scientific parlance, prokaryotic sex is said to include "lateral gene transfer" between disparate lineages, allowing a prokaryotic cell to acquire totally novel genetic ideas.

Emergence: The salient outcome of prokaryotic sex is that one organism gains genetic information by acquiring DNA from a second organism, the emergent outcome being the creation of *recombinant organisms*. The recombinant organism may acquire selective advantages from such acquisitions, a contemporary example being the acquisition of genes that confer antibiotic resistance. Therefore, the capacity to engage in recombination is under positive selection. That is, as with all biological traits, recombination is "for" something; it has a purpose, or *telos* (a concept expanded in Sherman and Deacon 2007).

A second emergent outcome of prokaryotic sex relates to the very pattern of prokaryotic evolutionary history. Whereas the lines neatly radiating out in the Archaea and Bacteria bubbles in Figure 1 describe useful groupings based on metabolic and habitat specializations, there are important ways that such branching trees are false (Doolittle and Bapteste 2007). Given that lateral gene transfer is so prevalent, a given bacterial lineage is likely to harbor genes acquired from very different bacterial lineages, meaning that prokaryotic relationships are more aptly depicted as a vast network or reticulum. Tidy branching trees are appropriate only to organisms that restrict recombination to organisms of their own kind or species, which, as we shall see, is the overwhelming case for eukaryotes.

Ploidy Transitions and Recombination

Eukaryotic sex also features recombination as a key emergent endpoint, and the enzymes involved in cutting and pasting DNA are often very similar to those employed by prokaryotes. But this endpoint is achieved via very different means.

For a start, eukaryotic sex entails *ploidy* transitions, usually haploid → diploid → haploid (the occasional polyploid lineage obeys the same fundamental rules). A haploid nucleus contains one genome, one complete set of the genetic information possessed by that species; a diploid nucleus contains two genomes, two complete sets. These sets are not expected to be identical in detail; one genome may contain a gene specifying brown fur while the equivalent gene in a second genome specifies black fur. The alternatives are called *alleles*. But both genomes include equivalent fur-color genes, pyruvate dehydrogenase genes, and so on, the total for humans being some 22,000 genes in a haploid genome, apportioned to 23 chromosomes. We now understand that genes are by no means the only carriers of genetic information; allelic versions of regulatory DNA associated with genes and allelic versions of regulatory RNA that is not translated into protein are also key players. But these elements obey the same rule—one copy in haploids, two copies in diploids—so we can continue to focus on genes.

So how are these ploidy transitions accomplished? The haploid → diploid transition occurs when two haploid *gametes* (for example, eggs and sperm) of the same species fuse together, and their nuclei then fuse together, to form a diploid *zygote*, a process known as *fertilization*. The diploid → haploid transition occurs during a process called *meiosis* during which the diploid chromosome complement is apportioned into complete-genome haploid sets that come to reside in gametes. Although variations on this theme generate stunning eukaryotic life-cycle diversity, the haploid gamete → diploid zygote → meiosis → haploid gamete theme is always encountered during the course of a eukaryotic sexual life cycle.

Reduction: It is during meiosis that recombination takes place. One form of recombination, occurring early in meiosis, resembles what we have described in prokaryotes: DNA from one chromosome is spliced into a second chromosome. Importantly, the process is rigorously homologous. If we focus on one chromosome, say #9, in an egg-derived haploid set, it lines up with the similar #9 sequences in the sperm-derived haploid set, much as we saw for prokaryotic homologous recombination. There then occurs a cut-and-paste event such that the first sequence replaces the second. Also importantly, the process is set up to be *reciprocal*: as the first sequence replaces the second, the second simultaneously replaces the first. Hence the two chromosomes that participate in reciprocal homologous recombination wind up with the same amount of information that they

started with, but each often carries different alleles of that information from the version it originally carried.

A second form of eukaryotic recombination, called *independent assortment*, occurs later in the meiotic process and relates to the mechanics of apportioning complete-genome haploid sets to gametes. Each human gamete resulting from meiosis will carry a complete set of 23 chromosomes, but some of these (on average, half) were contributed during the prior fertilization event from the sperm of the paternal parent and the rest from the egg of the maternal parent. Moreover, if homologous recombination has occurred—and each chromosome typically engages in at least one homologous exchange along its length during early meiosis—the gamete is more accurately described as carrying 23 maternal-paternal mosaic chromosomes. When this gamete (sperm) fuses with an egg that also carries 23 maternal-paternal mosaic chromosomes, the resultant diploid zygote, with 46 chromosomes, is splendidly recombinant.

We have been using human examples, but the capacity for such ploidy transitions is in fact ubiquitous. Modern organisms in all eight of the eukaryotic subdomains depicted in Figure 1—opisthokonts, amoebozoans, plants, and so on—have been either directly observed to engage in sexual behavior or found to harbor a set of genes expressed exclusively during meiosis. This means that the common ancestor to all modern eukaryotes most likely possessed this capacity as well. The alternative, that the invariant features of meiosis were independently invented multiple times in multiple lineages, is quite as implausible as proposing that the triplet DNA code was invented multiple times rather than being a feature of the common ancestor to all three evolutionary domains.

Whereas most of the lineages in the eukaryotic bubble propagate themselves much as prokaryotes do—copying their genomes and transmitting one copy to each daughter cell—and engage in sex only infrequently (where "frequency" is often a function of whether human observers are watching at the right times!), members of two subdomains, the opisthokonts and the plants, require sexual interactions in order to propagate. We return later to this special requirement.

Emergence: As with prokaryotes, cut-and-paste DNA exchanges in eukaryotes generate recombinant genomes. But eukaryotic sex introduces a whole new dimension to recombination: the wholesale reshuffling of genomes achieved by independent assortment. In an interbreeding eukaryotic population, new diploid complements arise at each sexual encounter even if cut-and-paste exchanges never occur, with exchanges serving to increase the variety of outcomes.

Importantly, eukaryotic-style recombination entails the shuffling of existing genomes *within a species*. With the exception of certain amoebas, eukaryotes carefully exclude the promiscuous uptake and incorporation of DNA derived from other lineages that occurs in prokaryotes. As a conse-

quence, the linear branching patterns in the eukaryote bubble in Figure 1 is an appropriate description of eukaryotic evolutionary history; as considered more fully later, species remain discrete until they branch to form new species. Thus the eukaryotic pattern of evolution is an emergent property of eukaryotic sexual patterns.

GENDER

Because *sex* is used both to designate an overall process and to designate, for example, male vs. female, I use the term *gender* to distinguish this second feature. *Gender* derives from *kind* or *type* (as detailed in *http://en.wikipedia.org/wiki/Gender*). It is used in many languages to classify nouns. More recently, it has come to connote often arbitrary cultural distinctions. I use it here in the sense that, with informative exceptions, eukaryotic sexual activities that generate recombinant offspring entail interactions between organisms that have differentiated along one of two gender paths, generating one of two types of gametes (for example, eggs versus sperm). We can stick with male/female and egg/sperm terminology to avoid unnecessary complexity, but other nomenclatures designate the same arrangement, like plus/minus or a/alpha. Exceptions include hermaphrodites, like some worms, and dioecious plants, where one organism produces two types of gametes in separate organs. Importantly, however, such organisms typically out-cross as well as self-mate, and many possess elaborate mechanisms to avoid self-mating altogether, presumably to promote the generation of recombinant offspring.

Probably all humans know that animals come in two genders, and many know that flowers include male and female organs, but most are surprised to learn that unicellular eukaryotic organisms, like yeasts and diatoms and dinoflagellates, also are gendered and engage in sexual haploid/diploid transitions. Indeed, of the eight eukaryotic subgroups in Figure 1, only the opisthokonts and plants include widely distributed multicellular lineages, yet, as noted earlier, all eight harbor sexual lineages, indicating that the common eukaryotic ancestor was undoubtedly a sexual unicell.

Reduction: As noted earlier, sexual eukaryotic unicellular organisms usually propagate by copying their genomes and dividing into two daughter cells, a process called mitosis. The mitotic cells do not display gender-related traits, but when they perceive signals that sex is in order, sometimes from the environment, sometimes from one another, one set of sex-related genes is expressed in cells of one gender and a second set of sex-related genes is expressed in the other, the outcome being that they display complementary sexual traits. The traits may include the secretion of mutually attracting hormones, the display of complementary recognition proteins on their external membranes or cell walls, and the elaboration of surface specializations that allow them to fuse together into zygotes. The operant

concepts here are mutuality and complementarity—a female secretes a pheromone that binds to a pheromone receptor displayed by males but not other females; male recognition proteins adhere to female but not male recognition proteins.

Unicells alternate between being mitotic organisms and sexual gametes. By contrast, with multicellularity, we encounter male or female organisms that produce male or female gametes (sperm/pollen and eggs) in distinctive reproductive organs (such as testes and ovaries). Nonetheless, the same principles apply: multicellular organisms switch on gender-related genes at specific life-cycle stages (such as early embryonic development and adolescence) and produce gametes with complementary features that mediate their adhesion and fusion.

The first eukaryotic unicellular organisms to differentiate along two distinct pathways to produce two different but complementary genders achieved a milestone in evolutionary history. No such differentiation has been described in prokaryotes. Why did this innovation occur, and why has it continued for at least 1.5 billion years through countless evolutionary radiations? True, meiosis "works" only if there are two input genomes, but if this is all that matters, why not restrict fusions to pairs of nongendered gametes? The time-honored answer is that the gender requirement means that unicells are unable to mate with their genetically identical mitotic clones. Instead, they are forced to find organisms that are genetically different from themselves, at least on the gender axis, and this promotes the likelihood that recombinant meiotic offspring will be generated. Hence we encounter yet again the drive to recombine as the engine of sex, in this case impacting on the very nature of self-identity.

Although there is nothing wrong with the logic of this time-honored answer, it may be incomplete. Some investigators suspect that there was, and continues to be, some additional adaptive feature associated with mating-with-another-gender that served to first initiate and then maintain this requirement. A candidate second answer is sufficiently arcane that I will only outline it here to give a sense of the territory.

All eukaryotic cells/organisms have mitochondria, or mitochondrial analogues. Hence, our posited first sexual unicells presumably had mitochondria as well. Mitochondria derive from bacteria that were taken up and domesticated by eukaryotic hosts, who transferred most but not all of the bacterial genes to their nuclear genomes. The remaining genes persist in small mitochondrial genomes that replicate independently of the nuclear genome. Following fertilization, and for as yet unclear reasons, the mitochondrial genomes from one gender are prevented from moving through the zygote and hence into the next generation—in a number of cases, including mammals, the mitochondrial DNA is literally digested by enzymes—while those from the other gender are protected from these exclusion or destruction mechanisms and are inherited by all the products

of meiosis. That is, regulation of this bizarre but ubiquitous activity is entrusted to the products of nuclear genes that are selectively expressed in one gender but not the other. Therefore it is plausible that the "invention" of gender was driven, at least in part, to supervise the inheritance of mitochondrial genomes.

Emergence: For whatever reason(s), gender happened, and gender persists to this day. Sexual eukaryotes within a species are not only different because of recombination; they are also of two different kinds. Moreover, each kind is required to find, interact, and fuse with the other if the species is to continue over the long haul. Gender thus marks the emergence of dyadic organismal relationships. No longer, in the eukaryotic domain, do organisms get along on their own.

Mate Recognition, Mate Choice, and Sexual Selection

Embedded in our consideration of gender was the need for recognition: Are you of the opposite gender? Importantly, the question has two parts: Are you of the opposite gender *and* a member of my species? Speciation, which we consider in more detail later, is enmeshed in mate recognition, and for good reason. Diverging species eventually lose their capacity to produce fertile offspring, if only because meiosis becomes increasingly flawed as genomes lose their similarity, meaning that erroneous matings are toxic to lineage continuation.

Once mate recognition is in place, there arises the opportunity for mate choice. Of the various males of my species in my population, are there some I would choose to mate with over others? Such language casts mate choice as a conscious decision, which of course is how humans experience it, but the same outcome can and does arise at simpler levels. A female unicell producing more pheromone, or a more potent version of a pheromone, is more likely to attract males, and in this sense she is more likely to be chosen.

Once mate choice is in place, there arises the opportunity for what is known as sexual selection. Using the example of peacocks, a peahen is programmed to look for a particular display of colored tail feathers by the peacock; her visual program and his feathers constitute one of our complementary mate-recognition dyads. Making colored tail feathers is "expensive," requiring good health and nutrition; hence a male with longer and brighter tail feathers is judged to be a higher-quality male than other suitors and is selected as a mate (mate choice). As generations pass and this choice process continues, tails lengthen and colors brighten, while peahens become increasingly choosy about this parameter, until we get the modern peacock, with a tail so long he can barely fly. Such runaway sexual selection has been described in numerous lineages, and while *choice* is clearly an appropriate word for the peahen's neural activity, the same selective

cycles can generate extreme sexual features even when brains are not involved.

Not yet mentioned is an important asymmetry in gamete production. In both plants and animals, males produce an abundance of sperm or pollen whereas females produce a small number of eggs. Hence it is in the male interest to be both promiscuous and competitive (the pollen tubes growing down into ovules engage in fierce competition to reach their egg targets) and in the female interest, as with the peahen, to be choosy. It presumably goes without saying that these male-female differences are stubbornly persistent.

Reduction/Emergence: One of the truly mind-boggling features of sex is that there are countless ways that mate recognition is accomplished. If we look at closely related species, they usually employ the same overall strategies: sperm-egg adhesion dyads will be sufficiently different from one species to the next to prevent interspecies fertilizations, but they will all use the same *kinds* of adhesive proteins. By contrast, if we compare distantly related lineages, like honeybees and fruit flies, they use very different strategies, and very different protein complements, to bring about the same goal. The same can be said for gender specification. The genes that specify male versus female differentiation are similar within closely related species but completely different between honeybees and fruit flies. Indeed, when investigators are sequencing a eukaryotic genome and encounter genes that have never been seen before (that is, are not found when they search the gigantic computer databases that store all genomic sequences), it is a good bet that the genes will prove to be related to sex.

So we arrive at an apparent paradox. Having established that all eukaryotic lineages engage in highly conserved haploid-diploid-haploid transitions, highly conserved meioses, and gender duality—meaning that their common unicellular ancestor doubtless displayed these features as well—we now find that countless means have evolved to achieve these common ends. Whereas we were able to compile a list of three core prokaryotic sexual strategies—conjugation, transduction, and transformation—there is no such thing as a core eukaryotic strategy, either for gender determination or for mate recognition. Why is this?

The etiology of disparate sex-determination mechanisms represents a central unsolved puzzle, but the evolution of disparate eukaryotic mate-recognition systems presumably operates much as the generation of eukaryotic biodiversity writ large. Organisms in each eukaryotic lineage make a living by pursuing particular adaptive strategies in the ecological context they occupy. Some swim, some fly, some float; each attempts protection from specific sets of predators and infectious agents; each seeks different forms of nutrition; and so on. Because mating is as central a trait as motility or protection or energy acquisition, each lineage comes up with mating strategies that "work" in the context of its other adaptations and environmental constraints.

Emergent, then, is a planet shimmering with endless forms of sexual awareness, provisioning us humans with such wonders as salmon runs, firefly flashes, birdsongs, floral displays, and, of course, our own intense individual and cultural versions of sexual sensibilities.

Nurture

As noted earlier, eukaryotic sex generates an emergent category of planetary beings: offspring. A bacterium that acquires a new gene by transduction is still the same bacterium, whereas the diploid zygote that results from fertilization is a new being. The unicellular soil algae that we study in my lab live in temperate zones, and their zygotes are invested with thick cell walls that resist freezing and desiccation; the zygotes therefore can survive the winter, and undergo meiosis when weather and soil conditions improve, whereas the gametes are killed under such adverse conditions. The walls, that is, provide *nurture,* as do seed coats and egg jellies and cocoons. While we are accustomed to think of nurture in terms of direct parental care of offspring, nurture in fact goes all the way down and presumably all the way back, and for good reason. Once all that effort is made to generate recombinant offspring, it follows that resources will also be invested in assuring their survival. Thus nurture is yet another emergent property of eukaryotic sex.

Multicellularity and Death

When a unicellular organism, be it prokaryotic or eukaryotic, copies its genome and divides, and its daughters do the same, and their daughters the same, the resultant population is called a clone. Individual cells in the clone may, of course, die for many reasons—they may carry toxic gene mutations or dry out or be poisoned or be eaten—but death is not an obligate feature of their life cycles. Moreover, if they are sexual eukaryotic unicells, they may differentiate into gendered gametes that fuse to yield diploid zygotes that yield recombinant meiotic progeny. Again, however, there is no obligate death in the system.

Life cycles with obligate death are restricted to multicellular plants and animals. In both lineages, haploid gametes are produced in special organs (flowers and gonads), but the zygotes that result from their fusion do not simply undergo meiosis as is the case for most unicells. Instead, they divide by mitosis into 2, 4, 8, 16, etc., cells that stay together to form an embryo. Moreover, groups of cells are induced to switch on the expression of different groups of genes, the result being that some go on to form shoots and others roots, or some livers and others brains. Along the way, flowers and gonads form as well, and these generate the gametes—the germ line—that yield the next generation. Meanwhile, the rest of the organism, the soma, eventually dies. The germ/soma dichotomy, as this arrangement is called,

essentially allocates the business of being alive to two venues. The soma does all the work of acquiring energy resources and defending against predators or disease and finding mates, but once mates have been found, the germ line is entrusted with perpetuity, and the soma, from a biological perspective, is irrelevant. It may live for weeks or for hundreds of years, but eventually it undergoes aging and death.

From a human perspective, of course, the soma is anything but irrelevant. It is who we are. Even if we have children and take comfort in their capacities to perpetuate our legacy, we are nonetheless deeply mindful, and often regretful or even fearful, of our inevitable demise. The fact that we will die shapes every facet of the lives that we live.

As developed in more depth elsewhere (Goodenough 1998), there is an upside to this picture. The invention of the multicellular soma, and its capacity to differentiate into numerous cell types in numerous organs, gave rise, in the animal radiation, to the invention of brains and, very recently, to the advent of human minds and their sensibilities, including their knowledge of death. When I ask myself whether I would prefer to be a potentially immortal soil alga or a certainly mortal human, the choice is easy. Knowledge of death may be burdensome, but knowledge itself is worth the price.

Speciation

If there is any unanimity among researchers investigating biological speciation, it is agreement that speciation is poorly understood. Charles Darwin's *The Origin of Species* brilliantly laid out the agenda, but 150 years later, most reviews of the topic begin with sentences like "There is little consensus on how or why organisms undergo speciation."

Despite this state of affairs, our focus on sex allows us to lift up a few germane features.

1. At some point in the speciation process, a freely shuffling deck of genomes—a species—diverges into two freely shuffling decks of genomes that can no longer productively shuffle with one another, at which point one species has become two species. Some argue that speciation may occur prior to the establishment of sexual incompatibility, but all acknowledge that once incompatibility is established, speciation has definitively occurred.

2. Sexual incompatibility arises at one or both of two junctures: (a) in pre-zygotic isolation, mating signals are not recognized, or copulation fails to occur, or sperm fail to bind to eggs, such that zygotes fail to form; (b) in post-zygotic isolation, zygotes form but either fail to undergo successful development or meiosis, or the resultant offspring are themselves infertile.

A major sticking point is understanding how these isolation mechanisms may become established. To take a simple pre-zygotic case, if fertilization in an established species involves an adhesive interaction between sperm protein *A* and egg protein *a*, if a gene mutation generates protein *A′*

with a divergent shape and hence specificity, there arises the requirement that it encounter an egg carrying protein *a′* with a complementary shape and specificity, because adhesion to the original *a* is no longer an option. If this fails to occur, the *A′*-bearing sperm will fertilize no eggs, and the *a′* egg will not be fertilized, and the potential new dyad will, as it were, die on the vine rather than initiate a potential speciation event. It all looks rather improbable.

There is, however, another way to think about these matters. The deck-shuffling feature of meiotic sex, for all its advantages in generating recombinant organisms, is in fact a bad idea if an organism has come up with a novel recombinant genome that confers a strong selective advantage. For example, the novel genotype may permit survival under drought conditions; the population as a whole may be dependent on humid conditions, and now a prolonged drought sets in. If our drought-resistant organism mates with the general population, the deck is shuffled and its adaptive genome is lost. But suppose mutations to *A′* and *a′* occur with sufficient frequency that our organism also happens to produce protein *A′* and encounters a mate carrying eggs with protein *a′*. In this case, the pair would effectively establish an inbreeding population, privately shuffling their vastly smaller number of possible genome configurations and generating offspring that preserve the drought-surviving trait while the rest of the population dies off. That is, should a variant pre-zygotic feature (*A′*) happen to be coupled with a selectable trait, the potential for reproductive isolation arises that could drive the speciation process.

A just-so story? Of course. At present, all speciation scenarios are just-so stories. But this one has some data going for it. Many sex-related genes have been shown, in numerous lineages, to be far more prone to mutation than other genes. Hence the premise that *A′* and *a′* proteins might arise with some frequency is not a rabbit out of a hat. Possibly, then, species that carry mutation-prone sex-related genes are thereby rendered "speciose," poised to capture novel ideas and drive them into reproductively isolated breeding groups.

Another way to think about these ideas is in the context of extinction, the overwhelmingly likely fate of a biological species. Figure 2 presents this perspective in cartoon form. Depicted are three kinds of clades—taxonomic groups consisting of a single common ancestor and all the descendants of that ancestor. An asexual clade (left), with no recombination, can expand its "niche dimensions" only by generating variants via mutation, a slow and incremental process. Should the niche become compromised (the drought in our example; the gray bar in the diagram), if no drought-resistant mutants have arisen, the whole clade goes extinct.

The two other clades in Figure 2 are sexual. Each teardrop-shaped unit is a species, shuffling its collective deck of genomes to generate organisms that are highly adapted to a particular narrow niche dimension, but thereby

vulnerable to extinction should that dimension be compromised. Speciation (depicted as branching teardrops) generates variant decks that are adapted to different narrow niches. When a given niche is compromised (drought) and some species go extinct, there remain others, in different niches, that continue to propagate the clade. The clade on the right, with the wherewithal to speciate more often, generates more modern descendants (gray circles), and a more diverse array of descendants, than the less speciose clade in the center.

I linger on this topic in part because our laboratory research is currently focused on the speciation question but primarily because it allows me to make a central point. At such time that a consensus view on the origin of species is reached, the theory will, I predict, be replete with research results pertaining to sex-related traits and their modification. Put another way, another emergent property of sex is likely to be its capacity to drive speciation and hence eukaryotic biodiversity (Figure 2).

Human Sexuality

That sexuality is a dominant feature of human experience and interest scarcely requires documentation. Its regulation has been, and continues to be, of central importance to religions and to religiously motivated political systems; it figures in all forms of art; it is used to sell products and celebrities. We have a long history of male dominance and gender inequality. Sex and criminal behavior are often coupled. Each human experiences her/his sexuality as a core feature of his/her persona—waxing or waning, coherent or confusing, satisfied or dissatisfied. It's a big deal.

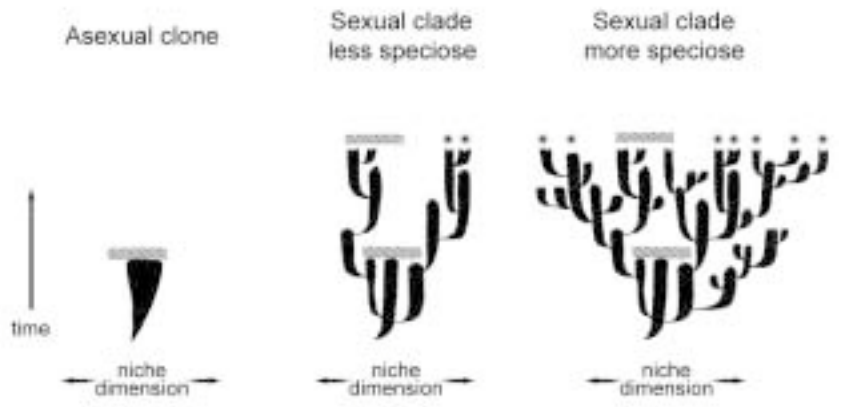

Fig. 2. Cartoon of evolutionary patterns. Gray bars denote events that wipe out major niches; circles indicate extant members of a clade. The speciosity of a clade influences its niche dimensions and hence its representation in present-day ecosystems (after Stanley 1975).

Human sexuality is an abstraction and therefore by definition a human construct. To our knowledge, nonhuman apes do not contemplate their sexuality, although they are robustly interested in engaging in sexual behavior. The emergence of human sexuality from sex, like the emergence of morality from prosocial emotions, or the emergence of justice from strategic reciprocity, marks the human capacity to transfigure our "ape minds" symbolically. We do not experience sex the way nonhuman apes do because we think in importantly different ways.

A particularly striking feature of human sexuality is its many manifestations. Many animals, for example, have been observed to engage in homosexual activity, but the significant percentage of humans with a robust and invariant homosexual orientation is noteworthy. Also noteworthy is the variety in preference for sexual behaviors; for some persons, activity *X* is stimulating and exciting, for others it is of no interest or even repellent. Moreover, the range of sexual activities that appeal to at least some persons is quite remarkable.

Where does all this variability come from? No one (yet) knows, but let me offer a hunch. It is clear that the evolutionary trajectory that produced the modern human entailed major rearrangements in what we can loosely call brain wiring modalities. Even though we know little about which rearrangements were important for supporting particular human traits, or how the novel wiring configurations actually work, significant reorganization took place that probably entailed both the loss of ancestral brain features and the development of new ones. The hunch is that during the process, sexual wiring was rendered far more indeterminate, more plastic, than in our brethren species.

Human sexuality is not, of course, a stand-alone trait. It is deeply enmeshed in human versions of relationship and nurture, traits that we encountered in simpler forms as we tracked sexual evolution. And, of course, it is enmeshed in that quintessentially human emergent property called being in love.

In his book *The Mating Mind* (2001), Geoffrey Miller proposes a winsome just-so story about the relationship between romantic love and human language, suggesting that our distinctive language-based traits evolved in the context of sexual selection. The idea is that sexual partners were chosen (and arguably continue to be chosen) on the basis of not only their looks but also their language facility—their capacity to express their romantic desires in the likes of poetry and love songs. In sexual-selection terminology, such courtship displays would be "expensive," like peacock tails, heralding a putative partner's linguistic creativity and hence his or her human-style intelligence. The enhanced mating success of such articulate wooers would translate into an accelerated, perhaps even runaway, evolution of language capabilities.

All this from cut-and-paste enzymes and independent assortment! An emergence story for the books.

NOTE

A version of this paper was originally delivered at the Star Island conference, "Emergence: Nature's Mode of Creativity," organized by the Institute on Religion in an Age of Science, 29 July–5 August 2006.

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