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COMMENTARY AND PERSPECTIVE

JEZ-B MOLECULAR AND DEVELOPMENTAL EVOLUTION WILEY

The evolution of evolution

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Abstract

In the past, most biologists, myself included, did not think of evolution as changing over time. The wonders of natural selection were always at hand and went into operation once there was life. However, with a little reflection it becomes obvious that evolution has changed—there has been an evolution of evolution. Evolution can be separated into four phases, or eras, that may or may not overlap. The *first era* starts with the evolution of life on earth, which led to single cells that multiply asexually. The *second era* takes advantage of the invention of sexual reproduction as evolution could now gallop forward because of a richer fare of diverse offspring for natural selection. The *third era* begins with the introduction of multicellularity. In the *fourth era* there is a radical innovation: the nervous system that arises animals by standard Darwinian selection. This has allowed major rapid changes to proceed, such as language that led to all the rapid progress we call civilization; a true revolution, and one that does not depend on the slow genetic changes of all other standard gene-controlled evolutionary steps.

I have spent my laboratory life of many years working with cellular slime molds, a most interesting group of microorganisms. At the same time, I have been surrounded by macro-organisms, such as trees, birds, dogs, and people. For many years I kept these macro and micro worlds apart, even though I was totally immersed in both. Only recently did I think of comparing the two and soon realized that there were some most interesting differences. I published the beginning of these thoughts in two places (Bonner, 2013, 2015) expecting to be burnt at the stake, but the silence was the only response. Either the thoughts were old hat, or the world was not ready for them yet. This essay is a further attempt to make what I think is a very important point. There have been changes in the way evolution has occurred over time: there has been an evolution of evolution.

In the four major eras, there are evident differences in the character of evolutionary change. Era 1 begins early and involves small organisms and initially, all reproduction is asexual. Everything changed in era 2 when sexual reproduction (defined here as meiosis and cell fusion) came to the fore with the origin of eukaryotes and evolutionary progress made a radical spurt forward. Next, in era 3, multicellularity as an easy way to become larger and dominant. In era 4, everything changes again and this only occurs in animals and their fantastic nervous system that has led to the brain and in humans, the miracle of language.

1 | BACKGROUND

My interest in this matter began some years ago (Bonner, 1965, 1988) when I became intrigued by the fact that the maximum size of any plant or animal increased as we gallop through geological time; initially there was nothing but bacteria on the earth but now, while we still have those bacteria, we also have giant sequoias and blue whales and all those organisms of intermediate size created along the way. This rise has now been put on a firmer footing by Payne et al. (2009). They managed this by measuring both actual fossils and living forms to produce a definitive graph (see Figure 1).

As one can see from the graph, there are immense spans of time where microscopic forms are the only living organisms, quite different from what exists today, where there are large numbers of different size species living together. It was immediately obvious that the process of evolution must have been very different early and late over the vast period.

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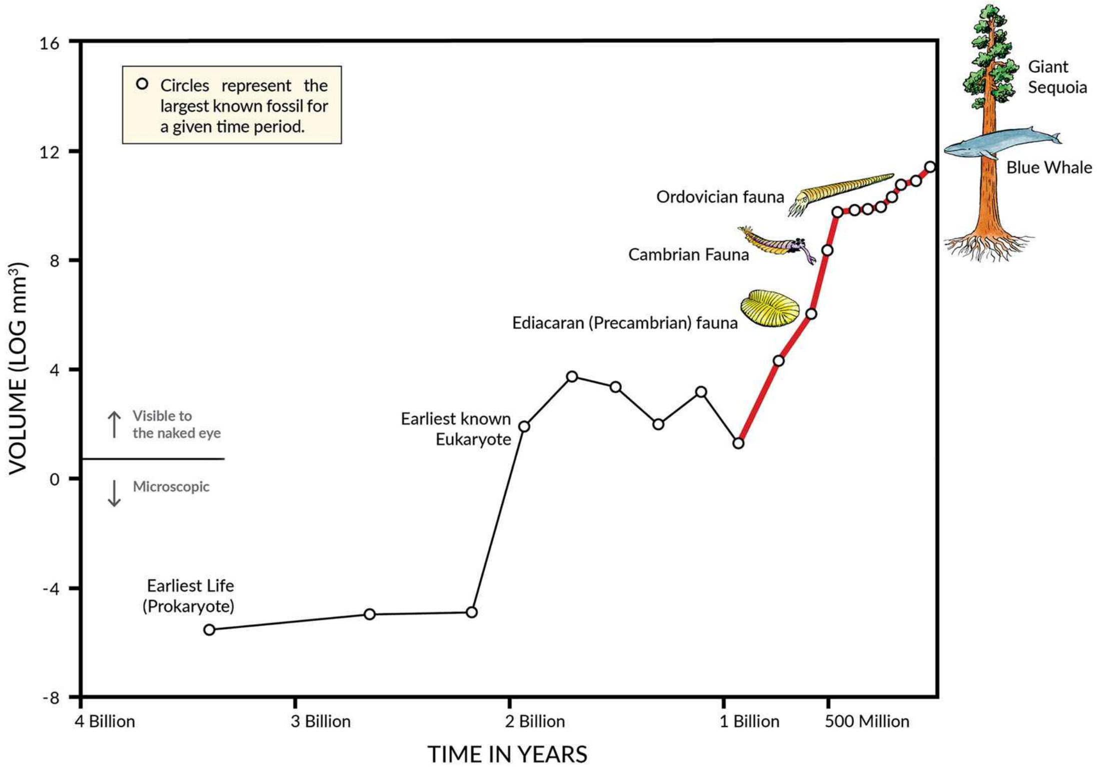

FIGURE 1 This is a redrawing of figure 1 of Payne et al. (2009) that emphasizes those features that are relevant to this essay. They also point out that over this great span of time, there has been an increase in the atmospheric oxygen [Color figure can be viewed at wileyonlinelibrary.com]

2 | ERA 1: MICROBIAL LIFE

The *first era* involves the evolution of microorganisms and starts with the earliest beginnings of life on earth. These microorganisms are still with us today and because some of them build mineral skeletons we know many have not changed significantly, for the modern ones show considerable similarity to the ancient fossils found in some rocks, as Darwin noted in the third edition of the *Origin* (1861, p. 135). The small size of microorganisms has a big effect on the way natural selection operates among them. Let me illustrate this point from some observations on cellular slime molds. Their amoebae feed on bacteria in the soil and therefore the amoebae become abundant wherever bacteria are available.

In cellular slime molds, there is essentially no competition. The amoebae ignore one another and go for the bacteria that attract them as desirable food. And once all the bacteria have been eaten the amoebae go into storage; they either turn into spores or microcysts that can remain dormant for an extended period of time, even years, only to burst open if they are blessed with the arrival of fresh bacteria. The easiest way of seeing how little interest slime mold amoebae have in one another is to study them with time-lapse photography and clearly, the feeding amoebae pay no attention to one another as they glide past their fellows—sometimes even briefly touching.

There is another bit of evidence that illustrates this behavior. Schaap et al. (2006) did a molecular phylogeny of 75 species of cellular slime molds and showed in this way that some of the species were ancestral to the more modern ones. This means that today the species of recent origin and the ancient ones are living side-by-side; we could say that the ancient ones are living fossils. Of course, there is no evidence for fossils or extinctions; cellular slime molds are very different from dinosaurs.

I know of only two examples where there is competition between species. My first example is from the work of Waddell (1982) who found a species among bat dung in caves whose amoebae will enter the aggregate of any other species and its amoebae will methodically eat—engulf—all the amoebae of the host. This predation is rather a severe form of competition. A different, but an equally extreme case comes from the work of Hagiwara (1989) who found a unique species that produced a chemical that utterly destroys the amoebae of other species of cellular slime molds. No doubt there may be other examples that have not yet been discovered, but it is fair to say that these kinds of competitive warfare are rare among these organisms. There have been some studies sampling areas of soil in, for instance, in a forest and what they have shown is that different species and strains may be present side-by-side, ignoring one another (e.g., Sathe et al., 2010). The evidence is overwhelming that competition is largely wanting in the cellular slime molds, although it may be common in larger animals and plants.

The apparent lack of competition is found in other free-living microorganisms. Consider, for instance, the great masses of different species of diatoms, or radiolaria, or foraminifera, and similar microorganisms. None of them exhibit any kind of competition; they just exist side-by-side, totally ignoring one another. As has been pointed out to me, they all fit the old adage: *Live and let live.*

3 | ERA 2: SEXUAL REPRODUCTION

The ancestral state that led to the invention of sexual reproduction (i.e., alternations between meiosis and cell fusion) was the eukaryotic cell. As we cast our eyes on this series of events from bacteria to cells with chromosomes capable of meiosis, fertilization and the rise of two sexes it is an extraordinary voyage full of events that involve huge and intricate steps. It is difficult to believe that we must explain all this as the fruits of natural selection, but there is no alternative. The fact that these changes took vast numbers of generations to achieve helps us to some extent accept the enormity of these inventions. Because sex plays such a big role in evolution, let us pause and examine it carefully.

In this essay, I make the fundamental point that any significant evolutionary change requires sexual reproduction; it could never have happened without it. It follows that the invention of sex was one of the most important events that ever occurred on our globe. First, I want to show how elaborate and intricate are the mechanisms that arose to hang on to this newly invented sexuality, and finally, to show when in earth history the invention was likely to have taken over.

That sex and evolution are closely associated, has been appreciated for many years. It was way back in the 1930s that independently Fisher (1930) and Muller (1932) showed that sexual reproduction was an ideal vehicle to promote evolutionary change. This seemed odd because it is far more costly than asexual reproduction; it involves two sexes, its joining of the genes of those two parents in fertilization, whose genes have been rearranged or shuffled in meiosis. It provides an ideal way to lay out a diversity of traits so they can most effectively be culled by natural selection—the perfect *smorgasbord*. They supplied the rationale of why sex and its complicated apparatus has been retained in essentially all animals and plants (and fungi) and their evolution.

In asexual reproduction, it is often far easier to make many more babies, but with rare exceptions, they will all be genetically the same. In sexual reproduction, there will be fewer offspring, but they will all be different; grist for the mill that is natural selection. I have seen this in my own family: all of my three siblings were male, and the four of us could not have been more different. With asexual reproduction, we would have been the same, like identical twins. With asexual reproduction an adverse change in the environment could wipe out a clone in one generation, whereas in sexual reproduction, because of the genetic diversity it creates, there may be one or more individuals among their diverse offspring that can thrive despite the change. The diversity that comes with sex will keep a lineage preserved for generations to come.

Some rotifers have completely lost their ability to reproduce sexually and have propagated asexually for millions of years. What is so special about them that they seem to be an exception to the rule? Perhaps they found a stable niche that suited them perfectly; a world in which they continue to thrive, but the price that they pay is that their evolution has essentially ceased. The roughly 50-million-year-old fossil rotifers found in amber are very similar to the forms that exist today.

4 | THE UBIQUITY OF SEX

The degree that sex has clung to the life history of living organisms is quite extraordinary. At the lower end, we have single-cell green algae (such as *Chlamydomonas*) which are not even dignified by being called male and female; there are no morphological differences between the sexes; they are called plus and minus mating types. At the other end of the scale, in higher animals, we have the most incredible variety of distinctions between the sexes. Think of the fruits of Darwin's sexual selection (Darwin, 1871): the Birds of Paradise with their glorious male plumage; the huge male elephant seal and his harem of small females; and even in human beings where the male alone has hair covering his face in contrast to the smooth-skin female.

And it is not just morphological differences, but the fantastic variety of behaviors as well. For instance, courtship rituals in animals come in all guises, from simple encounters to extraordinary dances and displays. And there are esoteric variations of marital behavior that seem quite inconceivable, as for instance in some species of praying mantis where the large female eats the smaller male, starting with his head, when deep in *flagrante delicto*. Two appetites satisfied at the same time.

If sex is an absolute requirement for significant evolution, then it is not surprising that natural selection has fostered many special adaptations to ensure that egg and sperm meet so they can achieve fusion, that is, fertilization. There are a vast number and a great variety of different ways in which this is assured, each one of which has evolved through natural selection and made possible by sexual reproduction. The fact that there are so many ways to ensure fertilization is clear evidence of how imperative sex is for efficient evolution. Without fertilization, there would be nothing but a direct plunge into extinction (or stasis, as in the rotifers).

In the unicellular green alga *Chlamydomonas*, where the indistinguishable sex cells (gametes) are swimming about, with the help of various chemical signals, they fuse in fertilization if they are of opposite mating types. In *Volvox*, a primitive multicellular descendent of the unicellular *Chlamydomonas*, there is a large, immobile egg and a small motile sperm. The egg gives off an attractant that guides the sperm to its target. For organisms that are large and complex the way in which the sperm finds the egg can become extremely elaborate involving many gene-controlled steps, often behavioral ones. I will give some well-known examples to illustrate the extraordinary lengths organisms have gone to make sure a sperm will find an egg.

Among animals, scent often plays a key role. I have long known this: When our children were small we had a female spaniel dog that came into heat. Being a somewhat impoverished assistant professor at the time, we decided not to send her to the kennel but keep her at home. We soon found out that this was a big mistake because we all picked up her scent, and we saw in the yard outside our window huge dogs stalking our infants. The climax came when I was lecturing to a large class in the rather steep, old lecture hall. Somehow an Irish Setter and a Dalmatian found me and came tearing down the aisle and tried to mount me in front of the whole class. That was, without doubt, the most arresting lecture I have ever given.

This kind of communication we find among dogs and other mammals is bested in a big way by some of the larger moths, as I discovered as a boy reading the magical prose of Jean Henri Fabre. The males have large and intricate antennae and should some molecules given off by a female descend on them they start flying up-wind to find her. There are records of males successfully finding females in this fashion some miles away. My heart has always gone out to the technician in Seattle who was working on a moth attractant in the laboratory and she was singled out at a football game by a fluttering cloud of eager male moths surrounding her in the stands.

My reason for giving these examples is to show how intricate and complex are the peripheral inventions to assure that fertilization takes place, and it must always be kept in mind that it is not genes in isolation that get selected, but their bodily manifestation (the *phenotype*) is what is culled, and the genes that are responsible for the phenotype are carried along each successive generation. Genes are the somewhat malleable, environmentally sensitive blueprints for the phenotype.

Finally, sound in the guise of a song is another way for uniting the sexes, leading to fertilization. In many species of songbirds, the male arrives early in the spring and will stake out a territory to entice a female partner which he attracts and advertises by singing. One of my most vivid memories as a young boy was in a boarding school in Switzerland. Right outside my bedroom window, there was a small wood. Every night in the spring as I fell asleep, with my window wide open, letting in the cool spring air, I would hear in the dark outside a nightingale sing its haunting song—I could not believe anything could be so beautiful.

The examples given so far are animals and they can move so handy to get the motile sperm to the egg. Plants cannot move; how can they bring about fertilization? Besides taking advantage of the wind to carry the male pollen great distances, they also do so by devising one of the cleverest of ploys: by evolving ways of attracting motile animals—especially flying insects, and even birds—with their colorful flowers, the scent they give off, and the nectar they provide as the ultimate reward; all so that the male pollen reaches the ovules of a distant plant. This involves the coordinated evolution of both a plant and an animal; think how many genetic events have been established by natural selection in two species, just so a plant can accomplish fertilization.

Also, it should be kept in mind that sexual reproduction plays another significant role in evolution. It is the guardian that keeps species separate. A species is defined as a group of individuals that can only produce their own kind, that is, it is reproductively isolated. The exception is in the formation of hybrids by crosses between closely related species, as in a horse and a donkey. This means that the species of all nonsexual organisms can only be defined on the basis of their morphology.

Sexual reproduction plays a central role in evolution. By the mixing of two genetic lines in fertilization, a new line has been created and can be repeated in the successive generations that follow. The result is a great increase in the diversity of the progeny and therefore evolutionary progress is made easier though; both richer and more rapid. This is set up for era 3 (evolution of multicellular lineages) that accounts for the most conspicuous life that exists on the earth today.

5 | ASEXUAL REPRODUCTION WITHIN SEXUAL LIFE CYCLES

In many organisms, such as among fungi and algae, and among various invertebrates, such as aphids, one finds numerous species that have both asexual reproduction along with the sexual cycle. The asexual cycle can be quite separate from the sexual one, or it may be directly derived from it; for instance, this is the case for aphids that are capable of parthenogenesis, where unfertilized eggs can develop into offspring. This means they can take advantage of what both kinds of reproduction have to offer. In an unchanging, benign environment of the summer the best strategy is to produce many offspring rapidly, which is the hallmark of parthenogenetic asexuality; and if the growing conditions become unsettled and unknown the following spring, then the best strategy is sexuality that produces genetically diverse offspring some of which might thrive in a new environment. Some years ago I became intrigued by the green alga *Volvox* for it provides a perfect example (Bonner, 1958). The sexual cycle appears in the fall and fertilization produces thick-walled cysts that can hold everything in safekeeping over the harsh winter. Come spring and gentle, but often capricious weather, they give birth to new, diverse colonies some of which might be quite capable of thriving in the new environment. Having both a sexual and an asexual life cycle allows *Volvox* (and aphids) to reproduce optimally throughout the seasons of the year.

6 | ERA 3: MULTICELLULAR ORGANISMS

The third era began with the evolution of multicellularity. This has occurred a number of times: the two most successful size increases by multicellularity are the rise of multicellular plants and multicellular animals. They are in a more crowded world where competition comes to the fore: it is the era of the struggle for existence. Different species of tall trees compete with one another to get at the top of the canopy to best catch the sun's rays, or carnivorous animals who compete with one another to capture their prey. Competition is inevitably also present in solitary microbes but its manifestation is harder to detect.

In both animals and plants becoming multicellular is the most obvious way of becoming larger for natural selection constantly pushes for small organisms to be larger and large organisms to be smaller—until the optimal size in a given environment is reached. The size of organisms plays a key role in their evolution. It is something that can easily be modified by natural selection, even in small, incremental steps. With an increase in size, there is bound to be an increase in the division of labor, which amounts to an increase in complexity: what I have called the *size–complexity rule* (Bonner, 2004). It means also an increase in the duration of the life cycle. During the course of history on earth, there arrives a point where the supply of food for many species of predators reaches a limit; there is no longer an endless supply of prey. This heralds the era of active competition.

7 | ERA 4: ANIMALS WITH COMPLEX NERVOUS SYSTEM

This era 4 is special because it only involves animals: to be involved, one needs a complicated nervous system with a brain. Brains allow for learning and social transmission of acquired knowledge. This immediately brings us to *Homo sapiens* and we are very self-satisfied with how smart we are compared to all those less-fortunate animals. This has led to communication by language, a big step forward, for in addition to the transfer of information in the genes through each generation of the sexual cycle, information (*memes*) can now be instantly transmitted at any point within the life cycle; it does not have to wait for the next generation. This produces cultural evolution that has been made possible following biological evolution and it has produced a whole new world. To make this leap from biological to cultural evolution certain innovations are required, the most important of which is the invention of language that can produce immediate communication between individuals. This is our world, the world of *H. sapiens*. The world of books, the world of nonstop invention, the world we call civilization. There has been continued interest in how animal behavior evolved into human behavior, where we no longer have to wait for at least a generation for the information to be passed on; compare that to the speed of reading a book or taking a telephone call. Richard Dawkins has proposed the word *meme* in contrast to a *gene* for this kind of information. (The fascinating subject of how our behavior shows its origins in the behavior of other animals has been refreshingly examined in a new book by Laland (2017)).

Many of the points in this essay dovetail with those of Maynard Smith and Szathmáry (1995, 1999). They also have looked at the great span of evolution and characterized it by its sequential progress in terms of transitions from one level to another. They go from the very beginning of life upward. Like my breakdown of the stages of evolution, they also include our most-recent stage that involves transmissions by behavioral means.

This is a major transition because in animals information need not require genetic transition: instead, information can be passed directly from one individual to another by language. Animal behavior has become a more efficient and certainly more rapid means of passing information. It has led to a system that is built on the foundation of rapid change. To put the matter in a lighthearted way, evolution has been extended from primeval soup to alphabet soup.

8 | TIME

For some while, I have been interested in the fact that there has been a progressive increase in the maximum size of animals and plants over geological time (Bonner, 1965, et seq.). My primitive description of this progression has happily been reexamined by Payne et al. (2009) who looked at the same phenomenon from a paleontologist's view (see Figure 1). Based on measuring actual fossils they greatly expanded the span of time. (Their figure has been pared down to include those features that are relevant to this essay).

Note that in the roughly one and a half billion years of the first life on earth only very small organisms existed, but this ends before two billion years ago when much larger organisms appear. (Remember that in the graph the size of the organisms is plotted logarithmically, so that an increase in size in a larger fossil appears *much* smaller than it would on a linear plot). This first step forward in size is thought to be related to the rise of cells with nuclei (eukaryotes); as we saw earlier, more primitive bacteria and similar organisms (prokaryotes) lack nuclei and their DNA lies directly within their cells.

On top of that, there arose a new invention: that of multicellularity. One also finds multicellularity among the bacterial prokaryotes, although it never progressed very far. In eukaryotes multicellularity truly blossomed and led the way to great increases in maximum sizes.

As is evident in Figure 1 there is a big turning point very roughly about a billion years ago and from then on to today, there has been a steady rise in the maximum size in the biggest animals and plants to our present day blue whales and giant sequoias. This surge upward is indicated on the figure by a red line; it is a span of maximum size from a microscopic single-cell organism to a whale made up of an incredibly large number of cells. These facts tell us some important things about evolution. Some of them are rather speculative but they all fit together.

That steady rise in maximum sizes that continues to this day is a splendid marker for the period where major evolutionary events have taken place. The fossil record supports this: there is a steady rise in the size of the largest animals and plants for approximately a billion years. Before that great rise, there has been only one earlier leap upward and that they attribute to the invention of the eukaryotic cell.

What this tells us is that sexual reproduction may have been invented—before the great rise, roughly a billion years ago, for the continued rise would not have been possible without it. And once sex had been invented, animals and plants select for its preservation with it's coming together of the sex cells (gametes) in fertilization. This is an absolute requirement for sexual reproduction, and therefore for rapid evolution.

Figure 1 provides some possible hints for a few of the big questions, as, for instance, when was sexual reproduction invented? When did it become prevalent? If my thesis is correct, it must have first appeared somewhat shy of a billion years ago, and once established we see a steady progression of evolution reflected in the steady increase in the maximum size of animals and plants. This fits in with the fossil evidence for there are known fossils from that period that show stages of sexual activity that clearly resemble those of a red alga that exists today (Butterfield, 2000).

The invention of sexual reproduction opened the floodgates of evolution and one of the consequences is that the maximum size rose steadily for about a billion years. This size increase is a convenient umbrella for all evolution that has taken place because it can be easily measured, and we know that size increase generally requires an increase in complexity—the size-complexity rule. The invention of sexuality was clearly the lynchpin of significant evolution. Once it was established, it began making a new and different world.

Not being a paleontologist, I have great troubles imagining what a billion years mean. My secular mind does not travel that far. I know the facts, but the numbers are so huge that I am left gasping by the wayside. It is almost like saying that if you wait long enough, anything might happen and the unlikely invention of sex—the handmaiden of evolution—is a pristine example.

9 | SEX AND MICROORGANISMS

It used to be thought that most eukaryotic microorganisms only reproduced asexually, but it looks less and less likely that this is so (e.g., Lahr, Parfrey, Mitchel, Katz, & Lara, 2011). They are very discrete about their sexual activities and do not show off like birds of paradise. In many cases, they indulge in sexual reproduction intermittently after a number of asexual cycles.

It has always been puzzling to me that there are so many species of diatoms, foraminifera, radiolaria, and other groups of microorganisms; there is nothing comparable among multicellular animals and plants with the exception of the coleoptera who have ~400,000 species. (As JBS Haldane famously said, God had an inordinate fondness for beetles). Among the microorganisms, diatoms have ~1,000,000 species; foraminifera, ~279,000; radiolaria, ~50,000. The difficulty vanishes if we remember that these organisms embraced sexual reproduction probably at a time near the base of the great rise in the figure which meant they could suddenly produce the many variant offspring that sex promotes.

But why are they suddenly so diverse? Perhaps because of their small size they revert to exist in their Era-1 world where there is little competition; which means many more of the mutant offspring survived and flourished, and did little in the way of competing with one another. Their small size allows them to revert to be “live and let live” organisms.

There remain many unanswered questions. For instance, how did unicellular organisms acquire sex? Modern thinking favors the origin of sex with the origin of eukaryotes (see, e.g., Speijer, Lukes, & Eliáš, 2015), but the “how” remains unanswered. Further, as mentioned earlier, Darwin (1861) noted that microorganisms that have left a fossil record remain virtually unchanged for eons, and I am adding that it is so because they live in a world essentially devoid of competition.

There has been an evolution of evolution. As the earth became more crowded over time, competition inevitably crept in and the world of “live and let live” faded. Natural selection gave rise to sexual reproduction that greatly enhanced the evolutionary progress of animals and plants by supplying offspring of increased variety. See the steeply rising red line in Figure 1 for the last almost billion years.

I rest my case.

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