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The Failure of Evolution in Antiquity

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The Failure of Evolutionary Thinking in Antiquity

Darwinian Evolution

When Darwin wrote the *Origin of Species*, Creationism was the dominant view, even among scientists. According to this view, each species of living thing is characterized by an immutable form created by God and transmitted from one individual to the next in the act of reproduction. Although minor variation between individuals may exist, deep permanent changes were not possible. Creationists took the fact that species cannot successfully interbreed as empirical evidence for the existence of real species boundaries: God had implanted in each individual a mechanism designed to prevent species from being altered by natural causes and thereby disrupting His divine plan. Darwinism (understood here as the theory articulated and defended in the *Origin*) changed all this. We can divide Darwin's theory into two main theses. The first is the basic idea of descent with modification. In chapters 5-13 of the *Origin*, Darwin presented a wealth of evidence showing beyond a reasonable doubt that biological species are not immutable but evolved over time. The other part of Darwin's theory is the claim that natural selection is the primary mechanism responsible for evolutionary change (*Origin* chapters 1-4). Evolution by natural selection, as Darwin understood it, can be seen as a consequence of four conditions (compare *Origin* 1859, 4-5):

(1) Variation.

(2) Struggle for Existence.

(3) Differential Fitness.

(4) Heritability.

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In the first place there must be variation within a population, which provides the raw material for selection. Without variation there can be no selection. Second, there must be a struggle for existence. Darwin argued that the conditions of life are such that, in every generation, more individuals are born than can possibly survive, given limited resources. This generates competition between individuals for resources, including competition for mates. Third, for selection to act on a population some variations must give their possessor a competitive advantag, which increases its chances of surviving and reproducing relative to other individuals in the population. (Selection is blind to ecologically neutral traits.) Finally, in order for evolution to result, those favorable variations must be heritable. If some individuals vary from others in ways that give them an edge in the struggle for existence, but those variations are not heritable, then no evolutionary change will result. Inheritance is necessary to ensure that those advantageous traits are preserved in future generations.

Darwinism incorporates several other ideas. (i) Evolution by natural selection is an adaptive process capable of fitting a population to its environment. (ii) Natural selection is capable of producing diversity, so that the number of different kinds of organism increases over time resulting in a branching "tree of life". Most importantly, selection is capable of generating new species, owing to what Darwin called 'The Principle of the Divergence of Character' (*Origin* IV, 111-26). (iii) All life on earth can be traced back to some unknown ancestor(s) in the remote past (the theory of common descent). (iv) Evolution is a gradual process that requires a large amount of time; no evolutionary changes occur instantaneously over a few generations (gradualism). '*Natura non facit saltum*,' Darwin said (*Origin* 1859, 194). (v) The individual organism is the unit of selection, not groups of organisms. Individuals, not groups, are locked in a continuous struggle for existence and natural selection favors variations that give those individuals an edge in that struggle.

The intellectual history of evolutionary theory really does not begin in earnest until the late 17th/early 18th Century.[1] Prior to that, the idea that species might have evolved over time was not a serious possibility for most naturalists and philosophers. There is certainly no substantive debate in antiquity about evolution in the modern sense. There were really only two competing explanations for how living things came to have the parts they do: design or blind chance. The ancient Greek Atomism, for example, taught that all composite bodies, including living things, are generated through the random collision of atoms as they "rebel and move in the void" (Aristotle, *On Democritus* [= Simplicius *in DC* 295,9]). Plato and Aristotle both dismissed this possibility on the grounds that living things are too complex and too well-adapted to be products of chance. This eventually became the central premise in Galen's own Argument from Design (see below). That species forms might have gradually evolved over time by a process of natural selection was not seen as a plausible alternative. Of course, such a theory had been proposed by Empedokles in the 5th Century BCE. But because his theory still relied heavily on chance, it was not taken seriously by any of later ancient Greek or Roman thinkers.[2]

This raises a question about methodology. How should one go about writing an essay on evolution in the ancient world? The most common approach has been to offer a survey of the scattered remarks that appear significant when read in the context of later evolutionary

[1] The first significant theory of transmutation was developed by French biologist Jean-Baptiste Lamarck (1744-1829), though Lamarck's contemporary, Comte de Buffon (1707-1788), also proposed a form of transmutation. See Mayr (1980, 309 ff.), Grene and Depew (2004, Ch. 3), Bowler (2009, Ch. 3).

[2] The Epicureans seem to have invoked Empedokles' ideas (Lucretius *ONU* V, 826 ff.), but evolutionary thinking did not form a major part of their system. They still saw chance as the only true alternative to design (e.g. Lucretius *ONU* II, 166-183; cf. IV, 823-76).

thought. But it is difficult to see what we might learn from that exercize. For example, Aristotle's student Theophrastos has plenty to say about variation and modification in plants, both in nature and under domestication (e.g. *Inquiry into Plants* II), which seem significant in light of the first two chapters of the *Origin*. But Theophrastos was not thinking about evolution, and so any comparisons with Darwin would be superficial.[3] Instead I shall concentrate on exploring the views of a few representative thinkers in detail. My aim is to investigate the reasons why evolutionary thinking failed to gain momentum in antiquity after its introduction by Empedokles.

Empedokles of Akragas (fl. 460-430 BCE)

The only recognizable transmutation theory to survive from antiquity was developed by Empedokles in the 5th Century BCE. Empedokles's cosmology posited four basic elements—earth, air, fire, water—and two cosmic forces—Love and Strife (see MATTER). Strife is an entropic force that causes things to separate, while Love is a magnetic force bringing them together. Empedokles thought that all of the diversity and change in the universe could be adequately explained in terms of a general theory of mixture in which a small number of basic materials combined and recombined in different ratios (*logoi*) under the periodic influence of Love and Strife. It is within this framework that he developed his transmutation theory of the

[3] Theophrastos also discusses what has come to be called "heterogony", the belief that the seeds of one species of plant can give rise to plants of another species (*Inquiry into Plants* II 4). In the *Vestiges of the Natural History of Creation* (Chambers 1844) this was offered as a major piece of 'evidence' for evolution. But Theophrastos's remarks are about different methods of propagation and have nothing to do with evolution (cf. Mayr 1982: 309).

origin of species.[4] Unfortunately his account can only be reconstructed from fragments, the most important of which are the following:

> Empedokles held that the first generations of animals and plants were not complete but consisted of separate limbs not joined together. The second generation, arising from the joining of these limbs, were like creatures in dreams. The third was the generation of whole-natured forms. And the fourth arose no longer from the homogeneous substances, such as earth or water, but by interbreeding, in some cases as the result of the condensation of their nourishment, in other cases because the beauty of the females excited the sexual urge; and the various species of animals were distinguished by the quality of the mixture in them…. (DK 31A72, translated after KRS)
>
> Here sprang up many faces without necks, arms wandered without shoulders, unattached, and eyes strayed alone, in need of foreheads. (*Fr.* 57, KRS)
>
> Many creatures were born with faces and breasts on both sides, man-faced ox-progeny, while others again sprang forth as ox-headed offspring of man, creatures compounded partly of male, partly of the nature of female, and fitted with shadowy parts. (*Fr.* 61, KRS)

The details of Empedokles's theory are unclear, owing to the fragmentary nature of the evidence, making it difficult to piece together a coherent picture. But the basic idea is relatively straightforward.

[4] *Fr.* 23. Cf. Kirk, Raven, and Schofield (1995: 294). There is no scholarly consensus surrounding Empedokles's cosmic cycles (see O'Brien 1969). For convenience, I shall assume that the evolutionary processes that follow occurred during the reign of Love.

Empedokles clearly envisioned some kind of evolutionary account for the origin of species. According to this theory, life evolved from simple inorganic materials (the four elements) through a combination of random variation and some kind of selection process (*Physics* II 8, 198b29-32). The primary forces that generate variation are Love and Strife. As Aristotle makes clear (e.g. *Gen. Corr.* 333a35-334a9), Empedokles treated these as blind mechanical forces ("blind" in the sense of not aiming at any specific outcome): Love is a cause of coming together *only*, not of coming together in *this* or *that* way; while Strife is a cause of dissociation *only*. Empedokles imagined Love generating variation by first bringing the elements together in random ways resulting in chance combinations (*Fr.* 59). For example, Empedokles tells us that flesh and bone were originally produced as the elements "happened to fall together" in different proportions "as each chanced to meet another" under the influence of Love. The resulting 'tissues' formed the basis for the first generation of living things to evolve.

As Love began to take hold of the universe the 'tissues' were brought together in different ways to form disembodied limbs ("the first generations of animals and plants were not complete but consisted of separate limbs not joined together"). There were "many faces without necks, arms wandered without shoulders, unattached, and eyes strayed alone, in need of foreheads" (*Fr.* 57). Of course these were not limbs in the proper sense (they were not parts of whole organisms) but proto-organisms, rudimentary life-forms that enjoyed an independent existence of their own.[5] The next evolutionary change produced the biggest explosion of diversity. As the various 'limbs' collided with one another, they produced a variety of complex

[5] DK 31A72 tells us that these proto-organisms constituted the first generation of living things. Though obscure, Fr. 20D (l.2-3) of the newly discovered Strasbourg fragments also suggests that Empedokles considered these 'limbs' to be living organisms. He says: "…at one time through Love, we [sc. the elements] all came together into one as limbs, which have acquired bodies at the height of their flourishing life."

organ-systems ("the second generation, arising from the joining of these limbs"), which Empedokles describes as being "like creatures in a dream". There were organisms with "rolling gate and countless hands" (*Fr.* 60), others with "faces and breasts on both sides" (*Fr.* 61), as well as "man-faced ox-progeny" (*Fr.* 61). Somewhere along the line Empedokles invokes what looks like a principle of natural selection, which Aristotle describes at *Physics* 198b29-32:

> Wherever, then, everything happened just as it would have if it had it come to be for the sake of something, those creatures that were spontaneously organized in a suitable way survived, while those that were not perished and continue to perish, just as Empedokles says of his man-faced ox-progeny.

The other details of Empedokles's full evolution story are murky. DK 31A72 mentions a third generation of "whole-natured forms" as well as a fourth generation (presumably the immediate ancestors of all contemporary species) who were capable of sexual reproduction. But it is unclear how these were both related to the previous generations. There are generally two ways of understanding Empedokles's account here.

Some read the fragments as positing a single continuous line of evolution from the elements to present-day species. Random mixtures of elements first threw up 'tissues', which eventually combined to form disembodied 'limbs' (the first generation of living things). The dream-like creatures of the second generation later emerged as these 'limbs' were fused together by Love. Contemporary species are descended from those advantageous fusions that out-survived and out-reproduced their more unprofitable counterparts. For example, Empedokles may have thought that modern sea urchins evolved from those creatures with "rolling gate and countless hands" (*Fr.* 60; cf. Aristotle *Part an.* 681a6-9), since that arrangement of limbs was better adapted for survival than other combinations. The whole-natured forms were intermediate between the dream-like creatures and present-day species. By calling them "whole-natured" (*tôn holophuôn*) Empedokles presumably means that, at some point in their evolutionary history, living things transitioned from being mere collections of limbs randomly joined together by Love to the sorts of functionally-integrated unities we see today. On this first reading, then, the evolutionary history of life on earth runs from (1) elements to (2) 'tissues' to (3) disembodied 'limbs' to (4) combinations of 'limbs' to (5) whole-natured organisms, which eventually evolve sexual reproduction to become (6) present-day species.[6] Other scholars deny that there is one continuous evolutionary sequence and instead posit a break in Empedokles's zoogony between (4) and (5).[7] The first sequence culminated in the dream-like creatures of the second generation, which immediately went extinct.[8] The second sequence began afresh when "the whole-natured forms" sprang up from the earth (*Fr*. 62) and then evolved into present-day species after acquiring sexual reproduction.

The fragmentary evidence is not sufficient to settle which of these two readings is correct. On the one hand, *Fr*. 62 does refer to whole-natured organisms that were spontaneously generated, like the earth-born race of Plato's *Statesman* (269b). This would have been consistent with traditional views about the origins of modern humans and non-human animals (cf. Aristotle *Gen. an.* 726b28-30). On the other hand, Aristotle's remarks could be read as implying that some of the dream-like creatures of the second generation evolved into present-day species. At the very least he suggests that Empedokles's principle of

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[6] This interpretation goes at least as far back as Lucretius 5.855-60.

[7] See O'Brien (1969, 196-200) for other interpretations that advocate a discontinuous sequence with a full break between the second and third generations.

[8] See Sorabji (1980, 176-7), who argues that these organisms were incapable of reproduction and died off after one generation.

selection was operating on the individuals of the second generation and so we should expect them to have left descendants. Whichever of these two interpretations is correct, the more interesting philosophical question is whether or not Empedokles can be said to have anticipated Darwin's theory of evolution by natural selection, as traditionally assumed.

Empedokles certainly grasped the basic concept of natural selection. Darwin defined natural selection in the *Origin* as "the preservation of favorable variations and the elimination of unfavorable ones" (*Origin* 1859, 81). This is exactly what we find in Empedokles. On Empedokles's account, the second generation of dream-like creatures arose as Love randomly joined together various limbs. Those forms that were "spontaneously organized in a suitable" were preserved, while those that were not were eliminated.

But there are good reasons to resist the conclusion that Empedokles anticipated *Darwin's* theory of evolution by natural selection (as traditionally assumed). First, Darwinian selection is an inter-generational process that depends on the inheritance of beneficial variations. While Empedokles's "dream-like" creatures exhibited differential fitness, there is a question as to whether or not they were reproductively viable. For example, *Physics* 198b29-32 says that some of these creatures survived; it does not say they survived *and reproduced* (Sorabji 1980: 177). If this is right, then Empedokles's brand of one-off selection (which occurs within a single generation only) would not be sufficient to count as Darwinian selection (cf. Dawkins 1986: chapter 3). I don't take this objection to be decisive. The fact that Aristotle only mentions survival does not necessarily mean individuals in the second generation were not reproductively viable. By saying those fusions that were spontaneously organized in a suitable way "survived", Aristotle could mean (a) those particular organisms survived for a single generation or (b) the lineage itself survived for several generations. None of the extant fragments helps us to decide between these alternatives.

Let us grant that, on Empedokles's theory, the history of life forms a continuous trajectory from simple inorganic materials (the four elements unmixed) all the way to contemporary species. Let us also grant that life evolved owing to a combination of random variation and some kind of inter-generational selective process. Still, this is not enough to conclude that Empedokles anticipated Darwin's theory of evolution. Empedokles's principle of natural selection is not Darwinian for at least two important reasons. First, none of the fragments mentions anything like the Mathusian principle of geometric increase, which says that many more individuals are born each generation than can possibly survive given limited environmental resources, or the struggle for existence that such conditions give rise to. This was a crucial step in Darwin's argument.[9] Second, and more importantly, Empedokles assigned only a negative role to his principle of selection, whereas Darwinian selection is a creative force capable of building organs through the accumulation of favorable variations over time (stepwise cumulative selection).

To see how natural selection can build complex adaptations, imagine an ancestral population of sightless organisms (Dawkins 1986). One day a mutation arises that generates a patch of photoreceptor cells on the heads of a small number of individuals, which allows them to detect shadows. While not a huge improvement, it is enough to give those individuals a slight advantage in the struggle for existence. If the mutation is heritable, then natural selection will preserve that new variation in the next generation. Over time, the trait will spread through the population as light-detecting individuals tend to leave more offspring than

[9] It is well-known that A.R. Wallace had independently discovered natural selection. And both of these were part of his account (see *On the Tendency of Varieties to Depart Indefinitely from the Original Type*, 1858).

their blind conspecifics. Eventually the population evolves as the proportion of light-detectors increases relative to the blind variants, which are driven to extinction. Those new light-sensitive cells now provide the basis for further modification. Imagine a few thousand generations later the gene that controls the growth of those photoreceptors again mutates causing an overproduction of cells. This expands the area, allowing in more light. This again gives its possessors an edge in the struggle for existence, causing the new mutation to spread through the population as individuals with the new expanded patches outcompete their original sighted ancestors, again causing a change in the relative frequency of the two variants (evolution). Next, imagine that several thousands of years later another mutation causes the expanded patch of skin to bend inwards forming a shallow cavity. These new organisms can not only detect light and dark, they can also sense the direction of an object. This would give those organisms a tremendous advantage over their conspecifics in the struggle for existence, again leading to an evolutionary change in the population, and so forth until eventually we arrive at something like the complex vertebrate eye. In this way, natural selection is able to build complex organs piece by piece through the gradual *accumulation* of beneficial (yet random) modifications of preexisting traits over hundreds of thousands of generations.

By contrast, the production of new forms in Empedokles's system is entirely the result of chance. At each stage of evolution, new forms are created through chance collisions of simpler bodies brought together under the influence of Love, a blind mechanical force that combines things wholly at random. Selection's role in this process is limited to removing those complex fusions that happened to be combined in ways that are not ecologically viable (see further Sorabji). On Empedokles's account, then, each generation of new forms is produced in a single step by randomly combining the bodies of the previous generation ('saltation'). There is no suggestion of any stepwise accumulation of slight variations over thousands of generation (no gradual cumulative selection). To use an analogy from Dawkins, Empedoklean evolution works like a hurricane blowing through a junk yard and randomly combining parts of a plane. When the dust settles, we are left mostly with clusters of parts that can't fly, but also some working planes. The principle of selection is merely responsible for removing those unprofitable combinations from the junk yard and leaving the viable ones behind.

Aside from Empedokles there were no other recognizable theories of transmutation in antiquity, and certainly no recognition of the mechanism of natural selection. Although Empedokles did not manage to achieve the sophistication of Darwin's theory, his idea that life evolved from simple inorganic materials through a combination of random variation and some kind of selective process was clearly ahead of its time. Unfortunately his ideas failed to gain momentum and were eventually eclipsed by the static worldview characteristic of Platonism and Aristotelianism.

Plato (429-347 BCE)

There is little in Plato that even remotely resembles evolutionary thinking. On the contrary, Plato is seen as the forefather of modern Creationism. At *Philebus* 28d-29a (Plato's) Socrates argues that the cosmos is an ordered whole and that only reason and intelligence could be the cause of such complexity. This commitment forms the basis for the Creationism articulated and defended in the *Timaeus* (Henry 2013: 226-9). There Plato sets out his two-world view, which divides reality into "that which always is and has no becoming" (the world of the Forms) and "that which comes to be but never is" (the sensible world) (*Ti.* 28ab). The world of being is "grasped by thought together with an account, and is unchanging", while the world of becoming is "grasped by belief together with unreasoning sense perception" and is characterized by instability and constant flux. Plato establishes, first, that everything that comes into being is necessarily brought into being by the agency of some cause (since nothing comes to be without a cause) and, second, that everything that is produced is produced according to some model. The Demiurge (aka *Nous*) and the Forms satisfy these two requirements, respectively. This yields an account of creation according to which visible nature is the product of an Intelligent Designer who constructed things by looking to the Forms as his models: "This, then, is how it has come to be: it is a work of Craftsmanship (*technê*), modeled after that which is changeless [sc. the Forms] and is grasped by a rational account, that is, by wisdom." (29a)

At the core of Plato's account is a distinction between intelligence, which serves as the primary cause of order (following the *Philebus*), and material necessities, which function as "co-causes" (*sunaitia*) that are used by intelligence to execute its plans.

> Now all of the above factors [sc. material-level forces] are among the co-causes employed in the service of the god as he does his utmost to bring to completion the character of what is most excellent. But because they make things cold or hot, compact or disperse them, and produce all sorts of similar effects, most people regard them not as co-causes but as the true causes of things. Things like these, however, are totally incapable of possessing any reason or intelligence about anything, and as secondary all those belonging to things that are moved by others and that set still others in motion by necessity. We too, surely, must do likewise: we must describe both kinds of cause, distinguishing those which possess intelligence and thus fashion what is beautiful and good

> from those which, when deserted by intelligence, produce only haphazard and disorderly effects every time. (46c-e)

For Plato, then, natural causes could never produce complex adaptations without the guidance of intelligence. For, only things that possess intelligence are capable of producing "what is beautiful and good", whereas natural causes operating according to blind necessity (when "deserted by intelligence") produce "only haphazard and disorderly effects every time".

Aristotle (384-322 BCE)

Aristotle is more direct in his rejection of Empedokles's biological views. At *Physics* II 8, 198b10-29, he entertains Empedokles's theory as a possible rival to his own, which relies heavily on intrinsic goal-directed principles of change (or "natures"):

> We must speak first about why nature is among the causes that operate for the sake of something. ...Here a puzzle arises, namely, what is to prevent nature from acting, not for the sake of something and because it is better, but just as Zeus sends the rain: not so that the crops would grow, but from necessity (for that which goes up must fall, and what is cooled must become water and descend <as rain>; the growth of the corn results from this). Likewise, if a man's crop is spoiled on the threshing floor, the rain did not fall for the sake of this (so that the crops might be spoiled); that just happened. So what prevents the same thing from being the case with parts in nature? For instance, the teeth come up from necessity, the front ones sharp and adapted for tearing, the back ones broad and useful for grinding down food, since they did not come to be for

> the sake of that; rather, it was a coincidence. And similarly with all the other parts that are believed to be present for the sake of something.

Aristotle takes Empedokles's account to be an example of this sort of thinking (*Phys.* 198b29-32, above). As we have seen, Empedokles treats Love as a blind mechanical force that causes things to fuse together in no particular way. Most of the time these fusions are poorly-adapted for survival and die out. But every once in a while Love will throw up a combination of parts that happen to work together and the fusion survives. But that was purely coincidental, since Love does not act for the sake of creating a well-adapted forms anymore than it does for the sake of creating poorly-adapted ones. It is all a matter of chance.

Aristotle ultimately rejects Empedokles's account, not because its transmutation theory is antithetical to a world of changeless forms, but because it affords too great a role to chance in the process of development:

> Yet, it is impossible for this to be the true view. For teeth and all other naturally formed parts come to be in the same way either always or for the most part, while this is not the case with any of the products of luck or chance. ...If, then, it is agreed that things are either the result of coincidence or exist for the sake of something, it follows that they must be for the sake of something. (*Phys.* 198b34-199a5)

On Empedokles's theory, complex adaptations are the products of blind chance. But the development of the parts of living things is just too consistent to be the result of chance. Instead the causal mechanisms that generate adaptations must themselves be under the teleological control of the organism's "nature" (*Phys.* 199b13-18; cf. *Part an.* 641b23-8).

At first glance Aristotle's objection appears to rest on a confusion between what Ernst Mayr (1988: 28) calls the *proximate* versus *ultimate* causes of species forms. The former refer to the underlying developmental mechanisms that are responsible for generating the particular individual, while the latter refer to the historical (evolutionary) causes that operate on the species itself over thousands of generations. Since the account to which Aristotle refers in *Physics* 198b29-32 concerns the evolutionary origins of species, not the embryological origins of particular members of species, it looks as though he is guilty of a kind of category mistake. But there is some evidence that Empedokles tried to apply his basic evolutionary principles to embryology (*Gen. an.* 722b6-20, 764b15-20) and that this is the target of Aristotle's criticism. According to that account, each embryo contains a set of tiny preformed parts derived from the parts of the parent organism (see EMBRYOLOGY). As Aristotle understands the theory, those preformed parts are meant to resemble the proto-organisms that constitute the ancestors of modern species. And just as those disembodied 'limbs' fused together to form various complex organ-systems, so too the tiny preformed limbs grow together during development to create a new individual (*Gen. an.* 722b6-20). Thus, at least as Aristotle understands him, Empedokles thought that embryology recapitulated zoogony (to adapt a famous expression). If this is right, then Aristotle may have felt justified in extrapolating from Empedokles's evolutionary account (including the role assigned to Love in the process) to his explanation of development.

But modern also biology agrees with Aristotle's objection as it applies directly to Empedokles's theory of evolution (it affords too great a role to chance in the process). This was the point made earlier, where it was noted that Empedokles makes chance the primary cause of adaptive evolution. On Empedokles's account, Love creates organic forms by randomly fusing together simpler elements. Any good 'fit' that results between a particular fusion and its surrounding environment is thus purely coincidental (which is anathema to Darwinism). On this theory, selection is left to play only the negative role of culling those unhappy fusions that happen to be put together in ways that are not ecologically viable.

Aristotle no doubt opposed the idea of a transmutation of species. But it is worth noticing several features of his biology that are actually conducive to an evolutionary worldview. I mention only three here.

(1) The inclusion of humans within animal nature. Aristotle certainly believed that the possession of intellect (or *nous*) constitutes a unique feature of the human essence not shared by other animals. But Aristotle's biology does not define humans exclusively in terms of this feature. The human species, like other animals, is defined by multiple differentiae (*Part an.* 643b9-644a11) including various features of its *bios* or 'way of making a living', which is a single complex activity that incorporates a certain way of moving in space, a certain way of feeding, a certain way of reproducing, a certain way of sensing the world, and so forth (see, esp., *Hist. an.* I.1-5). (Modern ecologists refer to this multidimensional description that relates the organism to its environment as its "ecological niche".) This had implications for the way Aristotle understood the boundary between human and non-human animals. For he recognized that many dimensions of the human *bios* overlap with those of other animals. For example, humans are air-breathing land dwellers that give birth to live young, something they share in common with other mammals. Given this fact, it is doubtful that Aristotle conceived of the difference between humans and non-human animals as fundamentally a difference in kind. Instead he seems to treat it as a difference in degree: humans share many features in common with other non-human animals; they simply realize those shared features to a greater

degree of perfection. This is even true for some features of their moral character, which historically have been seen as separating humans from the rest of the animal kingdom (Lennox 1999). This is important because the biblical conception of humans as somehow separate from the rest of nature was a major barrier to accepting Darwin's claim that humans evolved from other animals (cf. Bowler 2009: 7).

(2) The elimination of Design. While Aristotle often characterizes the productive activity of "nature" using the language of design (*Part. an.* 645a9-11, 652a31; *Gen. an.* 730b24-33, 730b19-23, 731a24, 740b25-741a3, 743b20-5, 744b16-27, 778a4), his personification of nature can only be metaphorical. For there is little evidence that his biology relied on an Intelligent Designer. In *Physics* II, Aristotle argues that each natural substance contains within itself principles of change and stability, which together constitute its "nature". He goes on to defend the view that nature in this sense is a goal-directed efficient cause that acts "for the sake of something and because it is better" (198b17-18). And he explicitly contrasts natures with intelligence and craftsmanship as distinct kinds of moving cause (e.g. 192b8-34, 198a2-4, 199a20-8; cf. *GA* 735a2-4). Thus, Aristotle had no need to posit anything like Plato's Demiurge over-and-above the natures of particular natural substances. His natural teleology does not depend on intelligence as it does for Plato.

(3) The recognition of heritable variation. Perhaps the most overlooked feature of Aristotle's biology from an evolutionary perspective is his theory of heredity. In *Gen. an.* IV.3, Aristotle argues that an adequate theory of generation must explain a number of phenomena connected with heredity (767a36-b6). The bulk of his theory is devoted to articulating the causal mechanisms that explain how heritable variations are communicated from one generation to the next. According to his account, each organism's genetic material carries a set of

"movements" (*kinêseis*), drawn from a corresponding set of "potentials" (*dunamis*) in the organism itself. Once inside the embryo the "movements" trigger a sequence of changes that terminates in a particular phenotype. The main upshot of Aristotle's theory is that it became possible to explain how variations within a species are maintained across generations (Henry 2006). This is important because that kind of heritable variation provides the raw material for natural selection.

Aristotle's theory of heredity also included the possibility of heritable mutations. At *Gen. an.* 768b10 (cf. 769b9–10) Aristotle tells us that disruptions in the normal pattern of inheritance result when the spermatic movements become "confused together". On one reading, these "confused" movements produce mutated potentials in the offspring's genetic nature. Those mutations would then be perpetuated, since there will be a new set of movements in the offspring's own *sperma* derived from those mutated potentials (in accordance with *Gen. an.* 767b35–768a2). The possibility of heritable mutation thus opens up theoretical space in Aristotle's account for a source of new variations, which could potentially lead to an evolution of species forms in the way Empedokles suggests.

Aristotle, of course, never took this step. Although his biology included a mechanism for generating and perpetuating heritable variations (the raw materials for natural selection), he failed to appreciate the evolutionary significance of this fact. To see why, consider Darwin's synopsis of natural selection:

> Let it be borne in mind in what an endless number of strange peculiarities our domestic productions, and, in a lesser degree, those under nature, vary; and how strong the hereditary tendency is. Under domestication, it may be truly said that the whole organisation becomes in some degree plastic. Let it be borne

> in mind how infinitely complex and close-fitting are the mutual relations of all organic beings to each other and to their physical conditions of life. Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations useful in some way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations? If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind? On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favorable variations and the rejection of injurious variations, I call Natural Selection. Variations neither useful nor injurious would not be affected by natural selection, and would be left a fluctuating element, as perhaps we see in the species called polymorphic. (*Origin* 1859, 80-1)

While Aristotle recognized the importance of heritable variations between species members, his emphasis was never on differential fitness (in contrast to Empedokles). Rather, his main focus in *Gen. an.* IV.3 was on patterns of heredity as such — why offspring resemble their parents more than other members of the same species — and not on whether those heritable variations give their possessor an advantage over conspecifics. For one thing, though Aristotle's biology places great emphasis on what Darwin calls "the mutual relations of all organic beings to each other and to their physical conditions of life" (compare *Hist. an.* I.1-5), he did not recognize (or at least says nothing about) the struggle for existence that those relations can generate, which is so important to Darwinian evolution. For another thing, Aristotle seems to have viewed most intra-specific variations as ecologically neutral: those traits that he thinks differ within a species tend not to make any functional contribution to the species' particular way of life (cf. *Gen. an.* V). Thus, while Aristotle allowed for heritable variations between species members, he did not see the possibility of those variations increasing an individual's reproductive success relative to conspecifics. The main explanatory burden of his theory is simply to account for the maintenance of polymorphism in the form of family resemblances.

So why did Aristotle fail to see the evolutionary implications of his own biological views? What is the ultimate source of his blindness (if not outright resistance) to a transmutation of species? One place that scholars have looked for this is in a pair of passages from *De an.* II.4 and *Gen. an.* II.1. In both places Aristotle is thought to have derived the immutability of species from considerations of the individual's desire for immortality (see Balme 1992: 155-6; Cooper 2004: n. 4; Lennox 2001: chapter 6). In the *De an.* passage, Aristotle argues that reproduction is the best available means by which individuals can achieve immortality. What persists in this case is not the individual itself but its substantial form (415b3-7). In the *Gen. an.* version of the argument Aristotle concludes that "for this reason there will always be a *genos* of humans, animals, and plants" (732a1-2), where "*genos*" presumably refers to a continuous generation of things of the same form (cf. *Meta.* 1024a29-31).

But neither argument commits Aristotle to the claim that what passes from one generation to the next is an immutable species form. The *De an.* argument is compatible with the possibility of species gradually evolving over time through the accumulation of slight variations between parent and offspring. For Aristotle seems to allow for differences in the degree to which individuals manage to replicate their forms (415b3-6), something already implied by his theory of heredity. The *Gen. an.* version of the argument comes closer to positing immutable species forms, but the text is far from conclusive. Saying that there will always be a continuous lineage of animals and plants does not entail that any particular species of animal or plant must remain the same over time. The continuity in question applies at a much higher level of generality, which leaves room for evolution (even if within fixed limits). Aristotle does say there will always be lineage of humans as well, which seems to commit him to the view that at least one species is immutable. But he is not actually arguing for that claim here; that is not his point. The immediate context of the *Gen. an.* argument suggests that Aristotle is defending a more general conclusion.

One of the major puzzles driving Aristotle's *Generation of Animals* is why there are sexes. Of particular importance to the case of animal generation is why animal species are divided into separate sexes. *Gen. an.* 731b24-732a10 provides a teleological explanation for this fact, whose aim is to identify the reproductive advantage that is accrued to animals by having separate sexes (cf. 717a15-16). The explanation proceeds in two steps: first Aristotle provides an argument for why the sexes exist (731b24-732a3); he then goes on to show how the *separation of* the sexes makes reproduction better (732a3-10). Aristotle's remarks about a continuous generation of humans, animals, and plants is the conclusion to an argument that forms part of the first step in this explanation. That argument is itself a more specific version of an argument presented at *Generation and Corruption* II.10, 336b25-35.

According to the *Gen. corr.* argument, the best universe is one that contains as much being as possible. Since things in the 'sublunary' realm (e.g. elements, living things) are not capable of existing eternally, but must come to be and pass away, the closest approximation to eternal being in this part of the universe is an everlasting cycle of generation: "For that way existence would be most connected (*malista suneiroito*), because the fact that coming to be should itself come to be perpetually is the closest approximation it has to eternal being." The argument at *Gen. an.* 732b24-732a2 applies this general theory to the specific case of biological generation. Since no individual organism is capable of eternal existence, the closest approximation to eternal being in the biological realm would be to make the generation of living things perpetual. *This* is why there will always be a continuous generation of humans, animals, and plants: that is the best way to maximize the amount of being in the world, given the constraints imposed on living things by their material natures. This in turn provides the final cause for the existence of sexes. Males and females are present for the sake of this insofar as they constitute the first principles of generation (*Gen. an*. 716a2-7). On this reading, the existence of reproduction contributes to the overall good of the universe by helping to maximize the amount of being in the world in the only way that is possible for living things.

When read in the context of *Gen. corr.* II.10, we can see that the *Gen. an.* argument does not require the stronger claim that each particular species must be eternal and unchanging. The idea is that, since eternal organisms are not possible, the next best thing is to have eternal ancestor-descendent lineages. That way life (being for a living thing) will be "most connected" (*malista suneiroito*) because there will be a continuous series of things of the same form. When Aristotle mentions the forms of humans, animals, and plants it is reasonable to suppose that he is pointing to the three general types of soul from the *De anima*, namely, intellectual soul, sensory soul, and nutritive soul. If this is right, then all the *Gen. an.* argument commits Aristotle to is the claim that these three generic forms must be eternal. That leaves room for a closed-system of evolution within the limits of these general types.

What I would suggest that the primary impetus for Aristotle's anti-evolutionary views comes, not in his biology, but from his epistemology. According to *Posterior Analytics* knowledge in the strict sense (*epistêmê haplôs*) — the sense that is appropriate to science — is acquired through demonstration (*apodexis*). And the premises of a demonstration must be universal propositions that express necessary relations between natural kinds (*An. post.* I.2, 4), where 'necessity' is understood in terms of what is eternal and incapable of being otherwise. It follows that there cannot be scientific knowledge of non-eternal truths:

> It is also clear that, if the premises of the syllogism are universal, then the conclusion of a demonstration of this kind (demonstration in the strict sense) must be eternal (*aidion*). Therefore there is no demonstration of things that pass out of existence nor is there knowledge of them in the strict sense but only in the incidental sense in which an attribute belongs to the subject not universally but only at a given time or under certain circumstances. (*An post.* 75b21-6; cf. *Eth. nic.* VI.3)

In this way the formal requirements of Aristotelian science impose constraints on the objects of knowledge that seem to be incompatible with an evolutionary world view. For Aristotle, the objects of scientific knowledge must be eternal and unchanging. So there could not be an Aristotelian science that took as its objects evolving populations that come into being and go extinct. Scientific knowledge of biological species is only possible if those species did not undergo any permanent changes in their essential nature.[10]

[10] It is a matter of great controversy whether or not Aristotle's biology conforms to the strict standards of knowledge developed in the *Analytics*. Indeed, it is a matter of scholarly debate whether or not those standards are in fact as strict as I have suggested here.

Galen (*ca.* 130-200 CE)

Aristotle's argument for teleology in *Physics* II.8 laid the foundation for the first genuine Design argument, formulated by Galen in the second century CE. Galen's *On the Usefulness of the Parts of Animals* (*OUP*) can be read as an extended defense of Aristotle's argument supported by his extensive knowledge of animal anatomy. In Galen's version of the argument, however, the key premise that things come about either by coincidence or for the sake of something (*Phy.* 199a3-5), becomes an opposition between the hypothesis of chance defended by the Epicureans and the hypothesis of design articulated in Plato's *Phaedo* and *Timaeus*.[11] The structure of Galen's argument is roughly:

1) The parts of living things perform functions that contribute to survival.
2) The ability of each part to perform its function depends on a precise structure. Any deviation from that structure, however slight, would destroy its ability to execute that function.
3) The perfect fit between structure and function is either a product of chance or intelligent design.
4) It is highly improbable that chance could be responsible for the perfect adaptations we observe in nature.
5) Therefore, such adaptations must be the product of intelligent design.

Galen builds his case for Premise 4 in stages, moving from the internal coordination of the features of a single part, to the coordination of the parts of the whole system, to the fact that different species of animals with the same way of life possess these same adaptations. As the level of complexity increases, Galen argues, the possibility that blind mechanical forces (e.g.

[11] See, esp., *OUP* I.21, VI.12-13. By contrast Aristotle explicitly argues that the natures of living things operate for the sake of an end but not through intelligence (*Phys.* II.8).

the random collision of atoms) are responsible for the fit between structure and function becomes increasingly small. Galen's example of teeth illustrates this general argument (*OUP* XI.8, cf. XI.7).

When we examine the dentition of a carnivore, we can see that different kinds of teeth play different roles in mastication. And each tooth possesses its own unique set of characteristics optimally suited to its function. The different features of the molar, for instance, are all adjusted to one another in a way that allows them to execute the function of grinding. Change any one of those features and the function is destroyed. Even if we grant that each tooth might be the result of the random collisions of atoms, all the teeth must be coordinated in such a way that they work together to execute the overall function of mastication. There are an indefinite number of possible dental arrangements that carnivores might have had but only one that results in a working system of teeth suited to its particular way of life: there must be sharp incisors in the front for biting, followed by a set of canines for gripping and tearing flesh, with flat molars at the back fitted with the precise topography needed to grind the food down before swallowing. Altering that set up in any way, either by changing the shape and structure of any tooth or arranging them in a different order, would destroy the function for the sake of which that particular dentition arose. Finally, in order for mastication to contribute successfully to nutrition, the carnivore's teeth must be coordinated with its other organ-systems, each of whose own viability is in turn dependent on the same delicate balance between structure and function. The probability that all of this is due to the random collision of atoms, Galen argues, is vanishingly small.

Galen's argument has the familiar ring of modern Design arguments, which have their roots in Paley's famous watchmaker argument. Complex adaptations depend on a precise coordination between features that are all "adjusted" to one another in such a way that they work together to fulfill a specific biological need. Change any one of those features in any way and the whole function is destroyed. This has come to be known as the "irreducible complexity" of certain biological systems.[12] That argument now strikes us as weak because we are used to viewing adaptations from a Darwinian perspective. Galen is surely right that it is unreasonable to suppose that something as complex as the vertebrate eye or the dentition of a carnivore, let alone an entire organism, might arise in a single step from the spontaneous collision of atoms swirling around the void. But Darwinian selection is not like that. It involves the gradual modification of preexisting structures through the accumulation of random variations over thousands of generations, where each new variation is only a slight alteration in the preexisting structure. And the chances of slight variations arising in the course of many generations that are also profitable is much less improbable than a single massive variation (which usually crashes the whole system). However, the central weakness of Galen's argument is the assumption that *any* adjustment to a part, however slight, would destroy its ability to function. This is empirically false: a survey of the number of variations, not only among carnivores as a class, but among the members of each species of carnivore, shows that there are multiple adjustments that could be made to carnivore dentition that would preserve the function of mastication.

Conclusion

Galen's argument helps draw attention to how small an impact evolutionary thinking had on Greek and Roman naturalists. To Galen, the only two options for explaining complex adaptations were intelligent design or blind chance. Even Aristotle, who rejected intelligent

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[12] The fallacy of an appeal to so-called irreducible complexity to refute the explanatory power of natural selection has been well-documented.

design, saw chance as the only alternative to his own brand of naturalistic teleology. That adaptations might have been gradually built up over time by a slow process of cumulative selection was not considered an option. The failure of evolutionary thinking to gain any traction in antiquity seems to come down to two factors. First, and most obvious, there was a serious lack of empirical evidence for evolution in antiquity. So Empedokles's theory would have been viewed as pure speculation. The best *available* (empirical) theory at that time was that species forms are immutable. The fact of evolution was accepted by science only after we had amassed a large body of empirical evidence to support it.[13] Some of the most important evidence was provided by fossils. While there is some suggestion that the ancients may have encountered fossils, even if they recognized them as such, isolated fossils viewed out of context would not have been enough to suggest an evolution of species.[14] What is needed is a proper *fossil record* that reveals different species existing in different rock strata, together with a theory that allows us to map the different the layers of rock onto different periods in the earth's history. Without this systematic fossil evidence, there was simply no impetus for pursuing the evolutionary hypothesis. Second, Empedokles himself had failed to appreciate the creative power of natural selection. As we have seen, even on his theory, well-adapted

[13] Today, science accepts that species have evolved over time on the basis of several lines of evidence, including the fossil records, the distribution of species around the globe (biogeography), embryological patterns, DNA evidence, the existence of homologies, and so forth, all of which converge on the theory of evolution. For an excellent discussion of the main lines of evidence, see Dawkins (2009) and Coyne (2009). While Empedokles seems to have appreciated that embryology might be related to the evolution of life on earth, this idea failed to gain any support beginning with Aristotle (see above).

[14] Mayor (2011) claims that the ancient Greeks and Romans collected, measured, displayed, and pondered the significance of fossils and that this formed the empirical basis for much of their mythology. I will leave the reader to judge the persuasiveness of Mayor's argument. However, if she is right, then it is puzzling why Aristotle — one of the most systematic and careful biologists the world has ever known and much of whose data is drawn from ordinary knowledge — never once mentions anything about observations of the bones of giant unknown animals. Even if we accept that the ancients encountered the fossilized remains of extinct species, including large vertebrates, there is no evidence that they recognized their evolutionary significance. For example, Xenophanes and Herodotus, writing in the fifth century BCE, apparently made passing remarks about fossilized shells. But neither of them saw this as evidence that species have evolved over time. Rather, both simply took them as evidence that the land in which they were found was once under water.

forms were seen as the products of blind mechanical forces that combined things entirely at random. That meant that any good fit that exists between organism and environment is entirely a coincidence. And few were willing to accept that.

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