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Aristotle on the Mechanism of Inheritance

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Abstract. In this paper I address an important question in Aristotle's biology, What are the causal mechanisms behind the transmission of biological form? Aristotle's answer to this question, I argue, is found in *Generation of Animals* Book 4 in connection with his investigation into the phenomenon of inheritance. There we are told that an organism's reproductive material contains a set of "movements" which are derived from the various "potentials" of its nature (the internal principle of change that initiates and controls development). These "movements," I suggest, function as specialized vehicles for communicating the parts of the parent's heritable form during the act of reproduction. After exploring the details of this mechanism, I then take up Aristotle's theory of inheritance proper. At the heart of the theory are three general principles (or 'laws') that govern the interactions between the maternal and paternal movements, the outcome of which determines the pattern of inheritance for the offspring. Although this paper is primarily aimed at providing a detailed analysis of Aristotle's account of inheritance, the results of that analysis have implications for other areas of Aristotle's biology. One of the most interesting of these is the question of whether Aristotle's biology is anti-evolutionary (as traditionally assumed) or whether (as I argue) it leaves room for a theory of evolution by natural selection, even if Aristotle himself never took that step.

Keywords: Aristotle, Aristotle's biology, *Generation of Animals*, genotype, phenotype, inheritance, evolution, nature

Introduction

Among Aristotle's most famous expressions is the often repeated mantra "human begets human" ("horse begets horse," etc.). But how does an

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Aristotelian form get passed on to an offspring in the act of reproduction? What are the mechanisms underlying the transmission of biological form? In other words, how exactly does human beget human (horse beget horse, etc.)?

The most obvious place to look for an answer to this is Aristotle's *Generation of Animals* (*GA*). I shall argue that the actual mechanisms behind the transmission of biological form are set out in *Generation of Animals* 4.3 in connection with Aristotle's theory of inheritance. This paper is an attempt to offer a detailed account of that theory. Of course, a complete analysis of Aristotle's views on inheritance would require a more lengthy discussion of the account of sex determination in *GA* 4.1-2, as well as a discussion of the problem of maternal inheritance.[1] In addition to being central topics in Aristotle's ontogeny (and thus necessary parts of any study of the *GA*), these issues are necessary precursors to the discussion of inheritance in *GA* 4.3. For example, in *GA* 4.3 Aristotle appears to assign a formal contribution to the mother. Many commentators have come to see this as being at odds with the strict reproductive hylomorphism set out in the first three books according to which the father provides the "form" while the mother provides the "matter."[2] Assuming the *GA* contains an internally coherent theory, a proper understanding of the mechanisms involved in the transmission of biological form (embodied in the phenomenon of inheritance) would have to begin with a solution to this problem.

Unfortunately I do not have space to explore these other topics here. For convenience I shall simply by-pass the discussion of sex determination altogether. Moreover, I shall take it for granted that, in addition to providing the material out of which the offspring develops, Aristotle thinks the female also makes a genetic contribution to reproduction.[3] The scope of this paper is limited to Aristotle's general account of the mechanisms of inheritance and how their operation serves to explain various patterns of resemblance (including both individual and species resemblances). In order to do that, it will be useful to introduce some terminology.

Two Senses of "Formal Nature"

In several key passages in the *Parts of Animals* (*PA*) Aristotle divides the "nature" of a biological substance into its "material nature" and its

[1] For a detailed account of these see Henry, 2004, Chapter 3 and 4 (respectively).

[2] Morsink, 1982; Furth, 1988; Cooper, 1988.

[3] For example, the female is responsible for the development of the offspring's nutritive soul (*GA* 2.5), as well as those aspects of its bodily form that make it look individuals on her side of the family (*GA* 4.3, see esp. 768a15–21).

"formal nature." The formal nature is then sub-divided into what he calls nature "as mover" (ὡς ἡ κινοῦσα) and nature "as end" (ὡς ἡ τέλος).[4] I shall not deal with the concept of material nature in any direct manner here. Roughly, the material nature of an organism (or organic compound) refers to what it is made out of, its matter. The formal nature is more important for my purposes, specifically the distinction between nature "as mover" and nature "as end."

An examination of the way Aristotle deploys these latter two concepts reveals that nature "as end" picks out the organism's fully developed adult form while nature "as mover" refers to the productive agent inside the developing embryo that directs the process towards that form. For example, at *PA* 1.1, 640b23–8 an organism's nature is identified with its shape (μορφή), configuration (σχῆμα), and visible character (ποῖοντὴν ἰδέαν). Here "nature" clearly refers to the shape and form of the adult organism (nature as end).[5] On the other hand, *GA* 2.4, 740b25–741a3 uses the concept of nature to pick out the active potential (ἡ ποιοῦσα δύναμις) inside the embryo that is responsible for generating the parts of the offspring's body (ἡ γεννῶσα). Here Aristotle is talking about an organism's nature understood as mover.

For convenience I will use the term "genetic nature" to refer to nature understood as mover (the thing that generates) and "phenotypic nature" to refer to nature understood as end (the visible form generated by it). My choice of terminology here is certainly not arbitrary. For when Aristotle distinguishes between the nature that generates and the nature generated by it, he seems to be drawing roughly the same distinction modern biology makes between the genotype and the phenotype.[6] Although these two concepts are not clearly defined even within modern biology, the phenotype basically refers to an organism's fully developed morphology, physiology, behavior, etc. (what we might generally call its observable form), while the genotype is the sum of underlying genetic factors which are in some sense productive of those phenotypic characters. To be sure, the extent to which the genotype is causally responsible for the development of the phenotype remains

[4] *PA* 1.1, 641a22–33 (cf. *Physics* 2.1).

[5] Compare *Metaphysics* Δ4, 1015a3–12 where nature in this sense is explicitly identified with the form at the end of the process of development (τοῦτο [sc. τὸ εἶδος καὶ ἡ οὐσια] δ' ἐστὶ τὸ τέλος τῆς γενέσεως).

[6] This insight has also been recorded by Morsink (1982, 167). Gutiérrez-Giraldo (2001) makes the reverse claim that I am making here. He argues, not that Aristotle made a distinction akin to the modern phenotype/genotype distinction, but that the modern concept of the genotype counts as an Aristotelian ψυχή. I shall not evaluate this interesting claim here.

controversial. What is important for my purposes, however, is simply the fact that modern biology recognizes a fundamental distinction between the phenotypic characters of an organism and the genes that underlie them.[7] It is in this sense that I think the phenotype/genotype distinction provides an effective model for understanding the relation Aristotle envisions between nature "as end" and nature "as mover" and the role that he assigns to each in his ontogeny.[8]

One of the things that led Aristotle to the distinction between the observable features of an organism and the productive sources of those features was the experiments he carried out on plants. Aristotle discovered that if you pull off parts of the parent plant before seed production, those missing parts will still show up in the seedling.[9] Aristotle took this as empirical proof that what is directly transmitted in the act of reproduction is not the observable part of an organism (the phenotypic nature) but its underlying cause (the genetic nature).

Mechanisms of Inheritance

In *Generation of Animals* 4.3 Aristotle states that an adequate theory of reproduction must explain at least eight different phenomena connected with inheritance:

1. Offspring tend to resemble their parents more than other members of the same species. (767a36–7)
2. Some offspring resemble the father while others resemble the mother, both (a) as a whole and (b) with respect to different parts (e.g. an offspring can have its father's eyes and its mother's nose). (767a37–b1)
3. Offspring tend to resemble their parents more than their ancestors. (767b2)
4. Offspring tend to resemble their ancestors more than any chance individual of the same species. (767b2–3)
5. Usually males resemble their fathers and females their mothers. (767b3–4)
6. Nevertheless, sometimes males resemble their mothers while females resemble their fathers. (769a3–4, b5–6)

[7] See, e.g., Laubichler and Wagner, 2000.

[8] Eventually I shall argue that an organism's genetic nature is comprised of several different active potentials, each of which governs the development of a specific part of its phenotypic nature.

[9] *GA* 1.18, 722a11–14.

7. Offspring who fail to resemble either its parents or its ancestors may still look like a human being at any rate. (767b4–5)
8. In extreme cases the offspring's observable form (τὴν ἰδέαν) may fail to bear any likeness to a human being, at which point it is a monstrosity (τέρας). (767b5)

I shall consider Aristotle's explanation for some of these later on (see "Aristotle's Theory of Inheritance" below). My aim in this section is to set out in detail the causal mechanism underlying Aristotle's account of them. My hope is that by grasping the details of this mechanism we shall not only be in a better position to understand Aristotle's theory of inheritance itself but also, more generally, how he thinks biological forms are transmitted from one generation to another in the act of reproduction.

The primary goal of the chapter is to explain the inheritance of features that make the offspring look like certain members of its own family more than other individuals of the same species (e.g. nose shape, eye color). As such, we can be sure that Aristotle thinks some features below the level of species are included in the form that is transmitted in the act of reproduction.[10] However, Aristotle does not confine the account of inheritance to these individual differences alone. What we find is that the causal mechanism at work in *GA* 4.3 actually underwrites the transmission of the species-form as well. For example, at *GA* 768a13 the mechanism is extended to include not only those properties that are peculiar to Socrates as an individual but also those that are common to all humans and animals (the universals).

The basic causal mechanism is introduced to us in the following passage from *GA* 767b35–768a2 (cf. 768a11–14):

> Therefore, there are κινήσεις present in the seeds <of animals> derived from the δυνάμεις of all of these sorts of things [e.g. male, Socrates, human, 767b24–6; animal, 768a13], and in potentiality even those of its ancestors, although those of the individual are always closer.

The two central components of the mechanism identified in this text are the "κινήσεις", which are said to be present in the parents' seeds (ὑπάρχουσιν αἱ κινήσεις ἐν τοῖς σπέμασι), and the "δυνάμεις" from which those κινήσεις are drawn (ἀπὸ τῶν δυνάμεων). (By "all these sorts of things" Aristotle means those phenotypic characters that are capable of being passed on in reproduction or, as Aristotle puts it,

[10] See *GA* 767b24–30 (discussed below).

those that belong to the organism insofar as it is capable of reproduction (καθὸ γεννητικόν, 767b23–9).) The main interpretive difficulty that arises in connection with *GA* 4.3 is how to understand this mechanism. More specifically, what are the "κινήσεις" and "δυνάμεις" supposed to be?[11]

I shall begin by examining (and subsequently rejecting) two possible interpretations of what Aristotle means by "δύναμις". On the first reading δύναμις simply refers to a property which is predicated of Socrates *qua* generator (it is a logical concept). The second reading also identifies a δύναμις with a property that belongs to the generator; however, it takes Aristotle to be identifying actual bodily characteristics rather than mere logical predicates (it has ontological significance). Against these two readings I shall take the concept to retain its more familiar sense of "potential" from *Metaphysics* Θ1–2 (causal power).[12] On the reading I shall defend the δυνάμεις refer to components of an organism's genetic nature, each of which is a potential for the formation of a different part of its phenotypic nature. In this way each δύναμις is associated with a specific characteristic in the teleological sense: it is a potential *for* that property.[13]

After identifying the nature of the δυνάμεις, I turn to the κινήσεις which are said to be derived from (ἀπό) them. All previous attempts to understand Aristotle's hereditary use of κίνησις can be roughly divided into three main readings (all of which are rejected here). The first reading identifies the κινήσεις with the formative motions *of* Socrates' sperm as it fashions the menstrual blood into parts of the offspring. On the second reading, the κινήσεις in question are not formative motions *of* the sperm but changes initiated in the menstrual blood *by* the sperm (those that make up the embryo's development). A third reading takes the κινήσεις in question to be the very same motions and changes that make up the process of development; however, unlike reading two, it identifies them with things carried inside the sperm (as in a vessel). On this reading the father's sperm "imports" changes directly into the menstrual blood, which then immediately set to work building that material into a new organism of the same shape and form.

[11] Until this question has been answered for each term I shall continue to employ the Greek as placeholders.

[12] For an excellent discussion of this sense of δύναμις see Gotthelf, 1987, 209–211. A simple example of an active δύναμις would be fire's power to melt iron. Iron has the corresponding passive δύναμις in virtue of which it is capable of being liquefied when exposed to fire. See also *Meteorologica* 4.8–12.

[13] By saying these are potentials *for* specific characters I mean that their activation during development initiates a set of changes that terminate in those characters.

In contrast to this, I shall argue that the κινήσεις in question refer to distinct units of inheritance carried inside Socrates' sperm. More specifically, they are *information-bearing vehicles* through which the parts of Socrates' form are physically transmitted to his offspring in the act of reproduction. (How this reading differs from the above three will become clear as we proceed.) This use of "κίνησις" is not peculiar to Aristotle's theory of inheritance. As we shall see, we also find the concept being used in this way in the account of sense perception in *GA* 5.

The "δυνάμεις"

Just prior to *GA* 767b35–768a2 (at 767b23–6) Aristotle remarks on his use of δύναμις: "I speak of each 'δύναμις' in the following sense. The generator is not only a male but also a particular sort of male, for example a Coriscus or a Socrates, and it is not only a Coriscus but also a human being." While this certainly provides a clue as to the reproductive significance of a δύναμις, Aristotle appears to be offering nothing more than a logical analysis of the concept here. If we take "the generator" (τὸ γεννῶν) as the subject, Aristotle's point in this passage is that the predicates "male," "Socrates,"[14] and "human being" all belong to the generator insofar as it is capable of reproduction (ὑπάρχει τῷ γεννῶντι καθὸ γεννητικόν) and not accidentally (κατὰ συμβεβηκός). The examples of genetically accidental properties are "being a good scholar" and "being someone's neighbor" (b26–9). Such properties are accidental to Socrates *qua* generator in the sense that they are not part of his heritable form: they are not features which are capable of being passed on in the act of reproduction. What 767b23–9 makes perfectly clear, however, is that those properties that make Socrates a unique individual (e.g. his particular shade of eye color and distinctive nose shape) *are* part of his heritable form. They are among those formal properties that belong to him "καθὸ γεννητικόν".

But how does this help us understand what a δύναμις is in this context? One of the meanings of δύναμις that Peck lists in the introduction to his translation of the *GA* is "distinctive characteristic."[15] This suggests that perhaps Aristotle is using δύναμις in a logical

[14] This stands for Socrates' distinctive characteristics falling below the level of species (his snub nose, blue eyes, etc.).

[15] Peck, 1990, li (Section 26; cf. Section 27). Peck claims that Aristotle's use of δύναμις in *GA* 4.3 reflects a specialized hereditary concept (liii, (Section 31)), though he does not say how we are supposed to understand that specialized use.

sense to refer to properties which are predicated of Socrates *qua* generator. On this first reading, 767b35–768a2 is simply pointing to the presence of κινήσεις in Socrates' sperm corresponding to those properties without making any claims about the actual presence of δυνάμεις in Socrates himself.

A quick glance at the text shows that Aristotle is quite clearly thinking of things which have some sort of physical (as opposed to logical) significance, things which are actually present in Socrates' body. For the δυνάμεις are supposed to be *the sources* of the κινήσεις in his sperm: the κινήσεις are "derived from" (ἀπό) those δυνάμεις.[16] Moreover, this first reading takes "male," "Socrates," and "human being" in 767b23–6 as the δυνάμεις themselves, whereas 767b35–768a2 refers to the δυνάμεις *of* these sorts of things. This implies some sort of ontological distinction between the phenotypic characters and the δυνάμεις of those characters.

Coles offers a second interpretation which attempts to preserve the identification of a δύναμις with a property of the generator's body while at the same time respecting its ontological status as the source of a corresponding κίνησις in its seed. According to Coles, by referring to the characteristics of Socrates' body as "δυνάμεις" Aristotle is assigning those bodily characteristics both phenotypic *and* genetic significance:

> ...the specific characteristics which make an individual what he is are also responsible for reproducing other specific individuals.... So to describe a characteristic of Socrates as a δύναμις must be to specify its particular hereditary significance as well as its phenotypic significance in characterizing Socrates.[17]

On Coles' reading the same characteristics which are displayed in Socrates' phenotype are also the δυνάμεις from which the κινήσεις in Socrates' sperm are drawn. For example, there is a κίνησις in his sperm corresponding to his snub nose which (on this reading) is drawn directly from his nose itself. In this sense Socrates' snub nose is both an actual part of his body *and* the source of a change that terminates in that same part in his offspring.

While I agree with Coles that the δυνάμεις in question are the sources of the κινήσεις in Socrates' sperm, they cannot refer to the actual parts of Socrates' body themselves. First, I am not sure that this

[16] Of course being *derived from* something as its source is not the only meaning of the Greek ἀπό; however, it is the most common meaning and the most likely one here.

[17] Coles, 1995, 73.

reading leaves room for the distinction Aristotle makes between a phenotypic character and the δύναμις *of* that phenotypic character. However, even if there is a way to preserve this distinction, Coles' understanding of the hereditary concept of δύναμις crucially depends on his assumption that Aristotle accepted the central tenet of the Hippocratic model of pangenesis, namely, that the capacity of sperm to transmit formal resemblances derives from its "pansomatic" origin in the parent's body. And this is an extremely difficult reading to maintain.

Coles refers to Aristotle's model as "formal pangenesis," as opposed to Hippocratic "material pangenesis." According to Hippocratic material pangenesis, the seed out of which the offspring grows is made of tiny bits of tissue drawn from each part of the parent's body.[18] Coles wants to argue that Aristotle picked up on this idea but held that instead of tiny bits of tissue, the parent's genetic material contains formal "κινήσεις." Coles takes these κινήσεις to be quite literally local motions (not *of* the sperm but *inside* the sperm) that preserve the shape and form of the parent's body.[19] His idea is this. Socrates' sperm is made from a residue of blood that has (according to Coles) traveled around to every part of his body during the nutritive cycle, the bit which is left over at the end of that cycle. The κινήσεις which are carried inside his sperm are the very same (local) motions that the blood underwent as it flowed around the contours of his body during nutrition; those motions are (somehow?) preserved in his sperm. Once inside the female, the sperm releases its motions into the menstrual blood which then sketch out the parts of Socrates' body by retracing the path his blood followed as it traveled around his own body.[20] It is in this sense, Coles argues, that the parts of Socrates' body are δυνάμεις or sources of motion ("parts can be sources or originators of movements, it seems, because blood flows around each and every part").

There are several reasons why formal pangenesis cannot be sustained as an interpretation of the *GA*. I shall confine myself to two.[21]

First, it is unclear why Aristotle's arguments against pangenesis in *GA* 1.17–18 should not also apply to so-called formal pangenesis. This is especially pressing in cases where Aristotle's attacks are focused not on the idea that what is drawn from the parts is some material component but on the idea that anything at all should be drawn from them. One

[18] The assumption here is that those bits of tissue have the ability to regenerate themselves. See *GA* 2.4, 740b12–18, 741b9–10.

[19] This is an example of the third reading of κίνησις discussed below.

[20] Coles, 1995, 61ff.

[21] In addition to these two arguments, there is sufficient textual evidence against Coles' reading. See especially *GA* 1.18, 725a21–7; 1.19, 726b9–15.

such argument appeals to his experiments with plants (722a11–14). Aristotle says that if you remove the parts of a plant, the theory of pangenesis predicts that those same parts will be absent from the offspring's phenotype. For there will be nothing in the seed drawn from those missing parts. Since this is not the case (the missing parts still show up in the seedling), Aristotle concluded that the reproductively significant units – whatever those might be – could not possibly be derived from the actual parts of the parent's body itself. This would equally apply to a formal pangenesis. Coles' reading predicts that if we amputated Socrates' legs prior to spermatogenesis, Menexenos would be born without legs. For according to formal pangenesis there will be no κινήσεις in Socrates' sperm corresponding to those amputated parts. For there are no such parts for his blood to flow around during the nutritive cycle.

Second, formal pangenesis (like material pangenesis) will not be able to account for the phenomenon of atavism, which Aristotle thinks any adequate theory of inheritance must explain. This is the most significant for my purposes here. Take the case of the woman from Elis, which Aristotle uses in Book 1 to undermine pangenesis.[22] The woman from Elis, who was pale skinned, had a daughter with a man from Ethiopia, who was dark skinned. Their daughter (call her Hypatia) was pale skinned, but her son was dark skinned. (The assumption here is that Hypatia's husband was also pale skinned.) Aristotle's theory explains this by pointing to a κίνησις in Hypatia's seed derived from a corresponding δύναμις in herself (in accordance with 767b35–768a2). Obviously the δύναμις which is the source of the dark-skinned κίνησις does not refer to an actual characteristic of Hypatia's body, since Hypatia does not have dark skin.[23]

Either of these objections would suffice to show that Aristotle rejects the idea that the reproductively significant units in an organism's genetic material are derived from the parts of its body. Accordingly, the δυνάμεις from which the spermatic κινήσεις are derived cannot be the parts themselves.

Morsink offers a third possibility for understanding what the δυνάμεις in our text might be. According to Morsink, a δύναμις is not an actual phenotypic character but the causal power behind that

[22] *GA* 1.18, 722a6–11.

[23] Nor can this refer to a potential characteristic, unless that potentiality has a strong ontological significance. For there must be some *thing* from which the corresponding κίνησις is drawn. I shall argue that this *thing* is a component of Hypatia's genetic nature (though one that is not actually expressed in her phenotypic nature). For Aristotle's own account of this case see below.

character (presumably the power to produce that part of the organism).[24] Though I think Morsink ultimately goes too far in calling these δυνάμεις "the most basic components of an organism,"[25] this interpretation at least takes us in the right direction. For it recognizes an ontological distinction between an organism's bodily characteristics and the δυνάμεις *of* those characteristics, which is implied by our focal text. This distinction is critical for accommodating Aristotle's rejection of the panspermatic thesis in Book 1 (the thesis that the units of inheritance are drawn directly from the parts of the body itself). For example, since the δυνάμεις in Socrates are not the actual parts of his body, there is nothing preventing Aristotle from postulating a set of δυνάμεις corresponding to the parts of Socrates' ancestors. Moreover, this account is not vulnerable to the objection raised by Aristotle's plant experiments. For the κινήσεις in an organism's genetic material are derived from the δυνάμεις of its parts, which on the current reading are ontologically distinct from the actual parts themselves. As such, removing the latter would not affect the outcome of reproduction.

Although Morsink argues that by associating the characteristics of Socrates' body with δυνάμεις Aristotle has extended the concept well beyond its ordinary meaning, he essentially takes these to be active potentials or causal powers. And this is one of the familiar senses of δύναμις from *Metaphysics* Θ. The problem with Morsink's reading is that it takes the δυνάμεις in question to be the reproductively significant units carried inside Socrates' sperm.[26] However, *GA* 767b35–768a2 is explicit that what is transmitted inside Socrates' sperm are not the δυνάμεις themselves but the κινήσεις derived from those δυνάμεις. So the δυνάμεις must refer to entities located in Socrates' body, which are nevertheless distinct from the bodily characteristics for which they are δυνάμεις.

The reading I shall defend can be seen as building on Morsink's insight. Following Morsink, I shall take "the δυνάμεις of all these sorts of things" to refer to the productive sources of an organism's formal characteristics.[27] However, I shall argue that these δυνάμεις are components of the organism's genetic nature (which for Aristotle are not

[24] Morsink, 1982, 134. Morsink compares the phenotypic characters of an organism to symptoms of underlying causes. He argues that what we find here is one of the earliest recognitions of the difference between phenotype and genotype.

[25] Morsink, 1982, 134–5. This claim implies a sort of genetic reductionism that I doubt Aristotle would accept.

[26] e.g. Morsink, 1982, 135.

[27] I am assuming that by saying a δύναμις is the "power behind" a given phenotypic trait Morsink means (as I do) it is the productive source of that trait.

directly transmitted in the parent's seed). Each of these δυνάμεις is a separate potential for the formation of a specific part of its phenotypic nature, not only those that make up its own observable form, but also those that correspond to various properties of its ancestors (which are not displayed in its observable form).

On my reading, the δυνάμεις that comprise an organism's genetic nature play two distinct roles in Aristotle's ontogeny. In the first place, each δύναμις serves a developmental function in the embryo as the primary source of a change that terminates in some part of its phenotypic nature.[28] However, we also know from our focal text that there are κινήσεις in the seed of the adult organism which are derived from these δυνάμεις. Thus, in addition to their developmental function, each δύναμις of the adult's genetic nature will play a major role in reproducing its phenotypic nature in another organism. I shall develop this interpretation further once we have a clearer picture of the nature of Aristotle's spermatic κινήσεις.

The "κινήσεις"

Having determined that the δυνάμεις in our text are the active potentials of an organism's genetic nature, the next thing to determine is the nature of the κινήσεις which are said to be derived from those potentials. According to the most common interpretation of *GA* 4.3, the κινήσεις in Socrates' sperm are simply motions *of* his sperm as it fashions the parts of the offspring's body out of menstrual blood.[29] On this first reading, to say that there is a κίνησις in Socrates' sperm corresponding to his snub nose is just to identify the motion *of* his sperm in fashioning that part of the offspring.

Although it is extremely tempting to read the text in this way (especially since Aristotle refers to them as "demiurgic" movements, 768a15), this cannot be what Aristotle has in mind. For example, in the closing argument of *GA* 2.1 Aristotle announces that "nothing generates itself but once it has been generated it makes itself grow" (735a12–14; cf. *Movement of Animals* 700a31–b4). It is supposed to follow from this

[28] See, e.g., *Physics* 2.8, 199b13–18 (cf. *Metaphysics* Θ 8, 1049b8–10). This is essentially what an Aristotelian δύναμις is, a source of change.

[29] This reading is held by Furth (1988, see esp. 118–9) and Cooper (1988). For example, Cooper (30) argues that the father is directly responsible for the shape and form of the offspring's entire body and that his sperm is "the instrument he uses to move, fashion and shape the matter so as to have that form."

that an animal's heart must contain the source of growth and development of necessity. And the reason is that the heart is differentiated *before* any of the other parts. The implication of this argument is twofold. First, an organism exists (it has come to *be*) as soon as its heart has been differentiated and begins to function. Second, once this part has been differentiated the embryo makes itself grow. Now by "makes itself grow" Aristotle must mean that at this point the offspring becomes responsible for constructing the rest of its body.[30] Indeed, this is the only reading that makes sense of Aristotle's claim that the heart must contain the principle of growth *because* it is the first part of the offspring to be formed. For at that point the embryo must be able to take over the job of building the rest of its body and so must of necessity contain the generative principle.[31]

Since the offspring is responsible for the construction of its own body (save for its heart), the κινήσεις that are said to be present in the father's sperm at *GA* 767b35–768a2 cannot be motions *of* his sperm as it literally fashions the offspring out of menstrual blood. To say that there is a κίνησις in Socrates' sperm corresponding to his snub nose cannot refer to the motion of his sperm as it fashions the offspring's nose; the sperm is not responsible for fashioning that part.

A second interpretation, suggested by Morsink, identifies the κινήσεις in question with the motions and changes that make up the actual process of development itself. On this reading the κινήσις corresponding to Socrates' snub nose *just is* the development of a nose. The picture Morsink has in mind looks something like this. Among the potentials that make up Socrates' genetic nature is a potential for the formation of a snub nose (of which his own nose is a product). During reproduction this potential (or a copy of it) is transmitted to the female inside Socrates' sperm.[32] Once there, that potential initiates a change (κινήσις) which terminates in a nose resembling Socrates.'

While I think this picture is right insofar as the changes that physically transform the embryo into its adult form are initiated and controlled by a corresponding set of potentials inside the embryo itself (the components of its own genetic nature), these changes cannot be the κινήσεις Aristotle

[30] Sometimes (e.g. *GA* 776a31–b3) Aristotle distinguishes morphogenesis – the primary differentiation of the offspring's major structures – from growth-proper – the period immediately following this when those newly formed structures are merely augmented. However, "growth" (αὔξησις) can also be used to cover both of these stages (e.g. *GA* 740a1). This is how I take Aristotle to be using the term in the present context.

[31] This is confirmed later at 740b25–741a3.

[32] Morsink, 1982, 135.

has in mind in *GA* 767b35–768a2. For those κινήσεις are said to be present in Socrates' sperm (ὑπάρχουσιν αἱ κινήσεις ἐν τοῖς σπέμασι; 768a11–14, b7–8: ἔνεισιν), while the changes that make up the process of development are located in the menstrual blood.[33]

Whatever the spermatic κινήσεις turn out to be, Aristotle is clearly referring to things which are present *inside* Socrates' sperm (presumably) while in transit into the female. This suggests a third reading: the sperm acts as a vessel for carrying the changes that make up the process of development into the female.[34] Although there are texts that seem to suggest this (e.g. *GA* 734b7–9, 737a18–24), this interpretation encounters several difficulties.

For example, at *GA* 768a11–14 we are told that some of the κινήσεις in the Socrates' sperm are present "in actuality" while others are only "in potentiality" (cf. 767b35, 768b5–7). According to this third reading, the κινήσεις which are present in Socrates' sperm while in transit are the very same motions and changes that make up the process of development. If some of those changes are present "in actuality," then they must be *actual* changes of Socrates' sperm, which implies that Socrates' sperm is *actually* changing (e.g. it is *actually* developing a snub nose). The problem with this is that Aristotle denies that the father's sperm is the subject of change: it is not the thing that develops into the adult at the end of the process (see esp. *GA* 1.21).

On the other hand, the idea that Socrates' sperm "imports" changes directly into the female which are not actual changes *of* his sperm is a

[33] Another suggestion is that the father's sperm is the mover and the κινήσις is the activity of that mover (e.g. a process of development effected by the sperm). However, a central tenet of Aristotle's physics is that the activity of the agent *and* patient constitute a single motion (though differing in account) and that this motion is located in the patient (*Physics* 3.3). There is one way of understanding κίνησις as the activity of the agent which does take place in the agent. At *GA* 2.4, 740b26ff. Aristotle says that, properly speaking, the products of art are formed by the motions of the craftsman's tools and that these motions are the activity of the art. Moreover, *GA* 1.22, 730b8ff. tells us that the father's nature uses the sperm "as a tool possessing motion in actuality" just as tools are moved when things are being formed in art: "for the motion of the art is *in* these things." However, this cannot be read in connection with the spermatic κινήσεις from *GA* 4.3. For that would amount to saying the father's nature uses the sperm to fashion the parts of the offspring (reading one), which is something Aristotle denies. Given the context, what is more likely is that Aristotle is simply referring to the sperm's causal role in the process of fertilization, not in constructing the parts of the offspring's body.

[34] Balme. 1972, 157; 1987a, 281–2; 1987b, 292; Coles, 1995 (see above); cf. King, 2001, 29.

very unAristotelian notion. For Aristotelian changes cannot be separated from their subject in this way (there are no free-floating changes).[35] Thus, we cannot speak of the motions and changes that make up the process of development (which are eventual changes of the menstrual blood) as being transported inside the sperm as in a vessel.[36]

So far I have considered three possibilities for what the spermatic κινήσεις in *GA* 4.3 could be:

1. Motions of Socrates' sperm as it fashions the parts of the offspring out of the menstrual blood.
2. Changes of the menstrual blood initiated by active potentials carried inside Socrates' sperm.
3. Changes of the menstrual blood initiated by active potentials in Socrates' body and carried into the female inside his sperm.

I have rejected reading 1 on the grounds that it is inconsistent with one of the central tenets of the *GA* (the offspring is responsible for the construction of its own body). The problem with reading 2 is that the κινήσεις in question are supposed to be present in Socrates' sperm while the δυνάμεις from which they are drawn are located in his body. Nor does it seem reasonable to suggest that Socrates' sperm might contain *actual* changes which are not actual changes *of* his sperm (something Aristotle categorically denies). In light of this, I want to propose a fourth reading of the text:

4. The spermatic κινήσεις are specialized vehicles through which an organism's form is physically transmitted to its offspring in the act of reproduction.[37]

This is the reading I shall defend. For lack of a better translation I shall simply use "movement" to refer to these entities. However, it should be stressed that by calling them "movements" I do not mean to suggest they are to be identified with any of the motions or changes that eventually transform the menstrual blood into the parts corresponding to those movements (they are not pre-set motions or changes).

[35] See *Physics* 3.3, 200b32: "There is no such thing as change over-and-above the things [sc. the subjects of change];" and 201a1–3: "Hence, neither will motion and change have reference to something over-and-above the things mentioned; for there is nothing over-and-above them." See also *Metaphysics* Z1, 1028a20–31.

[36] If by saying the sperm imports "preset" changes into the menstrual blood we mean potential changes, then this still leaves those actual changes unexplained.

[37] Gotthelf (1987, 216 *n*. 20) suggests something akin to this.

These spermatic movements are information-bearing vehicles of some kind.[38]

There is one other interpretation that I have not yet considered which would take the spermatic κινήσεις to be local motions like vibrations or wave-motions.[39] This is consistent with my reading, since these vibrations or waves would still have to be information-bearing vehicles that somehow encode the phenotypic characters they transmit. My own view is that Aristotle's theory inheritance is meant to be more abstract than this, and so we should expect the concepts deployed in *GA* 4.3 to be equally abstract. If this is right, then Aristotle's spermatic "κίνησις" would be more like Mendel's "gene" in the sense that both concepts attempt to abstract away from the concrete, physical basis of the vehicles of inheritance.

It is important to note that in taking the word "κίνησις" to refer to a vehicle for conveying biological form I have not extended its meaning beyond the Aristotelian corpus. We also find this use of κίνησις in the account of sense-perception in *GA* 5. There Aristotle deploys a concept of a κίνησις which refers to a vehicle for conveying an object's sensible form from the object to the perceiver.[40] For example, at *GA* 780a27–31 Aristotle says the thickness of the membrane around the eye-jelly (the organ of sight) can affect the direction of the κίνησις "coming into the eye from without" (θύραθεν) and whether or not it "passes straight through" the membrane (εὐθυπορεῖν). Again, at 780b34 Aristotle refers to a κινήσις "coming from distant objects" (πόρρωθεν) and "arriving at" (ἀφικνεῖσθαι) the perceiver's sense organs. The use of directional terms which ascribe locomotion to a κίνησις suggests that

[38] Witt (1985, 56 *n*. 26) also suggests that the spermatic movements are information-bearing vehicles, though she does not clarify what she means by this. For the idea of a κίνησις bearing informational content see Aristotle *On Memory* (e.g. 452b23–4: "the κίνησις of the fact" and "the κίνησις of the time"). The primary difference between my reading and reading 3 lies in the function assigned to the κινήσεις . The third readings identifies the κινήσεις with pre-set motions and changes that directly produce the parts of the offspring after being released into the menstrual blood. In contrast to this, I shall argue that the function of the spermatic κινήσεις is to directly reproduce the δυνάμεις which are the sources of those developmental changes.

[39] This interpretation was originally suggested to me by James Lennox (personal correspondence). It was also suggested by one anonymous referee who called these "micro-physical motions."

[40] Many of those who commented on earlier drafts of this paper suggest that Aristotle's use of κίνησις can also be understood (in the words of one anonymous referee) "without really reaching beyond the sense of the term as elucidated by Aristotle in the *Physics* (particularly, *Physics* 3)." This is especially true if the κινήσεις turn out to be micro-physical motions.

Aristotle is speaking about a vehicle that physically transmits the sensible properties of an object through the medium. For "κίνησις" here does not refer to the motion (or change) *of* something traveling but the thing which is itself in motion.

The sensory κινήσεις in *GA* 5 are not only subjects of locomotion. They are also subjects of other sorts of physical changes, such as being broken up into pieces. At *GA* 780b13–781a12 Aristotle introduces a mechanism whose function is to collect the sensory κινήσεις coming from distant objects and funnel them into the perceiver's eyes. He tells us that the concavity of an animal's brow literally shapes a portion of air between its eyes and the perceived object into a kind of "tube" (αὐλός). The further this tube extends, the more accurately the object is seen:

> Things at a distance, then, would be seen best if there were, so to speak, a continuous tube extending straight from the eyes to the object seen, for then the movements coming from the object would not be dissipated; but, if that isn't possible, still the further the tube extends the more accurately distant objects must be seen. (781a8–12)

Aristotle's idea is this. The sensory κίνησις coming from a distant object begins to dissipate or break up (διελύετο) almost immediately. How accurately that object is seen depends on the concentration of the signal the (κίνησις) when it reaches the perceiver's eyes. The more of the κίνησις that reaches the organ, the more clearly that object will be seen. This is where the perceptual tube comes in (the portion of shaped-air extending from the eye). The tube functions as a mechanism for collecting the κινήσεις coming from objects, which are then passed on to the organ where they produce sensation. And only those κινήσεις that enter the visual tube will reach the eye (cf. 780b18–21).[41] In this way the ability of an animal to see objects at a distance becomes a function of the length of its visual tube, which is in turn determined by the depth and shape of its ocular cavity. Thus, Aristotle says, animals with sunken eyes placed in a hollowed recess are able to see things at a distance "because the κίνησις does not get scattered (σκεδαννυμένη cf. 781b11: διασπῶνται) but goes straight to the mark" (780b35–781a2).[42]

[41] At *GA* 780b21–2 Aristotle remarks that this is why people in pits and wells can sometimes see the stars (a satirical reference to Thales' reputation for falling in wells?).

[42] Aristotle's perceptual "tubes" are not confined to vision. In *GA* 5.2 he discusses how the same mechanism accounts for the ability to smell and hear distant objects (781b7–16).

The fact that the sensory κινήσεις are themselves subjects of verbs of motion and change (εὐθυπορεῖν, ἀφικνεῖσθαι, διελύετο, σκεδαννυμένη, διασπῶνται) strongly suggests that in the present context a "κίνησις" is a vehicle for carrying sensory information to the perceiver about the object from which it came.

There is a nontrivial similarity between Aristotle's genetic use of κίνησις in *GA* 4.3 and the use of κίνησις in *GA* 5.1 as a vehicle for transmitting the sensible properties of an object. While at first glance the two may appear to be quite different events, from one perspective inheritance and perception are instances of the same general phenomenon. For they both involve the transmission of form *without* matter. It is well-known that Aristotle characterizes perception in the *De anima* as an event involving the transmission of an object's sensible form without its matter. In *Generation of Animals* 5 we are given the mechanism that underlies this event. There we are told that the formal properties of an object (e.g. its color) are conveyed from the object to the perceiver by means of "movements." Likewise, one of the central features of Aristotle's theory of reproduction is the idea that the father transmits his form to the offspring *without* transmitting any of his matter. And just as in the case of perception, we find Aristotle appealing to "movements" in Socrates' sperm that transmit that form.

What Happens at the Receiving End?

Up to this point the discussion has focused exclusively on what happens at the transmission end of the process (which is what we get in passages like *GA* 767b35–768a2). According to the interpretation developed here, an organism's form is transmitted to its offspring by means of "movements," which are said to be present in its seed. These movements are derived from the various "potentials" of its genetic nature, each of which is the productive source of a different part of the animal's phenotypic nature. The final step in the analysis is to ask what happens at the receiving end of this transmission when those movements reach the embryo. Although Aristotle never addresses this question directly, I think we can speculate as to a possible answer.

In order to bridge the gap between Aristotle's account of natural generation in the *Physics* and his analysis of the mechanisms of inheritance in *GA* 4.3 we must assume that the reception of the spermatic movements derived from potentials in the parent's body, on the one

hand, and the subsequent development of the offspring's body, on the other, are interposed by the formation of a new set of potentials: those that make up the offspring's own genetic nature. For the only way that the process of development will count as "natural" (according to Aristotle) is if all of the changes that make up that process originate directly in a set of potentials in the embryo itself (cf. *Metaphysics* 8, 1049b9–11).[43]

Assuming Socrates' son, Menexenos, is a naturally generated organism, the construction of his body must have been preceded by the formation of his genetic nature. This principle functions as a source of change in Menexenos himself. It follows from this that the movements transmitted inside Socrates' sperm cannot be those that make up the process of Menexenos' development (reading 3). First, if the movements imported into the menstrual blood by Socrates' sperm immediately set to work building Menexenos' body, then there would have been no time for the formation of his genetic nature. Second, those spermatic movements would be derived from the potentials of Socrates' genetic nature, which would be a principle of change *in another*. In that case it is not clear how Aristotle could distinguish Menexenos from a mere artifact.

Morsink's reading (reading 2) would avoid both of these problems. According to Morsink the potentials of Socrates' genetic nature (or copies of them) are carried directly into the embryo inside his sperm. Once there, these potentials are activated, which causes the matter to develop into an organism resembling Socrates in every respect. After all, they are (copies of) potentials of *Socrates'* genetic nature. The problem is that, while these potentials would count as sources of change in Menexenos himself, Aristotle is explicit that what is carried into the female inside Socrates' sperm are not the potentials of his nature but movements derived from those potentials.

An alternative answer (arising out of reading 4) is that the function of the spermatic movements is to directly reproduce the active potentials from which they were originally derived. On this reading Menexenos will resemble Socrates to the extent that the potentials reproduced by the movements in Socrates' sperm are copies of those in Socrates' own

[43] The main difference between natural generation and artificial production for Aristotle is that the former is initiated and controlled by a principle in the thing itself (its nature) while the source of the latter change is in another individual (the art in the craftsman). Cases like a doctor healing herself (which is an artificial change) complicate the story but do not significantly alter the point.

genetic nature. For each of the latter is a distinct potential for the formation of a different part of *Socrates*' body.

Aristotle's Theory of Inheritance

Now that the mechanisms are in place let me finally turn to the theory of inheritance proper. I shall leave most of the details aside here and instead provide a general overview of that theory. The theory itself consists of three "general suppositions" (καθόλου ὑποθέσεις),[44] formulated succinctly at *GA* 768b5–10:

> We must grasp the general suppositions, not only the one stated – (1) that among the movements present in the parents' seeds some are present in potentiality while others are present in activity – but also two others: (2) being dominated causes displacement into the opposite (κρατούμενον μὲν ἐξίσταται εἰς τὸ ἀντικείμενον), while (3) relapsing causes a change into the movement which stands next to it <on the blood-line> (λυόμενον δὲ εἰς τὴν ἐχομένην κίνησιν). If it relapses a little, it passes into the movement which stands closer; if it relapses a lot, it passes into the one farther away.

Supposition one concerns the existence of movements in the genetic material of all sexually reproducing animals, some of which are "in activity" while others are "in potentiality." The other two supply the principles (or 'laws') that govern the interactions between the maternal and paternal movements. The outcome of those interactions determines the pattern of inheritance for the particular offspring.

Having an account of the general contents of the parent's genetic material will make it easier to set out Aristotle's theory of inheritance. *GA* 768a11–14 is an important text in this respect:

> Some of the movements are present in <the father's sperm> in activity while others are in potentiality: in activity, those of the father and the universals (e.g. human and animal); in potentiality, those of the ancestors.[45]

[44] Lennox has suggested (personal correspondence) that the use of ὑποθέσις here probably reflects its scientific meaning from the *Analytics* (e.g. *An. Po.* 72a15ff.).

[45] Reading δὲ αἱ τῶν προγόνων for δυνάμει δὲ αἱ τοῦ θήλεος καὶ τῶν προγόνων. I argued for this emendation in Henry, 2004, Chapter 4.

Here Aristotle divides the paternal movements into three general groups: those of the father (τοῦ γεννῶντος); those of the universal (τοῦ καθόλου); and those of the ancestors (τῶν προγόνων).[46] Those of the first two groups are said to be "in activity" while those of the third group are "in potentiality." I shall return to this distinction later.

The movements "of the father" include two sets of movements, one for the sexual morphology proper to a male and another for those features of Socrates' phenotype that make him a unique individual. Both of these movements are derived from potentials of Socrates' genetic nature which correspond to those parts of his phenotype (768a 28–9: ἡ ἀπό τοῦ ἄρρενος κίνησις and ἡ ἀπό τοῦ Σωκράτους κίνησις).

In order to explain why some offspring resemble the father while others resemble the mother with respect to different parts (see above: phenomenon 2b) Aristotle postulates movements in the parents' seeds corresponding to each of their several parts (768b1–5). Each part-movement is itself a discrete unit of inheritance that can undergo "displacement" and "relapse" independently of the other movements in the set. This raises several difficult part-whole puzzles that would take us too far outside of the immediate project. To avoid unnecessary complications, I shall simply talk about the movement of "Socrates" (the movement for the whole) as being made up of the movements for the parts of Socrates. On this reading, resemblance to Socrates as a whole occurs when all of the several part-movements dominate together (though individually).

Although I shall not defend this here, I take it that "the movement coming of Socrates" (ἡ ἀπό τοῦ Σωκράτους κίνησις) is responsible for transmitting all of the peculiar details of Socrates' form, the color of his eyes, the shape of his nose, and so forth. The movement "human," on the other hand, will be responsible for transmitting those species-level properties, such as the basic organization of the body, the production of human-specific tissues and organs, and any other features that are characteristic of that particular kind of animal.[47] Finally, the universal movement "animal" is responsible for the inheritance of the parts of the sensory system, which is the feature that makes something an animal (its essence).

[46] The same applies to the maternal movements as well (*GA* 768a19–21, 768b13–15), although Aristotle's reproductive hylomorphism implies that "animal" will only be present in the father's sperm. In other words, the father's genetic contribution alone is causally responsible for the development of the offspring's sensory system, which is the form of an animal in the strict sense.

[47] Compare the analogy with an artist at *GA* 2.6, 743b20–5.

By postulating a set of movements in the parent's seed for conveying resemblances to other members of its family (the movements of the third group), Aristotle was able to account for the fact that offspring who do not resemble their parents tend to resemble their ancestors rather than any chance individual (phenomenon 4). However, the fact that these movements are only in potentiality while those corresponding to the parent's own phenotype are in activity is supposed to explain why offspring tend to resemble their parents *more* than their ancestors (phenomenon 3). I shall have more to say about this later. For it is not exactly clear what it means to say that some of the movements in the parent's seed are "in potentiality" while others are "in activity." However this distinction is cashed out, the way it figures into Aristotle's theory of inheritance is clear. The ancestor movements become active (ἐνεργείᾳ) whenever the parental movements undergo relapse.

Suppositions Two and Three: "Displacement" and "Relapse"

The real meat of Aristotle's theory of inheritance is expressed by suppositions two and three:

> Principle of Displacement: *being dominated causes displacement into the opposite movement*
> Principle of Relapse: *relapse causes a change into the movement which stands next to it on the blood-line*

Taking a movement in Socrates' sperm as a reference point, there are three things that can happen to it: that movement can dominate (κρατεῖν); it can be dominated (κρατεῖσθαι); or it can undergo relapse (λύσις). According to supposition two, being dominated causes displacement into the opposite movement, while relapsing causes a change into the movement which stands next to it (supposition three).

We are already familiar with the principle of relapse. If the movement corresponding to Socrates' nose relapses, the potential movement in his sperm corresponding to his father's nose is activated (becomes ἐνεργείᾳ). In this case Menexenos inherits his grandfather's nose. If Socrates' nose-movement relapses back two generations, Menexenos will inherit his great-grandfather's nose, and so forth down the blood-line.

The principle of displacement is somewhat more complicated than this, since Aristotle only says that being dominated causes "displacement into the opposite." This gives us a general idea of how the principle of displacement affects the outcome of inheritance. If displacement

occurs with respect to a property on the father's side, then the offspring will come to display the maternal version of the trait in which displacement occurred (and vice versa). However, the two principles of Aristotle's theory are supposed to govern the behavior of the causal mechanism that underlies the phenomena. And how displacement works at this level is extremely vague. Specifically, it is not clear *what* exactly changes to the opposite.

Although I will not offer a detailed defense of this, I take it that dominance in this context expresses a relation between opposite spermatic movements (the vehicles of inheritance).[48] On this reading both suppositions two and three refer to changes between spermatic movements. Displacement causes inheritance to change from the movements of one parent to those of the other (a change between movements on opposite blood-lines), while relapse causes it to change from the movements of the parent to those of the ancestor (a change between movements on the same blood-line).

Putting all of this together, if Socrates' nose-movement dominates, Menexenos will come to have the same nose as his father. However, if this movement is dominated, then it gets displaced which causes inheritance to switch over to Xanthippe's nose-movement (a change between movements on opposite blood-lines).[49] In this case Menexenos' nose will resemble his mother's not his father's. However, if Xanthippe's movement relapses, it passes into the movement of her mother (a change between movements on the same blood-line). When that happens Menexenos will come to have the same nose as his maternal grandmother.

Despite its brilliance, one of the shortcomings of Aristotle's theory is that it appears to lack any means for explaining how we get resemblance to the father's female ancestors or the mother's male ancestors. This phenomenon, which would have been just as obvious as those Aristotle

[48] The text appears to be inconsistent on this. On the one hand, *GA* 768a2–5 says that which is *not* dominated (μὴ κρατούμενον) changes into the opposite. Here Aristotle is referring to the embryo (or the matter supplied by the female). On the other hand, the official formulation of the principle of displacement at *GA* 768b7–8 says that which *is* dominated (κρατούμενον) changes into the opposite. The inconsistency can be avoided by assuming that the principle of displacement at *GA* 768b7–8 refers to the spermatic movements themselves. In this case supposition two can be read as supplying the causal mechanism behind the phenomenon described at *GA* 768a2–5. When the movement of the father is dominated (alternatively, when the mother's movement dominates), inheritance automatically switches over to the opposite movement coming from the mother. It will be the dominance of *this* movement that ultimately explains why the embryo develops the opposite maternal trait.

[49] Xanthippe was Socrates' wife.

discusses, cannot be explained by the principles the theory currently posits. For example, the principle of displacement explains how we get from movements on the father's side to movements on the mother's side, while the principle of relapse explains how we get from those of the father to those of his grandfather. What we need is an additional principle that works in combination with relapse. Relapse would cause inheritance to shift from the father's movements to his father's movements while this third principle, working in conjunction with relapse, would cause it to switch from his paternal ancestors to his maternal ancestors.

Supposition One: Actual versus Potential Movements

The final task in providing a general overview of Aristotle's theory of inheritance is to provide an account of supposition one. According to the first supposition of Aristotle's theory, some of the movements carried in the parent's genetic material are "in activity" (those of the parent and universals) while others are "in potentiality" (those of the ancestors). I shall ignore the universal movements and concentrate on the active parental movements, on the one hand, and the potential ancestor movements, on the other.

By postulating a set of movements corresponding to the parent's ancestors Aristotle was able to account for the fact that offspring who do not resemble their parents nevertheless resemble one of their ancestors rather than some chance individual (phenomenon 4). The fact that these ancestor movements are "in potentiality" while those of the parent are "in activity" is supposed to explain why offspring tend to resemble their parents *more* than their ancestors (phenomenon 3). While this may seem straightforward on the face of it, supposition one is actually quite puzzling.

On the reading I am defending, the κινήσεις in Socrates' sperm are separate entities carried inside the sperm: they are the vehicles through which Socrates' form is physically transmitted to his offspring in the act of reproduction. For Aristotle, it is the possession of these hereditary units that gives Socrates' sperm the capacity to generate formal resemblances. A thorough analysis of the puzzle about "potential" movements would require much more space than I can afford it here. My own understanding of the text is that by saying the ancestor movements in Socrates' sperm are "in potentiality" Aristotle means they are present in a kind of de-activated state. They become active

(ἐνεργείᾳ) whenever the movements corresponding to Socrates' own features undergo relapse.[50]

Whether or not this is the proper way to understand supposition one, any interpretation of Aristotle's theory must allow that there *really are* movements in Socrates' sperm corresponding to the features of his ancestors. They are not just there potentially in the sense that I am potentially (but not actually) in Manchester. For Aristotle not only needs to explain why Socrates' sperm does not actually have the ability to generate features that make his offspring look like Coriscus (a non-familial relation); he also needs to account for the fact that it does not even *potentially* have that ability. It is the fact that Socrates' sperm *really does* contain ancestor movements (they are actual entities inside Socrates' sperm) that grounds its capacity to generate features of those individuals who are, after all, just as removed from the current act of reproduction as any chance individual.

The Transmission of Biological Form: A Summary

In *GA* 4.3 Aristotle sets out the causal mechanism behind the transmission of biological form. There we are told that an organism's seed contains a set of "κινήσεις" derived from corresponding "δυνάμεις" within itself (767b35–768a2). According to the interpretation developed here, these δυνάμεις are the components of its genetic nature, each of which is a distinct potential for the formation of a given phenotypic character (including potentials for the formation of characters which are not displayed in its form). I have argued that the spermatic movements are the vehicles through which an organism's form is physically transmitted in the act of reproduction. Finally, I have argued that in order to bridge the gap between Aristotle's transmission genetics and his account of natural generation we must assume that the reception of spermatic movements from the parents, on the one hand, and the subsequent transformation of the embryo into its adult form, on the other, are interposed by the formation of new potentials like those from which the movements were originally drawn. Together these new potentials make up the offspring's own genetic nature, which constitutes a source of change in the thing itself *qua* itself, thereby satisfying the conditions for natural generation.

[50] For a defense of this reading see Henry, 2004, Chapter 6, § 5. Something like this reading is also suggested by Cooper, 1988, 23.

It follows from all of this that for each part of the offspring's phenotypic nature its genetic nature will contain *two* potentials (or two versions of the same generic potential), one corresponding to each spermatic movement received from its parents.[51] Since these will be potentials for the formation of contrary properties (e.g. snub nose versus straight nose), only one of them can be expressed in the offspring's phenotype at any given time. What I want to suggest here is that which version of a given potential gets activated at the appropriate stage of the embryo's development, and thus which version is eventually expressed in its phenotype, is determined by whichever parent's movement corresponding to that potential dominates (κρατεῖν) over the other according to the principles of displacement and relapse.[52]

This interpretation of the events in *Generation of Animals* 4.3 can be supported by appealing once again the case of the woman from Elis. Recall the example. The woman from Elis, who is pale-skinned, has a pale-skinned daughter with a dark-skinned man from Ethiopia. Their daughter (call her Hypatia) then has a dark-skinned child with another pale-skinned man. According to Aristotle's theory of inheritance, we first explain why Hypatia has pale skin rather than dark skin by pointing to the dominance of the pale-skin movement coming from her mother over the dark-skin movement coming from her father. The explanation for why her own son has dark skin is two-fold. First, the paternal pale-skin movement coming from Hypatia's husband is dominated, which causes inheritance to switch over to Hypatia's own pale-skin movement according to the principle of displacement. This movement then relapses into her father's dark-skin movement, which was present in her seed in a state of potentiality. The implication of this is that (looking back to the first generation) the defeated dark-skin movement coming from Hypatia's father must have still produced a corresponding potential in her genetic nature. For each movement in Hypatia's genetic material will have been derived from a corresponding potential in herself (in accordance with *GA* 767b35–768a2). It follows from this that Hypatia's genetic nature must contain *two* potentials for skin color, one for pale skin (the δύναμις produced by the κίνησις coming

[51] This follows from the fact that Aristotle's theory posits a set of κινήσεις coming from both parents which are functionally equivalent to one another (see, e.g., *GA* 4.3, 768a15–21). Thus for each potential, the offspring receives two movements, one from the mother and one from the father.

[52] See, e.g., *GA* 4.3, 768a28ff.: "And if the movement derived from 'male' dominates but the movement derived from 'Socrates' does not dominate [i.e. if the movement derived from 'Xanthippe' dominates], or vice versa, then the result is a male offspring resembling its mother or a female offspring resembling its father (respectively)." The passage continues to describe what happens if these movements relapse.

from her mother) and one for dark skin (the δύναμις produced by the κίνησις coming from her father). However, since her phenotypic nature cannot display both versions of that trait simultaneously, only one of the potentials will have been activated during her development; the other must be preserved in her genetic nature in a de-activated state.

If this is right, then one spermatic movement "dominating" over another does not determine which potential corresponding to those movements makes it into the offspring's genetic nature. Aristotle's account of atavism requires that *both* spermatic movements produce potentials in its nature. Rather, what the dominance relation must determine is which of those two potentials gets *activated* at the appropriate stage of development and thus which version of the trait is expressed in the offspring's phenotypic nature.

Is Aristotle's Biology Anti-evolutionary?

One of the important features of this study is that it can be used to shed new light on the question of whether or not Aristotle's biology is anti-evolutionary as traditionally assumed. Specifically, it allows us to ask in much more detail questions about Aristotle's views on the possibility of heritable genetic mutations.[53]

At *GA* 768b10 (cf. 769b9–10) Aristotle tells us that disruptions in the normal pattern of inheritance may result when the spermatic movements become "confused together" (συγχέονται). On my interpretation, these "confused" movements will produce mutated potentials in the offspring's genetic nature.[54] And those mutations will be heritable. For in that case there will be movements in the offspring's own genetic material derived from those mutated potentials (in accordance with *GA* 767b35–768a2). This opens up theoretical space for an evolution by natural selection. Of course even if this is right Aristotle either did not recognize it or did not appreciate its implications. For while his account of the mechanisms of inheritance might leave room for evolution, this is

[53] Of course evolution can occur even without genetic mutations, as long there is a sufficient amount heritable variation already available. Genetic mutations are really only necessary for the possibility of building new structures through cumulative selection.

[54] Compare *De sensu* 4, 446b6–10. Aristotle says that sometimes when a person speaks the κίνησις transmitting the sound undergoes a physical transformation in mid-air. The result is that the letters of the word get jumbled (in mid-air) and the listener hears something different than the speaker intended.

not something Aristotle actually entertained. But is this something Aristotle could even accept?

First of all, I don't think the theoretical barrier here is Aristotle's famous rainfall argument at the beginning of *Physics* 2.8, which many take to be an explicit rejection of Empedocles' ideas about natural selection. Whatever it is about Empedocles' suggestion that Aristotle thinks is implausible there, it is *not* his account of the origin of species.[55] Rather, the problem I have in mind is Aristotle's belief in the fixity of species, which he argues for in *GA* 2.1 and *DA* 2.4. Aristotle clearly does think that species are "eternal" and "unchanging" in some sense. And this would certainly appear to be antithetical to an evolutionary world-view. But what is not clear is *why* Aristotle thinks species are eternal. Leaving this question aside for a moment, let us consider whether or not Aristotle's account of inheritance taken by itself is compatible with Darwin's theory of natural selection. One way to test this idea is to look at the essential features of Darwin's theory and see if any of them are incompatible with Aristotle's biology.

Compatibility with Darwin's theory of evolution by natural selection requires at least five essential features:[56]

1. Organic populations must be part of an ancestor-descendant history.
2. The members of such populations must inherit traits from their ancestors and pass them on to their descendants.
3. They must also vary with respect to those heritable traits.
4. There must be a struggle for existence in which the members of populations compete for limited environmental resources.
5. The environment in which they live must be infinitely complex and subject to change.

Given these facts, Darwin argued that it is extremely likely that some of the heritable variations in a population will give their possessors an edge in the struggle for existence by increasing their ability to survive

[55] The crucial line in the argument is *Physics* 198b34: "Yet, it is impossible for things to be *this* way." What way? Most commentators take Aristotle to be referring to Empedocles' idea that contemporary species were forged through a combination of chance and natural selection. However, Aristotle goes on to explain, "For these and all the things that exist by nature *come to be in a given way either always or for the most part*, while not one of the results of luck or spontaneity do." This suggests that Aristotle is concerned with normal patterns of development for members of already existing species (e.g. the normal development of human teeth). His point is that the kind of explanations that Empedocles likes to give, which mostly appeal to chance, cannot explain the remarkable constancy of biological development. Compare *Generation and Corruption* 2.6.

[56] The following is adapted from Lennox's analysis of Darwin in Salmon et al., 1999, 271.

and reproduce. As a result of this increased ability, organisms with those advantageous variants will tend to leave a disproportionate number of offspring in successive generations. Eventually this will lead to a gradual change in the population as a whole, with more favorable traits accumulating over generations.[57]

Clearly Aristotle's biology is compatible with (1), (2), and (4). First, Aristotle has an historical concept of species. In *Metaphysics* Δ28, for example, a biological species is defined as a "continuous generation of individuals of the same form." Second, we have already seen that the members of an Aristotelian species inherit properties from their ancestors and pass them on to their descendants according to the principles set out in *GA* 4.3. As to (4), one might argue that even if Aristotle did recognize a struggle for existence, he certainly didn't appreciate its implications or recognize that this struggle is a direct result of the tendency of populations to over-reproduce in an environment with finite resources. However, this is certainly not incompatible with anything he says. So far so good.

What about (3)? Did Aristotle hold that organic populations vary with respect to their heritable traits? Clearly he did (as we have seen). However, the trick is to show how this is compatible with Aristotle's views about the eternity of species. One way to do this would be to think of the eternal species-form as a subset of those features that are capable of being passed on in the act of reproduction (those that belong to the individual καθὸ γεννητικόν). On this reading, while a population's species-specific properties would remain constant over time, there will be heritable variation in those other traits falling below the level of species, such as eye color and hair color in humans. Mutations in *these* properties would then open up the possibility for some evolutionary change.[58] However, this reading requires us to assume that organisms possess a built-in mechanism that either prevents mutations from occurring in its species-specific properties or else prevents those mutations from being passed on in reproduction. And there is no indication that Aristotle posits such mechanisms.

There is an alternative interpretation of Aristotle's account of species that allows for heritable variations *within* the eternal species-form itself. According to Lennox, species-level properties such as "nose," "eyes,"

[57] *ibid.*

[58] Even without mutations, Aristotle allows for a degree of phenotypic plasticity with respect to some (regularly occurring) non-essential traits. See, e.g., *GA* 5.6, 30–2: "The reason for this is that it is a natural attribute of the species *not* to be of a single colour; for the species is quite mobile (εὐκίνητον) in both directions."

and "leg" do not pick out *actual* features of any particular human being (as they would on the previous interpretation). Rather, they represent what Lennox calls "features with range": possible ways that human noses, human eyes, and human legs may be concretely realized in different individuals.[59] On this reading, Socrates' snub nose, blue eyes, and short legs and Callias' bulbous nose, brown eyes and long legs are two concrete realizations of *the same generic human features*. In other words, there is no "species-form" per se, only different versions of that form concretely realized in different individuals.

What this means is that the "eternal" form (the form that is continuously reproduced from one generation to the next) will display a certain amount of phenotypic plasticity within a certain allowable range of differences. This allowable range is defined by the creature's environment. For example, all curlews have elongated beaks, which is essential for their survival in their particular environment. However, the beaks of individual curlews (which are all concrete realizations of this same generic feature) differ from one another along a finite continuum, or by what Aristotle calls "the more and the less." What this means is that while all curlews have elongated beaks, some will have beaks that are slightly longer or slightly more curved than others. The continuum of differences here is finite in the sense that there is a fixed range of beak sizes and shapes that will be suited for life in a curlew's natural environment. If a mutation occurs outside this allowable range, then the offspring will no longer be adapted to its particular environment and so possessing that feature will be detrimental to its ability to survive and reproduce.

From this perspective Aristotle's account of inheritance allows for an evolution of species by natural selection, since populations would eventually be forced to adapt to a changing environment. For as the environment changes, the allowable range of possible ways of realizing the species-form changes.[60] Here is where the essential difference between Aristotle and Darwin lies. Although Aristotle was well aware of the fact that an organism's environment is infinitely complex, there is good reason to suspect that he did not think the environment itself was capable of undergoing change. In Aristotle's cosmological system, the motions of the heavenly bodies determine the nature of the sublunary environment. And for Aristotle these celestial motions are eternal and unchanging. The implication is that for Aristotle species are fixed, not because individuals possess some sort of innate capacity to maintain the species-form against all odds; rather, the fixity of the species is parasitic

[59] Lennox, 2001, 160–81.

[60] This much has also been suggested by Lennox, 2001, 178.

on the fixity of the environment. Thus an evolution of species is ruled out only on *cosmological* grounds. So it is Aristotle's cosmology, not his biology, that is ultimately incompatible with an evolutionary world-view.

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