

Was Aristotle the ‘father’ of the epigenesis doctrine?

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Abstract Was Aristotle the ‘father’ and founder of the epigenesis doctrine? Historically, I will argue, this question must be answered with ‘no’. Aristotle did not initiate and had no access to a debate that described itself in terms of ‘epigenesis’ and ‘preformation’, and thus cannot be considered the ‘father’ or founder of the epigenesis-preformation controversy in a literal sense. But many ancient accounts of reproduction and embryological development contain analogies to what early modern scientist called ‘epigenesis’ and ‘preformation’, and, in this analogous sense, Aristotle can be considered a precursor of the epigenesis-preformation controversy. But is Aristotle’s position actually epigenetic (in this analogous sense), as most of the traditional interpreters hold, or preformationist, as some of the recent scholars believe? I will argue against the one-sidedness of both readings that Aristotle’s account of reproduction and heredity contains mainly epigenetic, but also a few preformationist characteristics. Whereas, for instance, Aristotle’s idea of a successive development of the embryo’s parts is doubtlessly epigenetic, Aristotle’s idea that the development of the embryo is an actualization and enlargement of potential parts, which are simultaneously present in the semen, can be considered a preformationist feature.

Keywords Aristotle · Biology · Embryology · Epigenesis · Preformation

I.1

Philosophers and historians of the life sciences often point to Aristotle as the ‘father’ of the doctrine of epigenesis, when they discuss the opposition between ovist or animalculist theories of preformation and mechanical or vitalistic theories of

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epigenesis. Morsink (1982, 50–51), for instance, writes that Aristotle’s account of animal generation in book 2 of the *Generation of animals* (*GA*) “has set the stage for the entire history of the debate between preformationists” and “those who defend epigenesis (like Aristotle himself)”. Also Needham (1959, 54–55) says that Aristotle was “the first” who “realized that the previous speculations on the formation of the embryo could be absorbed into the definite antithesis of preformation and epigenesis”, and “decided that the latter alternative was the true one”. In the *GA* 2.1, so Needham (1959, 40), Aristotle gives “a brilliant discussion of epigenesis or preformation”, in which he defends a version of the doctrine of epigenesis, according to which the parts of the embryo develop gradually, whereas he rejects the doctrine of preformation, according to which tiny parts of a living being are already present in the male or female seed. Similarly, Peck notes that

Aristotle fully appreciated the greatest problem of embryological theory, a problem which gave rise to centuries of controversy. Does the embryo contain all its parts in little from the beginning, unfolding like a Japanese paper flower in water (“preformation”), or is there a true formation of new structures as it develops (“epigenesis”)? Aristotle was an epigenesist. (Peck 1942, 144)

Scholars often have passage *GA* 2.1.734a16–21 in mind, and book 2 of the *GA* in general, when they set Aristotle’s account of animal generation at the beginning of the preformation-epigenesis controversy. But if we look at the text, these claims can hardly be substantiated in a literal sense. In *GA* 2.1 Aristotle neither coins the term ‘epigenesis’ and a Greek equivalent of the term ‘preformation’ nor does he characterize his own account of reproduction as ‘epigenetic’ nor opposing accounts as ‘preformationist’. But we can find lines like these: “How, then, are the other parts [of the embryo] formed? Either they are all formed simultaneously—heart, lung, liver, eye, and the rest of them—or successively, as we read in the poems ascribed to Orpheus, where he says that the process by which an animal is formed resembles the plaiting of a net” (*GA* 2.1.734a16–20),¹ and we can find three descriptions of the successive emergence of the heart, primary blood vessels, and other parts of the animals in the *GA* 2.6.741b6, the *GA* 2.6.743a1, and the *GA* 2.6.743b25. But though it is true that the simultaneous (ἄμα) or successive (ἐφεξῆς) generation of the parts of an embryo are defining characteristics of what early modern philosophers called ‘preformationist’ and ‘epigenetic’ generation theories, these characteristics alone neither expend the defining features of the doctrines of preformation and epigenesis nor can they be understood without additional context.²

To name Aristotle the ‘father’ of the epigenesis doctrine, it seems, anachronistically applies terms, which were not in use before the early modern period, most

¹ Τὰ οὖν ἄλλα πῶς; ἢ γάρ τοι ἅμα πάντα γίνεταί τὰ μόρια, οἷον καρδία πλεῦμων ἦπαρ ὀφθαλμὸς καὶ τῶν ἄλλων ἕκαστον, ἢ ἐφεξῆς, ὥσπερ ἐν τοῖς καλουμένοις Ὀρφείως ἔπεσιν. ἐκεῖ γὰρ ὁμοίως φησὶ γίνεσθαι τὸ ζῶον τῆ τοῦ δικτύου πλοκῆ.

² The terms ‘simultaneous’ (ἄμα) and ‘successive’ (ἐφεξῆς) also cannot, or at least cannot directly, be considered Greek roots of the English terms ‘epigenesis’ or ‘preformation’. While the term ‘epigenesis’ itself contains the Latinized Greek terms ‘ἐπί’ (on top of; above, over, on, in addition to), and ‘γένεσις’ (origin, source, manner of birth, creation), the term ‘preformation’ is deduced from Latin ‘pre’ (before, in front) and ‘formatio’ (the process of giving or achieving shape or form).

notably in William Harvey’s neo-Aristotelian treatise *De generatione animalium* (1651).³ Thus, it seems more appropriate when Preus (1975, 91, 53), sensitive to the history of these concepts, claims that “epigenesis” was the “theory suggested by Aristotle”, even though the terms ‘epigenesis’ and ‘preformation’ were in use not before the “modern times”. Or when he cautiously characterizes the Aristotelian account of animal generation as epigenetic, but also reflects on its historical distance to the early modern conceptual framework: “Aristotle rejects... the pre-formationist theory, that there is a homunculus present in the male semen, in favor of the idea that the menstrual fluid for example and the semen have the powers (dynameis) necessary to bring about the development of a new individual, a theory later called epigenesis” (Preus 2015, 172; my emphasis).

But even if it is true that Aristotle himself had no access to a debate which already used these terms Aristotle deals with distinctions analogous to those between the doctrines of preformation and epigenesis, both, in his own account in the *GA* and in accounts of his time that he studied. In passage *GA* 2.1.734a16–21, Aristotle himself points to an (unspecified) Orphic text, which spells out elements of a position analogous to what was later called an epigenetic view. Föllinger (1996, 62) has argued that Plato’s *Timaeus* 91b–d contains incipient epigenetic ideas.⁴ And also ancient variants of what was later called ‘preformation’ were already available. Lesky (1950, 1275) sees a variant of preformation in Anaxagoras’s fragments DK 59B4 and DK 59B10,⁵ and she considers Democritus’s atomistic idea of the coitus preformationist (Lesky 1950, 1296–1297), since Democritus claims that a “coitus is

³ Harvey (1651 in 1965, Lat. 154, Engl. 334; see also Lat. 155–156, Engl. 336–337) defines the “method of epigenesis” as follows: “Some, out of a material previously concocted, and that has already attained its bulk, receive their forms and transfigurations; and all their parts are fashioned simultaneously, each with its distinctive characteristic, by the process called metamorphosis, and in this way a perfect animal is at once born; on the other hand, there are some in which one part is made before another, and then from the same material, afterwards receive at once nutrition, bulk, and form: that is to say, they have some parts made before, some after others, and these are at the same time increased in size and altered in form. The structure of these animals commences from some one part as its nucleus and origin, by the instrumentality of which the rest of the limbs are joined on, and this we say takes place by the method of epigenesis, namely by degrees, part after part; and this is, in preference to the other mode, generation properly so called.” (“Quaedam ex materia prius coctâ & auctâ formantur, & transfigurantur; omnesque partes simul per metamorphôsion oriuntur, ac distinguuntur, perfectumque animal enascitur: quædam verò, factâ parte unâ præ altera, ex eadem materiâ postea simul nutriuntur, augentur, & formantur: habent scil. partes alias aliis priores ac posteriores, eodémque tempore & augentur, & formantur. Horum fabrica à parte aliquâ, tanquam ab origine, incipit; ejúsque ope reliqua membra adsciscuntur: atque hæc per epigenesin dicimus; sensim nempe, partem post partem; éstque istæc, præ altera, propriè dicta generatio.”) Lennox (2006) has written one of the most careful comparisons of Aristotle’s and Harvey’s accounts of animal generation, though he does not focus on epigenetic characteristics in both accounts.

⁴ Föllinger (1996, 62) thinks that epigenetic ideas are present in Plato’s *Timaeus* when Timæus compares the generation and development of an embryo to the plucking of a fruit from a tree, which is then sown in the female womb as in a field. This fruit, first unseen due to its smallness and lack of form, gets separated and matured within, and is finally brought out in order to complete the generation of the embryo.

⁵ In DK 59B4 Anaxagoras notes: “And since these things are so, we must suppose that there are many things of all sorts in everything that is being aggregated, seeds of all things with all sorts of shapes and colours and tastes...”; and in DK 59B10 he asks: “How could hair come from what is not hair or flesh from what is not flesh?” (I am quoting the fragments according to Diels and Kranz 2004). Lesky (1950, 1275) writes in view of these embryological remarks that at this point, for the first time in ancient natural science, the idea of preformation was formulated clearly and unambiguously.

a light apoplectic stroke”, in which “a man is falling out of another man and is cut loose as if separated through a stroke” (DK 68B32).⁶ In addition, Morsink (1982, 51) and Mayhew (2004, 28–30) think that Aeschylus in his *Eumenides* mentions an animalculist preformationist view, when he puts the myth of Athena’s birth⁷ into Apollo’s mouth and lets Apollo say: “The mother [Metis] of what is called her child [Athena] is no parent of it, but nurse only of the young life that is sown in her. The parent is the male [Zeus], and she [Metis] but a stranger, a friend, who, if fate spares his plant, preserves it till it puts forth” (Aeschylus, *Eumenides*, 658–661). One could add a lamentation of Jason in Euripides’s *Medea* who imagines a variant of an animalculist preformationist view, when he wishes that “[m]ortals ought to beget children from some other source, and there should be no female sex” (Euripides, *Medea*, 573–574). And many other ancient mythological stories suggest generative narratives similar to those later referred to as either ‘epigenesis’ or ‘preformation’.

I.2

Aristotle had no direct access to what early modern philosophers called the ‘preformation-epigenesis debate’, but had access to ideas and theories that could (but do not have to) be considered similar or analogous to early modern preformationist and epigenetic approaches. Is it then advantageous to characterize Aristotle’s account of animal generation in terms of, or analogous to, the epigenesis-preformation distinction? Or does it make more sense to follow scholars who try to interpret Aristotle’s account of reproduction in relation to ancient theories of animal generation, which do not presuppose a conceptual antithesis that did not exist in Aristotle’s time? Let us have a look at alternative historical discussions which situate Aristotle’s account of reproduction in his own time.

I.2.1

In her classical analysis “Die Zeugungs- und Vererbungslehren der Antike und ihr Nachwirken (On ancient doctrines of generation and heredity and their impact on later thought)”, Lesky distinguishes five groups of ancient theories of animal generation: encephalo-myelogenic doctrines of seed, the warmth-theory, the right-left theory, the pangensis doctrine, and the haematogenous account of semen.⁸ The criterion of Lesky’s classification is the nature and the place of origin of the seed,

⁶ Lesky (1950, 1275–1276) associates this idea with Nicolaas Hartsoeker’s defense of animalculist preformation in early modern philosophy in his *Essay de dioptrique* (see Hartsoeker 1694, 230).

⁷ According to popular versions of this myth, Athena’s father Zeus once lay with Metis. But Zeus immediately feared the consequences of his act since Uranus and Gaia had prophesied that Metis would bear children more powerful than Zeus himself. In order to prevent this, Zeus swallowed Metis, but Metis had already conceived. Zeus experienced an enormous headache, and Hephaestus cleaved Zeus’s head with an axe. Athena leaped from Zeus’s forehead, fully grown and armed. See further discussions of this passage in Peck’s (1942, 372–373) translation of Aristotle’s the *GA*, and in Needham (1959, 43–46). Peck and Needham support the claim that this doctrine was of Egyptian origin.

⁸ See Lesky (1950, 1233–1254) for the encephalo-myelogenic doctrine (“enkephalo-myelogene Samenlehre”), Lesky (1950, 1255–1262) for the warmth-theory (“Wärmethorie”), Lesky (1950, 1263–1293) for the right-left theory (“Rechts-Links-Theorie”), Lesky (1950, 1294–1343) for the pangensis

and the (resulting) explanation of the generation of male and female sexes or of inherited resemblances in general.

Lesky attributes the first, the encephalo-myelogenic doctrine of reproduction, mainly to Alcmaeon of Croton, to Hippo, and to Plato. In Alcmaeon’s account the seed origins in the central organ of the body, the brain or encephalon (DK 24A10, DK 24A13); in Hippo’s view in the spinal marrow (Lesky 1950, 1235). In Plato’s *Timaeus* (73b–c, 77d, and 91a) man’s semen origins in the spinal marrow; and in some passages Plato even describes the spinal marrow as generative itself (Lesky 1950, 1243). According to Lesky’s (1950, 1247, 1249, 1251–1252) classification, defenders of encephalo-myelogenic doctrines of seed explain the hereditary mechanisms as an agony between two kinds of semen in which the semen of one of both copulating partners prevails.

Lesky sees the main defender of the second, the warmth-theory, in Empedocles. In Empedocles’s theory of reproduction, both, male and female, produce semen, and Empedocles seems to indicate that semen origins in a fluid, which is not blood (Lesky 1950, 1256; see DK 31A4). Empedocles claims that the opposition of the generation of male and female sexes begins in the womb and is dependent upon its temperature: “semens which enter a hot womb become males, those which enter a cold one, females” (see *GA* 4.1.764a1–6). The cause of this heat and cold is “the menstrual flow, according as it is hotter or colder, older or more recent” (DK 31A81).⁹ The differentiation of male and female takes place during conception (see *GA* 1.17.723a24–26). Into “clean vessels were they [male and female semen] poured forth; some spring up to be women, if so be they meet with cold [some to be men, if so be they meet with warmth]” (DK 31B65).

Parmenides and Anaxagoras defend what Lesky calls the ‘right-left theory’. In Parmenides’s view semen origins in blood (Lesky 1950, 1272): “when women and men mingle the seeds of love that spring from their veins, a formative power maintaining proper proportions moulds well-formed bodies from this diverse blood. For if, when the seed is mingled, the forces therein clash and do not fuse into one, then cruelly will they plague with double seed the sex of the offspring” (DK 28B18). Parmenides also expresses views on the origin of the offspring’s sexes in the right and left sides of the uterus: “on the right boys, on the left girls” (DK 28B17; see Lesky 1950, 1265). This fragment is closely related to an indirect testimony of Parmenides’s views on inherited resemblances in DK 28A54: “Parmenides explains, if semen is segregated from the right side of the uterus, offspring is generated which resembles the father, if it is segregated from the left side, offspring resembles the mother”, and “Parmenides’s view is that if the right sides segregate semen, children resemble the father, if the left sides, the mother”.¹⁰ Anaxagoras, the main defender of the right-left theory, notes about the origin of semen that “in all that is unified many and manifold

Footnote 8 continued

doctrine (“Pangenesislehre”), and Lesky (1950, 1344–1417) for the haematogenous doctrine (“hämatogene Samenlehre”).

⁹ Most of the Empedoclean fragments on reproduction confirm this classification, though some do not, for instance DK 31B92.

¹⁰ Fragment DK 28B18, however, supports an explanation of inherited resemblances that cannot be easily connected to Parmenides’s right-left theory.

materials are contained and sperms of all things [σπέρματα πάντων χρημάτων]... and that so are composed also men and all other animated living beings” (DK 59B4), since “how could hair origin out of non-hair and flesh out of non-flesh” (DK 59B10)? With regard to the generation of male and female offspring Anaxagoras claims that the opposition between male and female exists right back in the semens, and that males origin in the right side and females in the left side of the uterus (DK 59A107; see also *GA* 4.1.763b32–764a1).

The atomists and the Hippocratic physicians hold what Lesky calls the ‘pangenesi doctrine’. In the atomists’ version of the pangenesi doctrine the seed is derived from all parts of both parents’ bodies. The differentiation of the sexes takes place in the womb, but depends on whether the mother’s or the father’s seed preponderates; it is neither dependent upon temperature nor on the distinction between right and left sides of the whole body or of the reproductive organs, but upon the fact, which of both semens prevails (*GA* 4.1.764a6–11, DK 68A141). In the Cnidian variant of the pangenesi doctrine major parts of the semen are constituted by all four humors: black and yellow bile, phlegm, and blood (Lesky 1950, 1302–1303); in the Coan version just by two of them (Lesky 1950, 1304). According to Lesky’s understanding the Hippocratic physicians develop the new insight that both, the mother’s and the father’s semen, contain male and female patterns that they transfer to the embryo.¹¹

Aristotle’s account of reproduction in the *GA*, Herophilus’s, and Galen’s theories, belong to the last group of Lesky’s classification, to the hematogenous doctrines of seed. According to Aristotle semen origins in blood, the concocted nutrition of the body. Lesky (1950, 1355) thinks that Aristotle bases his claim on the observations that the body appears weak after sexual intercourse, since its blood has been used to form semen. In addition, sexual excess leads to the excretion of blood, the uncooked, raw matter of semen, since the cooked, refined matter of semen has been used up. Aristotle also thinks that children obtain their hereditary patterns from their parents’ blood. As for Aristotle’s account of inheritance, Lesky (1950, 1349–1350) points to the importance of the doctrine of the four causes (formal and material, efficient or motive and final causes) and the dominance of the teleological perspective. The male semen contains the formal, the female menses the material cause of animal generation; both together constitute the embryo.

I.2.2

Another discussion of Aristotle’s account of reproduction in the context of historical theories of Aristotle’s own time can be found in Coles’s (1995) piece “Biomedical models of reproduction in the fifth century BC and Aristotle’s *Generation of animals*”. Coles (1995, 49–50) claims that Empedocles and the “school of Acragas” were an indirect or “partial influence on Aristotelian physiology” and reproductive

¹¹ Lesky (1950, 1306) thinks that the “bisexual potency of the semen as a foundation of the inheritance of the sexes (*bisexuelle Potenz des Keimgutes als Grundlage der Geschlechtsvererbung*)” was an important step in the history of ancient embryology, since it for the first time allowed the explanation of multiple and crossed inherited resemblances.

biology insofar as both accounts associate semen with nutrition in general and with blood as nutritive substance in particular. However, and more importantly, Coles says, the Aristotelian idea that semen originates in the nutriment of the body, has been formed also by “later influences”, “playing a larger role” than Empedocles. According to Coles these influences were the Coan, and even more the Cnidian medical schools and their “nutritive and reproductive physiology”. He believes that the “links between Aristotle and Cnidian biology” were “closest” in Aristotle’s conceptions “of the physiological origin of semen” and “of its hereditary properties”, and demonstrates that Aristotle develops his views on semen as a residue of concocted nutrition in opposition to earlier views, especially to the Cnidian doctrine of semen or spermata as σύντηγμα, that is as a colliquescence or “morbid bodily discharge... produced as a result of an unnatural melting (συντήκεσθαι) of aliment around the body through the agency of heat” (Coles 1995, 54, 60).

I.2.3

Henry (2005), too relates his discussion of Aristotle’s account of reproduction to historical theories of Aristotle’s own time. In his paper “Embryological models in ancient philosophy”, he compares Aristotle’s account of reproduction with the approaches of Alexander of Aphrodisias and Simplicius of Cilicia. Henry’s main point of comparison is how the mechanism of the embryo’s matter brings about the embryo’s (teleological) form. In order to compare the various answers to his question, he distinguishes a variety of mechanical models such as marionettes, mechanical puppets, and self-moving automata (Henry 2005, 3). For instance, he imagines a marionette, which is a “puppet, whose limbs are moved independently of one another by a puppeteer manipulating strings attached directly to each limb” (Henry 2005, 3). In this model outer sources (various strings) cause the various movements of and inside of the marionette. Or he imagines a mechanical puppet, which is a device whose motion is also generated externally; however, in this case all of the puppet’s limbs are moved by pulling a single master cord rather than different strings attached directly to each limb. This model is similar to modern clocks (Henry 2005, 4), in which the mechanism has an outer source of its motion but the variety of the motions of and in the puppet are caused by internal gears. In addition, he construes the model of a self-moving automaton, which is a device that generates its motion “internally” (Henry 2005, 4). Henry compares this model to modern computers in which the computer program serves as the internal cause of the mechanisms of the computer; though Henry admits correctly that also a computer program is finally designed by an external cause, and is, in the end, similar to the master cord case. In addition, Henry describes a sheer mechanical automaton.

Henry ascribes to Alexander a marionette model or mechanical automaton. According to Alexander nature as a non-rational agent is an internal principle of the embryo that aims at the completion of the species form of the embryo (Henry 2005, 9), whereby the network of gears inside the automaton is an internal source of motion and an internal source of form (Henry 2005, 24). The process leading from embryo to adult is a causal sequence in which each member in the series is itself

both productive of, and capable of setting in motion, the thing which comes after it. This chain of causes and effects continues in succession until what exists is an organism with the same shape and form as its parents (Henry 2005, 12). Simplicius, in contrast, uses the model of a mechanical puppet in order to describe the development of an embryo. This puppet has an external source of motion, the operator pulling the cord, but an internal source of its form, the organization of its gears (Henry 2005, 24). Simplicius's mechanical puppet moves only as long as the operator is pulling the cord. Thus, the operator is not only active at the beginning of the embryo's motion, but continues to move it right up to the end (Henry 2005, 25). In Simplicius's account nature is co-responsible for the reproduction of offspring, since the mechanism of nature is not only a product of nature but also of an intelligent designer (Henry 2005, 27). Aristotle defends what Henry describes as the model of a pre-programmed automaton, similar to a self-building ship, an example, that Aristotle mentions in *Phys.* 2.8. It is a "device that is moved by an *internally* generated *continuous* motion... generated by a single common source of motion inside the device itself" (Henry 2005, 39). A pre-programmed automaton relies on "the actualization of a single potential" (Henry 2005, 40) that leads to the generation of the automaton's end.

I.3

Given the alternative historical discussions mentioned, is an anachronistic characterization of Aristotle's account in terms of, or analogous to, the epigenesis-preformation distinction somehow advantageous? Or does it make more sense to interpret Aristotle's account in relation to historical theories of his own time, as scholars like Lesky, Coles, or Henry suggest?¹² Lesky's classification concerns the sources and origin of male and female semen, and inherited resemblances, which result from them. According to her, Aristotle holds a variant of the hematogenous doctrines of seed. In this account semen origins in blood, the nutrition of the body. Lesky thinks that Aristotle also explains children's hereditary patterns by their parents' semen, which is digested blood, and transfers matter (female semen) and form (male semen) to the embryo. Coles's analysis focuses on one of the most central aspects of Aristotle's views on reproduction: the nature of semen as a concocted residue of nutrition and the nutrition model of generation. Coles argues that Aristotle's nutrition model of generation is rooted in Empedocles's views and is strongly related to Coan and Cnidian medical treatises of Aristotle's time. Henry debates the mechanical and teleological powers in various historical accounts of animal generation and analyzes how they can account for the formation of the embryo. Each of these approaches relates Aristotle's account of reproduction to positions of his own time, and offers valuable insights into central aspects of Aristotle's theory, which call into doubt whether anachronistic characterizations of the same features (as preformationist or epigenetic) result in more informative

¹² One could also mention Connell's (2016, 292–324) discussion of Aristotle's explanation of inherited resemblances in relation to Galen's and pangenetic alternatives.

analyses. Though tracing back ancient roots of early modern ideas is telling, the more authentic historical contexts of Aristotle’s account can be found in Aristotle’s own time.

II.1

At the beginning of this paper, I introduced a number of claims in which Aristotle is considered a defender of epigenesis (as opposed to an advocate of preformation). So far I have argued that these characterizations are anachronistic. They rely on a pair of terms (and doctrines) that do not belong to Aristotle’s own time, but to the early modern period. These anachronistic characterizations can be challenged by valuable historical discussions which analyze Aristotle’s account of reproduction in relation to and in comparison with theories of his own time. Let us now assume for a moment that the epigenesis-preformation distinction is a helpful tool for an analysis and characterization of Aristotle’s account of reproduction. Is it then right to call Aristotle a defender of epigenesis (in an analogous sense)?

The majority of scholars who characterize Aristotle in terms of preformationist and epigenetic characteristics, describe him as a defender of epigenesis, for instance Föllinger (1996, 163) who claims with reference to *GA* 2.1.734b9–13 that Aristotle interprets the development of the embryo epigenetically. Beginning with the heart, she says, the parts of the body develop successively by transferring the motion from a part which develops first to another part which develops next. Föllinger points to Aristotle’s comparison of reproduction with miraculous marionettes, in which a part set in motion subsequently moves other parts of the puppet’s body.¹³ Also Kosman (2010, 149–150) claims that Aristotle rejects ovist or animalculist theories of preformation and interprets the generation of animals as a kinetic epigenetic process, in which the collaboration of active and passive powers in the male and female semen leads from potential to actual states of the embryo: “Aristotle’s theory is... that the male, in an act analogous to what we call fertilization, begins the process by which the female grows within herself and bears their mutual offspring... Aristotle’s theory is through and through a theory of epigenesis”. And Balme claims:

Aristotle begins as usual from an accepted starting-point.... The current view was that th[e] seed must somehow contain all the bodily parts, drawn from the corresponding parts of one or both parents—a combination of the views later known as preformationism and pangensis, whereby the embryo’s development is merely the enlargement and manifestation of structures already present and fully diversified in the seed. (Balme 1985, 140)

However, so Balme’s (1985, 141) argument, Aristotle favors the doctrine of epigenesis, since the “seed cannot consist crudely of bits of each part”. And, as mentioned already, also Morsink (1982, 50–51), Needham (1959, 54–55), Peck

¹³ Föllinger (1996, 163) writes: “Die Entwicklung des Embryos stellt sich Aristoteles epigenetisch vor (*GA* 2.1.734b13–15): Die Körperteile entstehen, mit dem Herz beginnend, sukzessive, indem jeweils das vorher entstehende die Bewegung an das nächst entstehende weiterleitet. Aristoteles gebraucht den Vergleich mit bestimmten Automaten, um den Vorgang der Embryonalentwicklung anschaulich zu machen”.

(1942, 144), and Preus (1975, 91, 53; 2015, 172) think that Aristotle holds epigenetic views.

But there are also a few scholars who think that Aristotle is an advocate of preformation (Elsthain 1981; Bleier 1984; Blundell 1995). According to their views Aristotle holds that the female contributes nothing else than a container and nutrition to the generation and development of the foetus. Its function is to protect and ‘unwrap’ the embryo. Elsthain (1981, 44), for instance, writes that in Aristotle’s account “the male... implants the human form during mating” and “deposits within the female a tiny homunculus for which the female serves as a vessel until this creature matures. The female herself provides nothing essential or determinative”. Bleier (1984, 3) argues that Aristotle describes females as “totally passive beings” who “contribute nothing but an incubator-womb to the developing fetus that springs full-blown, so to speak, from the head of the sperm”. And Blundell (1995, 106) says that in Aristotle’s theory of reproduction the female contributes “space but also matter to the developing embryo. This matter, however, is entirely passive; it is the male who supplies the principle of movement and life”.

A major problem of this overall controversy is that scholars often do not spell out clearly which preformationist or epigenetic (early modern) accounts they have in mind when they characterize Aristotle as a defender of epigenesis or preformation, and that they do not say clearly and completely what the respective characteristics of these accounts are. But this is also not easy since the early modern preformation-epigenesis debate lasted one and a half centuries, a time, in which natural philosophers developed a wide variety of preformationist and epigenetic accounts.¹⁴

In order to decide which side of the debate is right, I will single out and distinguish only what I consider to be the most widely shared systematic characteristics of preformationist and epigenetic accounts of reproduction as they were used in early modern times and will investigate if and how they are present in Aristotle’s account. As an alternative to the oversimplified either epigenetic or preformationist readings mentioned, I will argue that Aristotle’s account is close (r) to epigenetic views, but contains a few preformationist elements also.¹⁵

II.2

What are the most widely shared characteristics of preformationist theories in the early modern period?¹⁶ According to my view, most of the defenders of

¹⁴ I have conducted a comprehensive analysis of preformationist and epigenetic early modern accounts of reproduction in Goy (2017, 288–385).

¹⁵ I think that Lesky (1950, 1364–1365) already tends towards such a more complex view. In some of her claims she seems to support the traditional epigenetic interpretation of Aristotle’s account. But she also points to the fact that the embryo contains all dispositions of its future parts in potency though no actually, which, I guess, is a preformationist idea.

¹⁶ See Goy (2017, 288–308). Marcellus Malpighi (1628–1694), Jan Swammerdam (1637–1680), Albrecht von Haller (1708–1777), Charles Bonnet (1720–1793), and Abbé Lazzaro Spallanzani (1729–1799) defended ovistic variants of preformation theories in the sixteenth to eighteenth centuries. Animalculistic interpretations of preformation appeared in the second half of the seventeenth and at the beginning of the eighteenth centuries, most prominently defended by Antoni van Leeuwenhoek (1632–1723), Nicolaas Hartsoecker (1656–1725), and Gottfried Wilhelm Leibniz (1646–1716).

preformation assume the existence of God and God’s creation. They claim that God preforms the germs of living beings such that they contain in miniature all characteristics of the prospective living being. These characteristics are generated simultaneously; and the development of the embryo is just an unfolding and enlargement of these simultaneously created characteristics. Among the two main kinds of preformation theories defenders of ovist preformation hold that the preformed germ is the female egg; advocates of animalculist preformation believe that the preformed germ is the male sperm. In both variants of preformation theories only one of the parents—either the mother or the father—transfers its characteristics to the offspring which means that advocates of both models of preformation theories hold highly counterintuitive unisexual theories of inherited resemblances. In ovist preformation the egg transfers the mother’s, in animalculist preformation the sperm the father’s characteristics to the offspring.

Does Aristotle hold what was later called ‘preformationist’ claims? Does Aristotle, for instance, assume the existence of a divine creator, that is, an ultimate generator of preformed germs, as defenders of preformation hold? Though in the *GA* Aristotle does not explicitly speak of a preforming creator of the potentially given material and formal characteristics of an offspring in male and female semen, as defenders of early modern Christian doctrines, in the *GA*, as in *DA*, Aristotle claims that reproduction aims at the eternity of the species, and thus, at a share of the divine: “because since the nature of a class of this sort [finite living beings] is unable to be eternal, that which comes into being is eternal in the manner that is open to it. Now it is impossible for it to be so *numerically*, since the ‘being’ of things is to be found in the particular, and if it really were so, then it would be eternal; it is, however, open to it to be so *specifically*” (*GA* 2.1.731b31–35, see also *DA* 2.4.415a22–415b8). And in Aristotle’s metaphysics, God moves all beings like a beloved (*Met.* 12.7.1072b3). Thus, in some sense, Aristotle claims the divine as a final cause of generation and reproduction that steers the generative process and directs the development of the offspring to an end; though God is not the creator of preformed germs as in preformationist accounts.

Does Aristotle claim the simultaneous generation of all characteristics of living beings, as defenders of preformation hold? Most of the traditional interpreters consider Aristotle an opponent of theories of preformation, especially because he claims the successive development of the parts of an embryo.¹⁷ Even though this is true, Aristotle also claims that the female semen contains all material and the male semen all formal characteristics of the offspring—in potency but not actually (*GA* 1.19.726b15–19)—and that the successive development of an embryo out of semen

¹⁷ For instance, Needham (1959, 48–49) writes with regard to *GA* 2.1.734b20–735a4: “Thus Aristotle... decided against preformation and pictured at one and the same time the unformed catamenia as containing a kind of clockwork mechanism which, once set in motion, would inevitably produce the finished embryo, and also as an inchoate substance on which the seminal essence should act like a swordmaker producing a sword according to the motions of natural art. The two ideas are not completely reconciled in Aristotle”.

is a successive unfolding, enlargement and actualization of *simultaneously* (ἄμα) given potencies (*GA* 2.1.734a16–21).¹⁸ This claim seems to belong to the preformationist view that the parts and characteristics of an offspring are *generated* simultaneously.

Does Aristotle explain the resemblance of children and parents by preformationist (either ovist or animalculist) unisexual theories of heredity? Does he think that either the male or the female characteristics alone fashion the offspring actively? As Aristotle repeats at numerous places, even though the male parent contributes the formal and the female the material characteristics of the offspring, an embryo is generated only if male and female contributions to animal generation cooperate (*GA* 2.1.732a9–11, *GA* 4.2.767a13–23). This collaboration is not only required at the most general metaphysical level, since the generation of a substance presupposes the existence of matter (contained in the mother's semen) and form (contained in the father's semen), but also in a more complex way, when the father's semen provides the form of the male as much as of the female offspring and the mother's semen the matter of the male as much as of the female offspring.¹⁹

II.3

What are the most widely shared characteristics of epigenetic theories in the early modern period?²⁰ According to my view, in epigenetic accounts of animal

¹⁸ In *GA* 1.19.726b15–19 Aristotle writes, that the male and female “semen of the hand or of the face or of the whole animal really *is* hand or face or a whole animal though in an undifferentiated way; in other words, what each of those is *in actuality*, such the semen is *potentially*... because it has some *dynamis* within itself”. What precisely is Aristotle's view on the male and female as potentialities or *dynamis*? Aristotle characterizes the potentiality of the male semen as a potentiality to form, to shape, to animate, to give a particular character, or to move. In *GA* 1.21.730a14–15 he writes: the “semen of the male...; in virtue of the *dynamis* which it contains... causes the material and nourishment in the female to take on a particular character”. In *GA* 2.1.734b19–24 he notes: “[w]hatever is formed... by Nature..., say X, is formed by something which is X *in actuality* out of something which is X *potentially*. Now semen, and the movement and principle which it contains, are such that, as the movement ceases, each one of the parts gets formed and acquires Soul”. The potentiality of the female semen Aristotle characterizes as a potentiality of matter, since it contains the material parts of the offspring potentially, but not in actuality. The “female's contribution”, Aristotle says, “is a residue” that “contains all the parts of the body *potentially*, though none *in actuality*” (*GA* 2.3.737a22–24). The “residue provided by the female is *potentially* the same in character as the future animal will be, according to its nature; and although none of the parts is present *in actuality* in that residue, they are all there *potentially*” (*GA* 2.4.740b18–20).

¹⁹ The preformationist aspects in Aristotle's account that I focus on are not identical with what Blundell (1995), Bleier (1984), or Elsthain (1981) have identified as preformationist elements in Aristotle. Blundell, Bleier, and Elsthain focus on the passivity and container-like function of the female in animal generation. But Aristotle neither considers the female entirely passive (though some isolated passages seem to support this view, e.g. *GA* 1.21.729b12–14) nor is the view that the female serves as a container for the embryo most central (though Aristotle mentions it at some points, e.g. *GA* 1.21.726b1). The important aspect of the female in reproduction is that its menses is the source of the embryo's potential matter, which, beside the potential form, provided by the male, is one of the two essential components of an embryo as a particular substance.

²⁰ See Goy (2017, 315–344). Among the defenders of the mechanical variant of epigenesis were Pierre-Louis Moreau de Maupertuis (1698–1759), Georges-Louis Leclerc de Buffon (1707–1788), and John Turberville Needham (1713–1781). The vitalistic direction of epigenetic theories was represented by Caspar Friedrich Wolff (1734–1794) and Johann Friedrich Blumenbach (1752–1840).

generation, the assumption of God and God's creation loses its significance. Defenders of epigenetic accounts explain the generation and development of the living being not by means of a preforming divine designer, but by an undifferentiated, unstructured matter and creative powers and laws of nature. They further replace the preformationist assumption of the simultaneous preformation of all features of an embryo with the view that the generation and development of the offspring's parts and characteristics occurs successively. As in preformation theories there are two major variants of epigenetic theories: earlier representatives of epigenesis tend to understand the powers and laws of nature mechanically and often explain the self-organizing processes of organisms in Newtonian terms of attraction and repulsion. Later defenders of this doctrine claim vitalistic laws and powers of nature and ascribe entirely new capabilities to the epigenetic powers of nature, such as sensitivity, irritability, intelligibility, and spontaneity. In either variant advocates of epigenesis explain inherited resemblances bisexually. Both parents, they say, transfer their characteristics to the offspring.

Is there any evidence that Aristotle holds later so-called 'epigenetic' claims? Does he, for instance, claim the beginning of the development of the embryo out of undifferentiated, unstructured matter? An account of this kind can be found in Aristotle's claim that the female contributes all potential matter to the generation of the prospective living being. This matter is unstructured insofar as it, in the beginning, contains the characteristics of the embryo in potency only, though not actually (*GA* 1.19.727b14–16, *GA* 2.3.737a22–25).

Does Aristotle claim the successive generation of all characteristics of living beings as defenders of epigenesis hold? As in epigenetic theories, in Aristotle's account, the actual development of the parts and characteristics of the embryo occurs successively. For this reason, most of the traditional interpreters consider Aristotle a defender of epigenesis. In *GA* 2.6 Aristotle presents three lists, in which he describes the successive development of the embryo's parts. In the first list (*GA* 2.6.741b25–743a1), Aristotle claims that the heart and surrounding blood vessels or the counterpart of the heart are formed first, followed by internal parts, which develop prior to external parts. Parts above the diaphragm develop earlier than parts below the diaphragm. Though larger parts are visible at first, they are not always formed prior to smaller parts. In a second list, which starts in the *GA* 2.6.743a1, Aristotle claims that the heart develops first, followed by blood vessels, uniform parts of the embryo such as flesh or its counterpart, and nails, horns, hoofs, bills, sinews, bones, and skin. In a third list (*GA* 2.6.743b18–745b20), Aristotle claims that the upper portion of the body is marked off first, before the lower part(s). The heart is the first part of the whole animal. It is warm by nature, and is the source of sensations. Its counterpart is the brain, which is cold by nature and fluid, similar to the eyes. The remaining parts are formed out of nourishment; the most valuable ones out of the most concocted nutrition (flesh and sense organs), the necessary ones out of less concocted nutrition (bones, sinew, hair, nails, hoofs, and bills). Teeth, finally, are formed out of bones.

Does Aristotle provide an account of creative powers and laws of nature? In the *GA* Aristotle does not explicitly speak of creative powers and laws of nature, but he claims material, formal, efficient, final, and motive causes of reproduction instead

(*GA* 1.1.715a4–15), which could be spelled out in terms of natural powers and laws. We neither find a mechanical description of the self-organizing processes of animals in early modern Newtonian terms of attraction and repulsion nor vitalistic descriptions of the powers of nature, which cause the sensitivity, irritability, intelligibility, and spontaneity of living beings. But one can identify something analogous to early modern natural powers and laws: one could see Aristotle's claim that the female contributes the nutritive and the male the more complex sentient and cognitive parts of the soul to animal generation (*GA* 2.4.740b25–2.5.741a18) as analogies to early modern animating principles of the living. Aristotle also claims that the male semen contributes primary and the female semen secondary moving powers to the process of reproduction, which are powers analogous to early modern mechanical forces (*GA* 2.1.734b7–17, *GA* 2.5.741b7–9). Finally, the female contributes matter to reproduction, which, on the elemental level, contains powers that cause the tendencies of the various kinds of matter to move towards their natural places: the periphery or the center of the cosmos. Also these powers could be considered analogies to early modern mechanical natural forces.

Does Aristotle defend a bisexual account of heredity? Apart from a few cases, such as the spontaneous generation of animals (*GA* 1.1.715a18–25, *GA* 3.11.763a25–34), in which offspring is generated out of mud and soil, Aristotle holds a bisexual account of heredity and inheritance. This is true also for plants, though several species of plants have two separate male and female sexes in one and the same individual plant.

III.

Let us summarize. Was Aristotle the 'father' of the epigenesis doctrine? In part I of this paper, I have argued historically that this question must be answered with 'no'. Aristotle did not initiate and had no access to a debate that described itself in terms of 'epigenesis' and 'preformation', and thus cannot be considered the founder of the epigenesis-preformation controversy in a literal sense. The preformation-epigenesis debate arises in the early modern period, and any claim, which describes Aristotle's account of reproduction in these terms, is anachronistic. I have also argued that there are a number of valuable scholarly discussions which consider Aristotle in historical contexts of his own time and which call into doubt whether an anachronistic characterization of Aristotle's account is particularly advantageous. In part II of this paper, I have investigated whether Aristotle's account of reproduction and heredity can be considered epigenetic (in an analogous sense), as most of the traditional interpreters hold, or preformationist, as some of the recent scholars believe. I have argued against the one-sidedness of both readings that Aristotle's account of reproduction and heredity contains mainly epigenetic, but also a few preformationist characteristics. Whereas, for instance, Aristotle's idea of a successive development of the embryo's parts is an epigenetic characteristic, Aristotle's idea that the development of the embryo is an actualization and enlargement of potential parts, which are simultaneously present in the semen, can be considered a preformationist feature.

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