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Epistemic Competition between Developmental Biology and Genetics around 1900: Traditions, Concepts and Causation

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Epistemische Konkurrenz zwischen Entwicklungsbiologie und Genetik um 1900: Traditionen, Begriffe, Kausalität

Der Artikel führt den Begriff der epistemischen Konkurrenz ein. Im Gegensatz zu „wissenschaftliche Kontroverse" beschreibt er eine Situation, in der sich zwei Forschungsfelder gegenseitig als mit demselben Bereich von Phänomen befasst wahrnehmen, wobei ihre methodischen Ansätze und theoretischen Erklärungen jedoch so unterschiedlich sind, dass ein offener Konflikt über die Wahrheit oder Falschheit bestimmter Aussagen oder die Genauigkeit in der Anwendung einer Methode nicht stattfindet. Nichtsdestotrotz streben beide Parteien danach, die maßgebliche Erklärung der entsprechenden Phänomene anzubieten. Indem die erweiterte Gemeinschaft der Forschenden oder die Öffentlichkeit einen Ansatz als maßgeblich anerkennt, handeln sie als eine dritte, gewissermaßen neutrale Partei, die einen Preis vergibt, um den die anderen Parteien konkurrieren. Der Artikel beschreibt das Verhältnis von Genetik und Entwicklungsbiologie um 1900 als epistemische Konkurrenz. Diese Forschungsfelder geben unterschiedliche Erklärungen für die Phänomene der organischen Reproduktion. Die Erklärungen unterscheiden sich bezüglich der Formbegriffe und entsprechend hinsichtlich der Begriffe der Vererbung von Aspekten der Form eines Organismus. Zudem basieren die Erklärungen der beiden Felder auf unterschiedlichen Arten kausalen Schließens, die in unterschiedliche experimentelle Ansätze eingebettet sind. Diese Unterschiede können als Instanzen eines allgemeineren Unterschieds zwischen der Tradition der Naturgeschichte, die sich mit Unterschieden zwischen Organismen auseinandersetzt, und der Tradition der Anatomie, die sich mit den Teilen der Organismen beschäftigt, angesehen werden. Dieses Bild der Genetik und Entwicklungsbiologie als Zweige unterschiedlicher fest verankerter Traditionen widerspricht dem Narrativ der Trennung des Begriffs der Vererbung von dem der Entwicklung im Zuge einer Trennung der Disziplinen der Genetik und der Embryologie, das in der Historiographie der Biologie nach wie vor weit verbreitet ist.

Schlüsselwörter: Epistemische Konkurrenz, Genetik, Entwicklungsbiologie, Merkmale, Kausalität

Keywords: Epistemic competition, genetics, developmental biology, characters, causal reasoning

The relation of genetics and developmental biology[1] around 1900 is often described as problematic. Although both fields are concerned with phenomena of organic reproduction, they appear surprisingly little integrated at least until the 1930s. On the level of detailed results, it seems that researchers largely

ignore the work done in the respective other field, at least when it comes to the planning and interpretation of their own work. On a more polemical level, they sometimes comment on the irrelevance of the results or the inappropriateness of the approach of the other field for gaining an understanding of the phenomena in question. We might thus say that they see each other in epistemic competition, without engaging in direct controversy. I will briefly characterize the notion of epistemic competition, distinguishing it from scientific controversy as it has been characterized in science and technology studies (Sect. 1). I will then analyse in detail what the competing approaches to and accounts of the phenomena of reproduction provided by genetics and developmental biology consist of in the first decades of the twentieth century. This reconstruction suggests that these fields stem from separate traditions that are characterized by different concepts of form with respect to organisms and, accordingly, different understandings of the inheritance of form (Sect. 3). In genetics and developmental biology, respectively, these traditions give rise to alternative notions of causation, which are embedded in different types of experimental methods (Sect. 4). The latter part of the argument offers the opportunity for a fruitful interaction of history and philosophy of science. The picture drawn in this article runs counter to a persistent narrative in the historiography of biology, which holds that development and heredity were seen as one and the same phenomenon and were studied as such, before—mainly through the work of Thomas Hunt Morgan (1866–1945) and his group in the 1910s—genetics was split off from developmental biology. I will use this narrative as a contrast against which the view proposed here, of two traditions that develop into a situation of epistemic competition with respect to questions of reproduction, gains contour (Sect. 2). Like many authors writing on the relation of the two disciplines, I restrict my analysis mainly to the American and German speaking context.[2]

Epistemic Competition

Competition and cooperation can take place on many levels in science. Concentrating on competition, a distinction can be drawn between competition for resources (CR) on the one hand, and epistemic competition (EC) on the other hand. CR is competition for access to technologies, materials or collections, as well as funding, academic positions or influence, students or personnel, among other things. EC, instead, is competition regarding the production of relevant knowledge concerning a phenomenon. According to Kärin Nickelsen (2014: 355), who refers to Georg Simmel's analysis, one of the hallmarks for competition is that parties compete for a prize awarded by a third party. Competition thus usually does not entail open conflict. Competitors in

CR have to convince a third party (funding institutions, universities, potential new group members, etc.) that a phenomenon is important and thus worth studying and should best be understood, investigated and explained in the proposed way. The third party must have the authority to grant institutional rights, the means to distribute money or material, or the ability to join a project. The third party is considered neutral and is typically explicitly acknowledged by the competitors, and in case it is only implicitly endowed with the capacity to award a prize, this is at least obvious to all competitors. The professional specialization that shaped genetics and developmental biology around 1900 can often be understood in terms of CR. Research fields can, however, also compete in providing the most relevant knowledge with respect to a phenomenon. This then would be a case of EC. The question is, who would be the third party in that case? I suggest that the prize awarding party here is the broader scientific community, but also the general public, when they evaluate a research field as successful in producing knowledge that they can accept and rely on. With Ludwik Fleck, one might say that a specialist field acquires a circle of general experts and even an exoteric circle of educated amateurs (Fleck 1979: 111). When other fields that are not participating in the competition draw analogies or integrate knowledge or methodologies from one of the competing fields in their framework, this probably represents the most explicit prize awarded by the scientific community to competitors in EC. That Mendelian genetics fared very well in this respect is probably best illustrated by its integration into agriculture, medicine and the discourse of eugenics (or racial hygiene in Germany, see Weingart et al. 1988). Such acceptance will result in more resources being granted by the relevant institutions, but in itself, it is an epistemic matter. CR and EC are thus similar in that they are structured by an indirect contest, where both parties compete to win the support or acceptance of a third party, but do not engage in open conflict. But apart from the fact that one is about resources and the other about knowledge, they are also different with respect to the nature of the prize and the third party awarding it.

Having compared EC with CR, I shall now distinguish it from scientific controversy (SC). EC and SC are both conflicts concerning knowledge claims. However, most situations described as scientific controversies in the STS literature are characterized by open conflict (see Sismondo 2010 for a summary of the literature). Although the aim of a party is the acceptance of a knowledge claim, in SC we typically find no neutral third party awarding the prize of acceptance. Opponents in SC are involved in direct confrontation, and even if they want and need to persuade other members of their narrow community, these are far from being neutral. The other members might not engage at first and act as bystanders for some time, but they can at any time and eventually will be asked to take position, and this position will not be an outsider's acceptance, but an insider's commitment. Since the third party and

the indirectness of the conflict that it enables are hallmarks of competition, SC is different from EC in this respect. SC often takes place within a field or community, but also in cases where the opponents belong to different communities, they typically share a narrow understanding of a phenomenon and presumably also of the questions and problems that can be posed with respect to the phenomenon. They also share at least most of the terminology and recognize the same entities and relations on the observational level that describe the phenomenon in question, though probably with different emphasis. Differences might occur on the theoretical level, with respect to the validity of a result, the significance of a measurement or a proposed explanation. It is hard to see, however, how parties could disagree explicitly if there was not a large amount of shared understanding. Accordingly, opponents in SC engage in direct and ongoing confrontation because the positions openly contradict each and the theoretical coherence of the field requires a solution.

"Epistemic competition" instead, is suggested as a term for situations in which parties perceive each other as working on the same phenomena, broadly conceived. They share an understanding that they both work on the same realm of things or processes, but the phenomena in question are construed differently and often divided into partial phenomena and research problems in a different manner. Reproduction in the sense of organisms giving rise to organisms of the same kind is such a broadly conceived phenomenon. Genetics and developmental biology came to reconfigure this common problem quite differently, as we will see, as the inheritance of difference and the growth of parts, respectively. Competitors in EC also use different observational categories to describe the entities and relations that make up the phenomenon as they understand it. Accordingly, if explanation is the task, they not only provide different explanations but also explain the phenomenon as something different, and typically their explanatory strategies are embodied in different experimental approaches. In the case at hand, this shows most clearly in the categories used to describe the form of organisms, in particular the notions of a trait or character in genetics and the understanding of tissues, organs and body parts in developmental biology, as well as in the different understanding of causation as they are embedded in the hybridization experiments in genetics and the practices of tracking processes in developmental biology.

It has been said before that parties in EC compete for the acceptance of their accounts as authoritative by a larger community. Accordingly, the conflict is indirect. While there is little direct dispute on conceptual or methodological detail, one occasionally finds remarks on the general inappropriateness of the other approach for the study of the phenomenon in question. If comments on the other account are made at all in EC, then it is the relevance of statements that is challenged rather than its truth. Criticism might also address the very way the phenomenon is understood or what kind of questions are asked about it. Competitors claim that other aspects of it are

more interesting or important. For instance, developmental biologists often complained that genetics is only concerned with superficial properties of organisms. This is nicely illustrated by a remark on characters studied in genetic research employing the fruit fly *Drosophila melanogaster* that Ernest Everett Just (1883–1941) made in an AAAS symposium (Dec. 30, 1936), according to which "he is interested more in the back than in the bristles on the back and more in the eyes than in eye color" (quoted in Burian 2005: 205). With respect to method, it is rather the kind of experiment or observation that is questioned in EC than the details of the experimental procedure. Concepts and theories are not found inconsistent, but rather unintelligible, mainly because the experimental context in which they are formed is not well known by the respective other party. Developmental biologists and physiologists were often irritated by the mathematical character of genetic formalism. Even for a period as late as the 1960s Symour Benzer (1921–2007) recalls that neurophysiologists were ignorant of genetics because they thought "All those symbols to study the genes were just complicated and unnecessary, because, you know, to figure out how a nerve membrane potential is propagated, what do you need genetics for?" (Benzer 1991: 88).

While SC typically arises when members of a community diverge from the mainstream, differences in EC, being more about overall approaches than specific positions, often stem from pre-existing differences in traditions, proponents of which happen to find themselves dealing with phenomena, broadly conceived, that are also investigated by researchers from other traditions. As I will argue below, the conceptual and experimental frameworks of genetics and developmental biology are part of larger traditions that might be addressed as natural history and anatomy, respectively. Certainly, researchers who participate collectively in such a tradition have made substantial investments in elaborating experimental cultures, material collections and infrastructures of exchange, which, accordingly, they will not give up or compromise easily. When it comes to how conflicts end, STS speaks of closure with respect to SC, which typically consists in the rejection or at least marginalization of one position by the majority of researchers in the field (Sismondo 2010: 130–133). In contrast, I suggest three ways EC might end: (1) one possibility is that approaches awkwardly co-exist. It might be perceived as unnatural that the phenomenon under study is also investigated with another approach, generating different kinds of results, but there is also no urgency to settle the matter, given that the communities are separate. (2) What happens often, however, is that the phenomenon, broadly conceived, becomes separated in clearly defined sub-phenomena. The fields thus become more clearly separated in their approach, concerning the realm of things for which they are responsible, and also as communities. Social and institutional mechanisms of discipline formation facilitate the process. This process can result in situations where it is easier for the former competitors to simply ignore each other's

work, or, more positively, see the two strands of research as complementing each other (Nickelsen 2014: 363). However, while discipline formation can often dissolve CR because every discipline develops its own funding or recruitment structures, EC can be sustained albeit in a mitigated form. But for both (1) and (2) one can say that one party wins EC if it more successfully acquires a circle of general experts and educated amateurs. However, this is obviously a gradual process rather than a momentary decision. (3) There is also the possibility that approaches become integrated, which would imply not only a theoretical integration of the ways to understand the broad phenomenon, but also material integration of the experimental cultures.

Genetics and developmental biology have coexisted for a long time, especially in Germany under the umbrella of broader disciplines such as zoology—a situation that is mainly characterized by ignorance, critical remarks notwithstanding. In other places, such as in the American context, discipline formation helped to demarcate genetics from other fields (see Harwood 1993). Genetics was probably more successful in finding application in other fields of science, medicine and industry, and possibly also in influencing the public perception of phenomena of reproduction, thus winning the rather abstract prize of being accepted as providing the authoritative account of problems of heredity. But this does not imply that developmental biology did not flourish as a discipline in its own right. Consider, for instance, that two years after Morgan received the Nobel Prize in Physiology and Medicine in 1933, the embryologist Hans Spemann (1869–1941) received the same prize for his work on the organizer effect. However, it seems that the discourse of genetics migrated more easily into exoteric circles, while embryology remained more esoteric in Fleck's sense. There were also attempts of integration, as instantiated, for instance, by the work of Goldschmidt and Kühn (Allen 1974; Harwood 1993; Rheinberger 2000). This suggests that several paths of ending competition can be pursued simultaneously if the communities in competition are large enough.

It was said that ending, or at least mitigating competition, regarding both resources and relevant knowledge, was largely facilitated by processes of discipline formation in the case of genetics and embryology. As Allen remarks in this respect, "competition between fields […] makes the delineation of separate disciplines advantageous, especially to a new field trying to establish its own identity, its own areas of research focus, its own funding, and its own students" (Allen 1985: 119). However, neither the enforcement of disciplinary boundaries nor the clear separation of partial phenomena implies that before these efforts there was a disciplinary or conceptual unity. The apparent split of heredity from development or genetics from embryology that some authors suggested seems to be motivated by the observation of processes of mediating competition through discipline formation. But this becomes necessary because the fields are already quite separate. Before I characterize the research fields of

genetics and embryology in terms of the genealogy of their concepts of form and heredity (Sect. 3), and regarding the types of causal reasoning and investigative practices they employ (Sect. 4), I will discuss the idea of a split in more detail.

Revisiting the Split Narrative in the Historiography Of Genetics and Developmental Biology

The difficult relation between the concepts of heredity and development and the fields that investigated the process(es) they address is a frequent topic in the historiography of biology in the late nineteenth and early twentieth century. Authors have emphasized different aspects, such as, among others, institutional factors, in particular with respect to discipline formation, different national contexts, the intellectual development of individual researchers, the effect of broader political and cultural developments or simply the role of model organism based experimental systems.[3] One persistent narrative, however, is that of a separation of a formerly unified concept of heredity and development, which is often seen as embodied and institutionalized in a split of genetics from embryology. The main advocates of this view are Garland Allen (1985) and Scott Gilbert (1998). In the nineteenth century, or so the story goes, questions of heredity, development and evolution were seen as inseparable and, accordingly, theoretical frameworks were developed that encompassed all three issues. As exponents of such overarching views Ernst Haeckel (1834–1919) and August Weismann (1834–1914) are frequently mentioned (e.g. Allen 1985). Allen characterizes their view by listing three features. First, they saw the transmission of hereditary material from parents to offspring and its translation into adult form as one process. Second, they did not differentiate between what came to be called genotype and phenotype. Finally, they saw nucleus and cytoplasm as one integrated and interacting whole (Allen 1985: 108). The next step in the narrative has it that, when towards the end of the nineteenth century the experimental ideal was imported from physiology to other fields of biology by a younger generation, speculative theory lost its credibility (Allen 1985: 108; Burian 2000: 1129; see also Maienschein 1987b). Instead, after the experimental turn, researchers attempted to isolate problems, or to break down complex processes and study their parts separately. This is not only a matter of changing epistemic virtues that value controlled experiments over speculative theory, but there is also a motivation or attitude that several authors describe as pragmatic style (Allen 1985: 116; Maienschein 1987a: 88; Burian 2000: 1130; see again Harwood 1993 for an account on different national styles in this respect). Following a research program that consistently generates results has advantages over working on potentially more

intriguing, but hard and intractable problems. While the Mendelian research program, and in particular the *Drosophila* system developed by Morgan and his co-workers, combining cross-breeding with cytological techniques and thus establishing the chromosome theory of heredity, proved to be highly productive, development instead was seen as a notoriously difficult subject with respect to experimental investigation (Allen 1985: 116). A productive system enables the generation of publications, attracts students, builds a community and secures funding (Allen 1985: 119; see also Sapp 1987). The pragmatism described by these authors as one factor in the disciplinary demarcation of genetics and embryology is thus largely, even if not exclusively, explained by competition for resources, as introduced above. Before turning to the conceptual and methodological dimensions engendering the epistemic competition between the fields, we have to address the unity that the authors discussed here assume for the period before the separation.

The unified view is characterized by Amundsen as holding that "[h]eredity is the passing on of developmental processes" (Amundsen 2005: 148). The view that is ascribed to Morgan before 1910 by Amundsen as well as by Allen and Gilbert, is probably best illustrated with a quote from the embryologist and friend of Morgan, Edwin Grant Conklin (1863–1952), who writes: "Indeed, heredity is not a peculiar or unique principle for it is only similarity of growth and differentiation in successive generations" (Conklin 1908: 89, quoted by Allen 1985: 108, as well as Amundsen 2005: 184). A similar outcome of reproduction required nothing more than a similar starting point of development under similar conditions. Only the species' specific principles of growth had to be transmitted, and the conditions in terms of temperature, nutrients and so on that are typical for a species had to be in place. Development would then always lead to the same outcome: a body of the form typical for the species. No particular aspects of form needed to be transferred individually. We can contrast this view with a statement by Morgan from a time when the separation according to the split narrative had been achieved:

> For purposes, then, of closer analysis, it seems desirable in the present condition of genetics and embryology to recognize that the mechanism of distribution of the hereditary units or genes is a process of an entirely different kind from the effects that the genes produce through the agency of the cytoplasm of the embryo (Morgan 1917: 25).

Here is a clear conceptual separation of heredity and development. Heredity concerns the distribution of hereditary units in the offspring, presumably corresponding to the distribution of characters, while development concerns the process of growth as mediated by the activity of these units. Allen lists four factors for Morgan's separation of genetics from embryology (Allen 1985: 111–117): First, the Mendelian and chromosome theories were best suited to explain the results he obtained in *Drosophila* crosses. Morgan had started to work with *Drosophila* in order to address questions pertaining to evolution

(Allen 1975b; Kohler 1994). When he found the white-eyed mutant in his stock and started crossing experiments, the chromosome theory of Mendelian inheritance allowed an explanation in terms of a sex-linked inheritance pattern. This analysis in turn came to be seen as the first conclusive evidence for this integrative theory (see also Darden and Maull 1977). Second, Johannsen's distinction between genotype and phenotype came to be interpreted as pointing out that no conclusions could be drawn from the appearance of the organism to the hereditary material it is endowed with (see also Churchill 1974). Nevertheless, as we will see, the phenotype came to be seen as indicative for the composition of the hereditary material in the context of complex hybridization experiments. A third factor mentioned by Allen is Morgan's underlying philosophy of mechanistic materialism, inspired by Jacques Loeb (1859–1924), and motivating his turn to experimentalism, especially after his contact with German proponents of developmental mechanics at the Zoological Station in Naples. As mentioned above, an experimental approach can motivate a narrowing of the problems addressed. Finally, Allen points out the role of the American agricultural revolution that was brought about by many developments in society at large such as urbanization, and which also induced significant and specific changes in the scientific landscape, in particular concerning the scientific management of agriculture and its institutions, such as the creation of agricultural colleges and research stations. It also led to increased funding for Mendelian research programs which Morgan took advantage of. Thus, this point again relates to the competition for resources.[4]

Although Allen's and Gilbert's accounts are valuable reconstructions of the shifts in Morgan's career and his conceptual and methodological outlook, they are less helpful for understanding the relation of genetics and developmental biology at large in the early twentieth century. Morgan was an embryologist and, like many other embryologists such as Conklin, held a unified view of heredity and development. Accordingly, it makes sense to say that Morgan separated the problem of heredity from that of development in his reasoning when he entered the work with *Drosophila* mutants. It is less accurate to say that he thereby brought about a split of genetics from embryology. Rather, he turned to the field of the study of heredity and variation for which William Bateson (1861–1926) had coined the name genetics in 1906 (Bateson 1907; see also Powell et al. 2007), and, for sure, Morgan and his group were to transform this field substantially. Geneticists at the time already held a view of heredity that was largely independent from questions of development. Nevertheless, it seems as if many authors read Allen and Gilbert as providing an account of the overall relation of genetics and development, taking Morgan's intellectual development in a *pars pro toto* manner as representing a broader trend. But the latter, unsurprisingly, turns out to be much more complicated. Take the characterization of late nineteenth century biology in terms of the unified view of heredity, development and evolution. It is evident

from the literature that the speculations and investigations with regard to issues relating to heredity and development were extremely diverse in the second half of the nineteenth century (Müller-Wille and Rheinberger 2012: Ch. 4). Even figures such as Haeckel and Weismann changed their conceptions over time, and their respective ideas are not easily brought under one description with respect to these themes. In short, while in the context of the split narrative, for the period after 1910 the focus of the literature is too much on the American context and in particular on the person of Morgan, the period before 1910 is painted with too broad a brush.

One might want to claim that neither heredity nor development were separated conceptually, nor did genetics split off from embryology, but instead a unity remained intact. There are indeed a number of researchers after 1910 who attempted to study the transmission and the translation of hereditary material in an integrated way. Richard Goldschmidt (1878–1958), for instance, is frequently cited as someone counteracting the split (Allen 1974). But Goldschmidt was also a Mendelian and it rather seems that heredity and development were separate for him and he tried to bring them together.[5] In fact, I find the claim that most researchers treated heredity and development independently in the early twentieth century quite convincing. My unease with the narrative does not stem from the observed separateness after 1910 but arises from the suggested unity before. In the following, I will argue that there were several notions of heredity in play before 1910 and that some were conceived independently from the process of development all along.

A Biology of Organization and a Biology of Kinds: Two Concepts of Form, Two Concepts of Heredity

In the following, I will identify two distinct notions of form with respect to organisms, which can be identified with the separate traditions of natural history and anatomy. I will then argue that these two traditions gave rise to different notions of heredity.

According to the *Oxford English Dictionary* (*OED*) the word "character," derives from the Greek word for "a distinctive mark impressed, engraved, or otherwise formed; a brand, [or] stamp." In ancient times the term had already acquired the metaphorical meaning of a defining quality or a distinctive mark that was not artificially introduced. A character thus either distinguished an individual from all other individuals, or marked it as belonging to a kind of things. Finally, the term acquired the additional specialized meaning in natural history as—again *OED*—"One of the distinguishing features of a species or genus." The word "character" as used in genetics was not only taken from taxonomy to refer to aspects of form, it entered the study of inheritance as the

taxonomic concept, addressing the difference between forms, and was gradually transformed into an unit connected to a gene rather than to a species. The notion of an individual or idiosyncratic mark that is recognized as being passed on between individuals is another root of the genetic character concept. The history of this concept seems closely related to the English word "trait" and the German "Zug," as in "Gesichtszug" ("Merkmal" seems to be used for both taxonomic characters and idiosyncratic traits). Furthermore, this history is connected with the history of the legal origin of the word heredity and the logic of kinship relations and genealogical knowledge (Müller-Wille and Rheinberger 2007). The idiosyncratic trait concept comes in two variants: the difference in form of a specific mark (e.g. a mole or eye colour), or the individual deviation from a norm with respect to a property (e.g. being tall). The study of difference in the latter sense in the late nineteenth century is mostly associated with the work of Francis Galton (1822–1911) (Bulmer 2003). Both character concepts, the taxonomic and the idiosyncratic, deal with difference in form and are thus quite distinct from the notion of a part of an organism. "Part" from the Latin *pars* is "one of the portions into which a thing may be divided" (*OED*). It is much more connected to anatomy and serves in the explanation of the meaning of "anatomy": "The artificial separation of the different parts of a human body or animal" (*OED*).

It is possible to distinguish two traditions in the history of the study of living things. One is concerned with the composition and organization of organisms. Accordingly, it regards aspects of form as parts, organs or tissue regions. When organisms are compared, differences are ignored. The question is more what can be learned from the organisation of one organism about the organisation of others. The other tradition is concerned with the sorting of organisms of various kinds. Aspects of form appear as characters or traits. Comparison is all about finding similarities and differences. I use tradition here in a sense similar to Kuhn's (1976) use of the term when he speaks of "Mathematical versus Experimental Traditions in the Development of Physical Science," that is, as long-term differences in approach and emphasis that do not map neatly on to individual actors who might participate to some extent in both traditions, or to institutional structures such as university faculties. Traditions in this sense are akin to what John Pickstone—who cites Kuhn's essay next to Foucault's (1970) notion of episteme as one of his influences—called ways of knowing (2001). As opposed to the Foucauldian picture as well as to Kuhn's notion of paradigms, ways of knowing—although emerging or coming to prominence at different times—coexist in parallel and appear in specific combinations in actual research programs. Pickstone (2001: Ch. 1) distinguishes *natural history* (concerned with classification and description), *analysis* (taking things apart into their elements) and experimentalism (the bringing about of new phenomena). While the first two categories seem to fit my distinction of traditions in the study of organisms, Pickstone's emphasis

regarding natural history is on making inventories of "what we have." Accordingly, descriptive anatomy of the sixteenth century falls under natural history, while nineteenth century histology is analytic. I wish to emphasize, instead, the different role assigned to the organism and the aspects of form in different approaches across time. In one tradition, organisms appear as organized composites and aspects of form as parts, while in the other organisms appear as belonging to certain kinds but not to others, and aspects of form appear as characteristics in which they are similar to or different from other organisms. And since I am mainly concerned with the constellation of these two ways of knowing organisms at the end of the nineteenth century, I will speak of a biology of organization and a biology of kinds, respectively. Systematics, whether taxonomic or phylogenetic, studies relations among organisms on the basis of their similarities and differences (characters) and thus belongs to the biology of kinds, while anatomy and physiology, which are concerned with the parts and their structural and functional relations in the organism, belong to the biology of organization. Again, the two traditions do not map clearly on to disciplinary or institutional boundaries. We find both approaches in the medical faculties as well as in the zoological and botanical departments of the philosophical faculty, which were established in the nineteenth century (Rheinberger 2010). Also, individual researchers can often not be placed in one tradition or the other unequivocally. They might emphasize one perspective on organisms over the other at different times or entertain various research programs simultaneously. Even a single research program might consist in a certain constellation of the two ways of knowing about organisms, but typically one perspective has priority over the other. It might be necessary to perform careful anatomical studies in order to classify organisms, but when the aim is to place the organism in a taxonomic system or in a phylogeny, rather than understanding its composition and the functional relation of parts, the program overall belongs to the biology of kinds.

Let me now spell out the different notions of heredity associated with the biology of kinds and the biology of organization. At first sight, it appears as if embryology, as well as the study of heredity in fields concerned with genealogy, classification and evolution, had the same notion of heredity: the similarity of parent(s) and offspring. But taking a closer look, their questions appear different: on the one hand, embryology asked how the new organism acquired form; how the seemingly heterogeneous mass of the early embryo gives rise to the differentiated organism. As will be shown below, to answer this question it had to dissect the process of sequential cell division and differentiation. Embryology was the anatomy of growth. For this question and approach, it was not important to think of one species as being different from another species. The question for those concerned with difference, on the other hand, was how the gametes of one species or of an individual marked by certain traits, gives rise to an organism showing the characters or traits of this species rather than

that of a closely related one, or of one parent rather than the other. Hybridization experiments crossed two species, genealogies tracked the traits of both parents and evolution was concerned with the divergence of characters in geographically closely related variants.

That genetics around 1900 emerged from earlier studies of heredity in the context of plant and animal breeding and family genealogies is well known (Müller-Wille and Rheinberger 2007). In 1910 genetics was an established practice that grew from concerns with variation on and below the species level, either for genealogical, taxonomic, evolutionary or agricultural reasons. It was a comparative practice of relating differences among organisms. It operated with a concept of inheritance of difference that was separate from the outset from the notion of heredity we find in developmental biology at the time. Why then should we say that the concept of heredity that we associate with genetics was split off from the unified notion of heredity and development in developmental biology, and with it the discipline of genetics itself? While I have identified discipline formation as one source of the impression of a split, I believe the split narrative is also motivated by the role of cytology in the study of heredity. The boundary between cytology and embryology is difficult to draw in terms of researchers' identities as much as in terms of research objects. Biologists such as Oscar Hertwig (1849–1922), Theodor Boveri (1862–1915) or Edmund Beecher Wilson (1856–1939) were as much cytologists as they were embryologists and the zygote is as much a cell as it is an embryo. Cytology emerges from anatomy, which drove the resolution of the body from organs to tissues to cells—it belongs to the biology of parts. Cytological findings became central to the idea of heredity because it became possible to demonstrate the material continuity between parent(s) and offspring. First it was shown that the gametes were derived from other cells through division, second it was shown that in cell division the nucleus was not dissolved and reassembled but stayed intact, and third it was shown that the nucleus of the sperm entered the egg cell and the nuclei fused (Coleman 1965). Thus, material continuity between the female and the male parent organism (in case of sexual reproduction) and its offspring was demonstrated. Accordingly, similarity between parents and offspring had to be mediated by the nucleus and its components.

From the perspective of the tradition concerned with differences, different species, varieties or individuals must give rise to different germ cells. In Mendel we can already observe a shift of focus from different forms (i.e. kinds) of organisms to different forms of gametes. According to his minimal species concept, two organisms that differ in one character belong to different species. If they differ in one aspect of their germ cells, it is possible to think of that which makes the difference on the level of germ cells as being responsible for the difference in species, and thus for a difference in a single character. Mendel switched from speaking of the inheritance of species membership to the inheritance of individual characters. However, it is less clear whether he

implied that the difference in kinds of gametes was due to a difference in particulate constituents (see the analysis in Müller-Wille and Orel 2007: 193).

For cytology, it was not possible to detect differences in the germs cells or zygotes of different species. Embryologists, who were interested in how the parts of the zygote gave rise to the parts of the organism, were less concerned with differences among germ cells or zygotes and, instead, more focused on the organization of the nucleus, asking how it could give rise to the organization of the organism. Questions as to the nature of nuclear particles and the role of the cytoplasm were debated (Sapp 1987). But the resolution of the nucleus in cytology was again not sufficient to identify parts and their organization. Morgan and his co-workers found a new way to combine cytology, the study of parts of the cell, with genetics, the study of inherited difference (Sect. 4). But this did not mean that they split off genetics from embryology, the study of inheritance as growth of form. What it does mean, however, is that they employed the study of difference on the level of the organism to study parts on the level of the cell. They were interested in the architecture of the genetic material in the chromosomes. Differences in characters came to be seen as merely instrumental. After all, Morgan et al. made maps of genes, not of alleles. In a way the Morgan school indeed used genetics to address a cytological concern shared by embryologists: the organization of nuclear material. In this limited sense, genetics, if narrowly defined as the study of chromosomes, had one of its origins in embryology, or at least in cytology as seen from an embryological perspective, namely regarding the study of the organization of nuclear material (Gilbert 1978). But rather than splitting off genetics from embryology, in this way it built a bridge. Morgan and his colleagues employed the notion of inheritance of difference for the study of parts of cells, thereby creating an interfield theory (Darden and Maull 1977) and practice, we might add. It turned out, however, that the knowledge of the organization of nuclear material in these terms (chromosome maps) did not answer the question of how the organization of the organism arises. This expectation of embryology was disappointed, but many embryologists never shared it anyway. They highlighted the role of cytoplasm instead. That the study of cytoplasm was not pursued to the same extent as the study of chromosomes might have to do with mechanisms of competition for resources (Sapp 1987), but it seems not to be due to a separation of heredity from development.

On the side of genetics, other researchers, who remained focused on the organism (as opposed to chromosomes) due to investments in the study of characters important from agricultural, medical or eugenic perspectives, or who were interested in the consequences of the inheritance of difference for the theory of evolution, adhered to the explanation of patterns of differences through the distribution of genes, that is, differences in the constitution of germ cells. Genetics, even in its early days, was far from being one monolithic enterprise. In the next section, drawing on work by Kenneth Waters, I will

show that geneticists, whether they were interested in the pattern of the inheritance of a pathological trait in medicine, an useful trait in agriculture or a trait as an index for a gene's location on the chromosomes, relied on a notion of causation as difference-making. In contrast, developmental biologists were interested in causation in terms of production, as I will illustrate with an example that has been analysed by James Griesemer.[6] Before, however, I shall briefly introduce the two forms of causal reasoning as elaborated by philosophers of science.

Forms of Causal Reasoning: Developmental Biology and Genetics

Excursion into Philosophy: Pluralism Concerning Causation

Philosophers of science have long been concerned with phenomena of or statements about causation. They try to identify criteria by which it can be decided whether something (object, property, event) is a cause of something else, or analyse statements about causality with respect to their structure, their implications and their relation to other statements. A number of authors (e.g. Hall 2004; Godfrey-Smith 2010) suggest that there are two large families of theories of causality, which might be referred to as dependence theories (also called difference-making theories) and transference theories (also called production or process theories), respectively. In the framework of dependence theories, C is a cause of an effect E, if E depends on C. In other words, a difference in C entails a difference in E. The causal relata in dependence views are often construed as variables. The value of E is thus dependent on the value of C, such that if a change occurs in the value of C the value of E will change as well. What dependence amounts to is explicated differently in different accounts. Dependence has been characterized as counterfactual dependence (Lewis 1973), probabilistic dependence (Hitchcock 2012) or in terms of interventions (Woodward 2013). According to transference theories of causation, on the other hand, C causes E if C brings about E by some process that is embodied in a physical connection between the relata, which are, accordingly, described in terms of objects or events with all their relevant physical properties. The connection is described in terms of forces or more generally as some conserved quantity (Salmon 1984; Dowe 2008). The difference between the theories is usually made evident by examining the consequences of the respective views with respect to imagined causal situations, for instance, in cases of causation by prevention. If you take action to prevent someone from preventing an event that is leading to an accident, you are held responsible for causing the accident. You made the difference that made the accident happen. Had you not acted, the course of events would have ended differently. There is, however, no physical connection between you and the accident. Several

authors have discussed or suggested pluralism with respect to the two forms of causal reasoning (Hall 2004). Such a position understood in an epistemological way amounts to the claim that there are different, equally valid ways of rendering relations among objects (Godfrey-Smith 2010).

In the following, I will argue that one can find both types of explanation in the history of genetics and embryology. I will use the abstract philosophical reconstructions of patterns of causal reasoning in order to spell out the difference between instances of actual causal reasoning given in the sources. If this is possible, it shows that the philosophical theories of causation, even if very general, are adequate descriptions of science, and, additionally, it will corroborate pluralism with respect to patterns of causal reasoning. On the other hand, if the patterns of explanation map coherently on the two fields, genetics and embryology around 1900, or if they are at least differently emphasized and valued in the two fields, this offers the possibility to use philosophical analysis to explain the historical dynamics of the fields in terms of epistemic competition and integration by pointing to the forms of reasoning that are brought in competition or have to be integrated. Furthermore, these forms of causal reasoning are embedded in different observational practices that enable researchers to investigate and represent aspects of the form of organisms as relata in causal relations of the respective kind.

Transference Causation: Parts as Outcomes of Growth Processes

James Griesemer describes the epistemic practice of "Tracking Organic Processes" (Griesemer 2007) by looking at several case studies in embryology and genetics in the late nineteenth and early twentieth century. He characterizes the practice of tracking organic processes and the resulting view of transference causation as follows:

> Tracking work provides the basis for causal narrative accounts of prospective significance, which involves two shifts of attention: (1) from developmental outcome to some earlier stage of a central subject significant to the narrative from which to begin tracking, then (2) tracking the historical process forward in time, conceptually "back" to the future developmental outcome from which the narrative account began (Griesemer 2007: 399).

The developmental outcome, "the development of organized heterogeneity out of the apparent homogeneity of the fertilized egg," (Griesemer 2007: 397) is the ultimate explanandum of embryology. The local explanandum might be a certain stage of the embryo, which is explained by processes leading from an earlier stage to the stage in question, but ultimately these explanations aim at the form of the adult plant or animal (although the notion of adulthood is not very precise, or rather arbitrary, given continuous change of the life history of plants and animals). What is important is that the adult form is perceived as being composed of distinct structures. These structures came to be conceptualized as being composed of specialized, in the language of embryology,

differentiated cells. Cells in earlier stages of development came to be conceptualized as having a determined fate. Griesemer writes with respect to embryologists around 1900:

> These "cell lineage workers," already very familiar with the end results of development, shifted attention to early cleavage stages of blastulation. They sought to identify the fate or prospective significance of cells that did not yet manifest the differentiated states of the kind of tissue or organ to be explained, whether epidermis or mesoderm, neural plate or lens, notochord or somite (Griesemer 2007: 399).

The adult organism afforded anatomical decomposition, but the structures were not only defined as being different from other structures, with respect to position, shape, colour or reaction to some treatment, but they also differed with respect to what brought them about or was transformed into the structure in question, while the embryo in this context afforded to contrast structures in terms of what they, in turn, give rise to or what they transform into.

Embryologists had to "track a process of cell division leading from a determined state to a visible embryonic differentiation" (Griesemer 2007: 402). Developmental processes are transformations of structures in time. These processes were studied through visualizing differences in the fate of cell populations. This allowed the decomposition of the whole process of development into partial processes—the anatomy of a process one might say. Classical embryologists did so by "introducing and then following ‚marks' in order to establish the fate or prospective significance of marked parts of a dynamic process" (Griesemer 2007: 378). Griesemer imports this notion of marks directly from transference theories of causation, in which the physical quantity transferred in the actual interaction between components in a process is thought of as travelling through the process in the same way as a mark introduced upstream by some modification in one of the components.

Marking can consist in one of the following activities or a combination of them (Griesemer 2007: 399). The first activity is mental marking, which basically relies on the fact that some notable features in a process can be followed with the eye, for example under the microscope, by focusing one's attention on them as opposed to others and tracking their transformation by literally "keeping an eye on them." The trajectories of structures will typically be captured by physical marks in a diagrammatic representation, for example a *camera lucida* drawing. Secondly, marking procedures can make use of artificial substances that highlight some structures as opposed to others, as in the case of anatomical staining, but here they are observed over time. A third way to track processes consists in transplantation experiments, an approach

exemplified by the work of Spemann and Hilde Mangold (1898–1924) which led to the organizer concept.

In one case discussed by Griesemer, Conklin's *The Organization and Cell-Lineage of the Ascidian Egg* (1905), among other procedures performed, a strategy is followed that lies between the first and the third way of tracking processes. Conklin "relied specifically on pigment markings of cells, which behaved as though the observer had introduced a persistent physical mark directly on the embryo" (Griesemer 2007: 404). Conklin describes his discovery as follows:

> The very first lot of the living eggs of *Cynthia* which I examined showed a most remarkable phenomenon and one which modified the whole course and purpose of my work; for there on many of the unsegmented eggs, which were of a slate-gray color, was a brilliant orange-yellow spot, which in other eggs appeared in the form of a crescent or band. Further observation showed that this crescent became divided into two equal parts at the first cleavage and that it could be followed through the later cleavages and even into the tadpole stage (Conklin 1905: 7).

Conklin's approach shows how a contrast (gray/yellow) identifies a partial process. It makes a lineage stand out against the manifold process of development, made up of countless interdependent cell divisions. It allows the interpretation of parts, at least in the tadpole stage, such as the tail muscles, as originating from certain regions in the embryo, and structures in the embryo as having a "prospective significance for future states" (Griesemer 2007: 399). Griesemer writes: "Presence of yellow pigment in a cell at a later time meant membership in the cell lineage tracing back to the original mark" (Griesemer 2007: 404). Thus embryology developed strategies to study processes along the lines of transference views of causation. The form of the organism is seen as an outcome of a causal process involving cell division and migration, including the mechanical influence of cells on each other that has to be decomposed and followed over time.

While embryologists explained the form of organisms through mechanisms of growth, they were critical of geneticists' abilities to explain form. Sapp (1987: Ch. 1) gives a number of examples where embryologists evaluate the explanations in terms of genes as inadequate to the task of explaining what it is that bestows the zygote with the capability of bringing about a differentiated organism. Those embryologists sought the source of organization in the organization of the cytoplasm. A quote by Frank Rattray Lillie (1870–1947) might serve to illustrate the epistemic competition with respect to adequate explanations:

> Those who desire to make genetics the basis of physiology of development will have to explain how an unchanging complex can direct the course of an ordered developmental stream (Lillie 1927: 367).

Dependence Causation: Characters as Indexes for Studying the Constitution of Gametes

From a philosophical perspective, some authors criticise gene-centred explanatory accounts in twentieth century biology as inadequate. They maintain that the form of organisms can only be explained through a notion of heredity that involves development, that is, as the outcome of inherited growth processes (e.g. Amundsen 2005). While this might be a valid point for the philosophy of biology, it is not necessarily a guide to interpreting the history of biology. In this context, the split narrative often serves as a historical explanation of how the situation of the dominance of an inadequate explanation came about. In classical genetics, however, heredity is not taken as explaining the form of organisms. It can only explain the patterns of distribution of variation, that is, differences in form. One reason for the view that for Morgan and his followers heredity without development is taken to be explanatory with respect to form is that Morgan and his co-workers were in fact talking about the causation of characters. In a section titled "On the Relation Between Factors and Characters," Morgan et al. report that they found 25 genes affecting eye colour.

> Each such color may be the product of 25 factors (probably of many more) and each set of 25 or more differs from the normal in a different factor. It is this one different factor that we regard as the "unit factor" for this particular effect, but obviously it is only one of the 25 unit factors that are producing the effect. However since it is only this one factor and not all 25 which causes the difference between this particular eye color and the normal, we get simple Mendelian segregation in respect to this difference. In this sense we may say that a particular factor (p) is the cause of [the character] pink [eye colour], for we use cause here in the sense in which science always uses this expression, namely, to mean that a particular system differs from another system only in one special factor (Morgan et al. 1915: 209).

What this means is that causation is usually thought of as a relation between two states of a system as opposed to a relation among individual entities. A textbook on statistical methods of the time which is also quoted by Wilhelm Johannsen (1857–1927) illustrates the way that "science always uses the expression":

> We start with the assumption that everything that exists, and everything that happens, exists or happens as a necessary consequence of a previous state of things. If a state of things is repeated in every detail, it must lead to exactly the same consequences. Any difference between the results of causes that are in part the same must be explainable by some difference in the other part of the causes (Thiele 1903: 1).

Ken Waters describes this type of reasoning in genetics as a difference principle: "Differences in a gene cause uniform phenotypic differences in particular genetic and environmental contexts" (Waters 2007: 558). It is usually acknowledged that this is a very modest form of claiming causal explanation. Nevertheless, it is taken to indicate that the Morgan group was interested in

explaining characters. Amundsen, for instance, writes: "If a single allele can be regarded as the cause of pink eye color, then it is possible to causally explain characteristics without any reference to the embryological process that actually brought them about" (Amundsen 2005: 150). For Amundsen it seems obvious that if Morgan says that genes cause characters, then this causal relation must be explanatory and therefore the explanations of characters must be on the agenda of the Morgan group. This shows in another reading of Morgan et al. by Amundsen that seems to me to be not very charitable. Morgan and his co-authors write:

> The characters of the organism are far removed, in all likelihood, from these materials [factors = genes as chemical materials]. Between the two lies the whole world of embryonic development in which many and varied reactions take place before the end result, the character, emerges. […] Although Mendel's law does not explain the phenomena of development, and does not pretend to explain them, it stands as a scientific explanation of heredity, because it fulfils all the requirements of any causal explanation (Morgan et al. 1915: 226–227).

Such a statement indicates epistemic competition. Morgan et al. state here that despite the fact that both fields, Mendelism and developmental biology, are concerned with the same phenomenon, the coming about of characters, Mendelism is not concerned with development but that Mendel's laws are nevertheless sufficient to explain the heredity of characters. This, however, does not imply that they think that Mendelism explains characters in the *same sense* as developmental biology does. In fact, it does not even explain characters as the same kind of thing. Morgan et al. state that characters can be conceived of as "end results," meaning the result of the growth process studied by developmental biology. In Mendelism, instead, what is explained is characters as showing in a certain pattern of distribution. Although it is clearly stated by Morgan et al. that explaining characters as end results of growth is a matter of explaining development, and that Mendelian genetics does not explain development and thus does not explain characters as the outcome of growth, Amundsen maintains that a causal explanation of characters as products is attempted here: "The fact that correlations can be traced between the *end products* of ontogeny in successive generations (the traits of parents and offspring) is enough to declare that the causes of these end products have been found" (Amundsen 2005: 150, emphasis in the original). Instead, it is clear that the type of causal account offered by the Morgan group explains characters as differences in form, which implies that it explains the distribution of a character in an offspring population. It is not meant to explain the emergence of manifest form in itself, that is, of tissues or body parts. In which sense then is "Mendel's law" a causal explanation? In the formulation that it has been given by the Morgan group, it causally explains the constitution of the hereditary material of the offspring from the constitution of the hereditary material of the parents. It provides an "explanation of heredity" and what is inherited is

genetic material (chromosomes) not characters. Thus, we can go even further and say that for Morgan and his colleagues at least, not even the explanation of distributions of differences in characters was important (though this might have been the case for other Mendelians, especially if they worked with agriculturally important or pathological characters), but only the distribution of alleles which shows itself in the distribution of character differences. Genes and characters stand in a causal relation, though this causal relation is not explanatory but rather indexical.

In Morgan's later formulation of the *Theory of the Gene*, characters do not play an important role at all. What is said is that they "are referable" to genes, an expression Morgan uses several times and that can be read as "characters indicating genes." In any case, characters are not mentioned as explananda here:

> We are now in a position to formulate the theory of the gene. The theory states that the characters of the individual are referable to paired elements (genes) in the germinal material that are held together in a definite number of linkage groups; it states that the members of each pair of genes separate when the germ-cells mature in accordance with Mendel's first law, and in consequence each germ-cell comes to contain one set only; it states that the members belonging to different linkage groups assort independently in accordance with Mendel's second law; it states that an orderly interchange—crossing-over—also takes place, at times, between the elements in corresponding linkage groups; and it states that the frequency of crossing-over furnishes evidence of the linear order of the elements in each linkage group and of the relative position of the elements with respect to each other (Morgan 1926: 25).

Many authors would nevertheless agree with Amundsen that characters are somehow the explananda of Morgan's theory of the gene, even if some are more careful in stating that only patterns in the distribution of traits are explained (Amundsen offers this as a less problematic reading of Morgan, Amundsen 2005: 150–151), or that only differences between traits are explained (Waters 1994). I will sketch an alternative role for the difference principle, namely as an observational theory. Characters are then understood not as being explained through but rather as indexes for identifying genes.

One point that shows the role assigned to characters cannot be that of the explandum is that it does not matter which effect of an allele is chosen. This becomes obvious in the following quotation from *The Physical Basis of Heredity*:

> Clearly then the character that we choose to follow in any case is only the most conspicuous or (for purposes of identification) the most striking or convenient modification that is produced. Since, however, these effects always go together, and can be explained by the assumption of a single unit difference in the germ-plasm, the particular difference in the germ-plasm is more significant than the character chosen as its index (Morgan 1919: 240).

Even if Morgan uses the verb "to explain" here, this passage also clearly states that the interest is in the constitution of the hereditary material and that the role of characters is that of an "index." This term gives a hint to the appropriate understanding of the difference principle as an observational theory (on observational theories see Kosso 1988). A character is explained only in the sense that an instrument's readout is explained. An index represents because of its causal relation to the object it represents. But pragmatically, an index is used to measure the object; its explanation is not necessarily a purpose of stating the causal relationship but rather the justification of its use for measurement. The point is that Morgan and his group do appeal to difference-making causation in order to explain characters, but rather to justify their use in the identification of the difference-making causes, in this case the genes. But these in turn are not of interest *qua* causes. They are rather studies in relation to each other. Thus genetics, a branch of the biology of difference, is turned into a tool for cytology, a branch of the biology of parts. But studying parts of germ cells is not to explain the growth of body parts.

Waters has pointed out the role of difference-making causation in genetics, although he would probably endow this reasoning with more explanatory power and aspiration than I do. He writes: "inheritance of phenotypic characteristics can be explained by charting the transmission of genes and relating genotypes to phenotypes" (Waters 1994: 169). In any case, following him, I concentrated on Morgan's reasoning after 1910. In the following, I will argue that this kind of reasoning is in part already in place in Mendelism before Morgan turns to this field and is thus not the result of the alleged separation of heredity from development. This might best be illustrated with reference to Wilhelm Johannsen, whom, together with Bateson, we might count as co-rediscoverer of Mendel, adding to the acceptability of Mendelism after the initial rediscovery (Müller-Wille and Richmond forthcoming).

Johannsen already in 1911 provides a formulation that comes close to the difference principle (Meunier 2016):

> [I]t may be quite impossible to indicate whether a particular reaction (character) is due to something positive or to the lack of a factor in the genotypic constitution. All that can as yet be determined in this regard by Mendelian analysis is the *number of differing points* between the two gametes forming a heterozygote. Such differences may be termed "*geno-differences*" (geno differences; emphasis in the original). The well-known facts, that a "character" maybe dominant in some hybrids but recessive in others, and that segregation in different cases maybe very different, indicate that "characters" are complicated reactions (Johannsen 1911: 148–149).

While the elements that compose the zygote can be independently recombined, characters when understood as parts, as outcomes of processes, are (genetically and developmentally speaking) not such independent bits but outcomes of the reaction (i.e. the process) as a whole. Differences in the outcome, that is, characters as differential properties of parts, however, allow

zygotic constituents to be tracked. That genetics studies the constitution of gametes and is not concerned with the explanation of characters (or, if, then only in terms of their distribution, not their production) becomes clear from Johannsen's analogy of hybridization with chemical analysis:

> The Mendelian analysis of an organism through hybridization is in its restricted relativity of a rather primitive nature; the analytical reagents are other complex organisms, not simple pure bodies like in chemical analyses (Johannsen 1909: 439, translation R. M.).

Johannsen described organisms as the "analytical reagents" that are used to investigate the elements of the hereditary material. The genotype was the subject of research and it was investigated through phenotypes, which implied a construction of the phenotype as an idealized differential value of a variable, a measurement datum that informed the researcher about the genotype. This view was essentially already there in Johannsen's reasoning in 1909:

> The genes are not to be seen as "bearers" of hereditary properties. These properties should only be regarded as symptoms or reactions, which however are real and measurable—and they must be measured if one wants to proceed in exact research (Johannsen 1909: 482, translation R. M.).

The exact study of heredity is the study of the constitution of the gametes. However, as opposed to Morgan's later work, Johannsen remained in the biology of kinds. He was more interested in identifying different types of gametes, giving rise to different types of organisms, than in the study of the structure of constituents of the gametes (Falk 2008).

We can see now that causal reasoning in genetics and developmental biology was already structured and used quite differently before 1910. This adds to the understanding that they constitute quite different approaches to the phenomena of reproduction. Nevertheless, the communities perceived themselves as working on the same phenomena, broadly conceived, and thus felt that, concerning these phenomena, they were competing with respect to the production of valid and relevant knowledge.

Ending Epistemic Competition

I have presented the relation between genetics and developmental biology around 1900 as a case study for situations of epistemic competition. This relation is not characterized by open confrontation, as in cases of scientific controversy, but rather by mutual ignorance, occasional remarks on the inappropriateness of the approach of the respective other field notwithstanding. This is due to the fact that researchers in both fields on the one hand acknowledged that they were working on the same phenomena broadly

conceived—the form of offspring in biological reproduction. On the other hand, they had very different notions of form. Embryology belonged to the tradition of a biology of organization, which was concerned with parts of organism and how they are composed in the whole. Genetics instead, belonging to the biology of kinds, was concerned with differences on the level of the organism. Accordingly, the two fields strived to produce accounts that were accepted by a larger community or the public as authoritative with respect to the phenomena of reproduction. The point of this article was to analyse the differences between the fields, which were the basis for the competitive situation with respect to knowledge about reproduction. The different conceptions of form and heredity were embedded in different forms of experimental practice (hybridization versus tracking processes) and involved different forms of causal reasoning (dependence versus transference causation). If it is true that genetics was more successful in acquiring a circle of general experts, from doctors to anthropologists, as well as an exoteric circle of educated amateurs, who became literate in the discourse of genetics, not exclusively, but mainly in the context of eugenics, we can ask what made genetics so acceptable for outsiders. A possibility is that dependence causation, the correlation of certain differences with other differences is easier to find and apply for most pragmatic concerns requiring prediction and intervention, rather than a complete picture of all causal interactions spelled out in transference causation.

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Endnotes

1 I will sometimes use "developmental biology" although neither this term nor *Entwicklungsbiologie* is common before the 1940s. It is meant to cover the work of researchers who use different labels to describe their work, such as "causal morphology," "developmental mechanics," "developmental physiology" and "embryology," or their German equivalents (see also Burian and Thieffry 2001).

2 For the situation in France, see Burian, Gayon and Zallen (1988).

3 See Gilbert 1978, 1998; Sapp 1987; Allen 1985; Fantini 1985; Maienschein 1987a; Harwood 1993; Burian 2000; Amundsen 2005; and Griesemer 2007.

4 For differences in national contexts and their relation to styles of research, see Harwood (1993); Maienschein (1991); Fangerau and Müller (2005).

5 As mentioned, another example for such an attempt would be the work of Alfred Kühn (1885–1968) (Rheinberger 2000; see also Harwood 1993 on both, Goldschmidt and Kühn).
6 These authors have not taken the comparative perspective adopted in this article. Griesemer discusses practices of genetics and developmental biology in the relevant text (2007), but he is more interested in finding similarities than differences.

References

Allen, Garland 1974. Opposition to the Mendelian-Chromosome Theory: The Physiological and Developmental Genetics of Richard Goldschmidt. *Journal of the History of Biology* (7): 49–92.

Allen, Garland 1975a. *Life Science in the Twentieth Century*. New York: Wiley.

Allen, Garland 1975b. The Introduction of Drosophila into the Study of Heredity and Evolution: 1900–1910. *Isis* (66): 322–33.

Allen, Garland 1985. Heredity under an Embryological Paradigm: The Case of Genetics and Embryology. *Biological Bulletin* (168): 107–121.

Amundson, Ron 2005. *The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo*. Cambridge: Cambridge University Press.

Bateson, William 1907. The Progress of Genetic Research. In: William Wilks (ed.). *Report of the 3rd International Conference 1906 on Genetics, Hybridisation (the Cross-Breeding of Genera and Species), the Cross-Breeding of Varieties, and General Plant-Breeding*. London: Royal Horticultural Society: 90–97.

Benzer, Seymour 1991. Interview by Heidi Aspaturian. Pasadena, California, September 11–February 1991. *Oral History Project, California Institute of Technology Archives*. URL: http://resolver.caltech.edu/CaltechOH:OH_Benzer_S (last accessed 24.11.2015).

Bulmer, Michael 2003. *Francis Galton: Pioneer of Heredity and Biometry*. Baltimore, ML: John Hopkins University Press.

Burian, Richard M. 2000. On the Internal Dynamics of Mendelian Genetics. *Comptes Rendus de l'Académie Des Sciences. Série III, Sciences de La Vie* (323): 1127–1137.

Burian, Richard M. 2005. *The Epistemology of Development, Evolution, and Genetics*. Cambridge: Cambridge University Press.

Burian, Richard M., Jean Gayon and Doris Zallen 1988. The Singular Fate of Genetics in the History of French Biology, 1900–1940. *Journal of the History of Biology* (21): 357–402.

Burian, Richard M. and Denis Thieffry 2000. Introduction to the Special Issue "From Embryology to Developmental Biology." *History and Philosophy of the Life Sciences* (22): 313–323.

Churchill, Frederick B. 1974. William Johannsen and the Genotype Concept. *Journal of the History of Biology* (7): 5–30.

Coleman, William 1965. Cell, Nucleus, and Inheritance: An Historical Study. *Proceedings of the American Philosophical Society* (109): 124–158.

Coleman, William 1971. *Biology in the Nineteenth Century: Problems of Form, Function and Transformation*. Cambridge: Cambridge University Press.

Conklin, Edwin Grant 1905. *The Organization and Cell-Lineage of the Ascidian Egg*. Philadelphia: Academy of Natural Sciences.

Darden, Lindley and Nancy Maull 1977. Interfield Theories. *Philosophy of Science* (44): 43–64.

Dowe, Phil 2008. Causal Processes. In: Edward N. Zalta (ed.). *The Stanford Encyclopedia of Philosophy*. Fall 2008. URL: http://plato.stanford.edu/archives/fall2008/entries/causation-process/) (last accessed 24.11.2015).

Falk, Raphael 2008. Wilhelm Johannsen: A Rebel or a Diehard. In: Oren Harman and Michael R. Dietrich (eds.). *Rebels, Mavericks, and Heretics in Biology*. New Haven, CT: Yale University Press: 63–83.

Fangerau, Heiner and Irmgard Müller 2005. National Styles? Jacques Loeb's Analysis of German and American Science around 1900 in his Correspondence with Ernst Mach. *Centaurus* (47): 207–225.

Fantini, Bernardino 1985. The Sea Urchin and the Fruit Fly: Cell Biology and Heredity, 1900–1910. *Biological Bulletin* (168): 99–106.
Fleck, Ludwik 1979. *Genesis and Development of a Scientific Fact*. Chicago: University of Chicago Press.
Foucault, Michel 1970. *The Order of Things: An Archaeology of the Human. Sciences*. London: Tavistock Publications Ltd.
Gilbert, Scott F. 1998. Bearing Crosses: A Historiography of Genetics and Embryology. *American Journal of Medical Genetics* (76): 168–182.
Gilbert, Scott F. 1978. The Embryological Origins of the Gene Theory. *Journal of the History of Biology* (11): 307–351.
Godfrey-Smith, Peter 2010. Causal Pluralism. In: Helen Beebee, Christopher Hitchcock and Peter Menzies. *The Oxford Handbook of Causation*. Oxford: Oxford University Press: 326–337.
Griesemer, James 2007. Tracking Organic Processes. Representations and Research Styles in Classical Embryology and Genetics. In: Manfred D. Laubichler and Jane Maienschein (eds.) *From Embryology to Evo-Devo: A History of Developmental Evolution*. Cambridge, MA: MIT Press: 375–433.
Hall, Ned 2004. Two Concepts of Causation. In: John David Collins, Ned Hall and L. A. Paul (eds.). *Causation and Counterfactuals*. Cambridge, MA: Mit Press: 225–276.
Harwood, Jonathan 1993. *Styles of Scientific Thought: The German Genetics Community, 1900–1933*. Chicago, IL: University of Chicago Press.
Hitchcock, Christopher 2012. Probabilistic Causation. In: Edward N. Zalta (ed.). *The Stanford Encyclopedia of Philosophy*. Winter 2012. URL: http://plato.stanford.edu/archives/win2012/entries/causation-probabilistic/ (last accessed 24.11.2015).
Johannsen, Wilhelm 1909. *Elemente der exakten Erblichkeitslehre*. Jena: G. Fischer.
Johannsen, Wilhelm 1911. The Genotype Conception of Heredity. *The American Naturalist* (45): 129–159.
Kohler, Robert E. 1994. *Lords of the Fly: Drosophila Genetics and the Experimental Life*. Chicago: University of Chicago Press.
Kosso, Peter 1988. Dimensions of Observability. *British Journal for the Philosophy of Science* (39): 449–467.
Kuhn, Thomas S. 1976. Mathematical vs. Experimental Traditions in the Development of Physical Science. *The Journal of Interdisciplinary History* (7): 1–31.
Lewis, David 1973. Causation. *Journal of Philosophy* (70): 556–567.
Lillie, Frank Rattray 1927. The Gene and the Ontogenetic Process. *Science* (64): 361–368.
Maienschein, Jane 1987a. Heredity/Development in the United States, Circa 1900. *History and Philosophy of the Life Sciences* (9): 79–93.
Maienschein, Jane 1987b. Arguments for Experimentation in Biology. *PSA: Proceedings of the Biennial Meeting of the Philosophy of Science Association* 1986: 180–195.
Maienschein, Jane 1991. Epistemic Styles in German and American Embryology. *Science in Context* (4): 407–427.
Meunier, Robert 2016. The Many Lives of Experiments: Wilhelm Johannsen, Selection, Hybridization, and the Complex Relations of Genes and Characters. *History and Philosophy of the Life Sciences* (38): 42–64.
Morgan, Thomas Hunt 1917. The Theory of the Gene. *The American Naturalist* (51): 513–544.
Morgan, Thomas Hunt 1919. *The Physical Basis Of Heredity*. London: J.B. Lippincott Co.
Morgan, Thomas Hunt 1926. *The Theory of the Gene*. New Haven: Yale University Press.
Morgan, Thomas Hunt, Alfred Henry Sturtevant, Hermann Joseph Muller and Calvin Blackman Bridges 1915. *The Mechanism of Mendelian Heredity*. New York: Henry Holt Co.
Müller-Wille, Staffan and Martha L. Richmond forthcoming. Revisiting the Origin of Genetics. In: Christina Brandt and Staffan Müller-Wille (eds.). *Heredity Explored: Between Public Domain and Experimental Science, 1850–1930.* Cambridge, MA: MIT Press.
Müller-Wille, Staffan and Vítêzslav Orel 2007. From Linnaean Species to Mendelian Factors: Elements of Hybridism, 1751–1870. *Annals of Science* (64): 171–215.
Müller-Wille, Staffan and Hans-Jörg Rheinberger (eds.) 2007. *Heredity Produced: At the Crossroads of Biology, Politics, and Culture, 1500–1870*. Cambridge, MA: MIT Press.
Müller-Wille, Staffan and Hans-Jörg Rheinberger 2012. *A Cultural History of Heredity*. Chicago: University of Chicago Press.

Nickelsen, Kärin 2014. Kooperation und Konkurrenz in den Naturwissenschaften. In: Ralph Jessen (ed.). *Konkurrenz in der Geschichte: Praktiken – Werte – Institutionalisierungen*. Frankfurt am Main: Campus Verlag: 333–379.

Peterson, Erik L. 2008. William Bateson from Balanoglossus to Materials for the Study of Variation: The Transatlantic Roots of Discontinuity and the (Un)naturalness of Selection. *Journal of the History of Biology* (41): 267–305.

Pickstone, John V. 2001. *Ways of Knowing: A New History of Science, Technology, and Medicine*. Chicago: University of Chicago Press.

Powell, Alexander, Maureen A. O'Malley, Staffan Müller-Wille, Jane Calvert and John Dupré 2007. Disciplinary Baptisms: A Comparison of the Naming Stories of Genetics, Molecular Biology, Genomics, and Systems Biology. *History and Philosophy of the Life Sciences* (29): 5–32.

Rheinberger, Hans-Jörg 2000. Ephestia: The Experimental Design of Alfred Kühn's Physiological Developmental Genetics. *Journal of the History of Biology* (33): 535–576.

Rheinberger, Hans-Jörg 2010. Biologie in Berlin um 1900. In: Heinz-Elmar Tenorth (ed.). *Geschichte der Universität Unter den Linden 1810-2010. Band 5: Transformation der Wissensordnung*. Akademie Verlag: 735–775.

Salmon, Wesley C. 1984. *Scientific Explanation and the Causal Structure of the World*. Princeton, NJ: Princeton University Press.

Sapp, Jan 1987. *Beyond the Gene: Cytoplasmic Inheritance and the Struggle for Authority in Genetics*. New York: Oxford University Press.

Sismondo, Sergio 2010. *An Introduction to Science and Technology Studies*. 2te Aufl. West Sussex, UK: Wiley-Blackwell.

Thiele, T. N. 1903. *Theory of Observations*. London: Charles and Edwin Layton.

Waters, C. Kenneth 1994. Genes Made Molecular. *Philosophy of Science* (61): 163–185.

Waters, C. Kenneth 2007. Causes That Make a Difference. *Journal of Philosophy* (104): 551–579.

Weingart, Peter, Jürgen Kroll and Kurt Bayertz 1988. *Rasse, Blut und Gene: Geschichte der Eugenik und Rassenhygiene in Deutschland*. Frankfurt am Main: Suhrkamp.

Woodward, James 2013. Causation and Manipulability. In: Edward N. Zalta (ed.). *The Stanford Encyclopedia of Philosophy*. Winter 2013. URL: http://plato.stanford.edu/archives/win2013/entries/causation-mani/ (last accessed 24.11.2015).

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