

# Ecology and systematics: An archaeology of life science

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# Introduction

Perhaps no two questions bother the history and philosophy of biology as much as the following two: What happened in biology around the 1880s, after Darwin yet before genetics; and why is evolution such a crucial and central topic of discussion for the contemporary life sciences? Ever since Darwin, Weismann and Roux evolution has been debated intensely in all corners of life science and the philosophy of biology. No biologist has been discussed throughout academia and society as much as Charles Darwin, the author of the ‘theory of evolution’. For decades now, life scientists have been speaking of an ‘evolutionary synthesis’, which has been or should soon be accomplished. But why? Why has evolution been problematised so much?

Regarding the other question, about biology in the 1880s, historians write that a profound change in the study of life took place in this time. William Coleman already wrote in 1972 that “the final quarter of the nineteenth century marks a turning point in the affairs of biology” (160). More recently, Lynn Nyhart (1995: 205) pointed out that “[b]y the 1880s a new alignment was emerging.” In this same period, major contemporary sciences find their supposed origin. Ludwig Trepl (1987: 134-5) as well as Nyhart (2009a: 22-4) situate the emergence of ecology in *fin-de-siècle* Europe; the scientist Élie Metchnikoff, publishing his main works in this period, is widely seen as the founder of immunology; Auguste Forel is considered to be one of the founders of ethology; Santiago Ramón y Cajal established neurology with his neuron theory, to which Forel also contributed; and finally, Karl Möbius and Eugene Warming are widely seen as important initiators of ecology. All were scientifically active in the 1880s and 1890s. So, what happened in this time that was so consequential for the further course of the study of life?

The answer to each question lies in their combination: Evolution has been problematised so much because of what occurred in the 1880s, and the period around the 1880s has been and still is so important for life science because of the problematisation of evolution. But it has been very unclear and difficult to understand what really happened in the *fin-de-siècle* period. Was there a major increase of experimentalism in biology (Allen 1975)? Did biology shift from historical explanation to causal explanation and from inquiry into form to that into function (Coleman 1972: 63, 162)? Or do we rather see the emergence of systematics and ecology (Nyhart 2009a: 24)?

The historian of biology Peter Bowler is known for having researched the *fin-de-siècle* period, between Darwin and genetics. He introduced the notion of the ‘non-Darwinian revolution’, arguing that in the wake of Darwin evolution was simply absorbed by the old, nineteenth-century, teleological conception of the history and development of living beings. I, too, will argue that Darwin was not the key unlocking the world of contemporary life science but rather worked fully with and within (nineteenth-century) biology, as much as Cuvier did. But whereas Bowler then proceeds to portraying Mendelism, or more precisely the early genetics emerging in 1900, as the harbinger of a new age of studying life, I believe my research disproves this ‘Mendelian revolution’ (thus understood). The truth is in between: The real revolution, or epistemic shift, took place in between Darwin and genetics with the work of scientists such as Wilhelm Roux, Gottlieb Haberlandt, Fritz Müller, and Karl Möbius – to name a few that feature in this thesis.

Nyhart, I believe, has found the right angle from which to approach this complex period of the study of life. She has researched nineteenth-century German animal morphology and found that by the 1880s “morphology was associated on the one hand with the speculative elaboration of phylogenetic relationships and on the other hand with the study of microscopic sections of

developmental stages” while “[t]he study of the organism in its environment and the process by which adaptation changed an organism’s form, by contrast, was a separate topic called ‘biology’ or sometimes ‘ecology’” (Nyhart 1995: 205). My thesis enlarges and deepens Nyhart’s understanding of the *fin-de-siècle* shift which established ecology and systematics. The argument that I will develop, step-by-step, in five chapters is as follows:

Around 1880 *life science* began. The study of the forms and spaces of life units became intricately connected to the study of life functions. This new conceptual nexus created ‘systems’, functional forms, and ‘self-organisation’ as new research objects of such new sciences as “developmental physiology” (Driesch) or “*Entwicklungsmechanik*” (Roux), “ecological plant geography” (Warming), and “physiological plant anatomy” (Haberlandt). This one side of the contemporary study of life I will call *ecology*, expanding the conventional use of that term beyond one particular life science. At the same time, the comparative study of life forms became intricately connected to the study of their ancestry. This other new conceptual nexus created such new research objects as ‘phylogenetic relatedness’, ‘clades’, and ‘convergent evolution’: the elements of contemporary *systematics*. Systematics and ecology emerged in opposition to each other, in spite of early attempts at uniting them in a single life-scientific approach.

*Life science* is ecology on the one hand, and systematics on the other. The conceptual gap or tension in between the two should be understood as precisely that which makes life science viable and productive. Life science today usually refers to molecular biology and biotechnology but there is also a wider sense of its meaning, encompassing all study of organisms and life processes. In this archaeology, life science is understood as a particular, historically contingent configuration of the study of life. As we will see, it started in the 1880s and has persisted at least until today. Relying on Foucault’s archaeology of the modern (19<sup>th</sup>-century) and of the Classical (18<sup>th</sup>-century) study of life, we can say that life science replaced *biology* in the last great reconfiguration of the study of life. Biology, in turn, had replaced natural history around 1800.<sup>1</sup>

Returning to the question of the vast discourse on evolution and Darwin, the reason why evolution has been problematised so much is because it divides ecology and systematics. In biology, evolution was not a central and always recurring theme because biology was a different epistemic structure. The aporia separating ecology and systematics will be debated and reflected upon as long as there is life science. The set of questions in the discourse about evolution that keep recurring – the real problematisation that is at stake – is part and parcel of life science itself. Making an attempt at showing, as this archaeology does, how these aporia came into being when biology was deconstructed and life science put together perhaps allows one to rethink and transform the ongoing problematisation of evolution.

The statement that life science started in the 1880s, and that it consists of ecology and systematics may appear strange to those who do not share the assumptions that underlie this project. An *archaeology* of life science aims to discern and represent the originality of life science, just as one may search for the originality of linguistics or alchemy. This originality is geographical as well as historical: it is found in a certain place and time and not in another. My research into life science has focused on its historical contingency, by distinguishing perspectives and ideas that are prior to life science from those that operate with life science, even though the geographical contingency is no

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<sup>1</sup> Natural history started around 1650, after the Renaissance. See Foucault (1966: 71, 137-176/1994: 57, 125-165) for natural history. For biology, see Foucault (1966: 238-245, 275-292/1994: 226-232, 263-279), Lenoir (1982), and Gambarotto (2018).

doubt an equally important concern. I found life science mostly in the 1880s, and mostly in the German scientific community devoted to the study of life. This does not mean that it may exclusively be found there – but I do argue that there is, in all likelihood, no life science prior to the epistemic shift of around 1880.

What does this originality of life science consist in? It is not a certain worldview, a certain perspective on life nor a theory, philosophy, or paradigm of life. It is not a science of a new object nor a new science of the same object. An archaeology does not separate beforehand the research objects from the methods and knowledge. The originality of life science refers to life science as such, with all its objects, methods, mindsets, and theories. Such a vast scope for a such a small term is only possible by way of abstraction. The philosophical effort of archaeology consists in this careful work of abstracting from the endless particularities of singular scientists, viewpoints, and objects in space and time in order to represent precisely the originality of what is being researched.

The result of this archaeology is an epistemic structure called life science, and this structure is not only historical but also relational. Life science is conceived as nothing but the division and coexistence of ecology and systematics. In this thesis, writings and diagrams by scientists are made to express and construct step-by-step the intricacies of the epistemic structure that is life science. At any moment this is a balancing act between the particular and the general aspect of the material, for whereas the particularities are equally life science, they can barely be used to understand it. Naturally, prior to the writing, I selected the material and divided between the relevant and the redundant. I have generally zoomed in onto the period from 1860 to 1900 and onto the scientists that are (widely) discussed by historians of biology.

The divided structure of life science, as ecology and systematics, is elucidated positively and negatively, that is, by texts which show ecology or systematics or the dividing of the two, and by texts which rather show a radically different epistemic structure, namely biology. For the epistemic shift that I consider – the shift through which life science emerged – is rife with notions and perspectives of the old, mostly nineteenth-century study of life: biology. Since my research focuses on life science, I rely on the work of others when it comes to biology; in particular, I rely on Foucault's archaeology of biology (a part of his *The Order of Things* (1966)) and, complementing this, Lenoir's *The Strategy of Life* (1982).

Foucault implied in *The Order of Things* that the modern 'episteme' endured until the moment he was writing this book, meaning that modern thought and knowledge, which had started with Kant, Cuvier, and others, and thus included biology, still held sway in the 1960s. In a lecture three years later he repeated this view, arguing that even such a revolutionary figure as Charles Darwin worked fully within the modern episteme's study of life (Foucault 1970/2017). Nonetheless, Foucault also left some ambiguity about the date of the modern episteme's ending: He believed to see, in the 1960s, an episteme-shifting 'return of language'; he considered Nietzsche's work to be a 'threshold' of modern, Western philosophy, beyond which there might be a 'future thought'; and he implied that the nineteenth-century 'obsession' with history had been replaced by an obsession with space.<sup>2</sup> But did this episteme shift take place in Foucault's time, the 1960s, or in Nietzsche's time, the *fin de siècle*? At least with regard to life science, my research shows that it already took place in *fin-de-siècle* Germany.

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<sup>2</sup> For the 'return of language', see Foucault (1966: 394-7/1994: 382-6). For Nietzsche as the threshold of a 'future thought', see Foucault (1966: 353/1994: 342). For the nineteenth-century 'obsession' with history, see Foucault (1966: 231-2/1994: 219-220), and in relation to the contemporary 'obsession' with space, see Foucault (1967/1984 (French) or 1967/1986 (English)).

Foucault and archaeology relate to a secondary, though important, aim of this thesis. I want to show that archaeology, ever since Foucault's iconic early work, is still a scientific approach that is able to provide valuable insights and contribute productively to the history and philosophy of science. Whereas Foucault focused too much on the philosophical aspect of archaeological inquiry, I hope to have found the right balance in this research project by incorporating a lot of careful historical-philological research. Of course, archaeology has also moved on after Foucault, as it became media archaeology in the work of Friedrich Kittler and historical ontology in that of Ian Hacking. Their studies, such as Kittler's *Discourse Networks 1800/1900* (1985) and Hacking's *The Taming of Chance* (1975) – especially the second half of either book –, complement this archaeology of '1900 life science'.

# Chapter 1 – Two aporia

## Introduction

Concerning the study of life at the end of the nineteenth century, historians (and scientists) have traditionally pointed at Darwin (1860>) and genetics (1900>) as the major changes. From this perspective, molecular biology was then added to these two in the 1950s and 1960s. A lot of work by historians (and scientists) has subsequently been focused on discussing the continuities and/or discontinuities between Darwin, genetics, and molecular biology. An example are the debates about ‘the evolutionary synthesis’ (Mayr & Provine 1980). Much of this historical research – *and* much life-scientific work in the early twentieth century – focused on questions relating to heredity: evolution, transmission, genes, embryology, Mendel, Darwin, etc.

Why was heredity so much problematised around 1900 and subsequently, by scientists and historians alike? Surely life science is about more than just the questions of heredity, evolution, and development? This chapter shows that the intensification of discussion and theory about heredity had everything to do with the major epistemic reconfiguration that took place around the 1880s, and that substituted biology (19<sup>th</sup> century) for life science. Whereas heredity *and* development were one and the same thing in biology, life science is precisely divided with respect to this relation: Ecology deals with development (processes) while systematics considers heredity (ancestrality). Thus, what previously was a solid principle in science now constitutes a lacuna. Heredity *and* development form a gap where theory rather than knowledge flourishes, and where attempts at synthesizing life science perpetuate. The subject of evolution is a vast field of problematization in life science. It is here that ecology and systematics go separate ways while also seeking to bridge this gap that allows for their difference.

But there is another fundamental debate within life science. The tension between ecology and systematics does not only revolve around evolution (i.e. process vs ancestrality) but also around forms. Classifying life forms is done in two distinct ways, according to a physiological/ ecological hierarchy, or according to a genealogical/ phylogenetic hierarchy (Eldredge 1985: chap. 6; Salthe 1985: chap. 7). The dichotomy is as follows: Is a life form a part of a whole, and itself a whole composed of parts, as it is in ecology and physiology, or is it rather a relation of ancestral material between other life forms (notably, between ancestors and offspring), as it seems to be for systematics? This fundamental dichotomy in life science I describe with the terms ‘meronomy’ (part/whole) and ‘transitivity’ (passage).

The tension between meronomy and transitivity complements that between process and ancestrality. There is thus a vast field of conceptual – and no doubt political – tension within life science, as scientists disagree along the lines of these incompatibilities and develop theories to come to grips with these two aporia. The well-known discipline of evo-devo (evolutionary developmental biology), for example, seeks to bridge the gap between process (development) and ancestrality. In doing so, it draws inspiration from biology (notably, Darwin) because in biology no such gap existed, as process and ancestrality formed a continuity in the science of physiology.

Before exploring the two aporia of life science, what follows, first of all, is the archaeological diagram of life science (figure 1). It posits ecology (the study of the nexus process-part/whole)



opposite systematics (the study of the nexus transitivity-ancestrality) and the aporia, or dichotomy between process and ancestrality opposite that between transitivity and meronymy (part/whole). It is modelled after the two diagrams of the Classical respectively modern epistemes in Foucault's *The Order of Things* (1966: 225/1994: 201).<sup>3</sup> Figure 4 presents an adapted version of Foucault's diagram of biology (as part of the modern episteme) alongside my diagram of life science.

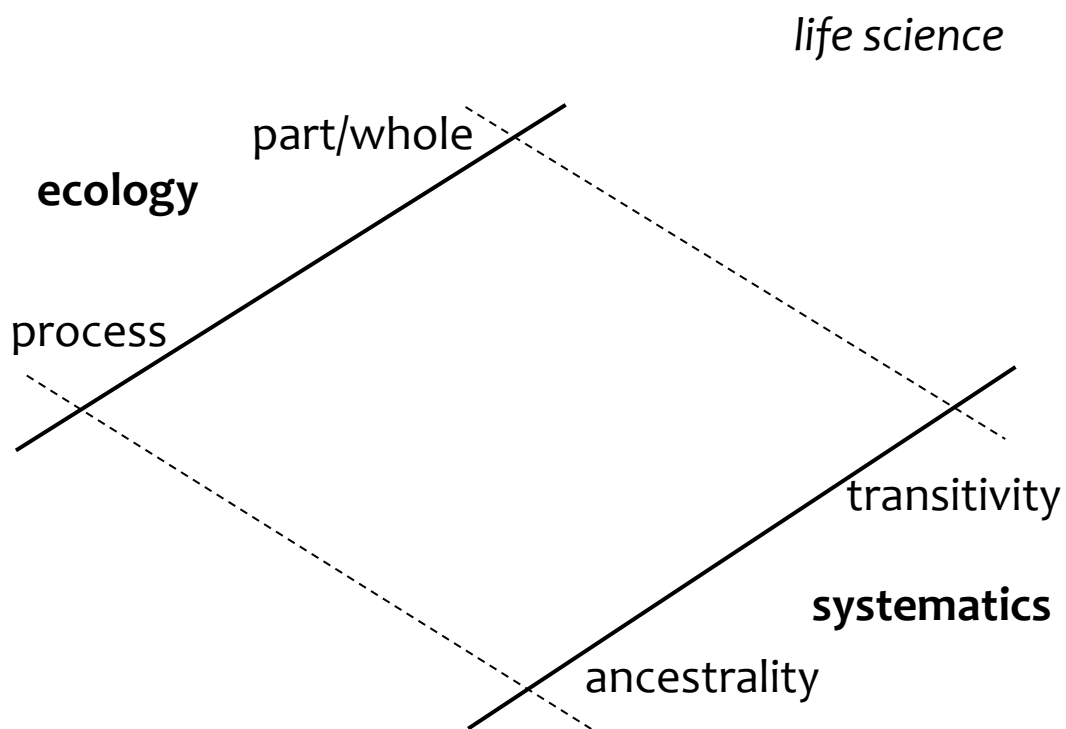


Figure 1. Archaeological diagram of life science

<sup>3</sup> I take from Foucault the general structure of the diagram, the division between a knowledge field (the realm of the solid lines) and a thought field (the realm of the dashed lines), and the places of four points. These four points or categories are not filled in arbitrarily; rather, they relate to the different terms in the archaeological diagram of *biology* (see figure 4). These latter terms are different because they are each part of an axis that does not exist as such in life science.

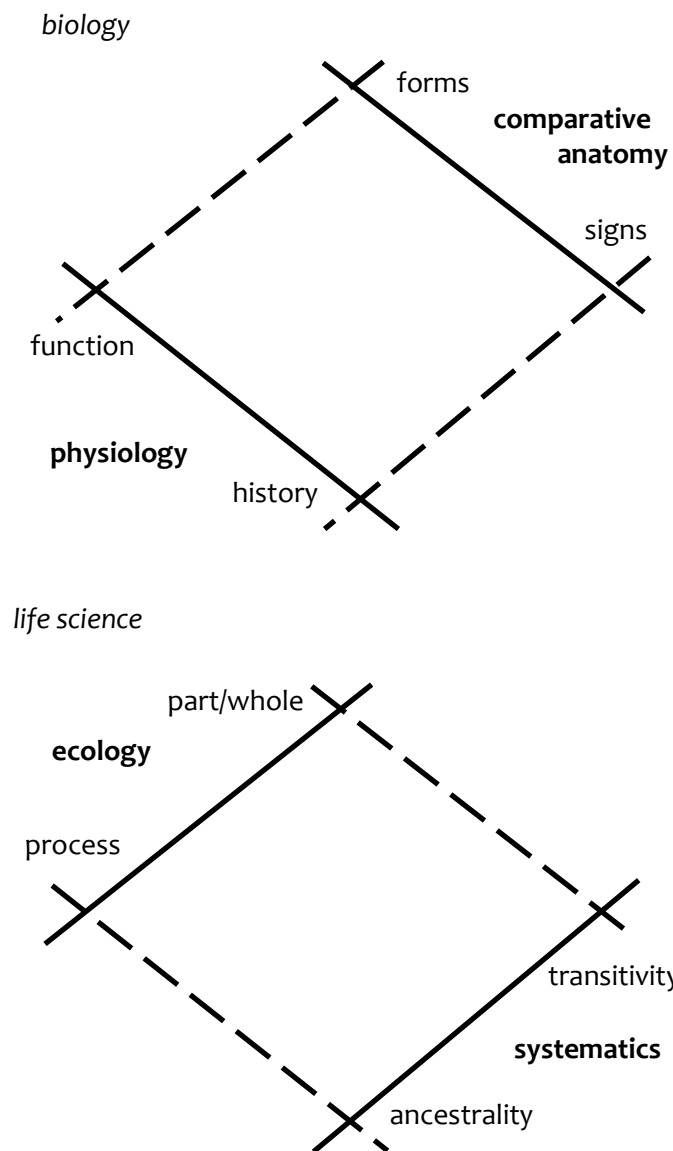


Figure 2. Above, an adapted version of Foucault's archaeological diagram of biology (from Foucault 1966: 225/1994: 201). Below, my archaeological diagram of life science.

## Section 1.1 – Heredity and development

Several historians have pointed out that nineteenth-century biology approached the subject of heredity in a way that is alien to contemporary life science, and alien specifically to new perspectives emerging at the end of the nineteenth century (Churchill 1987: 362; Coleman 1965: 125; Bowler 1989: 68). From Blumenbach's notion of *Lebenskraft* (life-force) to Darwin's use of the term 'prepotency', heredity used to be understood as development itself, as development 'by other means', as 'overgrowth'.<sup>4</sup> Even at the end of the nineteenth century, for Bronn, von Baer, Kölliker, and Haeckel, "the term *Entwicklung* did not have two different meanings, evolution and individual development. Instead, it had one meaning, development, which could be manifested in two ways, by species and by individuals. ... At least until the end of the century, descent was considered [by the German biologists] one facet of the more general phenomenon of development" (Nyhart, 1995: 139).

In biology, heredity was generally considered to be a manifestation of development, but development was more than heredity. Especially after Darwin, biologists recognised that development was an interaction of two opposing life forces: heredity and variation (Coleman 1965: 125). Together and against each other, they realised the organism's development. This development was intricately connected to the organism's true nature, or type. Heredity, as 'overgrowth', guaranteed the identity between development and type, as it transmits the organism's type and typical development to the offspring. The force of variation, then, is the cause of disturbances to this continuity of development and heredity.<sup>5</sup> Variation, or variability, is the discontinuity and difference that is always connected, within development, to that other force, of continuity and sameness: heredity.

At the end of the nineteenth century a new conception of heredity emerged. Frederick Churchill (1987: 364) has argued, based on a reading of the heredity theories of Hertwig, Weismann, Kölliker and others, that nineteenth-century heredity as development and 'overgrowth' changed "only with the recognition that a continuum of structure must be preserved during the development of the individual." In this way, "heredity assume[d] its modern and more narrow meaning of *Vererbung*, or transmission" (364). But this is not the full story: Churchill adds that "the new theories of heredity [*Vererbung*] required a mental dissection of the organism into a segment for transmission and a segment for development" (360-1; emphasis added). Now, this particular distinction points to a radical difference with nineteenth-century heredity. Biology worked with a distinction between heredity and variation, between continuity and discontinuity. Conceiving, instead, of a distinction between transmission and development seems to be at odds with biology.

Peter Bowler (1989: 6) later expanded on Churchill's argument by considering Mendelism. According to Bowler, the break with nineteenth-century biology (concerning heredity) consisted in the emergence of "a theoretical model of heredity [i.e. Mendelism] in which (a) the transmission of characters from one generation to the next constitutes a distinct and worthwhile field of study and (b) it is assumed that the characters can be treated as distinct units." This perspective, however, relies heavily on Mendelism, or genetics, which was not part of life science until 1900. The

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<sup>4</sup> For Blumenbach, see Lenoir (1980). For Darwin and 'prepotency', see Campbell (1983).

<sup>5</sup> Discussing Darwin, Bowler writes: "Variation was seen not as the circulation of different genetical characters within the breeding population, but as a departure from the norm produced by disturbances of individual growth" (1988: 32).

emerging distinction between transmission and development, discussed by Churchill, is situated in the 1880s. Now, Bowler (1989: 64-70) also discusses a scientist of the 1880s, Francis Galton, but surprisingly he is sidelined by the heavy emphasis on Mendelism. Nonetheless, Bowler (1989: 70) writes: “Evolution was uncoupled from the problem of generation, and in one stroke Galton undermined the whole complex of ideas that had upheld the developmental world view.”<sup>6</sup>

Galton broke down the nineteenth-century unity of heredity and development in a much more radical way than his German colleagues considered by Churchill. For Galton heredity is simply a matter of the sum total of germinal material that the individual organism inherits from all of its ancestors. This sum total he called the ‘stirp’, from the Latin *stirps*, meaning stock or stem (Bowler 1989: 68). In Galton’s view, this ‘stirp’ is not changed by any generation but rather remains constant, and is merely ‘blended’ in each separate organism without consequences to the offspring (Bowler 1989: 64). In this way, disregarding any functional development or interplay of heredity and variation, and lacking an understanding of the mechanism of character transmission, the ‘stirp’ is the singular presence of an organism’s larger history (its species history); it is the ancestral network of heredity condensed into a single, constant, all-encompassing node. Although no doubt a poor notion of heredity, Galton’s ‘stirp’ seems to have been a radically new, life-scientific research object, incompatible with biology’s integrated understanding of heredity and development.

These two notions – heredity and development – only became a site of problematization and attempted conceptual syntheses with the beginning of life science. Georges Canguilhem already said as much when he wrote in 1977 (1988: 110) that “[l]ike all his [nineteenth-century] predecessors, Darwin confounded the two questions of generation and heredity.” Viewed from today’s standpoint, biology was indeed confused about heredity and development – or more optimistically: Biologists knew better and realised that heredity and development should not be understood as separate phenomena as they are today. But what is really the distinction at stake here? Perhaps clarity about the conceptual situation can inspire bolder ideas for life science today.

Biology, according to Foucault, divided the study of life between physiology, on the one hand, and comparative anatomy, on the other. There was the study of form *and* there was the study of function, as two separate realms of biological research. Anatomists or morphologists sought to establish a life form’s identity by comparing different forms while physiologists tried to understand organisms by looking into their internal organization and conditions of existence. In the 1880s, new approaches to the study of life were built which collapsed the biological division between form and function, anatomy and physiology. Gottlieb Haberlandt, for example, tried to construct a new field of botany, ‘physiological plant anatomy’, and was initially reproached for doing so (Cittadino 1990: 33-44; Haberlandt 1884).

The biological configuration of development as heredity and variation, continuity and discontinuity, sameness and difference was reconfigured with the emergence of life science around the 1880s. Now, a life unit is on the one hand considered to be processes and systems, the construction and destruction of materials and functions, operations and transformations, each of which may have a certain temporality (e.g. circular, divergent, linear, short-term, etc.). On the other hand, a life unit is considered to be a passage of ancestral material and a network of ancestral relations. Galton’s ‘stirp’ is such a passage and network – though perhaps more static and unified: a unit of ancestral material.

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<sup>6</sup> Galton is better known for his innovations in statistics. For example, he constructed the concept of correlation. See Hacking (1990: 180-188).

For the gap between heredity and development, for this aporia of life science James Griesemer (2007: 378-8) has found an elegant expression in Hans Reichenbach's 'common cause principle':

If a causal process from A to B can be thought of as the 'development' of A, then this very abstract notion of causality contains the philosophical root problem of heredity/development. Heredity concerns the respect in which A stands in a certain causal relation to B, while development concerns the bringing about of B from A. (Salmon 1984: 148)<sup>7</sup>

Development (process), in this sense, may be visualised as follows (figure 3). Two units, A and B, are separated and connected by an arrow from A to B, indicating that B is 'brought about from A'.

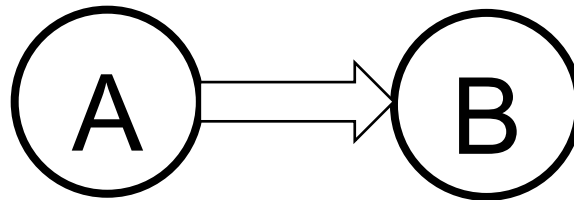


Figure 3. Process

Heredity (ancestrality), in the citation, refers to a network situation, I believe. It would thus be adequately visualised by figure 4, in which B stands in a relation to A (and to other possible units).

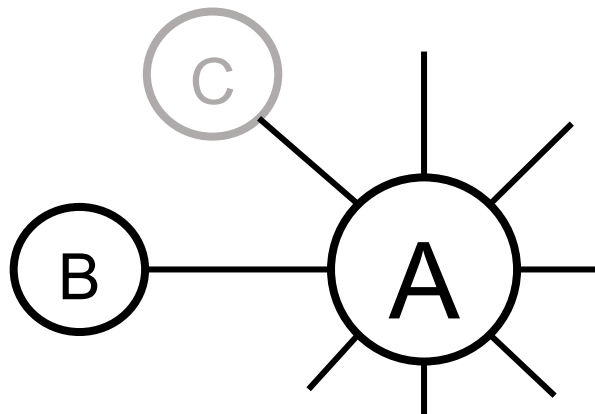


Figure 4. Ancestrality

The proliferation of research but, above all, theory and discussion about evolution and development since around 1900 testifies of the conceptual struggle with this aporia of process and ancestry. The solid and productive research area of physiology was replaced with a conceptual gap, which could be brushed over, ignored, or subjected to attempts at 'synthesis'. The ceaselessly repeated reanimation of Darwin's work perhaps also indicates that something irretrievable had indeed been lost. If life scientists today were the direct intellectual heirs of Darwin, reanimating him once would have sufficed to move on. It was not enough, and the theoretically-minded scientists keep going back to the nineteenth century for answers to the dichotomies of the present study of life.

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<sup>7</sup> For the original expression of the 'common cause principle', see Reichenbach (1925; 1956).

## Section 1.2 – Part/whole and transition

Now that we have gained a basic understanding of the ancestry-process dichotomy in life science, let us see if there are other major dichotomies at work, paying attention especially to those that do not concern the evolution of life units. Systematists Niles Eldredge (1985: chap. 6) and Stanley Salthe (1985: chap. 7) have suggested the existence of ‘the two great biological hierarchies’ (i.e. systems of classification): the functional hierarchy, or ‘physiological and ecological’ hierarchy, on the one hand, and on the other hand, the genealogical hierarchy, or phylogenetic hierarchy. This opposition seems to be derived from that of another systematist (and philosopher of biology), Ernst Mayr, who introduced a dichotomy between functional biology and evolutionary biology, where the former is understood to deal with ‘proximate causes’ and the latter with ‘remote causes’ (1980: 9). Let us take a closer look, however, at the conception of the hierarchy dichotomy as developed by the philosopher and historian of biology Gustavo Caponi.

Caponi (2016; 2018) refers to *systems* and *lineages* as the two distinct objects of the two different hierarchies in life science today. Systems are the elements of the ecological(-physiological) hierarchy, from the molecule and chromosome to the ecosystem and biosphere. Lineages are the elements of the hierarchy of systematics, that is, the different taxa, from the example (e.g. my neighbour’s cat), the sub-species, and the species to the genus, family and up to the super-kingdom. How do lineages and systems differ from each other? Caponi (2018: 46) writes that the sequence ‘*Panthera leo persica* > *Panthera leo* > *Panthera* > *Felidae*’ is conceptually similar to the sequence ‘square > rectangle > parallelogram > quadrilateral’. We say of a square that it is a rectangle, parallelogram, and/or quadrilateral, and in the same way, we say that *panthera leo persica* is a *panthera leo*, a *panthera*, and/or a *felida*. If we wish to speak similarly about a series of ecological(-physiological) units, however, we run into a conceptual barrier. The sequence ‘chromosome > tissue > individual > community > ecosystem’ is fundamentally different from the other two sequences, and we do not say that a chromosome is a tissue, an individual, a community, and/or an ecosystem as if these were equivalent names.

Now, Caponi and other thinkers have reflected on this difference, and provided a wide range of arguments, reasons, elements, and aspects, each of which covers a part of this dichotomy between the ecological and phylogenetic hierarchies. Ingo Brigandt (2009: 81; and referred to by Caponi 2018: 55-6) has argued that the difference consists in two kinds of cohesion: On the one hand, integrative cohesion, which means that “parts are spatially contiguous and there is a strong causal connection between the parties so as to facilitate integration into a whole.” This would characterise the ecological hierarchy. On the other hand, response cohesion, which means that “the parts of the entity [e.g. individuals of a species] respond together (respond in the same way) to external causal influences.” A pronounced difference between these two types of cohesion seems to be the spatial aspect, since units in ecology are always spatially determined and must be conceived as existing in a place, neighbourhood, area, or any other space, whereas units in taxonomy are not necessarily spatially determined. Another aspect of the dichotomy may be that the characteristics of a *panthera* are shared by *panthera leo* but the characteristics of an individual are not shared by a tissue – of that individual. This difference is that between taxonomies and meronomies: Whereas meronomies order things in a part-whole relation, taxonomies are based on the relation of the specific and the general.

Caponi ultimately argues that the dichotomy of the two kinds of hierarchies in ecology and systematics consists of two different types of cohesion, following Brigandt in this respect. But for Caponi (2018: 53-4) these types of cohesion are systematic cohesion and genealogical cohesion: Whereas systems are characterised by synchronic interdependence, lineages are characterised by diachronic connection. The *panthera leo persica* may go extinct – i.e. break the diachronic connection – but this would not entail any consequences for the African subspecies of *panthera leo*. However, if a chromosome is removed the consequences for the individual are virtually endless. Caponi (2018: 54) thus concludes that “the requirement of a *causal relationship between the parts of a whole* is only relevant in the case of systems.” The identity of lineages, on the other hand, is established by “the transitivity of the relation of descent, which is no less a causal link.”<sup>8</sup>

The opposition is therefore between part-whole relations and transitive relations. (We will leave out the notion of causality, as it appears redundant.) This fundamental dichotomy in life science takes place at the side opposite to the difference of heredity and development, ancestry and process (cf. figure 1). These two aporia (and hence, four categories) that we discuss in this chapter reveal, as their shadow, the research areas of ecology and systematics. Along the axes perpendicular to the aporia of life science, the four categories intimately connect and allow for two kinds of productive research. Ecology and systematics exist insofar as their basic conceptual connections (i.e. process and part/whole respectively ancestry and transitivity) endure.

Areas of research that seem particularly concerned with either of the two categories can, nonetheless, be singled out. Within ecology, for example, we may differentiate between ecological anatomy (the study of part/wholes) and ecological physiology (the study of life processes), even though process and part/whole would normally be studied in one conceptual movement. Ecological anatomy was also the title of a course taught by the American ecologist Henry Chandler Cowles in the summer of 1898 (Cittadino 1990: 151). It was based on Gottlieb Haberlandt's *Physiologische Pflanzenanatomie*, a work at which we will have a closer look in chapter three. Yet, the ecological study of part/wholes might also operate with a different name: mereology, or mereotopology. The logician Barry Smith has recently done some work in anatomy under this title, contributing to discussions about the conception of the mother-fetus relationship.<sup>9</sup>

The other half of the dichotomy separating ecology's and systematics' understanding of life forms – transitivity – still remains to be clarified. Just like the part-whole relation, transitivity is also a concept in set theory. This is the meaning to which Caponi refers: “Whenever an element *a* is related to an element *b* and *b* is related to an element *c* then *a* is also related to *c*” (‘Transitive relation’, n.d.). This transitive relation between *a* and *c*, therefore, is *b* itself. *B* is the passage from *a* to *c* and yet an element itself, too. Is this how species, haplogroups, and clades exist in systematics? Not as lineages but as passages, historical-geographical passages?

In the following chapters we will inquire into the primary source material and carefully build a more historically informed understanding of such notions as transitivity. For now, we need a

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<sup>8</sup> My translation. The original Portuguese is as follows: “a exigência de uma *inter-relação causal entre as partes de um todo* só é pertinente no caso dos sistemas. A identidade das linhagens é puramente genealógica. O que a estabelece é a transitividade da relação de descendência, que tampouco deixa de ser um vínculo causal ...”

<sup>9</sup> In the conventional use of the term, mereotopology refers to the branch of logic that deals with part-whole relations. Alfred North Whitehead was one of the first to develop such mereotopology, in the early twentieth century. A bibliography of Smith's work in this area may be found at <http://ontology.buffalo.edu/smith/articles/anatomical-parts.htm>.

conceptual awareness of the incompatibilities within life science, between ecology and systematics. Heredity and development, we have seen, seems to be a pervasive dichotomy, which we have conceptualised as an opposition of ancestry and process. Reichenbach's common cause principle succinctly expressed this dichotomy: "Heredity concerns the respect in which A stands in a certain causal relation to B, while development concerns the bringing about of B from A" (Salmon 1984: 148). Ecology, then, deals with such developments, transformations, and processes while systematics is concerned with the passages and networks, the nodes and lines, the shifts and situations of life units' ancestry, as they "stand in a certain causal relation to [each other]."

The other major dichotomy within life science – the one mostly discussed by systematists – is meronomy versus transitivity; in other words, part-whole versus transitive relations or forms. Let us express this dichotomy in a way similar to Reichenbach's principle: Meronomy concerns the respect in which A is a part of B, while transitivity concerns the passage (A) from B to C. Figure 5 presents the part in a whole (and in turn the whole as a potential part of another whole) while figure 6 shows the transitivity, the passage 'A', linking up B and C.

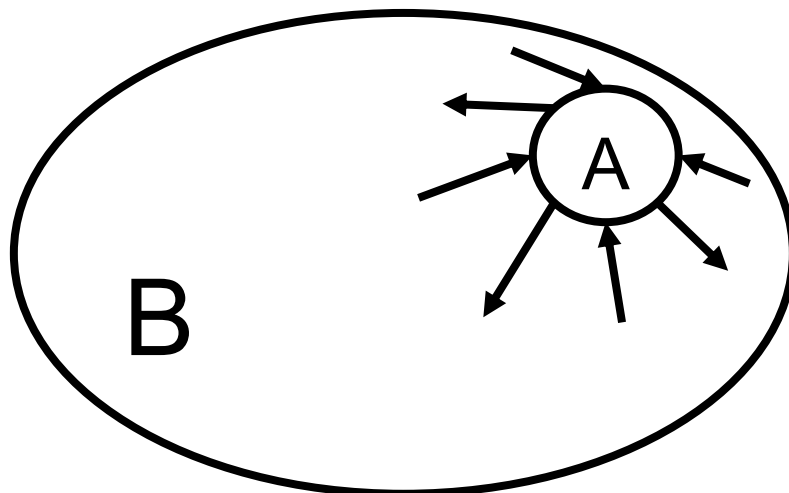


Figure 5. Meronomy

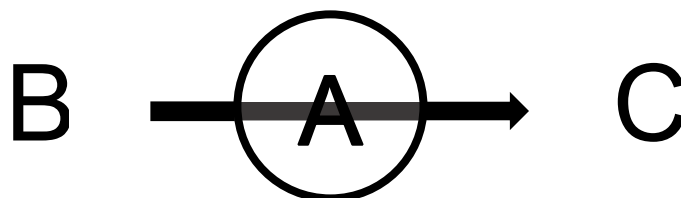


Figure 6. Transitivity



## Conclusion

The dissonance of life science is in large part due to the two fundamental aporias presented in this chapter. The incompatibility of seeing a life form as both transitive and a part of a whole, or the dichotomy between a life unit's transformations and its ancestral situatedness are conceptual tensions which divide life science from one end to the other. They shape the distinct, separate existence of ecology and systematics as much as the unbridgeable gap that divides the two. Research into life processes and systems flourishes today, and exists at all, insofar as it is conceptually incompatible with systematics, that study of the life form's transitivity and ancestrality. Attempts at synthesizing life science will fail as long as there is life science – which will endure as long as synthesis fails.

With the insight into the dissonance of life science acquired in this chapter, we should gradually move towards its dual harmony – ecology and systematics. All of life science, however, can only make sense in contrast to other epistemic studies of life. Life science is our historically (and geographically) dominant situation concerning the study of life but we must be able, sometimes, to experience the boundaries that generate doubt and innovation. Since we delve into the initial period of life science, the study of life that preceded it is most accessible to our inquiry, and will thus figure here as the other of life science. The next two chapters explore the twists and turns which divide life science from biology. In doing so, aspects of both will come to light. We might, moreover, appreciate the profundity and confusion of an epistemic shift as vast as that from biology to life science.

# Chapter 2 – Biology and systematics

## Introduction

The first set of twists and turns dividing life science from biology revolves around the ordering of life forms. In the next chapter we will delve into the epistemic shift from a different perspective, as we will rather consider the processes that make up life forms. Speaking of two distinct perspectives, in this sense, is misleading however. Biology became life science, and it is not the case that physiology transformed into ecology, and comparative anatomy into systematics. We have seen by way of the archaeological diagram that rather the conceptual axes have shifted, resulting in a fundamentally different configuration. Hence, this chapter does not explain how Cuvierian comparative anatomy gradually changed, in the second half of the nineteenth century, to become evolutionary morphology, an early form of phylogenetic systematics. The point is rather that there was no phylogenetic systematics in evolutionary morphology nor in Darwin himself. They practised the biological ordering of life forms. Fritz Müller, however, an intellectual friend of Darwin, deconstructed biology in significant ways, thereby constructing life science. No doubt other scientists did so too – and we will consider some of them in the next chapters – but specifically with regard to contemporary systematics, Müller’s work is pivotal: He drew the first cladogram, in order to understand the phylogenetic relatedness of certain, rather similar species. From an overly conceptual approach in the previous chapter, let us now zoom in on the epistemic rearrangement and become familiar with its many intricacies.

## Section 2.1 – A ‘new alignment’

Historians of life science have drawn attention to a certain epistemic reconfiguration at the end of the nineteenth century or around 1900. The discussion about this reconfiguration – the significance of which is not agreed upon – has centred around the relation between two revolutions in the history of life science: Darwin and genetics. At the same time, however, historians have pointed at another unmistakable ‘reorientation’ *in between* these two revolutions, sometime in the 1880s and 1890s. William Coleman argued in 1971 that “the final quarter of the nineteenth century marks a turning point in the affairs of biology” (160). For Coleman it concerned a shift from historical explanation to causal explanation and from inquiry into form to that into function (63, 162). “It was now much more important, [young scientists] held, to attempt to analyze the process of change than to seek probably unattainable detail regarding the products of change” (165). This “reorientation of biological thought that marked century’s end” Coleman believed to rightly characterise as “a revolt from morphology” (162).

Garland Allen (1975) reiterated this trope four years later, and more so than Coleman had already done, he argued that the shift consisted in a widespread increase of experimentalism; idealism in biological thought was replaced by materialism. Later, after criticism, he dropped the image of a ‘revolt from morphology’ and rephrased the rupture as one “between the descriptive-speculative

and the experimental traditions in biology” (1981: 166). However, this is more than a mere rephrasing of the same argument. In fact, Allen substituted the diachronic view of a ‘revolt from morphology’ for a synchronic one, concerning a new epistemic division (between descriptive and experimental science). This confusion is due to the double nature of the transition from biology to life science. It did not simply replace one ‘paradigm’ with another. Rather, a new entanglement of conceptual dichotomies and principles was constructed, which one might say was perpendicular to the previous one (i.e. biology). And so, in the time when life science replaced biology, historians see that young scientists profile themselves by contrasting their approach to that of their ‘old-fashioned’ teachers, but they also find that they express opposition against a contemporary, incompatible approach to the study of life (e.g. systematists emphasising history against ‘ahistorical’ ecology).

Lynn Nyhart, in her book-length history of nineteenth-century German animal morphology, is aware of these intricate tensions of a transforming scientific community. She argues that on the one hand, “[b]y the 1880s a new alignment was emerging,” and on the other hand, one cohort of scientists later, “the opposition [was] expressed between a rigorous causal, experimental approach that rejected evolutionary history and a morphological approach that was historical, descriptive, and speculative” (1995: 205, 308). “Only in the middle and later 1890s did it become more common to construe them as inherently incompatible intellectual orientations” (330). In this way, she corrects the view put forward by Coleman and Allen concerning a division between an experimental and a descriptive approach, construing it as a distinct opposition, separate from the ‘new alignment’ of the 1880s.

This new alignment I believe to be life science, i.e. ecology and systematics. Although she does not elaborate on it, Nyhart’s view does not seem to be very different:

By the 1880s a new alignment was emerging: for many younger zoologists, morphology was associated on the one hand with the speculative elaboration of phylogenetic relationships and on the other hand with the study of microscopic sections of developmental stages. The study of the organism in its environment and the process by which adaptation changed an organism’s form, by contrast, was a separate topic called ‘biology’ or sometimes ‘ecology’. (1995: 205; cf. p. 330)

Nyhart’s perspective is zoomed in on this particular period (the end of the nineteenth century) and restrains from finding a larger conceptual significance in these developments. The fact that there emerged a new study of the organism that went by such a general name as ‘biology’ or the fact that it was also called ‘ecology’, which would become one of the main, typically twentieth-century (and contemporary) life sciences, is not explored. What does it *mean* that that these words, in connection with the new kinds of research that emerged in this time? Why limit the interpretation to what the historical actors said and did when we have 140 years of hindsight to make use of?

In her attempt to adequately present *fin-de-siècle* German morphology in its own context, its own communities, and its own politics, Nyhart brushes over those scientists who worked in its margins. Now, in my archaeology these scientists appear to be most important. Fritz Müller, who studied crustaceans in the south of Brazil while corresponding with Darwin, is not discussed in Nyhart’s book: She only considers morphology at German universities, even though Müller’s book *Für Darwin* (1964; *For Darwin*, 1969) was crucial for the reception of Darwin in German biology (Mocek 1998: 154). The anatomist Wilhelm Roux is discussed only very briefly and his significance somewhat reduced to that of his colleagues (see Nyhart 1995: 279-305). Finally, Nyhart does not consider the important morphologist and ecologist Karl Möbius in her 1995 book, since he was not part of the German academic morphology community. However, she later wrote an article on him

and expanded this research into a book on the ‘rise’, in German society, of the biological/ecological ‘perspective’ that we just encountered (Nyhart 1998; 2009a) – material to which I turn in chapter four.

Besides ecology, the new alignment consisted, according to Nyhart (1995: 205), of “the speculative elaboration of phylogenetic relationships and ... the study of microscopic sections of developmental stages.” This is the field of evolutionary morphology (or “genealogical morphology” (Hatschek in Nyhart 1995: 205)) that flourished in the late nineteenth century. It largely replaced comparative anatomy, the doctrine of Cuvier (Foucault 1966: 275-292 / 1994: 263-279; Cassirer 1950: 128-136), as scientists increasingly started to consider the organism’s development (ontogeny) and genealogy (phylogeny) so as to understand its true nature and place within the natural system. They could in part work on the basis established earlier by German idealistic morphology (e.g. Goethe), which had already put ontogeny at the centre of attention (Cassirer 1950: 137-150).

Was evolutionary morphology the beginning of contemporary systematics? According to Nyhart (2009a: 22), it was not: “even in the revised project of systematics under evolution, what still counted were family relationships of closeness and distance, marked by similarities and differences of form. That is, to understand an organism’s “place in nature” was to set it into a framework of morphological similarities, differences, and degrees of relatedness.” In this view, evolutionary morphology and comparative anatomy, already established by Cuvier around 1800, were not very different from each other.

Lynn Nyhart has not been the only historian to point at the ‘non-revolution’ of Darwin-inspired morphology. This has been a common theme in the work of Peter Bowler (1983; 1988; 1996): “[T]he immediately post-Darwinian era did not exhibit a totally new world view, only an updated version of the old one” (Bowler 1989: 49).<sup>10</sup> Ernst Cassirer has been even more fierce in his judgement of evolutionary morphology:

Just as Columbus did not realize that he had discovered another continent but continued under the delusion that he had found only a new route to lands already known, so the Darwinians were not the founders of a new science of *historical morphology* but on the contrary simply took over the old morphology, “explaining” it in terms of evolution, the struggle for existence, adaptation, inheritance, etc., and trying to deck out its ideas in a phyletic form. Essential factors of all *true* historical study, such as strict chronology or “dating,” were totally neglected. ... Historical *description* was supposed to perform at once the whole duty of “explanation”: insight into the *evolution* of organisms was to open the way forthwith to the understanding of all problems relating to their structure and physiology. (Cassirer 1950: 171-2)

I think Cassirer is right to emphasise that Darwin’s evolutionary theory was considered by many at the time to be the holy grail that would solve all questions. It put the historical aspect of life at the centre and demanded that virtually all aspects of the study of organisms would revolve around their history and development. But did it also change the conception of history as such? Was evolutionary morphology, with Ernst Haeckel and Karl Gegenbaur as its two main protagonists, part of the shift from biology to life science? Where, finally, should we situate Darwin?

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<sup>10</sup> See Amundson (2005: 108) for a critique of Bowler’s account from the perspective of today’s evo-devo.

## Section 2.2 – Varieties and genealogy (Charles Darwin)

A crucial idea for Darwin was that of ‘transitional forms’, or ‘intermediate varieties’. Its significance becomes clear through this question that he posed in *The origin of species* (1859: 171, emphasis added; 1876: 133): “[W]hy, if species have descended from other species by fine gradations, do we not everywhere see innumerable *transitional* forms,” “closely-linking intermediate varieties”?<sup>11</sup> On the one hand, this is what a life form for Darwin is: a transitional form, a variety. On the other hand, variation is *linked* to others, it is genealogical. Given these beliefs, nature is expected to be a continuous pattern of variation, where species are virtually impossible to identify. But – and this is the wonder of Darwin’s question – there are clearly distinguishable species, even without the existence of transitional forms in between them.

In the previous chapter I introduced the notion of transitivity as one of the two aspects of systematics (the other being ancestry). Was Darwin already working with transitivity? A life form as a transitive relation is a link between other life forms (e.g. ancestors and offspring) but it is more than a mere connection, rather constituting the *passage* from one life form to another, that which Möbius (1886: 273) calls “passage point” (“Durchgangspunkt”) (cf. chapter five). Now, this is not exactly the way in which Darwin approaches his ‘transitional forms’. They may be connections but they are not passages. In his attention for these ‘intermediate varieties’, what concerns Darwin is the *succession* of forms and the gaps within this succession. Darwin’s ‘transitional forms’ are gaps in a series; they are places that connect to each other to form the chain of evolution’s forms. The quality of passage operates, *as it were*, at the general level of history (evolution), where the natural system is a space of ‘closely-linking varieties’.

At the level of the individual life form, then, there is really no conceivable transitivity: a life form, for Darwin, is not a relation but a variety, a unique entity. Whereas passage suggests movement and history, variety rather calls to mind spatial difference: on the one hand, the difference of the life form (the organism’s own space) and, on the other hand, the diversity of Nature (the mother space). Now, the latter is then thought physiologically, as it were, in terms of laws, the laws of evolution, and the mechanism of natural selection – a term which at the time constantly risked being interpreted as a hidden, omnipresent power. The differences of life forms, instead, are not so much approached as a realm of laws and mechanisms but more so as the signs of identities. They might reveal, through comparison, their place in the natural system, the reconstruction of which is the primary goal of classification in biology. What Darwin does is to temporalise this natural system, to add a historical axis to it, so that the identity of a life form is its genealogy, and it is only by way of the different genealogies that the true species are revealed.

But what is a genealogy? Given that a life form is a variety within the space of historical nature, in classification it will figure as an element in a succession of forms, in a thread, chain, or genealogy. At the same time, genealogy provides the possibility for a natural system which may encompass all varieties. Genealogy is thus, from this perspective, the key idea of Darwin’s morphology: it connects the view of life forms as varieties with the introduction of history into the natural system. This is possible, firstly, because individuals have the capacity or drive to vary: ‘variety’, as Foucault calls it when he discusses Darwin (2017: 210). Thus, there will be varieties of the varieties, and so on, to

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<sup>11</sup> See also Darwin (1859: 172, 174, 179/1876: 134, 138). Insofar as I cite *On the Origin of Species*, the differences between the sixth (1876) and first editions are very few and relatively insignificant. My citations are from the first edition.

be found in remote places, around the corner, in the fossil record, or potentially in the future. There is, in other words, a vast ‘historical’ space of “closely-linking (intermediate) varieties,” for which the notion of species (and its associated unity) becomes a rather inadequate classifier. These ‘historical’ varieties are better classified as successions of individuals than as strict unities of individuals.<sup>12</sup> These successions are the genealogies that Darwin suggests classification should reconstruct, on the basis of those characters which indicate their ‘history’ (i.e. the succession to which they belong) and not their adaptations (even if this difference is relative).<sup>13</sup>

Perhaps all of this has already been said by other scholars. Darwin scholarship has swollen to such vast proportions that a small discussion of his science cannot also encompass clear references to selected literature.<sup>14</sup> However, I have only rarely encountered references to the Darwin interpretation that I rely on here, namely that of Foucault. It features in his 1969 lecture “Cuvier’s Situation in the History of Biology” (1970/2017).<sup>15</sup> Arguing on the basis of his archaeology of biology (1966/1994), which focused so heavily on Cuvier alone, Foucault claims that Darwin’s transformation of biology “was achieved through the work of Cuvier,” by consolidating the fundamental configuration of the study of life that Cuvier had set up. Now, the singular importance of Cuvier for biology is definitely overstated – where are Blumenbach and Kiellmeyer, for example? – but in this lecture Foucault speaks of ‘transformation Cuvier’ as a way to circumvent the focus on a single founder. ‘Transformation Cuvier’ means biology (nineteenth century), understood as a transformation. Still, Foucault does not explain what this transformation within and of biology consisted of – apart from Darwin’s innovations (see Foucault 2017: 212-5).<sup>16</sup>

Let me briefly summarise Foucault’s view on Darwin here, separating it from the Cuvier-Darwin relation that makes up the actual subject of the lecture. For Darwin, first of all, the species is never

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<sup>12</sup> Foucault (2017: 212) said: “Darwin ..., on the one hand, eradicate[s] the epistemological threshold and show[s] that, in fact, we have to begin by knowing the individual with its individual variations; on the other, he ... show[s] how, beginning with the individual, what will be established as its species, its order, or its class will be the reality of its genealogy: a succession of individuals.”

<sup>13</sup> Perhaps it is worth mentioning that for Darwin genealogy is thus the only criterium for classification. Degree of similarity is not inherently relevant. Kevin Padian (1999: 353): “[T]he argument that Darwin advocated dual criteria of genealogy and degree of similarity is not supported by his writings on how classification should be done ... In fact, on several occasions, Darwin denied explicitly that similarity should be the basis for classification.”

<sup>14</sup> But see, for example, the important essay by Lynn Nyhart (2009b) on Darwin and embryology; and see Richards (181-8) for a general discussion on Darwin and classification.

<sup>15</sup> As far as I know, Foucault’s view of Darwin is not discussed in the history of biology or in Darwin scholarship. Two minor exceptions are an article by David R. Oldroyd (1986: 153-4) and a full-length discussion by Araújo & Araújo (2014). Foucault’s interpretation of Cuvier is discussed largely favourably in the work of Gustavo Caponi (2003; 2004a; 2004b) and his *The Order of Things* has been extended, in a general way, to the history of minerology (historical geology) in Albury & Oldroyd (1977). In a rather biographical reading of Cuvier, Dorinda Outram (1986) is critical of Foucault’s interpretation and argues for more continuity concerning classification from the Classical age to the modern episteme. See Michel Senellart’s editorial notes in Foucault (2007: 86) for the ‘Lamarck-Cuvier problem’ and useful references. In this lecture series (2007: 78), Foucault made the additional remark on Darwin that he introduced the idea that “population ... was, in fact, the element through which the milieu produces its effects on the organism.”

<sup>16</sup> Lynne Huffer, in the introduction to her translation of Foucault’s lecture (Foucault 2017: 208-9), writes that according to Foucault, Cuvier “created the conditions of possibility for modern biology,” which she equates with evolutionary biology. However, Foucault never makes this claim about biology in his time and is merely concerned with the time of Cuvier and Darwin. Moreover, Foucault’s book review (1970, November 15-16) of *La Logique du vivant* (*The logic of life*) by François Jacob clearly does not aim to understand molecular biology by means of his interpretation of Cuvier, Darwin, and biology but rather concerns itself with wholly different concepts and questions.

a “primary and ultimate reality” (Foucault 2017: 210). Secondly, “there is a progressive reinforcement of individual variation” (ibid.). Thirdly, “from variation to variation, individuals are linked with one another on top of and beyond the definition given for their species” (ibid.). With these standpoints comes an ontology of two realities, namely (1) the individual, since “all the taxonomic frames ... are, to a certain point, abstract categories,” and (2) “the ‘variety’ of the individual, its capacity to vary” (ibid.). Consequently, Darwin’s transformation of, and within biology consisted of two ‘operations’. He “eradicate[ed] the epistemological threshold of the unity of species,” proposing that we “rather begin by knowing the individual with its individual variations” (id., 212). Moreover, for Darwin, “beginning with the individual, what will be established as its species, its order, or its class will be the reality of its genealogy: a succession of individuals” (ibid.).

In chapter four we compensate for the singular focus on Darwin’s morphology and classification here by also considering Darwin’s ‘physiological’ side, that is, his theory of natural selection, as it was rethought by Wilhelm Roux. But genealogical classification, even if he never practised it, was perhaps even more important to Darwin (Padian 1999: 353; Richards 2009; Nyhart 2009b). In a letter to Thomas Henry Huxley he once wrote that most naturalists look beyond the “Cuvierian view of classification” and search for “‘the natural system’”, ‘the Creator’s plan’. Darwin believed “this further element” that they look for is “simply genealogical” (Darwin 1857). Thus, he suggests the following theoretical case:

Grant all races of man descended from one race; grant that all structure of each race of man were perfectly known—**grant** that a perfect table of descent of each race was perfectly known.— grant all this, & then do you not think that most would prefer as the best classification, a genealogical one, even if it did occasionally put one race not quite so near to another, as it would have stood, if allocated by structure alone. Generally, we may safely presume, that the resemblance of races & their pedigrees would go together. (Darwin 1857; cited in Padian 1999: 355)

History as a *table* – a “table of descent of each race” – would be the perfect classification. If only we knew the succession of all races, then we could establish once and for all the full system of the succession of life forms: the entire space of historical nature in one ‘natural system’.

Huxley replied to Darwin that “[y]our pedigree business is a part of Physiology ... Zoological classification is a Census of the animal world” (cited in Padian 1999: 355). This is the answer of biology: Integrating history and heredity into classification is to confuse morphology with physiology; the natural system can only be a “census”. Heredity, in biology, was a matter of development, and development was the domain of physiology. To study the development of an organism is to inquire into the function-history nexus that for the life scientist today rather constitutes an aporia: Life science inquires into either purpose-structures and processes or into historical relatedness. Darwin’s idea of genealogical classification *seems* to be at odds with biology because it suggests classifying the space of *historical* nature and not merely nature. In both cases, however, a space is classified: Visible (morphological or physiological) characters of a life form are taken as indications of the group to which they belong (i.e. the species, the genealogy).

Concerning Darwin, a final clue to discuss is his diagram of a hypothetical genealogy (figure 7), the only figure in the *Origin of Species*. We see two branching patterns, originating from genus A and genus I respectively; the other genera either go extinct or do not diversify (E and F). There are additional, merely indicative dotted lines representing the historical realm preceding the genera, and at the top, a temporal space subsequent to 10 and the species of 10. But what is 10? Ten is an element in a scale which organises the genealogical bushes. How should we understand this scale

in relation to the branching patterns? In fact, it divides them very strictly in two aspects: Thanks to the scale, the genealogies are structured by continuity and discontinuity, sameness and difference. For each point is the origin of a certain diversity and each lapse between such points is a continuity. Identity and difference, continuity and discontinuity figure as the two separate categories that enable the diagram to present knowledge. The scale is the master measure, or standard, dividing identity and difference, continuity and discontinuity.<sup>17</sup> It is how the different genealogies are all uniformly traced, thus enabling a means of comparison across genealogies at any moment (e.g. 1, 2, 8).

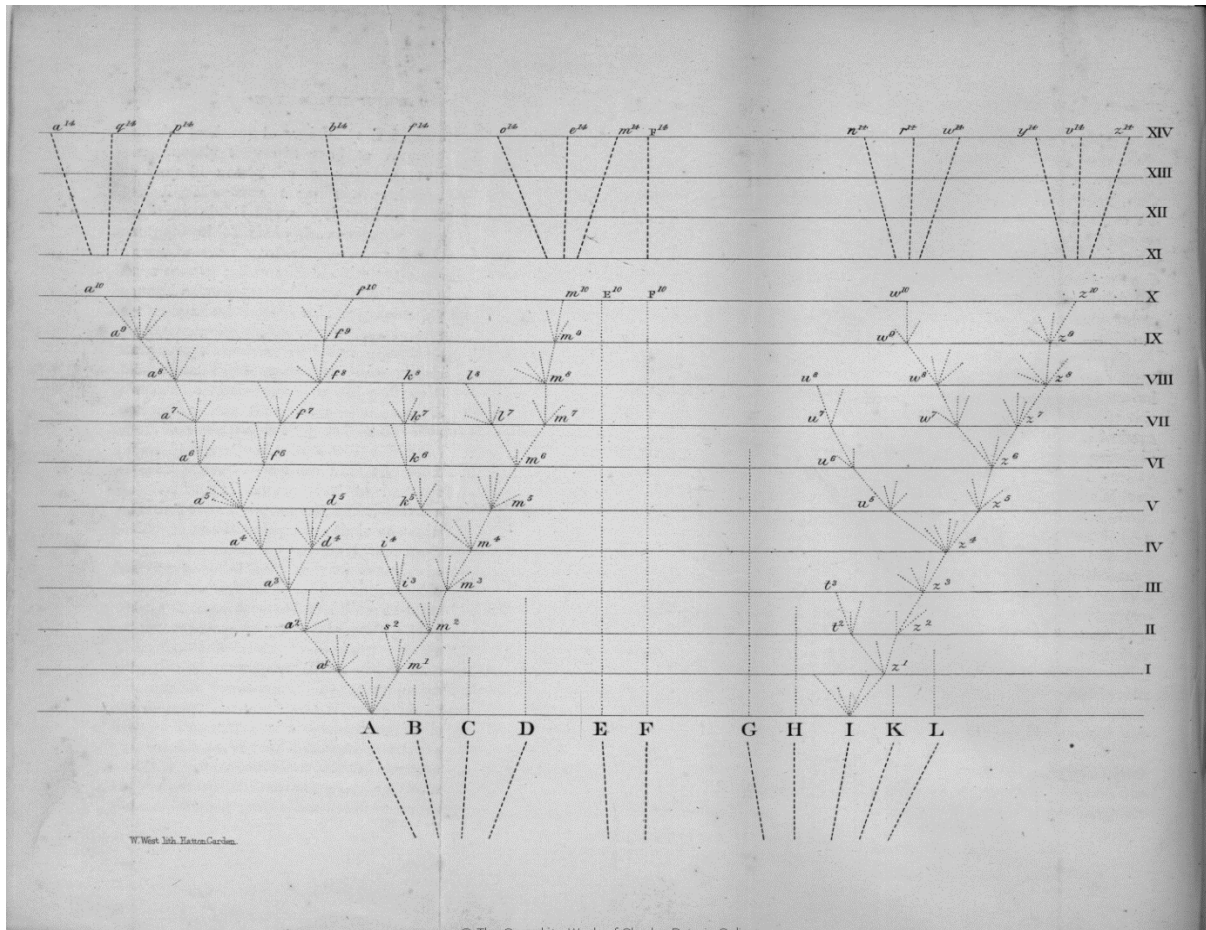


Figure 7. Darwin's hypothetical genealogy (1859: 117/1876: 108-9)

I avoided equating the scale with such general terms as 'history' or 'evolution' because now we see what is at stake. There are two histories: the branching patterns *and* the scale, history of differences *and* the history of a homogeneous timespace (the table). In Darwin's diagram they come together – but do not merge! They depend on one another to represent the natural system as a historical table. This was possible in the comparative anatomy of *biology*, constructed as it was with the nexus form-signs: A diversity of characters was interpreted by means of an ideal form, and this type was understood through its examples. It was a key innovation of Darwin to introduce some evolution into this static ideal form: For Darwin, the type is rather a *series* of varieties. And the signs, the characters of an organism – especially its embryological development – Darwin believed to

<sup>17</sup> Bowler has made a serious mistake in his book *The non-Darwinian Revolution* (1988: 12) by representing Darwin's model of evolution cladistically, that is, *without* the scale.



indicate this series, its ‘pedigree’. He never showed how this latter aspect worked, since he never practised genealogical classification – it remained an idea for a future project. The first aspect, however, is clear: the ideal form as rather a series of varieties, a succession rather than a species. And to classify organisms by means of such series is to refer them to identity and difference, continuity and discontinuity, the genealogical form and the diverse signs. Francis Galton collapsed the sign and the genealogical form into one thing, the ‘stirp’, as a total node of ancestral material. But Darwin’s idea of genealogical classification did not move in the direction of actual *historical* research. Understanding the ‘natural system’ with a ‘historical’ table, as he intended classification to be, was a matter of including and excluding organisms from series. The conceptual entanglement of *biology* operates through the work of Charles Darwin – not life science.

## Section 2.3 – Development and diversity (Fritz Müller)

Darwin’s idea of genealogical classification revolved around the identification of series of individuals, or genealogies. These would reveal the true species, insofar as species could still be conceived as distinct unities. Darwin sought to represent genealogies in history, not to represent history. Gegenbaur and Haeckel, and late nineteenth-century evolutionary morphology generally, did not differ much from this basic biological approach to classification. Cassirer was more or less right when he wrote that “the Darwinians were not the founders of a new science of *historical morphology* but on the contrary simply took over the old morphology, “explaining” it in terms of evolution, the struggle for existence, adaptation, inheritance, etc., and trying to deck out its ideas in a phyletic form” (1950: 171). Morphology could change into evolutionary morphology while consolidating its place in the conceptual entanglement that constituted biology. Gegenbaur, for example, as he built on the insights of Darwin and the legacy of German idealistic morphology, believed that “a particular form represented one moment in a continuous series, and ... an understanding of that form was to be achieved by uncovering the succession of forms in the series” (Nyhart 1995: 154).<sup>18</sup> A form in a series would thus be identified by understanding the succession of forms, much like Darwin approached varieties and the genealogies to which they belong. This thinking, this conceptual entanglement of biology has the scientist move from the discontinuity and diversity of nature – the distinctness of the life form’s moment and space – to the continuous series or genealogy the identity of which explains that of the life form.

Before Gegenbaur and late nineteenth-century evolutionary morphology, however, a German émigré scientist had already ventured into the entangled principles and dichotomies that I have called life science – though only in a dreamlike way, as no language community of that new study of life yet existed. Darwin’s “closest intellectual kin” and long-time correspondent, Fritz Müller had pushed himself as much to the edge of the Western world (the island of Santa Caterina in the south of Brazil) as to the edge of biology (West 2016: 1). He was one of the first to completely absorb Darwin’s *Origin of Species* and, on top of that, to develop it further in multiple directions. He did so mostly through the study of crustaceans (crabs, lobsters, shrimps) and some other marine invertebrates (jellyfish, marine worms) that he could find on the shore in front of his house. In 1864

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<sup>18</sup> For a more detailed and nuanced perspective on Gegenbaur, see Coleman (1976), Bowler (1996), and Rieppel (2016: 1-12; 25-33).

his first and last book was published, *Für Darwin* (*For Darwin*).<sup>19</sup> A major work of Darwinian thinking, it was crucial for the reception of Darwin in Germany (Mocek 1998: 154). Surprisingly, it is a neglected work in the history of biology. Besides his biographer, David West (2003; 2016), it has only been discussed shortly by Rieppel (2016: 51-6) and by Bowler (1996: 106-110).

What is most directly astonishing in Fritz Müller's book is the phylogenetic diagram on page 9 (11 in the English translation) (figure 8).<sup>20</sup> It is, we would say today, a cladogram – but cladistics is thought to have emerged only in the 1940s and 1950s with the work of Willi Hennig, a German entomologist. This style of systematics started to become dominant in the late 1970s and early 1980s, when it is said to have caused a paradigm change, 'the cladistic revolution' (Rieppel 2016: xii).<sup>21</sup> What then do we make of Müller's cladogram from 1864? We can say that it has nothing to do with cladistics, as Rieppel (2016: 54) does when he writes that "it had no historical connection to the rise of cladistics," and is separated from it by "100 years of history." But the fact remains that even "in its proper historical context" Müller's diagram is remarkably a diagram of today's systematics; as the almost identical diagrams of figures 8 and 9 show, its contemporaneity is undeniable.

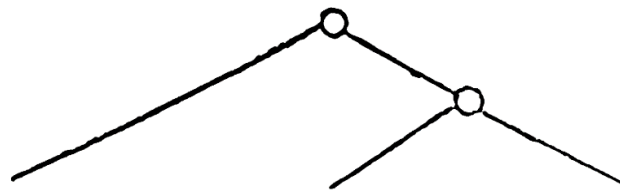
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<sup>19</sup> It was translated into English, thanks to Darwin's initiative and financial support, by William S. Dallas in 1868 as *Facts and Arguments for Darwin* (West 2016: 66-7; see Müller 1969).

<sup>20</sup> Surprisingly, historians of biology and systematists have so far overlooked the importance of Müller's cladogram. Exceptions are Robin Craw (1992: 68-9, 71, 73) who seems to have been the first to unearth it; Müller's passionate biographer, David West (2016: 73-4), discusses it and refers to Craw's text; Olivier Rieppel (2016: 54) mentions it rather dismissively, and without reference to Craw or West; Peter Bowler (1996: 322-3), finally, writes that Müller "produced diagrams resembling modern cladograms to depict the relationships [among certain crustaceans]."

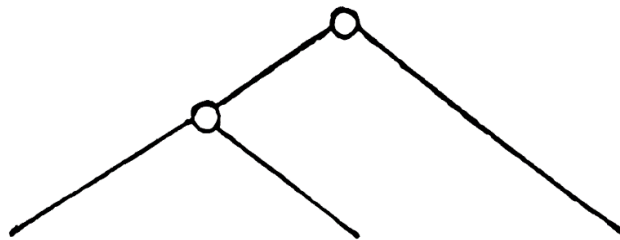
<sup>21</sup> This paradigm change is the subject of David Hull's well-known *Science as a process* (1988); cf. also Bowler (1996) and Rieppel (2016: 272-280 & chapter 8).

From the structure of the clasp-forceps :



*M. palmata*, &c. *M. exilii*, &c. *M. Fresnelii*.

From the presence or absence of the  
secondary flagellum.



*M. palmata*, &c. *M. exilii*, &c. *M. Fresnelii*.

Figure 8. Fritz Müller's phylogenetic diagrams (from  
Müller 1864: 9/1896: 11)

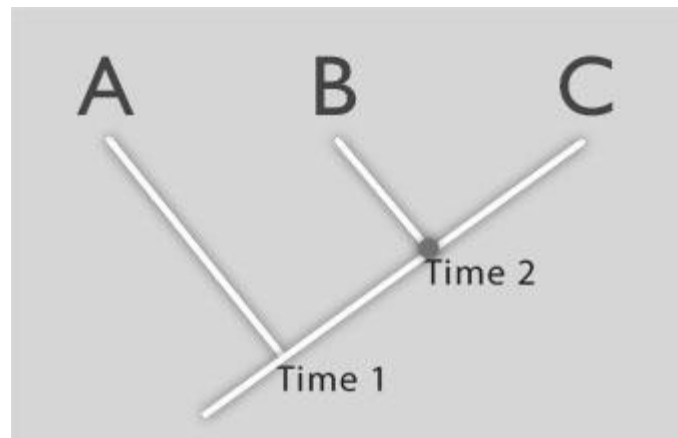


Figure 9. A phylogenetic diagram typical of contemporary  
systematics (from Peabody Museum of Natural History, 2008)

Whereas Darwin's hypothetical genealogy is incomplete without a second layer of history (the scale) structuring the first (the genealogies), the lines of Müller's diagram constitute their own structure. A connected structure of two dots, with two lines attached to each, is enough to represent ... To represent what? – In contrast to Darwin's branching patterns that signified the natural system (i.e. the system of dynamic species-genealogies), Müller's lines and dots present the relative network of ancestrality. There is no restless pattern of always diversifying history schematised by the solid stability of a sovereign time (the scale in Darwin's diagram). Instead, in Müller's phylogenetic diagram, time itself is diverse, and autonomous through difference. The lines never really end nor begin somewhere, they are not controlled by anything except the practicality of the diagram. The dots cooperate with the lines, providing them with switching points that enable

either continuity or discontinuity. Thus, both terms of this dichotomy, identity as well as difference, operate together, seamlessly. The active contrast, or productive tension is now rather one of transitivity on the one hand, and ancestry on the other: transitions and relatedness, switches and network, united in these diagrams of passage-networks. The notion of ‘phylogenetic relatedness’ in contemporary systematics covers precisely this productive conceptual tension. And so systematics did without the conceptual entanglement that operates through Darwin’s work and biology generally.

In chapter five I return to Müller’s diagram and method of classification, discussing systematics more extensively. Here, we must see how Müller’s book *Für Darwin* deconstructed biology not only concerning classification but also with regard to the crucial notion of development. In biology, development was a uniform phenomenon, studied with a conceptual axis of heredity and variation, continuity and discontinuity, sameness and difference. Rather, development followed the laws of life, understood as that which manifests itself through organisms and their development. Müller called all of this into question.

To start with, Müller makes a small comment on the influential criticism the German translator of *The Origin of Species*, Heinrich Georg Bronn, had voiced about the theory of natural selection:

When he [Bronn] says that “for the support of the Darwinian theory, and in order to explain why many species do not coalesce by means of intermediate forms, he would gladly discover some external or internal principle which should compel the variations of each species to advance in one direction, instead of merely permitting them in all directions,” we may, in this as in many other cases, find such a principle in the fact that actually only a few directions stand open in which the variations are at the same time improvements ... (Müller 1869: 24)<sup>22</sup>

Immediately we encounter the thinking of development in terms of variation and continuity, as Bronn criticises Darwin for allowing arbitrary variation, without one direction. But it is not a matter of direction or chance, Müller suggests: It is rather something in between, as “a few directions” are possible. There can no longer be, with Müller, laws of life which postulate the direction of development (i.e. life) because there is no single direction. From the start, development is diverse, multiple, plural – we see this also in Müller’s cladogram – and so it must ultimately be understood on the basis of probability rather than postulated, indiscriminate certainty.

Müller often refers to the ‘old school’ or ‘the schoolmen’, meaning his own teachers (among which the biologist Johannes Müller) and those scientists at his time who rejected Darwin’s new, evolutionary study of organisms, such as Louis Agassiz. Müller aims to show the absurdity of the old school’s science by taking key principles for biological study from Agassiz & Gould’s *Principles of Zoology* (1856). One of those principles is that “[t]he organs of the body are formed in the sequence of their organic importance; the most essential always appear first” (Agassiz & Gould in Müller 1869: 102). Müller comments:

This proposition might be characterized *à priori* as undemonstrable, since it is impossible either in general, or for any particular animal, to establish a sequence of importance amongst equally indispensable parts. Which is the more important, the lung or the heart?—the liver or the kidney?—the artery or the vein? (102)

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<sup>22</sup> Karl Ernst von Baer raised a similar, though more precise, criticism: “Throughout his examination of Darwin’s theory von Baer objected to the notion that chance variations having an internal source independently of any relation to the external environment could ever lead to functionally adapted organisms” (Lenoir 1982: 270).

In this way, he renders absurd the idea of a hierarchy of the organism's parts according to their physiological importance; an idea introduced already by Cuvier around 1800 (Foucault 1969: 277-280/1949: 265-7). Müller adds that not only do organs lack a physiological hierarchy, such a sequence often fails to correspond to developmental history. The latter may start with unimportant organs – “The development of the embryo [of *Mysis*] commences with the formation of the tail!” – or ‘essential’ organs may be insignificant from the perspective of developmental history: “in the Amphipoda the most important of all organs would be the “micropylar apparatus,” which disappears without leaving a trace soon after hatching” (1869: 64, 103). Development does not only lack a *single* direction and is diverse instead, it also lacks any progression of physiological importance.

A third aspect can be added to this deconstruction of development. Müller (1869: 103) cites another principle from Agassiz's & Gould's textbook: ““*The embryos, or young states of different animals, resemble each other the more, the younger they are,*” or, as Johannes Müller expresses it, “*they approach the more closely to the common type.*”” This pervasive idea of convergence as we go back in time and divergence as we move onwards here goes hand in hand with a belief in a shared origin (i.e. “the common type”).<sup>23</sup> Müller in fact agrees with the principle of diversification – “It is certainly a rule ...” – but he is quick to point out that

here, as in other classes, the exceptions, for which the Old School has no explanation, are numerous. Not unfrequently we might indeed directly reverse the proposition and assert that the difference becomes the greater, the further we go back in the development [ontogeny]. ... In other instances, the courses which lead from a similar starting-point to a similar goal, separate widely in the middle of the development. ... Finally, so that even the last possibility may be exhausted, it sometimes happens that the greatest similarity occurs in the middle of the development. (1869: 104-5)

Hence, while not directly rejecting the principle of diversification, Müller emphasises the diversity of development. Just as he “took character incongruence as a fact of nature that should not be ignored,” the strange ways of development are not denied their particularity (Rieppel 2016: 55). The queerness of development is not disturbance of a norm, not variation against continuity and identity, but a fact of nature that prevents us from studying development uniformly.

Given these important deconstructions of the notion of development, it is surprising that Müller nonetheless presents a theory of development as such. In contrast to what we have discussed, he even holds on to the idea that organisms develop progressively, towards perfection. Essential aspects of biology shine again in their last glory in Müller's theory of development, as he starts by proposing two distinct modes of new development: “*Descendants reach a new goal,*” he writes, “*either by deviating sooner or later whilst still on the way towards the form of their parents, or by passing along this course without deviation, but then, instead of standing still, advance still farther*” (1869: 111). Either new development takes place through deviation or it occurs by way of further advancement. The second mode of new development is very ambiguous: Is this ‘free’, ‘blind’ advancement, in the sense that we saw Bronn criticise Darwin for? Or is Müller's distinction between two modes of new development really the identity and difference dichotomy again, so that ‘further advancement’ means continuity and a kind of overgrowth?

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<sup>23</sup> Müller acknowledges that the notion of type lacks one distinct meaning: “Different as may be the ideas connected with the word “type,” ...” (1869: 103). He does not make any important remarks on the concept of type in *Für Darwin*.

In any case, the distinction of new development into two modes – deviating or further development – serves the purpose of identifying the correspondence between the organism’s developmental history and the historical development of the species. For if the organism’s new development deviated from “the way towards the form of their parents,” then it will not reflect the development of the species. If, however, the organism’s new development was a matter of further advancement, then “*the historical development of the species will be mirrored [sich abspiegeln] in its developmental history*” (Müller 1864: 76/1869: 112). The organism’s development will reflect that of the species in the mirror that it is. But it is a failing mirror since it may cause the “historical record” – i.e. the developing species – to be “*gradually effaced [verwischt]*,” ceasing to reflect it properly, or worse, to be “*falsified [gefälscht]*” (Müller 1864: 77/1869: 114; bold in original).<sup>24</sup>

Why does the mirror fade? Because, first, the course of the organism’s development may in fact become more and more perfect, “straighter,” so that the developing species can no longer be recognised in it. Secondly, “the struggle for existence” that the organism has to undergo may cause it to transform beyond recognition. Thus, the organism may change as a result of processes that occur, as it were, above and below the developing species. In the situation where the development of the organism reflects the species and the historical record that operates within it, the organism is at the same time subject to other functions, beyond this reflective one. It is also subject to functional processes particular to itself, particular to its own historical contingency: the progressive perfection that straightens out its development, and its role in the struggle for existence, which transforms its being. Instead of tightly connecting function and history, Müller, with the idea that the organism’s development may falsify its telos, opens up a space where the diversity of functions will be thought in connection with the particular life form and where history will be thought in connection with the interrelatedness of its episodes or developments.

Müller’s breaking up the old school notion of development initiated the study of a multitude of functional systems and a multitude of historical episodes. The organism, in *Für Darwin*, is much more a conjuncture of multiple episodes than a uniform functional development. Inheritance, Müller writes, may cause not only “individual variations with regard to the form of the parents,” but also changes of “the succession in time of the developmental processes” (1869: 114). The different episodes of developmental history are thought to be so independent that they are not tied to a particular time; their individual moments may shift. Moreover, their individuality may increase:

The changes of the larvae, independent of the progress of the adult animal, will become the more considerable, the longer the duration of the life of the larva in comparison to that of the adult animal, the greater the difference in their mode of life, and the more sharply marked the division of labour between the different stages of development. These processes ... increase the differences between the individual stages of development. (1869: 118)

But Müller also saw each of these stages as the material of natural selection, and this is what the Russian scientist Alexej Sewertzoff credited him for when he wrote that “[i]t was Müller who proposed that evolutionary changes of the adult forms arise not only from [selection among] these forms (what Darwin, Haeckel, and Weismann discussed), but proceed by means of *gradual*

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<sup>24</sup> William S. Dallas made the serious mistake of translating ‘gefälscht’ into ‘sophisticated’ (“it is frequently sophisticated [gefälscht] by the struggle for existence which the free-living larvae have to undergo” (Müller 1864: 77/1869: 114)). Perhaps Dallas (funded by Darwin) did not want a Darwinian phenomenon – the struggle for existence – to be associated with the negative term ‘falsification’.

*alterations of embryonic and larval development*” (West 2016: 90). In contrast to Sewertzoff, “Haeckel and his immediate followers neglected the idea of an evolutionary impact of ontogeny on phylogeny” (Levit, et al. 2004: 351).

Haeckel did, however, contribute to spreading Müller’s perspective on development – to which he made only minor changes. His significance for the deconstruction of biology further resides mostly in the fact that he coined many new terms to capture the new phenomena that new sciences were gradually starting to be concerned with. In relation to Müller’s innovations which contrasted the organism’s development with the development of the species, Haeckel called the former ontogeny and the latter phylogeny – although phylogeny refers to Haeckel’s particular notion of ‘species’, namely *phyla* (see Rieppel 2016: 50). Müller’s distinction between development which deviates and development which is rather a further advancement Haeckel also valued: He called palingenesis the kind of development which ‘recapitulates’ phylogeny and cenogenesis the breaks, “in ontogeny, of specially adapted stages” (Rieppel 2016: 56; cf. Nyhart 1995: 247-9).

## Conclusion

Insofar as idealistic morphology had not already done so, evolutionary morphology definitively recast comparative morphology into a historical mold. But this did not mean it broke with biology and initiated systematics. As Bowler, Nyhart, and Cassirer pointed out, evolutionary morphology was a non-revolution, failing to become a true ‘*historical morphology*’, as Cassirer put it. Müller’s breaking up of development into passages, transitions, or episodes at the edges of which a *few* directions stand open, as well as his cladogram – this diagram of passage-networks – should be seen as this historical morphology, or systematics. In contrast, Darwin’s ideal of genealogical classification was caught up in the conceptual entanglement of biology. Instead of structuring time, it would represent genealogies in its space, the historical table of the natural system. And instead of intimately connecting continuity and discontinuity – as Müller’s cladogram does by presenting phylogenetic relatedness – Darwin’s diagram opposed a sovereign history (the scale) to a diversity of genealogies. This sovereign history was also the pace, the function of nature’s diversity. For Darwin thought this diversity to really be, if properly understood, the continuous identity of *nature* in all its chained, ‘intermediate varieties’.

In Müller’s thinking the sovereign history is also the species history, but it does not determine the development of the organism; it is not its function. Rather, for Müller it has become so sovereign that the organism’s development only *reflects* the development of the species.<sup>25</sup> Whereas Haeckel reverts to biological thought when he writes that “phylogeny is the mechanical cause of ontogeny,” Müller breaks down the functional correspondence between phylogeny (or species) and ontogeny (or organism) (Haeckel (1874: 5) in Levit et al. 2004: 351). He does this *not simply* by turning the tables and writing that ontogeny may *erase* and *falsify* the *telos*, the ‘historical record’, since that would leave science within the opposition of ontogeny and phylogeny, of object and subject. Müller explains, *in addition*, that such fading and falsification of the species history is due to *other* functions affecting the organism. Function is multiplied, and intimately connected with different systems.

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<sup>25</sup> Although at the same time, Haeckel continued along this line and suggested that ontogeny and phylogeny are like two alphabets, punctuated by “simple deletions and interpolations” (Nyhart 1995: 249).

For it is not only function which is multiplied, the other half of the biological function-history nexus is multiplied too. Instead of a uniform development, Müller conceives of the organism's developmental history as more or less independent episodes or systems that are, in their own individuality, subject to such functional wholes as the struggle for existence. In this way, the separation between ecology and systematics is not so clearly present yet in *Für Darwin*. The life forms with which systematics and Müller's cladogram deal with as passages (dots in the diagram) related in a network of time(s) are also – in a rather continuous way – considered to be systems which take part in other functional wholes. This latter, ecological half of life science is, however, much more present in the work of Gottlieb Haberlandt and Wilhelm Roux.

Biology, and Müller insofar as he still works with this conceptual entanglement – let alone Darwin – are not part of life science. From this chapter we can conclude two key principles of biology, which show its difference: (1) life forms are nature's signs indicating their true identity; and (2) organisms are manifestations of life's functional history determining their organization and development (cf. figure 2 on page 10). Our recognition of a strange circularity in these principles is the distance that separates life science from biology. Whereas biology operated with a subject-object axis and a switch of representation between them, life science works differently. In order to see how, we must inquire further by proceeding chronologically to the scientists who were involved more with ecology than systematics.



# Chapter 3 – Biology and ecology

## Introduction

In 1885, the geographer Hanns Reiter wrote what he considered to be the first ecology, “an ecology of plants.”<sup>26</sup> He divided the study of plants into ecology, on the one hand, and morphology on the other. The historian Lynn Nyhart has also concluded that generally, in German biology at the time, a contrast emerged between ecology – or what was initially called ‘biology’ – and morphology: “the axis of tension lay not between morphology and physiology, between historical and mechanical causation, or between natural history and experiment, but between “biology” and systematics” (Nyhart 2009a: 24).<sup>27</sup> While the latter did not constitute much of a break with the nineteenth-century morphological tradition which had been dominated by Cuvierian comparative anatomy, ‘biology’ was in her view a new phenomenon in German society (Nyhart 2009a).

What is this ‘biological perspective’? Nyhart emphasises that it was identified in contrast to systematics, “as they implied fundamentally different ways of presenting and organizing information about nature” (2009a: 23-4). She equates systematics with evolutionary morphology, in this context, and we already saw in the previous chapter how she characterises it: as the study of “family relationships of closeness and distance, marked by similarities and differences of form. That is, to understand an organism’s “place in nature” was to set it into a framework of morphological similarities, differences, and degrees of relatedness” (2009a: 22). But we also saw that in the work of Fritz Müller emerged parts of a wholly different systematics, contemporary systematics.

Now, it is this latter systematics which I believe should really be contrasted to ecology. But systematics is more than the cladistics that we found in Fritz Müller. Ludwig Trepl (1946-2016), a German ecologist and historian of ecology, in his detailed and impressive history of ecology (1987), pointed at important developments in *plant geography* in the 1880s and 1890s, concerning questions about habitat (*Standort*), the place and space of plants, and vegetational types (Trepl 1987: 123-33). Although systematics is commonly seen, at first, as a historical study of life forms, it is surely also geographical. With Müller, then, we have inquired into the historical side of early systematics, which, if we rely solely on Müller, already emerged in the 1860s. The geographical side of systematics emerges in the 1880s, as does ecology, but unfortunately these Scandinavian and German plant geographers have not been part of my primary literature research, since only much later did Trepl’s book bring them to my attention.

However, we should discuss the insightful distinction that the plant geographer Oscar Drude made between ecology and systematics. He writes: “In explanations one should ... distinguish between the reason why a certain plant occurs in a certain locality, and the external and internal

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<sup>26</sup> The title of the book is *Die Consolidation der Physiognomik als Versuch einer Oekologie der Gewächse* (1885). Cf. Trepl 1987: 114, note 48.

<sup>27</sup> Concerning the historical shift from the word ‘biology’ to ‘ecology’, Nyhart writes: “[The] research stream [of biology] would win out in its claims to generality, and therefore its claim to the term “biology,” and as chapter 8 discusses, around 1910 advocates of the biological perspective would drop the term “biology” to use the term “ecology” for their field of interest” (2009a: 24). Trepl has a different view on this name change (cf. Trepl 1987: 78).

means by which it achieves its *enduring preservation*.”<sup>28</sup> Ecology would deal with this ‘ongoingness’ while systematics seeks to discern the occurrence, or the facticity of life and life forms. The verb for ecology, the noun for systematics. Drude continues with an example of a water plant that relies on warm standing water and which therefore can only expand to similar warm waters. These living conditions and the climate in which the plant lives are the subject of ‘biology’, he writes in the parlance of his time. “But the occurrence of such a plant *here and there*, its existence in the lands concerned at all, is a wholly separate question: the water plants concerned may have been dragged along by migratory birds ..., they may have first come into being here or there as a species on Earth ... In this area of inquiry rules a different being than in the biological field ...”<sup>29</sup>

Plant geography is interested in networks of passages, where at each passage a transformation and a new coming-into-being takes place, as the plant starts to live where, for example, it was dragged by migratory birds. We had so far assumed that systematics is the study of such a *historical* network, as it was for Müller and is today for cladists. But there is no historical passage for systematics to study that is not also a geographical one; ancestral relatedness is *historico-geographical*. Life forms *took and take place*: that is the subject of systematics, a historical as much as geographical study of life.

This concern for the geographical aspect was present not only in the ordering of life forms (among some Scandinavian and German plant geographers and botanists in the 1880s and 1890s) but also in the study of the organic processes that make up organisms. Nyhart writes that in the ‘biological perspective’ – which we understand as ecology,

the primary relationships were ... those ... of function, emphasizing relationships among organisms, their physical *environment*, and their *geographic* and ecological *place* in the world. ... an organism’s *place in nature* was established in good part by its *geographic* or physical “*place*,” as well as its *location in a web* of functional and physical relationships (Nyhart 2009a: 21-2; emphasis added).

If we follow Nyhart here, it thus seems that early ecology revolved largely around spatial inquiry. We may add that Wilhelm Roux – a major ecologist in this chapter – was not trained as a physiologist but as an anatomist, dissecting the spaces of the organism. Finally, as already mentioned, the first ecology was written by the *geographer* Hanns Reiter. Life science emerged with a great concern for the space(s) of life forms because biology, especially in the second half of the nineteenth century, had been saturated with the historical aspect of organisms. The conceptions of historical issues were so deeply entrenched in biology that conceptual progress in life science could initially be made more easily in geographical study of life. Thus, rather than an instant translation of all historical topics into life science, we might in part see an initial displacement of attention towards geographical topics.

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<sup>28</sup> “Man muß nämlich in den Erklärungen unterscheiden warum eine bestimmte Pflanze an einer bestimmten Lokalität *auftritt*, und mit welchen äusseren und inneren Mitteln sie daselbst ihre *fortdauernde Erhaltung* erzielt” (Drude 1890: 9; in Trepl 1987: 120; his emphasis).

<sup>29</sup> “Aber das Auftreten einer solchen Pflanze *hier und dort*, das Vorhandensein in dem betreffenden Lande überhaupt, ist als eine ganz getrennte Frage zu behandeln: die betreffende Wasserpflanze kann durch wandernde Vögel mitgeschleppt ..., sie kann hier oder dort als Art auf der Erde zuerst entstanden sein ...” (Drude 1890: 9; in Trepl 1987: 120).

## Section 3.1 – Ecology and Hanns Reiter

What is ecology? Trepl traces it all the way from its ‘pre-history’ in the Renaissance and in natural history to its emergence around 1800. It emerged due to the fact, “that ... the categorial horizon in the area of the concept of ‘living being’ shifted.”<sup>30</sup> Trepl here follows Foucault’s archaeology of natural history (early modern period) and of biology (nineteenth century). Without delving into this transition of around 1800, let us see how Trepl believes that ecology belongs to, and in fact emerged in biology. First, in biology the relation and interaction between structure and function is central. There is a morphological organism *and* a physiological organism, and there is an organism *and* an environment.<sup>31</sup> Life depends on certain conditions of existence that may disappear, and so they figure as the abstract counterpart to life, as the death which makes it possible. For Cuvier, a single bone of a skeleton was enough to deduce the internal organization and way of life of the once living organism.

Secondly, Trepl writes that biology confronted natural history essentially with the question “Why has ‘someone’ (God, ‘nature’) arranged something in this way?”<sup>32</sup> The purpose of life does not fully coincide with the life forms themselves; there is a space left to inquire into the relation between the purpose and the arrangement. Life forms are arranged in a certain way and it is the duty of the biologist to discern this purposeful organisation and development – because the purpose ‘is there’; it only requires some divination on the part of the scientist. Life forms reflect purpose, represent purpose, and the scientist will strive to understand that structure of representation. ‘How does the form indicate its function?’ Such interpretation of life’s ‘writings’ is what constituted the art of biology.

Trepl finds the emergence of ‘ecology’ in the importance that biology accorded to the relation between environment and organism (cf. Foucault 2017: 229). He cites Cuvier: “As nothing can exist unless it combine within itself certain conditions which render its existence possible, the component parts of each must be so arranged as to render possible the whole being, not only in itself, but also in its relations with those that surround it.”<sup>33</sup> The environment here thus figures as part of the conditions that underlie an organism’s existence, alongside its internal coherence. That is to say, the relation between environment and organism is functionally one-sided: The environment determines the organism. But in fact, it is more profound: Environment and organism are functionally separate entities in biology. Their relation is a clean and distant one, in which each retains its integrity (and in which the environment may swallow the organism, thereby ending the relation). This is how *adaptation* was studied at the end of the nineteenth century, in biology: The

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<sup>30</sup> “... daß sich in der Tat um 1800 der kategoriale Horizont im Umkreis des Begriffs des „Lebewesens“ derart verschob, daß man erst von dieser Zeit an von Ökologie in unserem Sinne sprechen kann” (Trepl 1987: 89).

<sup>31</sup> See Trepl (1987: 93-5) and especially Foucault (1966: 238-245, 275-292/1994: 226-232, 263-279).

<sup>32</sup> “Warum hat „jemand“ (Gott, „die Natur“) etwas so eingerichtet” (Trepl 1987: 98).

<sup>33</sup> I changed the translation of the last part, “not only with regard to itself, but to its surrounding relations” (Cuvier 1840: 14-5). The French original: “Comme rien ne peut exister s’il ne réunit les conditions qui rendent son existence possible, les différentes parties de chaque être doivent être coordonnées de manière à rendre possible l’être total, non-seulement en lui-même, mais dans ses rapports avec ceux qui l’entourent, ...” (Cuvier 1829: 5-6). Trepl’s German citation (1987: 94-5) of Cuvier differs yet again on the last part: “... so müssen die verschiedenen Theile eines jeden Naturkörpers so zusammengeordnet seyn, daß das Gesamtwesen derselben nicht nur in sich selbst, sondern auch in Beziehung auf seine Umgebungen möglich sey” (Cuvier 1831: 4).

organism changes due to a functionality that comes from a real outside, the environment. Haeckel's definition of ecology is revelatory:

By ecology we understand the entire science of an organism's relations to its surrounding environment [Aussenwelt], in which we may include, in a wider sense, all "conditions of existence". These are partly of organic, partly of inorganic nature; both are, as we have shown before, of utmost importance for the shape of organisms because they force it to adapt itself to them.<sup>34</sup>

At the same time, however, the relation between organism and environment started to be thought differently, more geographically – horizontally, one might say. The scientific efforts of plant geographers in Scandinavia and Germany in the 1880s<sup>35</sup> – the birthplace of ecology as a discipline, in Trepl's view – is related to the history of the nineteenth-century tradition of physiognomy. This study of the aesthetic appearance of life forms (in contrast to morphology's anatomical study) is also discussed by the geographer Hanns Reiter, who strives to surpass it in order to finally create a truly ecological classification of life forms. Following Reiter's compass, we may find work of physiognomy in Alexander von Humboldt's *Ideen zu einer Physiognomik der Gewächse* (1806), in Matthias J. Schleiden's lecture "Die Aesthetik der Pflanzenwelt" (1848: 285-329), and most importantly, in August Grisebach's *Die Vegetation der Erde nach ihrer klimatischen Anordnung* (1872).<sup>36</sup>

According to Trepl (1987: 123), physiognomy developed throughout the nineteenth century so that it increasingly sought to connect vegetational types (such as high forest or shrub-wood) to certain habitats (*Standorte*), such as steppe and marshes. Different vegetation thus increasingly related to its conditions of existence, the habitats, that made it possible. But "[t]he result was an image of the living community as determined in one direction, by external conditions, ahistorical and 'non-geographical'."<sup>37</sup> Non-geographical and ahistorical because "the concrete place was a matter of coincidence. In all places where certain habitat conditions reigned, one could expect (at least as a consequence of the approach) the corresponding living community."<sup>38</sup> In other words, this was a classification of aesthetic forms, free-floating and separated from their history and geography.

Now, Hanns Reiter, Eugene Warming – and no doubt other plant geographers such as those mentioned in note 35 – sought to break with this tradition and create instead a truer, ecological classification of life forms.<sup>39</sup> Reiter tried to do so by starting from three principles, based largely on

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<sup>34</sup> "Unter Oecologie verstehen wir die gesammte Wissenschaft von den Beziehungen des Organismus zur umgebenden Aussenwelt, wohin wir im weiteren Sinne alle „Existenz-Bedingungen“ rechnen können. Diese sind theils organischer, theils anorganischer Natur; sowohl diese als jene sind, wie wir vorher gezeigt haben, von der grössten Bedeutung für die Form der Organismen, weil sie dieselbe zwingen, sich ihnen anzupassen" (Haeckel 1866: 268; my emphasis).

<sup>35</sup> Besides Oscar Drude, they are Eugene Warming, Ragnar Hult, Rutger Sernander, Hampus von Post, Carl Schröter. See Nicholson (1996) for more on their scientific developments in what may be seen as early phytosociology, or syntaxonomy. Trepl writes about von Post on page 132.

<sup>36</sup> Soon after Reiter's effort also Eugene Warming (1895) and Andreas F. W. Schimper (1898).

<sup>37</sup> "Das Resultat war ein Bild der Lebensgemeinschaft, das in einer Richtung, und zwar durch äußere Bedingungen, determiniert, unhistorisch und „ungeographisch“ war" (Trepl 1987: 123).

<sup>38</sup> "Letzteres gilt in dem Sinne, daß der konkrete Ort zufällig war. Überall, wo bestimmte Standortbedingungen herrschten, konnte man, wenigstens in der Konsequenz des Ansatzes, die entsprechende Lebensgemeinschaft erwarten" (ibid.).

<sup>39</sup> Warming mentions Reiter's work rather dismissively, quickly concluding that "his 'system' must allow for improvement" ("Aber auch sein „System“ muss verbessert werden können") (Warming 1895: 6). On Warming himself, see Coleman (1986).

his criticism of Grisebach's physiognomy.<sup>40</sup> Firstly, whereas Grisebach had not distinguished between hereditary and adaptational characters (in the case of vegetative organs), Reiter (1885: 180-1) believed life forms should be classified exclusively according to characters that were due to adaptation. Secondly, Reiter states that the characters which explain the physiognomy should be taken not only from the total outward appearance, the "external bearing" ("*äußeren Habitus*"), of the form (as Grisebach did) but also from its internal condition (id.: 179, 181). Both are needed to explain "the gear [*Ausrüstung*] of forms for the performance of their life appearances."<sup>41</sup> Finally, whereas Grisebach had considered "only those forms which attract our attention with the plentiful occurrence of their individuals," Reiter believes "all types marked by a peculiar way of life and gear" should be considered for classification.<sup>42</sup>

In this way would be classified the vegetational form, that is, "living beings which accord with each other in each of their important parts qua life activity and corresponding gear [*Ausrüstung*]," regardless of their genetic or taxonomic relations.<sup>43</sup> This is therefore still an aesthetic classification, like those earlier ones in biology, because it is not concerned with hereditary characters. But crucially, the aesthetics of forms are now themselves historical and geographical. Forms of *adaptation* are classified because the focus is on "life activity and corresponding gear," which are understood to depend on the specific situation of the plant. The local contingency of a form is thus no longer incompatible with its aesthetics. For the vegetational form is precisely constituted, for Reiter, by everything that is contingent about it, whether this is external or internal (cf. the second principle).

However, in the distinction between "life activity and corresponding gear" we also find again the major biological notions of function respectively structure. Let us zoom out with Reiter and consider his view of the study of life. There is ecology and morphology, he writes. The former is supported by anatomy and physiology while the latter uses anatomy and developmental history. Ecology inquires into "the phenomena of adaptation, which are brought about by the nexus between variability and the natural conditions of existence."<sup>44</sup> Its anatomy half studies "the shape and structure of the finished form," while its physiology part deals with "the activity of the form

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<sup>40</sup> "1. Zur Unterscheidung der Vegetationsformen nur diejenigen Merkmale heranzuziehen, welche, soweit wir heute zu beurtheilen im Stande sind, als das Resultat nachheriger Anpassung erscheinen; 2. die Ausrüstung der Formen zur Verrichtung ihrer Lebenserscheinungen nicht nur nach ihrem äusseren Habitus, sondern auch ihrer inneren Beschaffenheit (CP181) nach darzulegen, und 3. nicht nur die durch massenhaftes Auftreten ihrer Individuen auffallenden Formen zu berücksichtigen, sondern, so weit es im gegenwärtigen Augenblicke möglich ist, aller durch eigenartige Lebensweise und Ausrüstung gekennzeichneten Typen zu gedenken" (Reiter 1885: 181-2).

<sup>41</sup> See note 39. Compare for the interesting notion of gear (*Ausrüstung*) Warming's use of the term 'Tracht' (attire): "Diese [die Lebensform] zeigt sich besonders in der Tracht und in der Gestalt und Dauer der Ernährungsorgane" (Warming 1895: 3).

<sup>42</sup> See note 39. The citation on Grisebach is partly from page 179: "und [Grisebach] zog zweitens nur diejenigen Formen in Betracht, welche uns durch das gesellige Auftreten ihrer Individuen in die Augen fallen"

<sup>43</sup> "sämmliche Lebewesen ..., welche in Bezug auf ihre Lebensthätigkeit und die dazu gehörige Ausrüstung in allen wesentlichen Stücken untereinander übereinstimmen, mögen sie nun nahe verwandt sein oder nicht, also derselben oder verschiedenen Arten, derselben oder verschiedenen Gattungen, derselben oder verschiedenen Familien u. s. w. angehören" (Reiter 1885: 5). According to Warming (1895: 4), Grisebach introduced the term 'vegetational form', which, however, was used differently by different authors, he notes.

<sup>44</sup> "die Erscheinungen der Anpassung, die der Connex zwischen der Variabilität und den natürlichen Bedingungen der Existenz hervorgerufen hat, zum Ausgangspunkte wählt" (Reiter 1885: 4).

and the adaptation of activity to the conditions of the surrounding nature” (1885: 5).<sup>45</sup> Thus, although the study of structure and function seem to be separated, physiology itself nonetheless also inquires into structure (activity) and function (the conditions). Reiter presents us with a mix of biological and life-scientific elements.

Yet, we read here in these few lines from Reiter’s ecology book an understanding of adaptation which has little to do with that of Haeckel’s biological one. The latter wrote that the conditions of existence (the external environment) force the shape of an organism to adapt itself to them. In this way, function is posited firmly opposite to structure (Haeckel 1866: 286). In Reiter’s considerations, however, adaptation is much more a phenomenon in its own right, to the expense of both structure and function. An organism’s internal and external sides are both necessary for understanding its gear – its *purposive form*. In turn, the gear is as important as the organism’s life activity for determining its vegetational form. Thus, if we should still consider gear to be form here, then the vegetational form – by encompassing both gear and life activity – might be a concept of a ‘form-function’, a vegetational system.

Nonetheless, the vegetational form is called a ‘form’ and the relations among the plants that it covers is based solely on homogeneity: It defines “living beings which accord with each other.” There is no conception of interrelations except for this sheer similarity. And so the functionality that we associated with the vegetational form also cannot consist in the interrelations of the different elements of a vegetational form; this is prevented by their homogeneity. The functionality of the vegetational form rather concerns, biologically, an unnamed outside, unnamed conditions of existence, which render the vegetational form functional in the sense of *adapted*. It is a functional form not because it entails functionality but because it relates to it, beyond its own structural integrity.

## Section 3.2 – Gottlieb Haberlandt

Some of Reiter’s main ideas were derived from the work of a revolutionary Austrian botanist, Gottlieb Haberlandt. He pursued precisely the integration of physiology and anatomy into one science, which Reiter called ‘ecology’, with his influential 1884 book *Physiologische Pflanzenanatomie*.<sup>46</sup> In contrast to Reiter’s work, classification plays only a minor role in it. Primarily focused on physiology and anatomy of individual plants, it had little to do with plant geography. But an integrated physiological-anatomical approach to plants was crucial and beneficial to young botanists with an interest in the geography and adaptation of plants. Many of Haberlandt’s students ventured out into the most non-European regions of the world then accessible for plant

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<sup>45</sup> “die Gestalt und Structur der vollendeten Form kennen zu lernen”; “die Ermittlung der Thätigkeit der Form und die Anpassung der Thätigkeit an die Bedingungen der umgebenden Natur” (id.: 5).

<sup>46</sup> This textbook for a new approach to the study of plants went through six editions up to 1924 (Cittadino 1990: 38). It inspired many German botanists at the time, including for example Georg Volken, A. F. W. (Andreas) Schimper and Heinrich Schenck. In 1898, Henry Chandler Cowles, in the USA, based his first independent course – ecological anatomy – on precisely this book (id.: 151). Reiter (1885) repeatedly refers to Haberlandt (1882a; 1882b) and uses an early version of his classification of tissue systems. Eugene Warming and Alexander Tschirch later also used it, taking the classification from his 1884 *Physiologische Pflanzenanatomie* (Haberlandt 1896: 62).

study, such as the Sahara and especially Java, through the Buitenzorg botanical research station.<sup>47</sup> It seems to me that in contrast to the Scandinavian botanists who were interested in vegetation and large-scale botanical phenomena, these German botanists, Haberlandt included, focused rather on the individual plant and the relations to its immediate environment in a more anatomical-physiological, less botanical way.

Adaptation, however, was a central subject for both approaches to the study of plants. Classification, too, was used and developed in the botanical study of the vegetative world and in the study of the physiology and anatomy of plants. To illustrate, the famous book *Oecology of Plants* by Eugene Warming (a botanist by training) is rife with anatomical and physiological observations of individual plants to support his order of ecological classes (such as lithophytes and hydrophytes) and Haberlandt's *Physiologische Pflanzenanatomie* elaborates a classification of tissue systems to guide and arrange his physiological-anatomical discussions of plants. Certainly there is a difference between ecological classes and tissue systems but, at bottom, they are both ecological units, as they cover structure and function without distinction.

Haberlandt was one of the first scientists of life who worked with and defended an approach beyond the structure-function division.<sup>48</sup> His new physiological anatomy appears to be completely at odds with biology. For biology hinged on the distinct existence of physiology and anatomy, separately inquiring into function respectively structure. It comes as no surprise, then, that Haberlandt's approach was cause for outrage among established botanists. "Opponents of Haberlandt's approach did not deny the functional significance of particular plant structures, they simply disagreed with Haberlandt's view that structure is best studied in terms of function. They insisted that structure must be studied in and of itself" (Cittadino 1990: 42). Now, this was precisely what Haberlandt rejected to do.

Instead of structures, Haberlandt started to study new, physiological-anatomical research objects, which he called 'systems', tissue systems in particular. He writes (1882a: 557) that one usually divides plant tissue in different tissue forms or types, and that these refer to conjunctions of cells which share one or more characters; the characters being topographical, morphological, physiological, or development-historical. It might appear, he continues, that it is of little significance which characters are used to determine the classification of tissues. Nonetheless, if the ordering is to be natural and grounded in the subject itself, then the determining characters should be the most characteristic ones. Moreover, since the plant body differentiates itself into different tissue types in close accordance with their physiological functions, any morphological character should really be considered an anatomical-physiological character (if it indeed accords with its physiological function). Now, it is clear then, Haberlandt concludes, that such anatomical-physiological characters would provide the most natural and widest foundation for the classification of tissues. "For plants the diversity of tissues only has a sense and a meaning if it is at

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<sup>47</sup> Georg Volken, a student of Simon Schwendener (like Haberlandt), studied desert flora in the Sahara (id.: 66). Andreas Schimper, Ernst Stahl, Alexander Tschirch, and many others visited Buitenzorg (run by the Dutch botanist Melchior Treub) in the 1880s and 1890s to carry out plant research (Cittadino 1990: e.g. page 110).

<sup>48</sup> Haberlandt, in turn, credits his mentor Simon Schwendener for having seen the light of a physiological anatomy (with his *Das mechanische Princip im anatomischen Bau der Monocotylen*, 1874) but, overall, Haberlandt's work was more significant and impactful. So far, not much has been written on Haberlandt within the history of science; a notable exception is Eugene Cittadino's *Nature as the Laboratory* (1990). Also see a biographical article on Haberlandt, written by one of his many students (Noé 1934).

the same time connected with a diversity of physiological functions” (Haberlandt 1882a: 559).<sup>49</sup> Only a classification of anatomical-physiological systems – tissue systems – is acceptable.

This diversity of physiological functions essentially constitutes, in Haberlandt’s view, the life of the plant: “a sequence of different physiological functions ..., which intertwine in a manifold and complex way” (id.: 557). They are not only diverse but some “even reach beyond the single individual, as their goal is the preservation of the entire species” (i.e. the reproductive organs) (ibid.).<sup>50</sup> Given all of this diversity and complexity, how is it possible that the physiological functions still maintain a required stability? The reason is not the correlation of parts, Cuvier’s famous principle. It is not because “in every being life is a whole, resulting from the mutual action and reaction of all its parts,” that the plant is an organised being (Cuvier 1840: 18).<sup>51</sup> Rather, “the most important means ... to attain the necessary equality and certainty ... consists in the realisation of the principle of the *division of labour*” (Haberlandt 1882a: 557).<sup>52</sup> Instead of an integrity at the core of the living being – i.e. organisation, life – a division is presupposed. Instead of a functionality which radiates from an abstract centre, there is a diversity of mutually irreducible physiological functions operating through their “most far-reaching accordance [with] the morphological structure” (ibid.).<sup>53</sup> An example are the cells of a plant body, those “innumerable small workers, basic organisms ..., which may be assigned diverse tasks with much greater ease than a single, undivided, large plasma body would” (id.: 558).<sup>54</sup>

But how should the scientist explain the plant’s cellular structure? How should organic phenomena be explained in a physiological-morphological way, accounting for the system rather than the function *and* structure? Haberlandt writes that, normally, scientific explanation follows one of two different paths. Research is either causal-mechanical – “What combinations of chemical and physical forces effects the realization of the morphological figure?” – or teleological: “What is

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<sup>49</sup> “Für die Pflanze hat die Verschiedenartigkeit der Gewebe blos insofern einen Sinn und eine Bedeutung, als damit zugleich eine Verschiedenheit der physiologischen Functionen verknüpft ist;”

<sup>50</sup> “Das Gesamtleben der Pflanze setzt sich aus einer Reihe verschiedener physiologischer Functionen zusammen, welche vielfach und complicirt ineinandergreifen und deren Endzweck in der Entwicklung des werdenden, in der Erhaltung des ausgebildeten Individuums besteht. Die Bedeutung gewisser physiologischer Vorgänge reicht sogar über das einzelne Individuum hinaus, indem dieselben die Erhaltung seiner ganzen Art zum Zwecke haben.”

<sup>51</sup> “Each part concurs in this general movement by a peculiar action, and experiences from it particular effects; so that, in every being, the life is a whole, resulting from the mutual action and reaction of all its parts. / Life, then, in general, presupposes organization in general, and the life proper to each being presupposes the organization peculiar to that being, ... ” The French original: “Chaque partie concourt à ce mouvement général par une action propre et en éprouve des effets particuliers ; en sorte que, dans chaque être, la vie est un ensemble qui résulte de l’action et de la réaction mutuelle de toutes ses parties. / La vie en général suppose donc l’organisation en général, et la vie propre de chaque être suppose l’organisation propre de cet être, ... ” (Cuvier 1829 : 14).

<sup>52</sup> “Das wichtigste Mittel, welches dem Organismus zu Gebote steht, um die nothwendige Gleichmässigkeit und Sicherheit seiner physiologischen Functionen zu erzielen, besteht in der Durchführung des Principis der *Arbeitstheilung*.”

<sup>53</sup> “Indem jede wichtige physiologische Leistung einem eigens dazu bestimmten Organe oder Gewebe übertragen wird, kann sich die weitgehendste Uebereinstimmung zwischen dem morphologischen Aufbau dieser einzelnen Apparate und den ihnen zugetheilten physiologischen Leistungen ausbilden.”

<sup>54</sup> “Es sind damit unzählige kleine Arbeiter, es sind Elementarorganismen gewonnen, welchen mit viel grösserer Leichtigkeit verschiedenartige Aufgaben zugewiesen werden können, als einem einzigen, unzertheilten, grossen Plasmakörper.”



the morphological fact's final purpose for the organism as a living being?" (id.: 561).<sup>55</sup> Causality is either a matter of efficient cause or of final cause – and they cannot exist independently from each other, Haberlandt notes. But, clearly – he seems to imply – neither is sufficient for a truly anatomical-physiological science.

At this moment, Haberlandt has Darwin enter the text, as the harbinger of a radically new way of doing science which breaks apart that distinction between efficient and final causes. "By a stroke of genius," Darwin found "the mechanical formula for the teleological mode of explaining" (ibid.).<sup>56</sup> How? By showing that "in the 'struggle for existence' only those morphological variations are fixed through inheritance which ensure as certain, complete, and smooth a progress of all physiological functions as possible" (id.: 560-1).<sup>57</sup> The stability of the organism is thus explained not by referring to the organism's internal dynamics themselves, but by referring to the 'struggle for existence', that is, to the dynamics of the population to which the organism belongs.

This idea that the 'struggle for existence' causes the organism to be the way it is, i.e. stable and of a particular form, Haberlandt considers to be the solution to the division of efficient and final causes. Darwin's theory, in his view, provides both causal-mechanical and teleological explanation for the organism's particular structure. With Darwin, "the efficient causes are connected with the final causes" – but they affect different life units! For "the ones [the efficient causes] effect the realisation of the morphological fact in the development of the single individual, while the others [the final causes] realise the same in the historical development of the entire species" (id.: 562).<sup>58</sup> Although Haberlandt himself disagrees, Darwin's theory (thus understood) certainly appears to be short of an integration (at the same level) of efficient and final causes.

But what is really at stake here are not these different kinds of causality but rather structure and function. For the stated goal, "the task of the anatomical-physiological research direction [is] to reveal the causal nexus between structure and function" (ibid.; emphasis added). Even here, however, Haberlandt appears to contradict himself when he adds that this means "to explain the structure of plant tissues on the basis of their physiological performances" (ibid.).<sup>59</sup> A causal nexus

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<sup>55</sup> "Welche Combinationen von chemischen und physikalischen Kräften bewirkt das Zustandekommen der morphologischen Erscheinung? ... Welchen Endzweck hat die morphologische Thatsache für den Organismus als lebendes Wesen? Mit anderen Worten: welches ist ihre physiologische Function, und in welcher Weise giebt sich die morphologische Thatsache als Mittel zu diesem Zwecke zu erkennen?"

<sup>56</sup> "Durch einen »Zauberschlag des Genies« wurde nun auf einmal die Scheidewand durchbrochen, welche die mechanische und teleologische Erklärungsweise trennte und der lang zurückgestaute Strom der Forschung konnte sich ungehindert in das neue breite Bett ergiessen. Dem Scharfsinne Charles Darwin's blieb es bekanntlich vorbehalten, für die teleologische Erklärungsweise die mechanische Formel zu finden."

<sup>57</sup> "Or, more precisely put, preserved through inheritance are those combinations of chemical and physical forces which induce causal-mechanically in each single individual of the species concerned the beneficial morphological characters." The German original: "Im »Kampfe ums Dasein« werden nur jene morphologischen Variationserscheinungen durch Vererbung fixirt, welche einen möglichst sicheren, vollständigen und glatten Verlauf aller physiologischen Functionen gewährleisten. Oder genauer gesagt, es bleiben diejenigen Combinationen von chemischen und physikalischen Kräften durch Vererbung erhalten, welche bei jedem einzelnen Individuum der betreffenden Species die vortheilhaften morphologischen Eigenschaften causalmechanisch hervorrufen."

<sup>58</sup> "So werden die wirkenden Ursachen mit den Endursachen verknüpft; die einen bewirken das Zustandekommen der morphologischen Thatsache in der Entwicklung des einzelnen Individuums, die anderen dagegen bewirken das Gleiche in der historischen Entwicklung der ganzen Species."

<sup>59</sup> "Weil es nun, wie wir oben gesehen haben, die Aufgabe der anatomisch-physiologischen Forschungsrichtung ist, den Causalnexus zwischen Bau und Function aufzudecken, d. h. den Bau der Pflanzengewebe auf Grund ihrer physiologischen Leistungen zu erklären, so hat diese Richtung selbstverständlich die Anerkennung der Grundlehren des Darwinismus zur Voraussetzung;"

between structure and function is different from a causal determination of structure by function. This confusion is tied to Haberlandt's misguided appreciation of Darwin in this text. According to Haberlandt, the efficient causes – although they are purely mechanical, devoid of functionality, of life – realise the individual's morphology while the final causes – although they exclude structure – realise the species' morphology. It seems to me that precisely this distinction between efficient and final causes (mechanism and vitalism) prevented Haberlandt from articulating a consistent new research programme truly integrating the study of structure and of function.

Despite Haberlandt's confusion about causality in the midst of a profound epistemic shift that transformed biology's entire basic entanglement of principles and dichotomies, he inquired productively into the causal nexus between structure and function, into plant tissue systems in particular.<sup>60</sup> Before even discussing the Aristotelian types of causes or Darwin's 'struggle for existence', Haberlandt wrote that he considered these different anatomical-physiological systems to be the product of morphological differentiation, driven by the principle of the division of labour (Haberlandt 1882a: 557-8; 1882b: 76; 1884/1896: 47, 51). This principle, as an abstract function or goal, is, for Haberlandt, the cause of morphological differentiation. As such, his explanation follows the structure of the final causes, as defined by himself: The purpose of the structure (the division of labour) is conceived of as the causal function that produced the structure all along. This is typically biological, function-causes-structure thinking.

On the one hand, Haberlandt breaks apart the unity of physiological function by introducing a plurality of different physiological processes or systems: the dermal system, mechanical system, nutrition system, photosynthesis system (still called 'assimilation system' at the time), and others. On the other hand, these systems and processes are governed by a more abstract function, namely the division of labour, which through morphological differentiation caused the existence of diverse structures in the first place. Unlike the systems, the division of labour is not tied to a specific life unit (e.g. the organism, a tissue system, a species, etc.), rather appearing as a general 'law of life', a biological function without place.

The central question which Haberlandt set out to answer was: How can we know from "an anatomical-physiological tissue system, ... up to the smallest detail of its anatomical structure, the adaptation to the task that the division of labour assigned it?"<sup>61</sup> The division of labour demands adaptation to tasks from the systems, and it is this adaptation – as it were in between an abstract function and concrete functional-structural systems – that needs to be explained. Cuvier claimed around 1800 that he could deduce the nature and way of life of an animal organism simply by looking at one of its bones, thus inferring its total functionality from a detail of its anatomical structure. At first glance, Haberlandt seems to suggest similarly that functionality will be explained by structure. But is it the division of labour or adaptation which explains structure? Functionality is strangely doubled. And so is structure, for one might equally ask whether the division of labour explains adaptation or the anatomical structure? In any case, the notion of a process – adaptation

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<sup>60</sup> I have not looked into his later work. Noé (1934: 854) mentions that Haberlandt researched plant hormones in the 1910s, and "expressed the hope that some day somebody else might give an independent treatment of evolutionary physiological anatomy of plants (Entwicklungsphysiologische Anatomie) as a counterpart of the functionally physiological anatomy which he formulated in his handbook" (id.: 852).

<sup>61</sup> "ob mit anderen Worten die chlorophyllführenden Zellen der Pflanze ein anatomisch-physiologisches Gewebesystem vorstellen, welches bis in das kleinste Detail seines anatomischen Baues die Anpassung an die ihm durch die Arbeitsteilung übertragene Aufgabe erkennen lässt?" (1882b: 75).

– is in the key position, right in between the two categories – function and structure – which organised the biological format of explanation.

Haberlandt soon considered the single principle of the division of labour insufficient and added more such principles, now calling them “structure and organisation principles,” or in Cittadino’s rendering, “organizing principles” (1990: 37).<sup>62</sup> He writes, in *Physiologische Pflanzenanatomie*, that these “principles of [the] histological structure and organisation” of any tissue “are given by [its] physiological function.”<sup>63</sup> This physiological function is in turn determined by the division of labour. However, one of the organising principles is, in fact, the principle of the division of labour. This occurrence of circular reasoning in Haberlandt’s conceptual framework no doubt relates to the fact that he attempted a reconciliation of biology and life science. But more interesting is the fourfold structure of his framework, in which the division of labour and the physiological function are on one side while the organising principles and the tissue systems are on the other. The first two elements are of a fully functional nature while the latter two are to some extent also morphological. Each set seems to consist of a relative part and a whole: The physiological function is the local functionality distributed at a general level by the division of labour; the tissue systems are local anatomical-physiological phenomena guided by organising principles which, in turn, are also such phenomena but operative on a wider scale.

Take, for example, the mechanical principle. It entails that “every detail of construction must satisfy the laws of mechanics” (Cittadino 1990: 37). But since every detail is nothing but a part of the plant’s mechanical tissue system, it is rather obvious that it accords with the laws of mechanics. Having introduced the idea of an anatomical-physiological system, it becomes redundant to speak of functionally determined structures. Haberlandt himself writes that an “anatomical-physiological tissue system ..., in our view, ... forms a closed unity, grounded in the identity of its function.”<sup>64</sup> Thus, any detail of construction is not so much a structure determined by a function, as it is a part of a whole, namely the mechanical system. Another conclusion we can draw here is that the notion of principle coincides with that of the system, a purpose-structure. There is no principle existing separately from the system; it is rather inherent to it. The only real distinction one may draw between the system and the principle is the pragmatic one that the principle resides in the realm of science – if it would be true that the system does not.

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<sup>62</sup> “die Bau- und Anordnungsprincipien” (1884/1896: 47). They were, alongside the principle of the division of labour, “(2) the mechanical principle (every detail of construction must satisfy the laws of mechanics); (3) the principle of economy of material (the greatest result must be obtained with the smallest expenditure of material); (4) the principle of maximum exposure of surface; [and] (5) the principle of efficiency” (Cittadino 1990: 37).

<sup>63</sup> “According to what we said previously, for each single tissue the principles of its histological structure and its organisation are given by the physiological function allocated to it.” The German original: “Für jedes einzelne Gewebe sind nach dem Vorausgegangenen die Principien seines histologischen Baues und seiner Anordnung durch die ihm zugetheilte physiologische Function gegeben” (1884/1896: 46-7).

<sup>64</sup> “Ein und dasselbe anatomisch-physiologische Gewebesystem kann ontogenetisch wie phylogenetisch sehr verschiedener Herkunft sein, wie z. B. das mechanische System, es bildet aber trotzdem von unserem Gesichtspunkte aus eine geschlossene Einheit, die in der Identität der Function begründet ist” (Haberlandt 1884/1896: 52).

## Conclusion

Haberlandt's thinking reveals the contours of life science. In his writing physiology recedes to the background, as function is thought less and less as the abstract, purposive history operating in the deepest core of the organism, as life, the counterpart to death, and the organism's purposive integrity. Comparative anatomy also recedes to the background, as Haberlandt does not inquire into the signifying parts of a meaningful whole – the characters of a type. Rather, these parts are functionally integrated within a whole, which is a concrete, purposive system. Any such a system or localised process is, then, understood not with causes but with principles inherent to it. The subject of research in ecology is the nexus between process and part/whole: How do processes that bring about B from A relate to the part-whole relation of A and B? How does the 'dividing of labour' relate to the 'morphological differentiation' of plant tissue, as Haberlandt may have asked himself?

We can also conclude that regarding the question of the emergence of ecology, it did not come about in the way Trepl believed it did. In his view, nineteenth-century physiognomy importantly connected the physiognomy with the habitat of vegetation. When the notion of species was added, the result was "an image of the living community as determined essentially by internal processes, by relations between organisms, which are, or at least may be, essential for the history and the concrete place."<sup>65</sup> In combination with the idea of competition, this notion of the living community established the conceptual basis for the ecological discipline, Trepl believes (1987: 134). Although, as we have seen, this is certainly not the case for ecology as I understand it, it might be true for a more narrowly understood ecology. In any case, from the archaeological perspective, the living community probably emerged as one among many new, anatomical-physiological, or *ecological* systems. We have discussed Haberlandt's tissue systems in this chapter and we will very briefly consider Karl Möbius' notion of 'biocenosis' in chapter four.

Finally, with regard to Darwin, we have seen that Haberlandt believed to have found a radically new understanding of the organism's purposiveness in the idea of the struggle for existence. In contrast to Haberlandt, "[m]any biologists, Ernst Haeckel and Julius Sachs among them, believed that Darwinism had spelled the end of teleology" (Cittadino 1990: 126). But they referred to something different: The teleology, or purposiveness, of function and structure had indeed met its end and only few scientists intuited a new purposiveness. Haberlandt did, as he "argued that ... purposiveness is the necessary consequence of natural selection, since the struggle for existence ensures the perpetuation of only those characteristics "that guarantee the safest, most complete, and most efficient operation of all physiological functions"" (Cittadino 1990: 126-7). Purposiveness would be the endurance of the best, the perpetuation of what works best ecologically, in a certain situation.

However, this insight is as grand as it is empty. Darwin's notion of the struggle for existence only explained purposiveness at the level of populations and not sufficiently at the level of the organism. "Many developmental and evolutionary biologists of the time, Haeckel included, were left dissatisfied by the Darwinian twin mechanisms of random variation and natural selection, as they

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<sup>65</sup> "Erst die Verbindung beider Begriffe [physiognomy and habitat] mit (3) [species] führte zum Bild der Lebensgemeinschaft als wesentlich durch interne Vorgänge, durch Beziehungen zwischen Organismen bestimmter, für die Geschichte und konkreter Ort essentiell sind oder es zumindest sein können. Diese Integration war die Geburt der Ökologie als Disziplin" (ibid.).

believed Darwin had not provided a satisfactory explanation for the perceived purposefulness of animal organization and adaptation” (Rieppel 2016: 115). Darwin had answered what Trepl believes to be the critical question of *biology* to natural history: “Why has ‘someone’ (God, ‘nature’) arranged something in this way?”<sup>66</sup> For Darwin argued that there was so much variation in nature because the function of nature is to only let the fittest organisms survive. But he had not answered the critical question of *life science* to biology: Why does something construct itself in the way in which it does? Why does a certain life form preserve itself like this? Why have life forms evolved in the way they have? These two latter questions would be the basis for life science, for ecology respectively systematics.

The next chapter discusses ecology by way of the early work of Wilhelm Roux. Roux worked fully within life science, in contrast to the other scientists we have considered so far (perhaps with the exception of Fritz Müller). Cassirer (1950: 178) signalled this new epistemic power of Roux’s new science when he wrote that,

[alt]hough in the first enthusiasm aroused by the theory of evolution it was assumed to have virtually settled the causal problem in biology, now the conviction grew steadily stronger that the question had not even been stated by the theory of descent in its usual form and that in order to do so one would have to go over to another foundation. It was the merit of the new science of “developmental mechanics,” especially as founded largely by Wilhelm Roux, that it was the first to have seen this problem and expressed it clearly.

Let us now see what Roux’s achievement really consisted in.

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<sup>66</sup> “Warum hat „jemand“ (Gott, „die Natur“) etwas so eingerichtet?” (Trepl 1987: 98).

# Chapter 4 – Ecology: Wilhelm Roux

## Introduction

Wilhelm Roux is mostly known for the research programme that he set up so ardently: *Entwicklungsmechanik* (developmental mechanics).<sup>67</sup> “Roux recognised that its methods were akin to physiology yet the object was the explanation of form” (Churchill 2008). Similarly to Haberlandt, Roux strived to do physiological anatomy, or in our terms, ecology.<sup>68</sup> He was one of the key scientists to bring about contemporary life science. However, he is remembered above all as a mechanist and experimentalist. This is due to early discussions of his work in the history of biology, which predominantly considered Roux’s embryological experiments (Allen 1978: 21-39; Coleman 1977: 164; Sander 1997; Magner 2002: 195-7).<sup>69</sup>

This view of Roux as a founder of experimental embryology is still dominant; but it has more recently been called into question mostly outside of anglophone academia, as scholars turn to Roux’s earlier work. His essential, largely theoretical book *Der Kampf der Theile im Organismus* (‘the struggle of parts in the organism’) (1881) has recently been translated into French, for the first time. It has also been the subject of important essays, in Portuguese, by Wilson A. Frezzatti Jr. (2013; 2015). The most comprehensive study of Roux’s work, *Die werdende Form* by Reinhard Mocek, was published in 1998 but has still not been translated.

Mocek’s history of ‘causal morphology’, entailing Wilhelm His, Roux, and Hans Driesch, is a landmark book in the history of biology, as it provides detailed analyses of the scientific thought of each of these important researchers, focusing on their view of organic self-organisation.<sup>70</sup> In 1974, before the fall of the Berlin wall, Mocek (1974) had already written a little-known study of Roux and Driesch but *Die werdende Form* is much more extensive and revises many of his earlier interpretations. With regard to Roux, Mocek deliberately moves away from earlier American discussions, rather considering his work in its entirety. He argues that it is a mistake to separate Roux’s earlier inquiries into functional structure from his subsequent embryo research. Instead of seeing the former as morphology and the latter as *Entwicklungsmechanik*, Mocek believes the two are in fact completely connected, as “the theoretical and methodical premises for both research directions had already been developed in his book on the ‘struggle of parts’.”<sup>71</sup>

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<sup>67</sup> Hans Driesch and Hans Spemann later called it ‘developmental physiology’ (Mocek 1998: 419). The term ‘causal morphology’ (*kausale Morphologie*) is also sometimes used to refer to Roux’s research style (see, for example, Rádl 1930: 520; Rieppel 2016: 116).

<sup>68</sup> Passariello (2016: 29) points out that “[Roux’s] work was strongly influenced by Schwalbe’s interdisciplinary concern for the relationship between anatomical form and physiological function.” G. A. Schwalbe was “Roux’s doctoral supervisor in 1878” (id.: 38).

<sup>69</sup> I chose to discuss only Roux and not those scientists intellectually close to Roux. August Rauber is left out because “Rauber was caught in the same ‘anatomical’ cage as His” (Brauckmann 2006: 447) and for this reason I have also left out Wilhelm His: He did not shift his science from anatomy to an anatomical-physiological study of life, that is, to ecology (cf. Mocek 1998: 178, 228).

<sup>70</sup> Reviewed in English by Sabine Brauckmann (1999).

<sup>71</sup> “Damit scheint die Sache klar zu sein. Die Arbeiten zu den funktionellen Struktur der verschiedener Gewebe gehören zur Morphologie, die Embryo-Forschungen zur Entwicklungsmechanik. Aber das ist eine rein klassifikatorische und äußerliche Aufgliederung! Schaut man auf die Inhalte, dann wird deutlich, daß beide

Although they ignore Mocek's analysis of Roux's work, Nyhart as well as Rieppel signal the importance of Roux having synthesised the study of form and of function. Nyhart, in her history of nineteenth-century German morphology (1990: 279-305), hardly discusses Roux's work, reduces it to that of his coworkers at the anatomy institute in Breslau (Hans Strasser and Gustav Born), and thus fails to see the uniquely radical nature and lasting significance of his project. She nonetheless points out, contra her American colleagues, that "[Roux's] first major innovation ... was not his championing of experiment, or even his stress on causal analysis, but his attempt to synthesize analytical approaches from the two disparate orientations of mechanical anatomy and evolutionary morphology" (1995: 282). Rieppel similarly credits Roux for "[having brought] the analytic perspective, that is, physiology back into comparative anatomy, thus forming a comprehensive and integrated research program, a *kausale Morphologie*" (2016: 116).

That is Mocek's argument in his book *Der werdende Form* (1998). For he writes that

[i]n contrast to the traditional morphology and its comparative methods, [causal morphology] inquired into the causes of form formation in animal ontogenesis, aimed at the 'becoming form' and researched these causes with a new method, the experimental one. No longer the 'finished form' – main starting point of the comparative research methodology of the past century – occupied centre stage but rather the causes of the realisation [*Zustandekommen*] of formed life entered the centre of attention.<sup>72</sup>

Since Mocek's understanding of causal morphology is delimited to the time period between Wilhelm His' *Untersuchungen über die erste Anlage des Wirbelthierleibes* (1868) and Hans Driesch's *Die Lokalisation morphogenetischer Vorgänge* (1899), with a second phase involving Hans Spemann, Alexander Gurwitsch, and Paul Weiss, after 1900 (Mocek 1998: 18), it covers material that we do not discuss here. Nonetheless, causal morphology certainly overlaps with our notion of ecology, as both refer to the study of physiological-anatomical processes and systems.

However, Mocek (id.: 28) believes that causal morphology is potentially the synthetic framework able to unite ecology and systematics. Since it inquires into the "causes of the realisation [*Zustandekommen*] of formed life," it covers both the processes, transformations, or 'realisations' and the emergences, occurrences, existences of formed life – both development and heredity, both process and ancestry. Mocek's view contrasts starkly with that of the plant geographer Oscar Drude, whose distinction between two kinds of life-scientific study we discussed previously (pp. 33-4). According to Drude, one either explains the "enduring preservation," or 'ongoingness' of a life form (within its environment and with its different parts) or one seeks to understand a life form's particular occurrence, "its existence [*Vorhandensein*] in the lands

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Bereiche eng miteinander zusammenhängen, die theoretischen und methodischen Prämissen für beide Forschungswege bereits in der Schrift über den »Kampf der Teile« entwickelt worden sind." (Mocek 1998: 213).

<sup>72</sup> "Im Unterschied zur traditionellen Morphologie und ihrer vergleichenden Methoden fragte sie [die kausale Morphologie] nach den Ursachen der Formbildung in der tierischen Ontogenese, zielte auf die »werdende Form« und ging diesen Ursachen mit einer neuen, der experimentellen Methode nach. Nicht mehr die »gewordene Form«, wichtigster Ansatzpunkt der vergleichenden Wissenschaftsmethodik des vergangenen Jahrhunderts, stand im Mittelpunkt, sondern die Ursachen des Zustandekommens geformten Lebens rückten in das Zentrum der Aufmerksamkeit" (Mocek 1998: 17-8).

concerned at all.”<sup>73</sup> These two modes, ecology and systematics, are mutually incompatible.<sup>74</sup> Mocek’s expression, “the causes of the realisation of formed life,” is an attempted synthesis of the two, on the basis of causal morphology. But do we find anything resembling such a synthesis, anything beyond ecology (and systematics) in the work of Wilhelm Roux? And, more generally, how did Roux accomplish a shift from biology to life science in his early work?

## Section 4.1 – Life and organism

Roux’s very early work (before *Kampf der Theile*) was concerned with blood vessels, their ways of branching, and the flow of blood that they accommodate and interact with. Alessandra Passariello (2016), in her important article on Roux’s early work, has pointed out that a distinctive incongruence divides Roux’s dissertation (1878) on blood vessels from his view on the same topic as expressed in *Der Kampf der Theile* (1881). Whereas Roux first seeks to “[find] anatomical generalizations that correspond to an optimal physiological condition,” he later inquires into “the capacity of a developing organism to react to internal-external stimuli and arrange its form accordingly” (Passariello 2016: 26). In his first study, mechanism means “a physical (hemodynamical) force,” while in the latter it is a “process” (ibid.).

“[T]here is a conundrum in Roux’s argument,” Passariello (2016: 36) concludes: “either he explicitly resorts to the principle of functional adaptation and explains the optimality of its outcome, or he calls for hemodynamical laws to be directly shaping the structure of the system without any need for an external stimulus.” I think the paradox – for there surely is one – is slightly different, however. It is not a change from an explanation based on hemodynamical laws (understood as analogous to hydrodynamics) to an explanation based on the principle of functional adaptation; not a change from a mechanistic to a functional account. That would be a shift within biology, which hinges on the division of form and function, mechanism and vitalism. Roux’s early work rather shifts from biology to life science.

In his dissertation Roux’s reasoning was that, if we know the difference between the lumen of vessel A and vessel B (i.e. the measures of their inside space), we can determine the ensuing bifurcation angles by applying hemodynamical laws (Passariello, 2016). These laws determine the bifurcation angles – but only once we know, once we fix the lumen of the vessels. The latter is the parameter that Roux kept independent. In this way then, a combination of unexplained form (the lumen of vessels) plus abstract physiological function (hemodynamical laws) results in a form that

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<sup>73</sup> “Man muß nämlich in den Erklärungen unterscheiden warum eine bestimmte Pflanze an einer bestimmten Lokalität *auftritt*, und mit welchen äusseren und inneren Mitteln sie daselbst ihre *fortdauernde Erhaltung* erzielt.” And: “Aber das Auftreten einer solchen Pflanze *hier und dort*, das Vorhandensein in dem betreffenden Lande überhaupt, ist als eine ganz getrennte Frage zu behandeln: die betreffende Wasserpflanze kann durch wandernde Vögel mitgeschleppt ..., sie kann hier oder dort als Art auf der Erde zuerst entstanden sein ...” (Drude 1890: 9).

<sup>74</sup> In an article on Roux, the early twentieth-century anatomist Hermann Braus (1920: 440) develops the comparable view that the causal study of life is concerned with the universal laws of life’s happenings (*Geschehen*) whereas systematics inquires into the happenings (*Geschehen*) as emergences forming chains of singular creations. He concludes that Windelband has called the former mode nomothetic and the latter idiographical.



is now physiologically explained (the bifurcation angles). As such, it would perfectly fit the nineteenth-century tradition of biological explanation.

But Roux adds something that makes this entire way of explaining biological phenomena obsolete. He introduces a principle: The whole branching structure of blood vessels will expend a minimum of energy to accomplish circulation. This principle of optimality was not at all needed to understand the phenomenon at stake: The lumen of vessels, with their specific bifurcation angles, were explained by the hemodynamical laws. Hence, the principle constitutes a fundamentally different explanation, perpendicular to the former one. It states that the vessel branching structure operates purposively; that it produces its own functionality, or at least a part of it: its energy efficiency. Surely, the shape of vessel branches is determined by hemodynamical laws, by an abstract physiological ‘function’ but the vessel branches also develop purposively on their own, expending as little energy as possible. They form a purpose-structure, a system, which relates functionally to the purpose-structure of blood; blood which in turn develops its movement according to its own principles.

In contrast to a physiological function determining anatomical development, the principle of optimality or any other such constructive principles – such as those used by Haberlandt (p. 41) – do not determine in the same sense. Instead of setting a goal for the structure to develop towards, or establishing the cause from which it is realised, these constructive principles are a relative, contingent causality. For example, given all the ways in which the many different elements of a system have so far mostly related to each other, principles x and y appear to be its most important guidelines or pathways for constructing itself. The complexity of the system is approximated with statistics and relations of probability and contingency, instead of uniform causality. In Roux’s early inquiries we find such an abundance of statistics and of rules which capture relative relations rather than causal relations. To illustrate:

*Rule V, a: In the case of a constant ratio of the strength of a branch to the diverted stem, the size of the diversion of the stem increases approximately proportionally to the diversion of the branch;*

*Rule XV, a: The origin of a branch follows, in relation to its strength, from a part of the width of the stem profile which is the larger, the weaker the branch in relation to the stem.<sup>75</sup>*

Instead of connecting a cause and an effect, these rules provide insight into a complex system of connected elements, the functional shapes of which depend, in a specific way, on that of other such elements.<sup>76</sup> The ways in which these elements relate reveals the constructive principles according to which the system develops.

How does Roux believe a living system should be understood? In Roux’s 1879 article first appears the metaphor of the state that he would use again later in *Der Kampf der Theile*. He writes that “in order to go a step beyond” the principle of optimality and the laws of hemodynamics

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<sup>75</sup> “Regel V, a: Bei constantem Verhältniss der Stärke von Ast und abgelenktem Stamme wächst die Ablenkungsgrösse des Stammes annähernd proportional der Ablenkung des Astes” (Roux 1878: 225). “Regel XV, a: Der Ursprung eines Astes erfolgt im Verhältniss zu seiner Stärke aus einem um so grösseren Theile der Breite des Stammesquerschnittes, je schwächer der Ast im Verhältniss zum Stamme ist” (id.: 234).

<sup>76</sup> Cf. Cassirer (1950: 191) and Mocek (1998: 24). Cassirer argues that with Roux it is no longer possible to distinguish cause from effect: ‘causalism’, which traditionally held sway in science, is replaced by what Max Verworn (1912) called ‘conditionalism’. Roux had a heated debate with Verworn about the issue of causality, see Cassirer (1950: 191-3) and Frezzatti (2015: 79-80). Mocek rather speaks of a shift from ‘mono-causality’ to ‘system causality’.

one could pursue that practice so common today, of appealing to the *ultima ratio*, to the struggle of individuals, to the struggle, first that of the cell states amongst each other, but this would appear here, as in other cases, as if one wanted to trace back all the good institutions of a state – government, legislation, administration, sciences, trade, industry, etc. – solely to the struggle with other states.<sup>77</sup>

One might expand the explanation with the all-encompassing principle of the struggle of individuals but it would reduce the multiplicity within a singular individual to an outside struggle. Roux laments that the different elements of a body are not properly explained by referring to the body's struggle with other bodies. The principle of the struggle of individuals (i.e. natural selection) can only be explanatory at the level of different individuals; it is unsuitable for explaining the different parts of a whole individual. Roux desires a mode of explanation that is more precise and restricted to a definite system. Different organs of, or in the individual may be understood as a system of struggle. Different individuals may also be understood by means of the notion of struggle but doing so would seem to be imprecise, in the eyes of Roux, if no place, field, or whole is defined where this process of struggle effectively takes place.

With this statement about the state and its different institutions, Roux set himself the task of avoiding to reduce the living system, that is the individual, to the principle of struggle amongst individuals, and to develop, instead, a conception of struggle that is at once more local and more general. This was necessary because the principle of optimality (i.e. expending minimal energy), of which he had made use in his studies of blood vessel branching, is severely limited for understanding a living system. It introduces a scale, the increase and/or decrease of optimality, without providing insight into the system itself, into the relations and tensions that make it be. It does not explain things in relation to other things but rather in relation to an abstract measure, optimality. As such, this principle is one-dimensional, with every application dependent on the definition of optimality, which should probably be different in the case of different organisms. It is not a life-scientific principle, since it does not introduce an aspectual reality of its own, only a scale of measurement. In contrast, the notion of struggle implies a dialectical reality, namely a world of loss vs a world of gain.

However, if one tries to translate the principle of struggle from the area in between organisms to the area within organisms, one is confronted with the question of how to still conceive of the 'individual' organism. What kind of whole is a living being if its parts can be conceived as elements in a perpetual conflict?<sup>78</sup> Or what is nature if there are only local parts and contingent wholes? What

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<sup>77</sup> "Um noch einen Schritt weiter zu gelangen ... könnte man das gegenwärtig so gebräuchliche Verfahren der Appellation an die *ultima ratio*, an den Kampf der Individuen, an den Kampf, zunächst der Zellenstaaten unter einander einschlagen, allein dies würde hier wie übrigens in vielen Fällen, erscheinen, als wollte man sämtliche gute Einrichtungen eines Staates in Regierung, Gesetzgebung, Verwaltung, Wissenschaften, Handel, Gewerbe etc. allein auf den Kampf mit den übrigen Staaten zurückführen" (Roux 1879: 335-6). Roux explicitly returns to this metaphor in *Der Kampf der Theile* (1881: 101), stating that competition and the regulating interplay between the different levels is one of the most powerful factors of progress. The term 'cell states' is from Rudolf Virchow, whom we will soon discuss.

<sup>78</sup> At the time of Roux's early writings, around the 1880s, scientists also turned their attention to the sociology and cooperation of organisms. Pëtr Kropotkin's *Mutual aid: A factor of evolution* (1902), which argued that "[s]ociability is as much a law of nature as mutual struggle" (p. 5), is an important work in this emerging study of associations of organisms. Kropotkin also points us to some other inquiries: "Les Sociétés animales, by Espinas (Paris, 1877); La Lutte pour l'existence et l'association pour la lutte, a lecture by J.L. Lanessan (April 1881); and Louis Buchner's book, *Liebe und Liebes-Leben in der Thierwelt*, of which the first edition appeared in 1882 or 1883, and a second, much enlarged, in 1885. But excellent though each of these works is, they leave ample room for a work in which Mutual Aid would be considered, not only as an argument in favour of a pre-human origin of moral instincts, but also as a law of Nature and a factor of evolution" (p. xii). Auguste Forel

is a life form if its life is divided between all its different, rather independent parts? For this is the perspective that Roux pursues, as he argues that, “just as the struggle of wholes [i.e. complete individuals] led to the remaining of the best ones, so it may have done, and still do, among the parts, if there is the opportunity for such an interplay of parts in the [organism’s] interior.”<sup>79</sup> And Roux believes such an opportunity exists, for he notes that

even in the highest organisms the centralisation towards the whole is definitely not so complete as one often imagines, not such that all parts can only exist in the organism to which they belong and only in the spot of their normal place, so that, completely dependently, they are only able to live as parts of a whole in a strictly standardised way.<sup>80</sup>

It appears that Roux’s main adversary is, as it were, Georges Cuvier and in particular Cuvier’s principle of the correlation of parts, which appears to be ludicrous from Roux’s viewpoint. In 1829 Cuvier (1840: 18) had written that

[e]ach part concurs in this general movement [i.e. life] by a peculiar action, and experiences from it particular effects; so that, in every being, the life is a whole, resulting from the mutual action and reaction of all its parts. Life, then, in general, presupposes organization in general, and the life proper to each being presupposes the organization peculiar to that being, ...<sup>81</sup>

For Roux, life is rather multiplicity, and multiplicity throughout. There is no overall purpose or purpose-structure that all the different parts add up to. There is no “life proper to each being.” Roux rather believes that each being is a self-regulating system which is able to endure even if its conditions gradually change (Roux 1881: 239).

Similarly to Cuvier, Rudolf Virchow, an important biologist in the second half of the nineteenth century, once stated that “the constituent elements [of an organism] will always only find their full significance in the Whole” (Virchow 1855: 20; in Rieppel 2016: 109). For Roux, there is no such total whole which encompasses everything, or differently put, into which all parts necessarily fit. And instead of seeing the organism as an organisation, it is a contingent ensemble of yet again other ensembles (e.g. organs, cells), with the different parts in each ensemble existing in a constant, ever-changing interplay.

Nonetheless, Virchow also seems to be a source of inspiration for Roux. Virchow introduced the idea that an organism is essentially composed of many individual cells, and Roux praises him for having “pointed out the autonomy of cells, and invoked in support of it the transplantability of cells

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also started studying the sociology and psychology of ants, resulting in his 1874 publication *Les fourmis de la Suisse*, and later in his five-volume *Le monde social des fourmis* (1923). The fact that ground-breaking inquiries into both the struggle and the cooperation among organisms proliferated in this time indicates that a fundamental reconfiguration of the notion of organism took place.

<sup>79</sup> “Wie dort [im vorigen Kapitel, bei Darwin und Wallace] der Kampf der Ganzen zum Uebrigbleiben des Besten führte, so kann er es wohl auch unter den Theilen gethan haben und noch thun, wenn Gelegenheit zu einer derartigen Wechselwirkung der Theile im Innern gegeben ist” (Roux 1881: 65).

<sup>80</sup> “Zunächst ist zur Beantwortung derselben zu erwähnen, dass selbst in den höchsten Organismen die Centralisation zum Ganzen gar nicht eine so vollkommene, wie man sie sich noch oft vorstellt, nicht derartig ist, dass alle Theile nur in dem Organismus, welchen sie angehören, und nur an der Stelle ihres normalen Sitzes bestehen könnten und somit, vollkommen in Abhängigkeit, nur als Theile des Ganzen in fest normirter Weise zu leben vermöchten” (ibid.).

<sup>81</sup> The French original: “Chaque partie concourt à ce mouvement général par une action propre et en éprouve des effets particuliers ; en sorte que, dans chaque être, la vie est un ensemble qui résulte de l’action et de la réaction mutuelle de toutes ses parties. / La vie en général suppose donc l’organisation en général, et la vie propre de chaque être suppose l’organisation propre de cet être, ... ” (Cuvier 1829 : 14).

of one organism to another and from one spot in the same organism to another.”<sup>82</sup> Although these findings support Roux’s conception of what we may call a dividual organism, Virchow believed, in contrast to Roux, that the different cells “remain united because they are interrelated to one another just as members of the same state” (Carl Reichert in Lenoir 1982: 224). “[T]he organism,” Virchow wrote in 1862 (p. 55), “is a community of living cells, a small State, well organized with all the required accessories, with super-ordained and subordinated officials, with servants and masters, leaders and followers” (in Rieppel 2016: 109).

As we saw earlier, it is precisely this metaphor of the state through which Roux seems to have reconfigured his understanding of the (dis)unity of the organism. Contrary to Virchow, Roux conceives of a state with internally competing and interacting institutions. Now, in support of his own view, Roux cites an excerpt from Virchow, in which the latter precisely sought to conceptualise for himself a more comprehensive notion of the organism’s unity. Whereas Virchow thus argued that “any organisation is not a united one in the traditional sense but rather a societal, or more precisely, a cooperative (social) one,” Roux takes this same conception to mean “that many parts are not absolutely dependent on the whole,” and that they have “a certain individual freedom,” even “a certain leeway [*Spielraum*], within which the happenings mutually regulate themselves” (at least during embryonic development).<sup>83</sup>

## Section 4.2 – Organism and development

The principle of optimality could not explain why some parts in the organism change in relation to others. Given a changing space of differences, there is little use in knowing that these different parts will develop so as to expend a minimal amount of energy. The principle of optimality says nothing about the mutual interplay between parts. It can only describe a history that is static in the sense of a timeline or scale of either more or less general optimality. If we only have the principle of optimality, then how would we understand the change of an organism as a space of many different, interrelating parts? Clearly, the principle of optimality was a conceptual dead-end for Roux, even if at the same time it entailed a study of purpose-structures, beyond the form-function dichotomy that characterised biology.

Roux’s escape and innovation was to accord the newly seen, irreducible differences and relative autonomy of all the different parts of the organism with a newly conceived principle of struggle.

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<sup>82</sup> “Virchow hat schon vor fast dreissig Jahren [note 1: Virchow’s Archiv f. patholog. Anat. u. Physiol. Bd. IV. 1852. p. 378] auf die Selbständigkeit der Zellen hingewiesen, und die Transplantationsfähigkeit von Zellen des einen Organismus auf den anderen und von einer Stelle desselben Organismus auf eine andere dafür angeführt” (Roux 1881: 65).

<sup>83</sup> “Wenn es möglich ist, aus dem Verbande des menschlichen Körpers gewisse Elemente oder Gruppen von Elementen zu trennen, ohne dass sie aufhören, Lebenseigenschaften zu äussern und sich zu erhalten, so folgt daraus, dass jener Verband nicht in dem hergebrachten Sinne ein einheitlicher, sondern vielmehr ein gesellschaftlicher oder genauer ein genossenschaftlicher (socialer) ist” (Virchow in Roux 1881: 66); “Ausser diesem Beweise, dass viele Theile nicht in absoluter Abhängigkeit von dem Ganzen stehen, spricht sich eine gewisse individuelle Freiheit derselben schon in der embryonalen Entwicklung dadurch aus, dass die vererbten Formenbildungen nicht durch eine vererbte Normirung der Leistungen jeder einzelnen Zelle, sondern bloß nach allgemeinen Normen für die Grösse, Gestalt, Structur und Leistung jedes Organes hergestellt werden, so dass für die Einzelausführung, für den Aufbau aus den einzelnen Zellen ein gewisser Spielraum bleibt, innerhalb dessen sich das Geschehen gegenseitig selber regulirt” (Roux 1881: 66).

Just as the individual organism, the principle with which to understand it should be divided. The solution was not two principles but rather a principle which is not functionally uniform, a principle which implies a fundamentally divided reality. Roux avoids stating that 'nature' separates the fit from the unfit, as a sieve, thus establishing an abstract, most general functionality, a total measure for all change, as Darwin did. Instead, Roux states that in the organic world difference in itself equals interplay, and specifically the kind in which some gain while others lose, namely struggle.<sup>84</sup> Instead of establishing a total measure or sieve – 'natural selection' – which causes change on the basis of difference, Roux installs difference itself in the very principle that explains difference: At any time, there is simply a struggle of parts, an interplay between two or more different elements.

Roux explains in his introduction to *Der Kampf der Theile* (1881: 1) that Empedocles already solved the question why nature seems to be so purposive. According to Empedocles, the world's basic material substance is a fundamental being, itself unchanging, which is however shaped and mixed by two opposing forces, love and hate. Their perpetual battle is both creative and destructive: All things that exist are merely that which endured, what remained from this struggle – before, yet again, stronger and better things will spring from it and take their place.<sup>85</sup> Roux continues: "Purposiveness was not a matter of will but a matter of becoming, not teleological but natural-historical, mechanically emerged; for what remained was not something corresponding to a preconceived goal but rather that which the necessary elements needed for their existence amidst the given relations."<sup>86</sup> This, Roux writes, is how he will understand purposiveness.

Purposiveness is thus the persistence of whatever persists, it is becoming itself – "purposive autogeny" – and I do not believe to be wrong that it is also, for Roux, the core duality, the switch, or interplay between the interacting 'parts', of which this becoming, this persistence really consists.<sup>87</sup> Note, however, that the struggle of parts is for Roux not one, all-encompassing system. Rather, he speaks of a struggle of parts *in the organism* (*Der Kampf der Theile im Organismus*). The locality and contingency of any system is also a point of critique towards Darwin, as Roux points out that "it should appear questionable whether selection through the struggle of individuals could create something – even if it would concern something very useful – which cannot exist victoriously in the struggle of molecules."<sup>88</sup> Conversely, things happen in the struggle of molecules, of cells, of tissues, or of organs (the four struggles considered in *Der Kampf der Theile*) "without the struggle of individuals, and possibly even against it."

Roux justifies his principle of the struggle of parts by first of all emphasising the heterogeneity, or inequality ("Ungleichheit") of the organism's parts (1881: 66-70):

No liver cell is completely similar to another in terms of size and shape, and yet they all join together to form a capable organ, built according to a certain type. It is impossible that it was determined beforehand by heredity that the hundredth or another liver cell would have exactly this size and shape which differs

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<sup>84</sup> This is how Roux defined struggle on page 67 in *Der Kampf der Theile*.

<sup>85</sup> This is Roux's version of Empedocles' theory; it is not a faithful representation of it.

<sup>86</sup> "Die Zweckmässigkeit war keine gewollte, sondern eine gewordene, keine teleologische, sondern eine naturhistorische, auf mechanische Weise entstandene; denn nicht das einem vorgefassten Zwecke entsprechende, sondern das, was die nothwendigen Eigenschaften zum Bestehen unter den gegebenen Verhältnissen hatte, blieb übrig. Allein in diesem Sinne reden wir im Folgenden von Zweckmässigkeit" (Roux 1881: 2).

<sup>87</sup> "das Princip der functionellen Selbstgestaltung des Zweckmässigen" (Roux 1881: 238).

<sup>88</sup> "Alles dieses geschieht ohne den Kampf der Individuen, ja eventuell wohl gegen denselben, denn es muss fraglich erscheinen, ob die Auslese durch den Kampf der Individuen, auch wenn es sehr Nützliches beträfe, etwas züchten könnte, was im Kampf der Molekel nicht siegreich bestehen kann" (Roux 1881: 83).

slightly from all others, and that it would connect with the already formed as well as subsequent cells under this angle. Rather, the subsequent cell joins to the previous one according to its individuality, thereby being determined surely by the needs of a certain contact with a capillary, with adjacent cells, etc. but, apart from that, it is free.<sup>89</sup>

If we consider these cells as building stones, then we cannot conceive how their heterogeneity implicates interplay. But these cells are alive, “the next ones are always the products, the offspring of the previous ones.”<sup>90</sup> Hence, if a certain one is privileged over the others due to a certain advantageous characteristic, it can grow faster and better through metabolism, and reproduce itself in greater numbers than the others can, thereby contributing more to the structure, that is, in this example, the liver. In this way, the liver itself might gain an advantage over the other organs, with due consequences in the struggle of organs.

In this way, every small difference in the organism’s make-up has consequences, creating an interplay of elements at once local and general. “The inequality of parts,” Roux writes, “will have to be the foundation of the struggle of parts.”<sup>91</sup> Roux thus seems to have shifted from biology to life science by way of replacing the *correlation* of parts with the *struggle* of parts.<sup>92</sup> Only five years earlier, though, a book-length discussion by one of the most renowned scientists at the time had included the statement that “the development of organisms is based on something which may be compared to a mathematical formula. That is the relationship that has been called the correlation of parts” (Von Baer 1876: 439; in Lenoir 1982: 266). Karl Ernst von Baer believed that the production and variation of organic forms through natural selection was governed not by the struggle of parts, as Roux would soon argue, but by the correlation of parts. This was the common thread within the organism, uniting the organism, which prevented any small modification of the organism that did not also “necessarily entail a total restructuring of its interrelated parts and a corresponding change in its developmental path” (Lenoir 1982: 266).

In an intricate reconfiguration of perspective, Roux does not exactly contradict Von Baer’s view that all parts are intricately related. Rather, he disentangles the old perspective from the inside. Surely all of the organism’s parts are interrelated, and surely both minor modifications and total transformations occur, but for Roux the interrelatedness of the organism’s parts does not necessitate a causal connection between a small change and major restructuring. With Roux, the organism is without its singular organisation, life, or correlation of parts; it is without this kind of integrity or unity. Recall the liver cell which, according to Roux, “joins to the previous one according to its individuality, thereby being determined surely by the needs of a certain contact with a

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<sup>89</sup> “Keine Leberzelle gleicht vollkommen in Grösse und Gestalt der anderen, und doch fügen sie sich alle zu dem nach (KT66) einem bestimmten Typus gebauten leistungsfähigen Organe zusammen. Unmöglich kann durch die Vererbung von vornherein bestimmt sein, dass die hundertste oder eine andere Leberzelle genau diese von allen anderen etwas abweichende Grösse und Gestalt haben und unter diesem Winkel, welcher für jede etwas verschieden ist, sich mit den vorhergebildeten und nachfolgenden Zellen verbindet, sondern die nachfolgende Zelle fügt sich nach ihrer Individualität an die vorhergehende an, dabei bloß bestimmt durch die in ihrer vererbten Qualität liegenden Bedürfnisse einer gewissen Berührung mit der Capillare, mit Nachbarzellen etc. im Uebrigen aber frei” (Roux 1881: 66-70).

<sup>90</sup> “Beim Organischen sind die Bausteine nicht vorher alle fertig gemacht und werden dann bloß nacheinander zusammengefügt, sondern hier sind die nachfolgenden immer die Producte, die Nachkommen der vorherigen” (Roux 1881: 67-8). See also pp. 106-7.

<sup>91</sup> “Die Ungleichheit der Theile wird also die Grundlage des Kampfes der Theile sein müssen” (Roux 1881: 69).

<sup>92</sup> In his habilitation defense, Roux also takes a distinct interest in Darwin’s notion of correlative growth, or correlative variation, that is, the phenomenon that if one part of an organism changes other parts change correspondingly; see (Roux 1880: 9-11).

capillary, with adjacent cells, etc. but, apart from that, it is free.”<sup>89</sup> Living beings are not fully determined, in Roux’s view: Chance has a distinct role to play in their ‘purposive autogeny’.

Von Baer’s perspective could not be more opposed:

the harmony of nature, ... is a relationship of mutual regulation. Just as tones only give rise to a harmony when they are bound together in accordance with certain rules, so can the individual processes in the wholeness of nature only exist and endure if they stand in certain relationships to one another. Chance is unable to create anything enduring, rather it is only capable of destruction. (Von Baer 1864: 228-9; in Lenoir 1982: 275)

The notion of the harmony or wholeness of nature is unacceptable within Roux’s conceptual framework.

But even the notion of self-control, which Roux believes to underlie the work of Eduard F. W. Pflüger, allows for too much integrity and too little flexibility:

Self-control is a self-regulation arranged for a certain range of variation from a central point towards both sides; the organism, however, has self-regulations of a most general character, whereby after persisting in a deviant position for some time, this position becomes the central point of a new range of variation: and if the deviation keeps departing further towards one side, then the new central point may be far off to the side, away from the maximum of the original range of variation. This distinction is not so pedantic and superfluous as it may appear to be; it should rather even be emphasised, for the latter characteristic [i.e. self-regulations] is the foundation of the gradually unlimited perfectibility inherent to organisms, while the former [i.e. self-control] simply constitutes a stability arranged for a great many cases.<sup>93</sup>

The central point of organic variation is always a displaced one. Even variation is without any fixed, stable centre. And so self-regulation, a key characteristic of life according to Roux, is always plural, as it covers inconceivably many different ranges of variation.<sup>94</sup> Note also that the perfectibility of organisms is here conceived as contingent and relative: It is “gradually unlimited,” dependent on the given range of variation, and the next, and so on; instead of a conception of the total range, it is a conception of the movement of the range itself.

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<sup>93</sup> “Dieser letztere Ausdruck [Selbststeuerung] ist eigentlich die richtige Bezeichnung für die Auffassung, welche Pflüger’s Arbeit zu Grunde liegt, nicht aber Selbstregulation. Die Selbststeuerung ist eine Selbstregulation, welche für eine bestimmte Variationsbreite nach beiden Seiten von einem bestimmten Mittelpunkt hin eingerichtet ist; der Organismus aber hat Selbstregulationen allgemeinsten Charakters, bei denen nach einiger Zeit des Verharrens in einer abweichenden Lage diese letztere zum Mittelpunkt der neuen Variationsbreite wird: und wenn die Abweichung immer nach Einer Seite hin weiter fortgeht, so kann der neue Mittelpunkt viel seitwärts abliegen von dem Maximum der ursprünglichen Variationsbreite. Diese Distinction ist nicht so spitzfindig und überflüssig, wie sie vielleicht scheint; sie muss sogar entschieden betont werden, da die letztere Eigenschaft die Grundlage der den Organismen innewohnenden graduell unbegrenzten Vervollkommnungsfähigkeit ist, während die erstere bloß eine für sehr viele Fälle eingerichtete Stabilität darstellt” (Roux 1881: 229-230).

<sup>94</sup> Cassirer (1950: 190) notes, in this respect, that “Roux distinguished nine “typical spontaneous activities” of the organism: variation, elimination, ingestion, assimilation, growth, movement, reproduction, hereditary transmission of characteristics (inheritance), self-formation, and self-preservation. Only through such a complex system of functions, “self-activities,” can an organism exist and be recognized as an organism.”

## Section 4.3 – The limits of ecology

Given a self-regulating, dividual organism, composed of a multiplicity of different parts, that is understood with a principle of difference (the struggle of parts), how does Roux deal with the topic of inheritance? At first, he approaches it *ex negativo*:

In case of absolute likeness, all similarly functioning parts would take an equal part in the setup or the regeneration of the organism, and only externally favoring circumstances, such as a beneficial location close to a blood vessel etc., would provide a benefit, which, however, would only be small and temporary, as they are not transferable to offspring. If they are transferred however, then this would be proof that they are grounded in the mother cell, that this would therefore be an internal, not an external privilege.<sup>95</sup>

Any transferred benefit (or deficit, for that matter) is understood to be grounded in the mother cell. These benefits can only be those within the space of the cell concerned; the cell's location or place cannot be a transferable benefit. Although this may appear to be a straightforward point, it is important that we closely consider it. Roux essentially states that even though both the cell's inner characteristics and its place matter in the struggle of cells, only those characteristics which may be conceived to take part in a lower-level struggle (of molecules) play a role in the process of reproduction. If we freely translate this distinction to other levels, we may say that even though an organism's inner characteristics as well as its place matter in the struggle of individuals, only the characteristics which also engage in the struggle of organs – i.e. the organism's inner characteristics – are transferable to the next individual. However, at a certain bottom level the transfer of characteristics depends fully on the struggle operative at that level (disregarding external circumstances): The place and inner characteristics of the next life forms are here determined by the place and inner characteristics of the former one.

Experiments with the very first life forms would thus provide essential insight into the effect and significance of place and other characteristics for the life form's subsequent development. Such embryological experiments, working at a level of relative organic simplicity, might also elucidate the core workings of organic struggle and interplay itself; in other words, the mechanism of purposive autogeny, i.e. life itself. It is no surprise, then, that Roux took a vital interest in embryonic development, already in *Der Kampf der Theile*. He would soon thereafter delve into embryology and in particular the study of cell division, starting with a small publication (*Über die Bedeutung der Kerntheilungsfiguren*, 1883), in which he suggests that the purpose of the division of the cell core is “not simply to divide itself with regard to its mass but also with regard to the mass and *nature* of its singular *qualities*.”<sup>96</sup> This is exactly what Roux's conception of purposiveness entails: The function of life itself is divided. The form of life surely does not exist; there is no nature encompassing all formal diversity. But Roux adds that organic ongoingness, that life, too – although existent – is a divide.

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<sup>95</sup> “Bei absoluter Gleichheit aller gleich fungirenden Theile müsste auch der Antheil aller am Aufbau des Organismus oder an der Regeneration desselben der gleiche sein und nur äussere begünstigende Momente, wie günstigere Lage zu einem Blutgefässe etc., könnten eine Bevorzugung hervorbringen, welche aber nur gering und vorübergehend wäre, da sie nicht auf die Nachkommen übertragbar ist. Uebertrüge sie sich aber auf die Nachkommen, so wäre das ein Beweis, dass sie in der Natur der mütterlichen (KT68) Zelle begründet, also eine innere, keine äussere Begünstigung war” (Roux 1881: 68).

<sup>96</sup> “Nach dieser Erörterung können wir den Zweck der Kerntheilungsfiguren definiren: Die Kerntheilungsfiguren sind Mechanismen, welche es ermöglichen, den Kern nicht bloss seiner Masse sondern auch der Masse und Beschaffenheit seiner einzelnen Qualitäten nach zu theilen” (Roux 1883: 15).



As we saw before, this divide, this ongoingness takes place in a certain space. These different spaces are for Roux the different levels of struggle (molecules, cells, tissues, organs, individuals). They are systems of interplay. But they cannot be a part in another system at the same time. A tissue is a system of interrelating cells but cannot simultaneously be a part of an organ. To see it as a part of an organ would require the scientist to consider it completely anew, this time ceasing to see it as a system. A piece of life at any one time is thus either a manifold, a multiplicity of forms and their interrelations, or it is a unit interrelated to others in a certain space. The title of Roux's book – *Der Kampf der Theile im Organismus* – precisely captures this distinction. There is the process or system – the struggle of parts – and the space or field: the organism. The struggle is precisely not of the organism because the organism itself does not engage in it. In the book's title, the organism is the place or location without which the process of struggle might be inconceivable.

However, the struggle is one of parts, and these parts may be organisms in the struggle of individuals. The organism or any other life form, thus, figures as both part and whole (in the sense of space, context). The concepts of part and whole are continuous in their relation to each other, allowing the shift of perspective from one level of struggle to another, as we zoom in, for example, on the organism as a part in order to see the struggle in the organism as a whole. At each step, moreover, the notion of part/whole is intimately connected with the concept of process or system (here, struggle). The purposive interplay that is life is, from one end to the other, the combination of process and part/whole. We already mentioned that it is the notion of part/whole which allows for shifting from one process to another. On the other hand, the notion of process reveals that the part/wholes are transformations as well as a singular, perpetual transformation. Roux's central idea – the struggle of parts – hinges completely on the nexus of process and part/whole.

Something escapes from this framework, however. As so many other ecologists after him, Roux spends a considerable number of pages in *Der Kampf der Theile* on speculations about the emergence of life and life forms. Compare his use of Von Baer's argument concerning the evolutionary shift from sea animals to land animals (Roux 1881: 39-46; Von Baer 1876: 378-9). Roux finds himself having elucidated the ongoingness or 'enduring preservation' (Drude) of living beings: their 'purposive autogeny', their 'self-regulations', their 'functional adaptation'. Yet, these processes do not explain the occurrence of, for example, lungs, eyes, or vertebrates; they only make us understand the ways in which these phenomena change, and in that sense, may have emerged. But emergence can ultimately not be explained as change, as process – there must be a threshold or shift of some kind that enables a *discrete* change, a true emergence.

Now, Mocek (1998: 206) argues precisely that Roux managed to progress from the investigation of the causes of existence ("Bestehens") to the causes of emergence ("Entstehens"), by moving from the theory of functional adaptation to the developmental mechanics of the embryo. In Mocek's view, Roux ultimately inquired into the "causes of the realisation [Zustandekommen] of formed life" (id.: 28). However, the developmental mechanics of the embryo Roux still conceives as processes, without a conception of discrete change. But, above all, what might the "causes of the realisation of formed life" really be in the work of Roux? I think this expression from Mocek is the cause of a confusion regarding the *principles* with which Roux sought to understand life. Surely, Roux established certain *principles* of the realisation of life but these are not causes!

The principle of the struggle of parts is not a cause. We have already said that it "implies" a reality but we have to push this point further. Now, several commentators have drawn attention to the fact that Roux spoke of 'natural experiments' (*Naturexperimente*): Diseases, injuries, free variations or other atypical events, which, just as 'artificial experiments', could yield valid causal

knowledge (Nyhart 1995: 294; Braus 1920: 441). This need to distinguish between two kinds of experiments – natural and artificial – shows that Roux did not consider experiments to be inherently artificial nor inherently natural. He introduces a third realm where nature and artifice are one and the same thing; he reconceives nature as something that is artificial too: “The great experiment of nature,” he writes in *Der Kampf der Theile*.<sup>97</sup> This view implies that nature itself explains itself to us, scientists, as parts of nature. The principles, then, with which we try to grasp nature, are not conceptual artifices that we say govern nature; they are rather the intellectually conceived pathways or ‘embodied knowledge’ of nature itself. And the scientist seeks to *translate* this knowledge or reality into scientific facts rather than to establish in science the hidden layer of causes that underlie the events of nature.

From Roux’s viewpoint, all events of nature are already in themselves the causes, as everything is a multiplicity of processes consisting of different, interacting parts. Given such a ‘nature’, the only way to gather important knowledge is to become such an interacting part:

*I was fully conscious of the crudeness of this attack on the secret workshop of all the forces of life and compared this act to the insertion of a bomb into a newly founded factory, perhaps into a textile work, with the undertaken purpose of making a conclusion about the factory’s inner organization from the change of production and its further development after the prepared destruction.* (Roux in Churchill 2008)

Roux entered the workshop of life as if he had never been part of it before. The scientist had been the subject interrogating the object called nature or life but with the dawn of life science, he might as well start investigating himself. Hermann Ebbinghaus started to do precisely this around 1880, when during specific periods he conducted a scientific inquiry, modifying his life, in order to measure his own memory capacity (“something that was previously deemed common knowledge and therefore beneath notice”) (Kittler 1990: 207). Roux’s ‘sting attempts’ (*Anstichversuche*) should be understood in continuity with Ebbinghaus’s self-science.

## Section 4.4 – Ecology and Karl Möbius

Roux’s new science, ecology, is potentially about everything. The study of life processes and part/wholes may cover all things. Anything may, arguably, be regarded as a process, and part/whole is an exponential category, since there is always the part of the part and the whole of the whole. One may delimit a certain process but it may always be seen as a part of a whole or a whole that is part of a greater whole. Haberlandt perhaps already intuited this problem when he not only praised but also criticised Roux in the second, 1896 edition of his *Physiologische Pflanzenanatomie*. He wrote that “it relies on insufficient consideration when the evidence that the external or internal arrangement [*Ausgestaltung*] of the organism is determined, respectively may be modified, by external influences, is already labelled an “explanation based on the principle of causality.””<sup>98</sup> I will not consider if this is a fair judgement but at the centre of the objection is the inner/outer distinction: As Cassirer (1950: 190) asks, “is there any justification for or even possibility of

<sup>97</sup> “das grosse Experiment der Natur” (Roux 1881: 120).

<sup>98</sup> “Auf unzureichender Ueberlegung beruht es aber, wenn der Nachweis, dass die äussere oder innere Ausgestaltung des Organismus von äusseren Einflüssen abhängig ist, resp. modificirt werden kann, bereits zu einer »auf dem Causalitätsprincip basirenden Erklärung« gestempelt wird” (Haberlandt 1896: 9). Cf. p. 2 and p. 60 (note 62).

discriminating between "inner" and "outer," as was done in [Roux's] theory; between what the organism performs of its own accord and the influences exercised upon it by external causes?"

We saw earlier that discrete change constitutes a problem for Roux's new science. Ecology cannot conceive of the emergence or sheer occurrence of something without already considering it as a process. Instead of the relatedness of the event, it will think the movement of the process. The issue of distinguishing between the inside and the outside is related to this problem. The end of a certain process, e.g. the death of an organism, will figure, in ecology, as a part of a whole, e.g. an ecosystem, where this death is a part of the system's processes. At once, the sheer occurrence of the organism's death is thus rather conceived as a process. At the same time, even though this death takes place within and through the organism, it also takes place beyond, outside of the organism. These two problems are not problems for ecology per se, as it is perfectly productive without contemplating them, but they do divide it from systematics. For systematics considers the organism precisely not as a part/whole but rather as a passage point, a transition (as we will see in the next chapter). Thus, in the problems and at the limits of Roux's thought we encounter the aporia of life science, which we approached schematically in chapter one, and which keep ecology and systematics at a certain distance from each other.

Max Verworn confronted Roux with one of these limits when he concluded that with Roux's new science, "there is no longer any occasion for our distinguishing between supposedly "inner" and "outer" causes of a phenomenon of nature" (Cassirer 1950: 192). Any phenomenon is both inner and outer since they are all conceived as processes taking place in parts and wholes. Verworn also argued that Roux's new science replaced the traditional causalism – i.e. the causality of cause and effect – with conditionalism, i.e. a causality in which all things affect all others, a causality of general, interactive conditionality. Roux, however, sought to counter Verworn's perspective and pointed out that "we call the ... factors which, as we say, "act" on the organism the "outer" ones, but we do not say, conversely, as we ought to do from the standpoint of a pure conditionalism, that the living being "works on" these "outer" factors, for example, oxygen" (Cassirer 1950: 193).

Perhaps Roux himself did not say such things but it is nonetheless implicit in, for example, his notion of the struggle of parts, in which all parts work on all others. And even before Roux's early work, Karl Möbius, with his more geographical focus, had already worked with precisely this perspective of conditionalism, in which indeed the living being also works on environmental factors such as oxygen. Already in 1877 Möbius wrote that "all living members of a life community keep, with their organisation, the physical relations of their biocenosis in balance" (80; emphasis added).<sup>99</sup> Möbius is specifically known for having coined the term 'biocenosis' and discussing it is a good way to displace this chapter's – and Roux's – focus on the individual organism.

Having worked mostly outside of academia, Möbius was asked to research the possibility of oyster farming along Germany's Baltic Sea coast, resulting in the 1877 publication *Die Auster und die Austernwirthschaft*.<sup>100</sup> Here we already find a view of life not as a pervasive developmental force,

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<sup>99</sup> "Alle lebendigen Glieder einer Lebensgemeinde halten mit ihrer Organisation den physikalischen Verhältnissen ihrer Biocönose das Gleichgewicht, denn sie erhalten sich und pflanzen sich fort gegenüber allen Einwirkungen äusserer Reize und gegenüber allen Angriffen auf das Fortbestehen ihrer Individualität."

<sup>100</sup> For an overview of Möbius' career, see Nyhart (1998; 2009a, chapter 4): "Before he arrived at Kiel in 1868, Möbius spent fifteen years in Hamburg working as a natural history activist ... In Hamburg, where he taught at the leading secondary school, he also became a leader of the natural history community, running the natural history association and serving on the governing committees of the natural history museum and the zoological society" (2009a: 125-6).

always threatened by death, or the conditions that enable it, but rather as whatever rest which persists; purposiveness is persistence, as it is for Roux:

The entirety of grown-up individuals of all species living together in an area is the leftover rest of all germs of the preceding breeding period. This rest of mature germs is a certain quantum life which occurs in a certain number of individuals and which, like all life, gains endurance through reproduction.<sup>101</sup>

But more useful here is what Möbius writes about the notion of 'biocenosis'. Biocenosis, from the ancient Greek words for 'life' (βίος) and 'to share, to make common' (κοινώω), refers to "a selection and number of species and individuals corresponding to the average, external living conditions, which condition one another mutually and which persist enduringly, by way of reproduction, in a limited area."<sup>102</sup> In contrast to Roux's understanding of the organism as a struggle of parts, the biocenosis – or living community, as Möbius also calls it – is a more neutral conception of a functionally integrated system of interacting parts. It became "one of the most familiar scientific concepts in Germany" and "has remained an enduring staple of the science of ecology" (Nyhart 2009b: 2).

In representing Möbius' notion of the living community, Nyhart, however, makes the mistake of strictly separating the organic from the inorganic: Möbius' "biological societies ... were characterised by the dependence of their members on one another and on their physical conditions of existence" (ibid.). This is to say that the living parts of a biocenosis affect one another and are all affected by the physical living conditions. Life on one side of the equation, matter on the other. But in fact, Möbius draws attention, throughout his study of the oyster biocenosis, to the fact that "all living members of a life community keep, with their organisation, the physical relations of their biocenosis in balance (1877: 80; emphasis added). Life and matter are seen as a spectrum, and the biocenosis is above all a system of physical relations, just like Roux's organism.

Möbius also explains, similarly to Roux, that any small change in the biocenosis has consequences for all of its parts:

If, at any time, one of the external conditions of life deviates for a long time from its ordinary mean, then the entire biocenosis would transform itself. But she also becomes different if the number of individuals of a particular species increases or diminishes due to the influences of man, or if one species entirely disappears from, or a new species enters into, the living community.<sup>103</sup>

Accordingly, if any one of the parts finds itself in a completely different system, consisting exclusively of parts it never interacted with before, then a total transformation of this part is necessary for it to persist. With regard to the oysters,

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<sup>101</sup> "Die Gesamtheit der herangewachsenen Individuen aller in einem Gebiet zusammenwohnenden Arten ist der übriggebliebene Rest aller Keime der vorhergegangenen Brutperioden. Dieser Rest der ausgereiften Keime ist ein gewisses Quantum Leben, welches in einer gewissen Summe von Individuen auftritt und welches, wie alles Leben, durch Fortpflanzung Dauer gewinnt" (Möbius 1877: 76).

<sup>102</sup> "eine den durchschnittlichen äusseren Lebensverhältnissen entsprechende Auswahl und Zahl von Arten und Individuen, welche sich gegenseitig bedingen und durch Fortpflanzung in einem abgemessenen Gebiete dauernd erhalten" (Möbius 1877: 76). One may find a slightly different definition of biocenosis in a later text by Möbius (1886: 247).

<sup>103</sup> "Wenn irgend eine der äusseren Lebensbedingungen längere Zeit von ihrem früheren Mittel abweicht, so gestaltet sich die ganze Biocönose um; sie wird aber auch anders, wenn die Zahl der Individuen einer zugehörigen Art durch Einwirkungen des Menschen sinkt oder steigt, oder wenn eine Art (AA76) ganz ausscheidet oder eine neue Art in die Lebensgemeinde eintritt" (1877: 76-7).

if [they] must live in today's East Sea, they would need to change their physiological operations in such a way that they would be able to prosper with greater fluctuations in salinity than in the North Sea, that is, they would need to become a different animal, while nonetheless retaining the taste of oysters.<sup>104</sup>

Finally, as Nyhart has pointed out, several peculiarities characterise Möbius' study of the oyster biocenosis, one of which is "the inclusion of a man-made "region" with the geographical ones" (1998: 624; 2009a: 144). Including "the artificial environment of the mussel-stakes [is] something one would not normally expect in a faunistic discussion" (id.: 623; 143). We can conceive of this in analogy to Roux's notion of 'natural experiments' which we understood to imply that with ecology a fundamental distinction between nature and culture cannot viably be made.

## Conclusion

In this chapter we have seen that in his early work on blood vessel branching Roux replaces the explanatory structure of function and structure, cause and effect, with one of constructive principles and systems or processes (i.e. function-structures). Haberlandt made similar innovations but Roux definitively departs from Haberlandt's approach since he is not satisfied with one-dimensional principles, such as the optimality principle. In order to explain the movement of a system consisting of many different interacting parts that all develop in relation to one another, in order to understand such a multifaceted reality, such an ensemble of phenomena that all mutually condition one another, no single dimension or principle will suffice. Rather, the principle itself must be a divided one: Roux introduces the principle of the struggle of parts to conceive of the organism as an endlessly divided system of parts none of which are equal, to conceive, in other words, of a dividual organism. Only a divided principle such as the struggle of parts is so comprehensive – it allows one to see a world of gain versus a world of loss – that it can explain part/whole development.

Cassirer (1950: 178) pointed out that it was the merit of Roux's new science to see that Darwin's theory of evolution had to be shifted across another foundation, but what did this shift consist in? Now, in contrast to Darwin who believed that nature separates the fit from the unfit, as a sieve, and who thus established an abstract, most general purposiveness, a total measure for all change, Roux instead implies that in the organic world difference in itself equals interplay: Any part is unlike any other, and since they are organic, they reproduce, thus resulting in a certain interplay. At the same time, Roux installs difference itself in the very principle that explains difference, as we just explained: The principle of the struggle of parts postulates the very interplay of difference. Yet, to say that it 'postulates' is to ignore that these principles are not so much conceptual artifices that a scientist says govern nature, as they are the intellectually conceived pathways or 'embodied knowledge' of life forms themselves. All of life 'and' science is the great natural experiment.

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<sup>104</sup> "Und wenn die Auster in der heutigen Ostsee wohnen sollte, müsste sie ihre physiologischen Thätigkeiten so verändern, dass sie bei grösseren Schwankungen des Salzgehaltes gedeihen könnte, als in der Nordsee, d. h. sie müsste ein anderes Thier werden, dabei aber doch den Geschmack der Auster bewahren" (1877: 86-7).

# Chapter 5 – Systematics: Karl Möbius

## Introduction

In chapter two it became clear that Darwin did not yet do systematics, and that we rather find it in the work of Fritz Müller. In 1864 Müller drew a cladogram (figure 8) in order to understand the phylogenetic relatedness of certain, rather similar species. Darwin, in his genealogical diagram (figure 7), had ordered forms according to a general scale, which determined, in a total way, whether certain forms were contemporary to each other or not. Müller, however, ordered forms according to their own interrelations of contemporaneity. He was not interested in determining the true identity of a form – the genealogy or *phylum* (Haeckel) to which it belongs. He rather sought to establish the probability that *M. exilii* was phylogenetically more closely related to *M. fresnelli* or to *M. palmata*.<sup>105</sup>

In order to acquire this knowledge about the probabilities of ancestral relations and the relative positions of forms Müller had to make an “assessment of the evolutionary significance of characters for classification not on the basis of their preconceived physiological importance, as Cuvier had done, but in terms of the regularity of their distribution across the group under examination” (Rieppel 2016: 53). For Müller, “a natural system must be based not on a few characters selected *a priori* according to their putative physiological importance, but on as many characters as possible” (id.: 55). Without a general scale of history, or without a general hierarchy of physiological parts to judge forms with, all of the form’s parts are relevant to classification; any minor detail may reveal something about its ancestral situation, and thereby also about that of other, related forms.

Müller’s work was greatly concerned with the transitions and transitional stages in the ontogeny of organisms, particularly crustaceans, some of which develop through as many as nine larval stages. Sexual dimorphism fascinated him too, and, generally, the moments and areas of development which seem to separate species. He asked himself, given these transitive life forms – always on the verge of becoming different, of constituting another shift – what correlations do we find? How is any one life form correlated with others, so that we may situate it in relation to those others? Whereas ecology sees life forms as processes and part/wholes, systematics sees transitions and correlations.

Darwin was interested in finding the ‘intermediate varieties’ that he supposed should exist somewhere. He asked himself why in nature – understood as continuous and unified – there are

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<sup>105</sup> David West (2016: 74) adds that “Müller was in essence recognizing the value in classification of what are now called shared derived characters, or synapomorphs [i.e. “a derived character state shared by two or more descendent taxa” (Avice 1994: 36)]. Even with Darwin’s genealogical approach, however, classification was at the time based on similarities among taxa, and the use of shared derived characters for determining phylogenetic relationships among living species was Müller’s innovation. Müller used the occurrence of a secondary flagellum in many other amphipod genera as an “outgroup comparison,” one of the ways of resolving cladistic ambiguities. His branch diagram is of the type now known as a cladogram, in which organisms are clustered in clades based on the branching order (cladogenetic splitting of lineages), but the method was fully developed only in the mid-twentieth century, and Müller’s discussion is fragmentary by modern standards.” Cf. Craw 1992.

nonetheless distinct species. Where are the transitional forms that guarantee the historical unity of nature? Whereas Müller sought to elucidate the historical diversity, the historical networks of life forms which connect, node by node, any one of them with all others, Darwin rather tried to understand the historical unities or genealogies underlying the only apparent diversity of nature. And so we also see that in contrast to Darwin, who is involved in representation and interpretation of the invisible behind the visible – the genealogy behind the forms – Müller rather tries to construct, along with the life forms themselves, their own ancestral relatedness. This succeeds insofar as the life forms construct that relatedness with the help of Müller, by showing, for example, their relevant characteristics.

Just as ecology is not only a geographical but also a historical inquiry into life, so systematics is not only historical (phylogenetic) but also geographical. In Müller's *Für Darwin*, however, this geographical aspect is not considered. And generally, my research into systematics resulted in very little material to discuss. Ludwig Trepl's history of ecology, though, pointed at a possibly useful direction of inquiry: the mostly Scandinavian plant geographers working around the 1880s, such as Ragnar Hult and Hampus von Post. All we can do here and now, however, is to look into systematics by way of another scientist active around the Baltic Sea: Karl Möbius.

## Section 5.1 – Species and the theory of evolution

Besides his mostly ecological and descriptive fieldwork, Möbius wrote an important and interesting article on the notion of species.<sup>106</sup> The paper “Die Bildung, Geltung und Bezeichnung der Artbegriffe und ihr Verhältniss zur Abstammungslehre” (1886) – or in English, ‘the construction, validation, and meaning of the species concept and its relation to the theory of evolution’ – was derived from a much earlier lecture on the same topic, delivered already in 1873 (according to Möbius himself (1886: 241)). Although its impact may have been small, I believe this text is of the greatest importance to the conceptual history of science, as it shows aspects of a radically new ordering of life forms, namely systematics. Moreover, its impact might not have been so small after all, since Willi Hennig, the founder of cladistics, is known to have read it and to have cited a quote by Carl von Nägeli from it (Rieppel 2016: 315).

One of Möbius' key points in this text concerns evolutionary morphology and the relation between the theory of evolution and systematics. He explains:

If the theory of evolution wants to prove that a species transforms itself into another, it first confronts itself conceptually with the congruent characteristics of genetically distinct series of individuals; subsequently, it *thinks for itself*, in between the two [series], as many transitional stages as it believes to be necessary for a sustained procreation of generations. For example, it can derive the species *Clupea sprattus* L. from *Clupea harengus* L., the species *Elephas indicus* L. from *Elephas primigenius* Blumb. or both *Elephas* species from a common original form which, however, it first conceives of. Yet the differences between the forms, which – made present conceptually – are also those that the theory of evolution calls *species*, always remain as large as the sum of the steps that it made from one species type to another. The

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<sup>106</sup> Möbius did research on all kinds of things, as Nyhart (2009a: 149) writes: “He published work after work, on flying fish (they don't); on phosphorescence in the oceans (for lay readers); on scientific experiments using aquariums to establish how deep-sea animals got their food; on the species concept; on the fishes of the Baltic, the Atlantic, and the waters around Mauritius.”

individuals, which are the *real* representatives of the species that have been blended into each other in thought, one has in this way precisely not placed in a real genetic connection.<sup>107</sup>

This is what the theory of evolution does: It thinks the transitional stages in between species, so as to explain the history of life forms, the genealogy of life. We already saw that Darwin believed in the existence of these transitional stages, these ‘intermediate varieties’ which, he supposed, would explain the existence of the species that they connect. However, the resulting genealogy would always only connect the different groups of forms and leave yet again other gaps in this more detailed series. All the while, the individual forms are not understood as parts of a real genetic process. Thus, Möbius goes so far as to state that “[i]f it were possible to connect all animal and plant forms with real transitions, then the theory of evolution would be made unnecessary.”<sup>108</sup>

This is an ecological critique of evolutionary morphology aimed at those scientists who, in the wake of Darwin’s work, “mix up hypotheses on the real origin of organic forms with the logical notion of species concepts.”<sup>109</sup> Möbius wishes to make clear that species concepts – their construction and application – has nothing at all to do with the origin of the forms that they represent (1886: 255, 267). To trace the descent of species, genera, and families is a fundamentally mistaken enterprise because those group categories are first of all constructed by comparing the different characteristics of individual life forms. Not species and genera but only individuals develop through time, and therefore only they may be studied in a genetic connection.

The botanist Carl von Nägeli (1865), as cited in Möbius’ text, stated that

the focal point of natural history is no longer in the species but rather therein that each systematical category is treated as a natural unity which constitutes the passage point of a great development-historical [evolutionary] movement. The genera and higher concepts are not abstract but concrete things, complexes of forms which belong together, which share a common origin.<sup>110</sup>

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<sup>107</sup> “Wenn die Abstammungslehre beweisen will, dass sich eine Species in eine andere umändert, so stellt sie sich die übereinstimmenden Eigenschaften genetisch verschiedener Individuenreihe begrifflich erst gegenüber; dann *denkt sie sich* zwischen beiden so viele Uebergangstufen, als sie für eine ununterbrochene Zeugung von Generationen für *nothwendig hält*. So kann sie z. B. die Species *Clupea sprattus* L. von *Clupea harengus* L., die Species *Elephas indicus* L. von *Elephas primigenius* Blumb. oder beide *Elephas*-Arten von einer beiden gemeinschaftlichen Urform, die sie sich aber auch erst begrifflich vorstellt, ableiten. Immer aber bleiben doch zwischen diese Formen, welche, begrifflich vergegenwärtigt, das sind, was auch die Abstammungslehre Species nennt, die Unterschiede so gross, wie die Summe der Schritte beträgt, die sie von einem Speciestypus bis zum andern machte. Die Individuen, welche die *realen* Vertreter der in Gedanken in einander übergeführten Species sind, hat man dadurch gewiss nicht in einen realen genetischen Zusammenhang gebracht.” (Möbius 1886: 270). Also: “The theory of evolution surely negates the boundaries between the plant and animal species; but still its entire structure leans on pillars which are performed by species concepts serving as building blocks. It merely closes the arches over the pillars with thought transitions. When one wants to convince someone visually that two different life forms belong to one species, one puts in between the two the intermediary transitional stages” (id.: 274).

<sup>108</sup> “Wäre es möglich, alle Thier- und Pflanzenformen durch reale Uebergänge zu verbinden, so wäre die Abstammungstheorie unnöthig gemacht” (id.: 274).

<sup>109</sup> “Ch. Darwins Werk über „die Entstehung der Arten durch natürliche Zuchtwahl“ hat jedoch viele Biologen veranlasst, dies zu bezweifeln und Hypothesen über den *realen Ursprung* der *organischen Formen* mit der *logischen Auffassung* der *Speciesbegriffe* zu *vermischen*” (id.: 268).

<sup>110</sup> “Der Schwerpunkt der naturgeschichtlichen Betrachtung liegt nicht mehr in der Species, sondern darin, dass jede systematische Kategorie als eine natürliche Einheit gefasst wird, welche den Durchgangspunkt einer grossen entwicklungsgeschichtlichen Bewegung darstellt. Die Gattungen und höheren Begriffe sind keine Abstractionen, sondern concrete Dinge, Complexe von zusammengehörigen Formen, die einen gemeinsamen Ursprung haben” (Möbius 1886: 273).



Now, Möbius does not disagree with the first sentence (in contrast to the second) for his reply merely emphasises that species and other such groups of forms must have been apprehended conceptually before they can be considered as passage points of evolution. They “must have been determined conceptually if they are to be compared and *ordered* in a *developmental series*.”<sup>111</sup> In this way, Möbius thus introduces an irreducible individuality of forms: They are always prior to group categories. To some extent, Darwin did so too but, unlike Darwin, Möbius also emphasises that groups such as species are conceptually constructed, not found.

Yet, constructed are also the individual forms, though not by humans. The systems in which the form takes part shape the life form and let it come into being. This is the direction of research that should be pursued – and that Roux, as we saw, did pursue – if one wishes to explain the real genetic descent and emergence of life forms: “[O]ne should verify that the force systems which developed the form – thus, for example, the herring – have altered in such a way that they finally let the sprat come into being.”<sup>112</sup> Yet, these force systems are not only internal but also external:

In the course of the specific development of an individual or of multiple individuals which together constitute a developmental cycle the inherited immanent forces of the germ express themselves. Yet, since it cannot let its immanent forces operate in isolation from all biocenotic living conditions, because no single organic *individual* is ever *isolated*, the being that develops from it is not just a child of its parents but rather, simultaneously, a child of its biocenosis, which is itself a spatially and temporally determined result of the force operations of our solar system.<sup>113</sup>

The passage point that is the life form is not only a transition of species but also a transition of a biocenosis. That is to say, the individual not only passes on to the next generation the species but also its biocenosis.<sup>114</sup> And in this way, the geographical aspect of systematics (and ecology) enters the picture.

## Section 5.2 – The construction of species

The historian and philosopher of systematics Joeri Witteveen has brought to the attention of scholars an important shift in the understanding of types between the nineteenth and twentieth centuries. Today, types in systematics represent names whereas in nineteenth-century taxonomy they represented nature (Witteveen 2016: 179). In contemporary systematics, a type is thus not required to be typical. One may encounter a statement such as “‘It is unfortunate that the biological average of *Planta vulgaris* is poorly represented by the specimen in the original publication’” (Croizat 1953: 124; in Witteveen 2016: 179). The type-specimen and the biological type do not

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<sup>111</sup> “Die Glieder der Stufenfolge müssen begrifflich bestimmt sein, ehe sie mit einander verglichen und in eine Stufenfolge geordnet werden können” (id.: 273).

<sup>112</sup> “... müsste man nachweisen, dass die Kraftsysteme, welche die eine Form, also z. B. den Hering bilden, sich so umgeändert hätten, dass sie endlich einen Sprott ins Leben treten liessen” (id.: 270).

<sup>113</sup> “In dem Gange der spezifischen Entwicklung eines Individuums oder mehrerer Individuen, welche zusammen einen Entwicklungskreis darstellen, drücken sich die ererbten immanenten Kräfte des Keimes aus. Da aber dieser seine immanenten Kräfte nicht isoliert von allen biocönotischen Lebensbedingungen arbeiten lassen kann, da kein organisches *Individuum* jemals ein *Isolatum* ist, so ist das Wesen, das aus ihm hervorgeht, nicht bloss ein Kind seiner Eltern, sondern zugleich auch ein Kind seiner Biocönose, welche selbst ein räumlich und zeitlich bestimmtes Resultat der Kraftwirkungen unseres Sonnensystems ist” (id.: 270).

<sup>114</sup> Möbius (id.: 272) provides several examples of “*real causes*,” encompassing the biocenosis, for morphological differences acquired through time.

necessarily correspond. In the same vein, some systematists in the first quarter of the twentieth century started to speak of ‘nomenclatural types’ to distinguish the new type from the old, biological type (Witteveen 2016: 163).<sup>115</sup>

Now, precisely this new understanding of the type as a name-bearing category, a logical category rather than a feature of nature we find in Möbius’ text. He conceives of the species, already in 1886 or possibly in the lecture of 1873, as nothing but a logical construction of the intellect. In his view, nineteenth-century taxonomists presupposed a fixed number of species to exist in nature. Consequently, their task was to connect the forms they found with those natural species; the matter of debate being how to connect them. But Möbius cleverly points out that they, therefore, did not let the diversity of characteristics shape their species concepts but rather themselves determined, a priori, what this diversity consisted of. “In truth they thus constructed that many *species*, as they established *species concepts* on the plant and animal forms that they researched.”<sup>116</sup> Species were natural and the taxonomists interpreted nature’s diversity to find these underlying types.

Nineteenth-century taxonomists asked themselves whether, in classification, they should look at the sexual organs, the organs of greatest physiological importance, or yet again other elements of the living being. In botany life forms were mostly classified on the basis of their sexual organs, their flowers, as Linnaeus had long since done. Haberlandt criticised this – what he called – ‘flower systematics’. According to him, the ‘flower region’ is only of the many different regions of the plant system, not deserving of special importance in classification (Haberlandt 1882a: 563-4). Most important, Haberlandt argued, are the physiological-anatomical characteristics of the plant. Yet, evidently, these encompass virtually all characteristics. Similarly to Haberlandt, Möbius also believes that a myriad of different characteristics best allows for a life form’s classification. He considers the most complete species concepts to be “biocenotic-physiological-genetic-morphological species concepts,” with the adjectives placed in order of their importance from left to right.<sup>117</sup>

Species concepts, Möbius writes, are “essential like the common names in language,” and never complete, since they are the results of induction.<sup>118</sup> Even if we could perfectly compare all living individuals within the next degree of kinship, we would still not be able to consider their common ancestors and offspring. In this sense, therefore, the species concept is endless, but effectively, it is limited – by the present state of induction.<sup>119</sup> All individuals (including common ancestors and

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<sup>115</sup> Surprisingly, the English systematist Hugh Edwin Strickland already wrote to Darwin in 1849 that “by *type-species* I only mean a conventional distinction, referring only to words, not to *things*, and like human titles, only used as a matter of convenience” (in Witteveen 2016: 160).

<sup>116</sup> “In Wahrheit creirten sie also so viele Arten, wie viele Artbegriffe sie auf die von ihnen untersuchten Pflanzen- und Thierformen gründeten” (Möbius 1886: 244).

<sup>117</sup> “Die **biocönotisch-physiologisch-genetisch-morphologischen Artbegriffe** sind die relativ inhaltsreichsten” (Möbius 1886: 248). In stark contrast to Möbius however, Haberlandt argued for *functional* classification, that is, classification based on the functional characteristics of life forms (Cittadino 1990: 33; Review 1879: 337). For a more recent defense of functional, ecological classification, see for example Grime (1998).

<sup>118</sup> “In den biologischen Wissenschaften sind die Artbegriffe ebenso unentbehrlich, wie die Nomina communia in der Sprache” (id.: 244).

<sup>119</sup> Möbius writes about this: “They [i.e. all species authors] do not demand a spatially and temporally *unlimited* succession of similar individuals but they would rightly also reject any demand to delimit beforehand the spatial and temporal limits within which real representatives of their species concepts might appear” (“Sie verlangen keine räumlich und zeitlich *unbegrenzte* Reihenfolge gleichartiger Individuen, aber sie würden mit Recht auch jedes Verlangen, im voraus Raum- und Zeitgrenzen festzustellen, innerhalb welcher noch reale Vertreter ihre Artbegriffe erscheinen könnten, zurückweisen” (id.: 260)). However, there

offspring) constitute, in Möbius' terms, a species concept's scope (*Umfang*) (Möbius 1886: 259). The counterpart of its scope is its content: "the congruent characteristics of all individuals of the next degree of kinship, scattered over space and time, [concentrated] in one mental presence [i.e. the species concept]." <sup>120</sup>

Möbius conceives of the content as the intensive side of the species concept, the scope its extensive side. Moreover, "both relate to each other like phenomena to laws" (Mob260): The kindred individuals (of an indefinite number) constitute the limits of congruent characteristics. Therefore, if one other characteristic is shown to be present in five percent of the individuals, this characteristic is deemed irrelevant. If, however, another individual, with one incompatible characteristic, is shown to be an ancestor of the kindred individuals, the individual is included with the species content's scope and the characteristic excluded from its content. In this way, the content of the species concept will always be "legitimate phenomena." <sup>121</sup>

Möbius warns against the belief that species concepts are mere disconnected abstractions. Classification, he writes, can never be fully abstract, completely arbitrary:

Nature provides the characteristics; only their selection and their classificatory appreciation is the author's work. The further the authors remove themselves from the real foundations of the classificatory concepts, from the singular perceptions, the more the classification is influenced by their logic. It can never make itself fully free from nature and therefore never become purely arbitrary. <sup>122</sup>

As long as "classification takes its concepts from experience," and is not like "the theory of evolution [which], led by ideas, goes beyond experience," any abstraction from the basic perceptions of the life forms will only further clarify the logic of their phylogenetic relatedness. Now, this work of abstraction, i.e. the very construction of species, which Möbius says the nineteenth-century taxonomists never realised they were actually involved in, that work is needed because the species is, in a certain sense, far removed from the individual forms. No single life form can exemplify it. There is no type; the 'nomenclatural type' being nothing but a name-bearer. "[T]he type purely as such cannot be drawn. Each animal image thus always also constitutes individual characteristics." <sup>123</sup>

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is also a pragmatical limit: "The species concepts should not refer to eternal but only to temporally real regularities" ("Die Artbegriffe sollen nicht ewige, sondern nur zeitlich reale Regelmässigkeiten bezeichnen" (id.: 260)).

<sup>120</sup> "Der Artbegriff drängt die übereinstimmenden Merkmale aller im Raum und in der Zeit zerstreuten Individuen eines nächsten Verwandtschaftsgrades in eine geistige Gegenwart zusammen; darin besteht sein Inhalt" (id.: 259).

<sup>121</sup> "gesetzliche Erscheinungen" (id.: 258).

<sup>122</sup> "Die Merkmale giebt die Natur; nur ihre Auswahl und classificatorische Verwerthung ist Autorensache. Je weiter sich die Autoren von den realen Grundlagen der classificatorischen Begriffe, von den Individualvorstellungen entfernen, je mehr Einfluss gewinnt ihre Logik auf die Classification. Völlig frei von der Natur kann sie sich niemals machen und daher nie rein willkürlich werden" (id.: 261-2).

<sup>123</sup> "Da wir in einem Artbegriff nicht einen bestimmten, sinnlich anschaulich auftretenden Grad des Typus denken, sondern damit die ganze Schwankungsweite desselben umfassen, so kann der Typus rein als solcher nicht gezeichnet werden. Jedes Thierbild stellt daher immer auch individuelle Eigenschaften dar" (id.: 262). Nonetheless, Möbius provides four kinds of "real representatives of a species concept," namely "(1) a hermaphroditic individual; (2) a male and a female of animals with separated sex; (3) in the case of polymorphic species individuals of any complementary form and function of a stock or community; (4) individuals of the different generations of a developmental circle" (Mob263).

Yet, precisely because the species can only be a fully conceptual ‘thing’, not existent ‘as such’, it is *constructed*. It must be constructed as nothing would suffice to signify it in an immediate way. Only the process of construction – the careful abstraction from many, endlessly different forms – gives off, almost as if it were some by-effect, the signification of the species. Life forms show characteristics, scientists select and interpret them, and as this process continues – life forms nor scientists ever remaining the same – species concepts gain scope and content while other such concepts are forgotten. The construction process is, however, not as boundless as it may appear here. Crucially, it takes place within limits; the limits of its own classification system and the limits of its own classification method (i.e. the limits of where in time and space one should look for characteristics and possibly kindred individuals). Regarding the classification system, construction of species will only take place in between the “unforeseeable wealth of an individual’s characteristics” and the emptiness of the genus concept in relation to it.<sup>124</sup> Concerning the classification method, life forms and scientist will only meet within a practical time limit (determined by their own times) and within a practical space limit (determined by their own places and movement).

## Conclusion

Systematics, as approached by way of Fritz Müller and Karl Möbius, studies the nexus of transitivity and ancestry. It studies life forms as passages or transitions and simultaneously as nodes in a network, as correlations of other forms. An organism, moreover, is not only a passage point of its ancestors but also of the biocenosis. For the ecologist, the biocenosis is a whole in which the organism is an interacting part whereas for the systematist it is something which its different members pass on to the next generation. In contrast to ecology’s mechanism of part/whole, it is in this way that systematics conceives of what is beyond the organism: through the conceptual dynamic of transitivity.

With regard to the development or sequence of organisms, ecology seeks to explain the real genetic process. As we saw by way of Roux, however, it is unable to account for discrete change: Any process may be part of a greater process but the shift from one process to another one that replaces it escapes the ecological nexus of process and part/whole. The genetic development, on the other hand, escapes the transitivity-ancestry nexus of systematics. Instead of seeing real development, the systematist sees sequences and networks of life forms. There is not a movement but a correlatedness: The form is a situation, functionally related to other such ‘abundant’ forms, as they all stand out in relation to each other. This is why classification needs to work with many different characteristics – biocenotic, morphological, genetic, and physiological ones – according to Möbius: All of this data will only add to the insight into and truthful reconstruction of the ancestral network of life forms, their phylogenetic history.

Möbius’ criticism of the theory of evolution should also be seen in this light. The goal of systematics he believes cannot be the reconstruction of evolution. Real genetic development must be studied by ecology, as it involves the always changing part-whole interaction of force operations and systems of organisms and biocenosis. Systematics should rather devote itself to the construction of species. It should not, like evolutionary morphology, interpret species. Möbius

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<sup>124</sup> “unabsehbaren Reichthum von Merkmalen eines Individuums” (id.: 263).

points out that in order to explain developmental series one may build as many bridges between the members as one likes but on the one hand, this does not improve our understanding of the real genetic connection between real individual life forms. On the other hand, our classification becomes fundamentally misguided. Species are logical constructs abstracted from the individual forms with their endless multiplicities of characteristics. Since they are conceptually constructed and not naturally found, it makes no sense to trace their descent.

Although construction is an important phenomenon in systematics, Möbius' focus on it might lead us to believe that it is a defining character of systematics. It is not. In the previous chapters, we saw that construction is also essential to ecology. Constructive principles such as Roux's struggle of parts and Haberlandt's 'organizing principles' are different from biology's causes and effects because they do not articulate a supposedly underlying reality but rather translate the pathways or 'embodied knowledge' of the organisms themselves. The scientist, making herself part of the factory of life, as Roux did with his experiments on embryos, does not gain the abstract knowledge of life's conditions and causes but rather becomes able to reconstruct the intimate knowledge of life's dispositions and ways of interacting in the discourse of science.

Is life science then all about construction? – No, it is certainly not. In fact, construction is just as essential as the perceived, radical multiplicity of forms. Not a single form is like another, not for Möbius nor for Roux. Forms are seen as being radically individual. This endless difference, this boundless surface of multiplicity without a second, 'more fundamental' layer is precisely for that reason also one enormous tapestry, factory, or biocenosis. Nature has been turned inside out: Its integrity and unity is not in the interior but out in the open and its difference is not on the outside but rather coupled with that superficial integrity or broken-up unity to form a shining everything of differentiating differences.

Roux distinguished in the practice of his science between a kinetics and a cinematics and I think that distinction adequately expresses the construction of being and the film of being – both in the sense of a thin layer and moving pictures – that we discuss here.<sup>125</sup> The former is studied by the kinetic domain of ecology and systematics, that is, the process half of the ecology nexus and the ancestrality half of the systematics nexus, while the latter is studied by the cinematic domain of life science, i.e. the part/whole half of ecology and the transitivity half of systematics.

The axis of cinematics and kinetics is situated where in biology we would distinguish between structure and function. In contrast to structure and function which divided biology in two – comparative anatomy and physiology respectively –, the construction and film of beings is in line with the sciences. Both ecology and systematics move between the kinetics and cinematics of life, as they both involve construction of life forms and the film of life forms – albeit in completely different ways which mutually exclude each other.

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<sup>125</sup> Evidently, Roux does not use the distinction in the way that I introduce here. For him, cinematics refers to "a total description of all developmental processes" and kinetics to "the causal doctrine of development [theory of evolution]." See Mocek (1998: 193): "Die Anlehnung an A. M. Ampères (1775-1836) Einteilung der physikalischen Bewegungslehre unterscheidet Roux zwischen einer vollkommenen Beschreibung aller Entwicklungsvorgänge (Kinematik) und der ursächlichen Entwicklungslehre (Kinetik)."

# Conclusion

Balancing between history-writing and philosophizing, this archaeology of life science has constructed life science as an epistemic structure consisting of, and divided by, ecology and systematics. First of all, it suggested the two aporia that keep ecology and systematics at an insurmountable distance from each other. We identified these areas of problematization as the dichotomy between heredity or ancestry and development or process on the one hand, and on the other, the dichotomy between part/whole and transition. Armed with this basic yet abstract understanding of the epistemic structure, we moved from predominantly philosophy of biology material to historical material.

In order to understand how biology precisely differed from life science, especially with respect to the ordering and development of life forms, we first approached Charles Darwin and Fritz Müller. Darwin's ideal of genealogical classification appeared to be firmly situated in biology, as it conceived of life forms as nature's signs indicating their true identity and considered organisms to be manifestations of life's functional history determining their organization and development – the two basic dogmas of biology. Müller, however, fiercely deconstructed these dogmas (without fully escaping them) and drew a cladogram to understand the phylogenetic relatedness of certain life forms. In combination with Möbius' important though equally overlooked article on the construction of species, we were able to construct the epistemic nexus of systematics (transitivity and ancestry). Further research into important work by Scandinavian plant geographers at the time would have further improved our understanding of systematics.

With regard to the relation between biology and ecology (life science), we first approached Hanns Reiter and Gottlieb Haberlandt. Whereas Reiter expressed a conception of the study of life, including ecology, much like our archaeological one, and showed an interesting concern for the tradition of plant physiognomy, Haberlandt's texts helped our construction of ecology even more. In a definite move away from biology's framework of function and structure, physiology and anatomy, cause and effect, Haberlandt rather established a physiological plant anatomy which conceived of plants as systems governed by organizing principles. Although at a closer look even Haberlandt's work was somewhat confused, in this complex shift from biology to life science, there was still the influential 'experimentalist' and 'mechanist' Wilhelm Roux for us to delve into. In contrast to his usual portrayal in the history of science, however, we found him – guided by his early work – to be a genuine ecologist, as he firmly worked with the part/whole and process nexus.

Finally, we were also able, with the historical material – especially Roux and Möbius – to conceive of a general axis of scientific practise shared by both ecology and systematics, namely the construction and film of beings. Ecology, by way of Roux, knows constructive principles, which are nothing but the pathways and dispositions of life forms translated to a scientific discourse. By means of 'natural experiments' and an intimacy with other life forms through experimentation, the system of scientist and research 'object' express their construction of life. Systematics, by way of Möbius, knows species constructed by the multiplicity of a life form's characteristics in combination with the scientist's abstraction. In both cases, construction is inseparable from the irreducible and always changing uniqueness of life (forms). There is only construction of species and principles, groups of forms and processes, because nature is no longer a wide, united expanse of forms which are ultimately one but rather differences throughout. As such, by virtue of being differences, all life

forms interact by differing. In that way, they also show themselves, and so the film of life forms connects with their construction.

In relation to the method of archaeology with which this research project has been produced, two potentially pressing questions may be asked. Firstly, has life science remained fundamentally unchanged ever since the epistemic shift of the 1880s when it replaced biology? The answer is 'no'. At every moment, life science is changing and, in part, also fundamentally. Within the epistemic structure represented by figure 1 (p. 9) there is in fact a lot of space for manoeuvre and change. Ecology may at certain times or in certain places be more concerned with the aspect of process than with that of part/whole, and similarly, systematics may sometimes be paying more attention to the phylogenetic relatedness of life forms than to their transitivity. These categories – of process, transitivity, etc. – may even shift their meaning somewhat and approximate, to a certain extent, another category. The shape of the diagram may change radically, yet its basic structure will have to be the same if we are still looking at life science.

The second question concerns whether life science is currently still ongoing or if it is perhaps at this very moment being replaced by a future study of life. This is hard to establish, for me, on the basis of this archaeology. However, I have reconstructed the epistemic structure of life science up to a relatively abstract level, at which it attains some generality. A major epistemic shift involving all of what we have discussed would not remain restricted to just the study of life but would also entail many other sciences as well as philosophy and the humanities. Looking around academia, and knowing what we know from this thesis, it is, in my view, highly unlikely that an epistemic reconfiguration of life science is currently ongoing or has already occurred – though we might always be looking in the wrong places.

Finally, this archaeology of life science also stimulates the reflection of archaeology on itself. As we discussed systematics by way of Karl Möbius in the final chapter, one may have drawn certain parallels between systematics and the very method that has produced this research project. Although we are here translating from one domain of the intellect to another – which is always more complicated than it seems at first glance –, archaeology would, in a different epistemic structure, be situated where we now find systematics. It approaches sciences as transitive forms which are historically correlated: Life science follows biology. Avoiding all the complications of translation that we immediately draw ourselves into here, one of the interesting questions may be: What is the study of science and thought opposite archaeology in a similar diagram? These and other questions will require another, different archaeology.

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