Evolutionary novelty:
a philosophical and historical investigation.

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To Sanja. Uskliknimo s ljubavlju Svetitelju Sanji.

Abstract

Evolutionary novelty, the origin of new characters such as the turtle shell or the flower, is a fundamental problem for an evolutionary view of life. Accordingly, it is a central research topic in contemporary biology involving input from several biological disciplines and explanations at several levels of organization. As such it raises questions relative to scientific collaboration and multi-level explanations. Novelty is also involved in theoretical debates in evolutionary biology. It has been appropriated by evo-devo, a scientific synthesis linking research on evolution and development. Thanks to its focus on development, evo-devo claims to explain the mechanistic origin of novelties as new forms, while the Modern Synthesis can only provide statistical explanation of evolutionary change. The origin of an evolutionary novelty is a *historical* emergence of a new character involving form and function. I focus on three neglected dimensions of the problem of novelty, the functional-historical approach to the problem, research on novelty in the Modern Synthesis era and novelty in plants.

I compare the evo-devo approach to novelty to a functional-historical approach of novelty. I focus on its origin in Darwin and its presence in the Modern Synthesis. The comparison of the two approaches reveals distance between conceptual frameworks and proximity in explanatory practices. This is partly related to unwarranted conceptual opposition. In particular, I list several ways of distinguishing novelty and adaptation, some of which are not conceptually sound. I then focus on the relation between novelty and adaptation in the Modern Synthesis era, and on the relation of novelty to other fundamental biological problems (speciation, origin of higher taxa, complexity). Pushing this approach further, I challenge the view that the Modern Synthesis excluded development and reached a hardened consensus. Finally, I analyse how Günter Wagner’s developmental theory of novelty applies to novelties in plant.

Table of contents

List of figures.

GENERAL INTRODUCTION

The emergence of organisms with new characters or novelties becomes a fundamental problem as soon an evolutionary view of life is adopted. What exactly is a novelty? It can be non-technically defined as a character that was not possessed by any of the ancestors of the organisms that possess it and which constitutes a qualitative difference compared to any character present in the ancestors. For an evolutionary theory, the problem is then how did these novelties originate? What kind of transformation happened? And what caused this significant transformation between ancestor and descendant? For Darwin's theory of evolution by natural selection, the problem was more precisely how can the latter act on small variations to gradually help produce new characters. The problem was especially acute for complex characters composed of many parts such as the vertebrate eye. How can evolution by natural selection gradually produce the eye when all the parts in their complex and specific arrangement are apparently needed to make the eye viable? Problematic were also characters about which it was hard to conceive any advantage provided by their hypothetical intermediate forms. These criticisms against Darwin's *Origin of species* were recognised by Darwin himself as the deepest challenge to his theory of evolution by natural selection (Darwin, 1872, chapter 7). The failure to convince that natural selection acting on small gradual variations could produce new characters was one of the reasons Darwin's theory fell out of favour between the end of the 19th and the beginning of the 20th century. It is still today one of the targets of defenders of contemporary versions of creationism such as Intelligent Design (Behe, 1996; Dembski, 1998; Johnson, 1991).

Conceived in contemporary scientific terms, the origin of a new phenotypic character such as the turtle shell or the flower is a complex phenomenon. Changes in entities and processes at multiple levels of organisation such as genes, gene regulatory networks, morphogenetic gradients, cell adhesion molecules, cell populations etc. can take part in the mechanisms of their origin. As historical events often set in the deep past, the occurrence of novelties has to be situated within evolutionary sequences with the help of different sources of evidence. As transformation occurring within organisms, they call for ecological functional and structural considerations.

This complexity and these multiple aspects of evolutionary novelty or innovation[1] make it a multidimensional scientific problem involving numerous disciplinary and interdisciplinary research projects. As an object of investigation for the philosopher and the historian of science it raises questions related, among others, to multi-level explanations, epistemic values, competing sources of evidence or research traditions.

Another level of investigation is added by the involvement of novelty, as a concept and research problem, within a contemporary scientific controversy. Novelty has been particularly promoted and investigated by researchers within the field of Evolutionary Developmental Biology or 'evo-devo'[2]. As indicated by its name, evo-devo is a multidisciplinary scientific endeavour ambitioning to bring together the study of evolution and the study of development. It progressively took shape in the 1980s and is now an established field with laboratories in many biological departments, dedicated scientific journals, international societies and conferences. As a synthesis of disciplines, evo-devo contains many research programs. However, empirical research in evo-devo is dominated by the study of development based on developmental genetic concepts, methods and tools; considerations of higher level of organisation and of evolutionary problems are undertaken only by a small part of evo-devo scientists (Diogo, 2016, 2018). At the same time, evo-devo can refer to a theoretical construct that is opposed by some scientists and philosophers to the still dominant paradigm in evolutionary

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[1] Different meanings have been given to the distinction between novelty and innovation. Some authors have argued that 'innovation' should be used for novel functions and 'novelty' for novel morphological structures (Love, 2003, 2006; G. P. Wagner, 2015). It is usually the term 'innovation' that is used to designate new behaviours in animals (Ramsey, Bastian, & van Schaik, 2007a, 2007b), the term 'novelty' is rarely used for this category (but see Brown, 2014). The latter usually designates new morphological characters. Some authors have used the term 'innovation' to describe the process of origin , and 'novelty' the product (Müller & Newman, 2005; Peterson & Müller, 2016). Here I will use 'novelty' as a default term, and qualify it (as functional, behavioural, genetic etc…) when needed.

[2] I will use the term 'evo-devo' throughout the rest of this work.

biology, the Modern Synthesis. Novelty is, among other problems, at the centre of the debate, primarily because it is argued that input from developmental biology has been neglected by the dominant framework and that this input is necessary to elaborate a mechanistic theory of the origin of novelties (Bonner, 1982; Carroll, 2005; Raff, 1996; Wagner, 2014; Wagner, Chiu, & Laubichler, 2000).

FOUR DIFFERENT PROBLEMS

At least four problems regarding evolutionary novelty can be distinguished:

_ The problem of the definition(s) of novelty.
_ The problem of the role of novelty in evolution.
_ The problem of the degrees of novelty in evolution.
_ The problem of the explanation of the origin of novelty.

In this thesis, I will only address the first and above all the fourth problem; I will however present the four problems in turn in order to provide context to the subject of this thesis.

The problem of the definition(s) of evolutionary novelty

Some researchers have linked the value of the concept of novelty to the agreement of the community of researchers on a single definition:

> “Evolutionary novelty is the subject of several edited works (including this one) as well as many papers and books (Jernvall 2000; Love 2006; Love and Raff 2006; Muller and Newman 2005a; Muller and Newman 2005b; Muller and Wagner 1991; Pigliucci 2008; Salazar-Ciudad 2006; Shubin et al. 2009; Stone and Hall 2004; Wagner and Lynch 2010), and is frequently used to justify the importance of work proposed in grant submissions. The origin of evolutionary novelty has even been proposed as the central question linking evolution and development (Muller and Newman 2005b; Wagner and Lynch 2010). *Given its importance to such a broad spectrum of evolutionary biology, novelty must therefore either have a workable and agreed upon definition or be discarded*.” (Hallgrímsson et al., 2012, emphasis added)

If one subscribes to the judgment of Hallgrímsson and colleagues, then the prospects of the concept of novelty seem grim since a review of past and recent literature reveals several coexisting definitions of novelty. At least four criteria to define evolutionary novelties and flesh out the idea of a qualitative difference stand out in the literature:

a) A *functional criterion*: Ernst Mayr proposed to ground the qualitative change associated with novelty in the concept of function. He thus defines an evolutionary novelty as: "any acquired structure or property that permits the assumption of a new function" (Mayr, 1960, p. 351). This definition is used across levels of organisation, for example for new metabolic pathways (Wagner, 2011) as well as for new morphological characters.

b) A *criterion based on evolutionary significance*: this type of definition is present both in ecologically minded and developmentally-minded researchers. It defines novelty based on its effect on further evolution. The concept of key innovation is used to refer to new characters that are connected with a rapid diversification of species or the invasion of a new ecological zone, such as avian flight (Alfaro, 2014; Galis, 2001; Liem, 1973; Schluter, 2000). In evo-devo, some definitions are based on the concept of evolvability, that is, a novelty is conceived as a change that allows for more developmental change or opens up new direction of variation (Brigandt, 2007).

c) A *criterion based on the concept of homology (character-based)*: homology is a concept from comparative anatomy. A "homologue" was originally defined by Richard Owen in 1843 as "the same organ in different animals under every variety of form and function". Novelty is defined using homology as a new homologue, that is, a trait that cannot be considered homologous to any pre-existing trait (Müller & Wagner, 1991). Because several interpretations of the concept of homology exist, there are debates among researchers who adopt this criterion (Arthur, 2000; Müller, 2010)

d) A *process or explanatory criterion*: Qualitative change is brought about by a specific process, or by specific processes, such as the overcoming of constraints or the switch between adaptive peaks (HallgrÍmsson et al., 2012); these processes are different from those governing quantitative change. This implies that the nature of the process determines the nature of the outcome.

The multiplicity of existing definitions of evolutionary novelty and the still ongoing debate among scientists about what is the proper definition (HallgrÍmsson et al., 2012; Müller & Wagner, 1991; Peterson & Müller, 2013, 2016; Wagner, 2014) appears as a first reason for philosophical investigation. The philosopher of biology might play a role in conceptual clarification, as with the concepts of adaptation and gene for example. Among the philosophers who have considered the question, few seem to agree with the judgment of Hallgrimsson and colleagues cited above (Brigandt & Love, 2012; Pigliucci, 2008).

Ingo Brigandt and Alan Love have recently pleaded for a move “beyond definitional debates” (2012). They argue that the main purpose of definitions of novelty is not to determine which traits are novel and which are not, but to formulate problems that research should answer. They interpret the plurality of definitions as a consequence of the complexity of the problem of novelty. This complex problem has to be decomposed into more local problems. By defining concepts of novelty as guide for research Love and Brigandt diffuse the problem of definitions and turn the attention of philosophers towards other problems. Indeed, the requirement of Hallgrimson and colleagues does not seem to fit with the nature of contemporary scientific investigation of complex problems. The search for the unique appropriate definition of novelty is probably harmful for research and bound to fail. However, one can reject the quest for a unique definition while defending the benefit of a critical appreciation of definitions and distinctions. This may be particularly justified when these definitions and distinctions are put to use in the theoretical and polemic literatures within the context of the controversy on the theoretical framework of evolutionary biology.

The problem of the role of novelties in evolution

A second problem, that I will not address directly in this thesis, is the one suggested by the second type of definition of novelty. The concept of key innovation is traditionally used in an ecological context, whereas the concept of evolvability has emerged from the domain of evo-devo. Despite their different disciplinary homes, these concepts share a focus on phenotypic changes that have important evolutionary significance, that is, changes that might have been responsible for initiating large-scale evolutionary trends, or for altering them in one way or another.

The rise of a developmentally oriented concept of novelty was paralleled by a move from an interest in how the power of selection is limited by different kind of constraints, to a more general and positive interest in the ways genomic and developmental changes open or close, broaden or narrow potential directions of phenotypic variation (Arthur, 2001; Brigandt, 2015; Wagner & Altenberg, 1996). The rise of the concept of evolvability led to a return of the criterion of evolutionary significance in the study of evolutionary novelty. Highly interesting were (and still are) to the student of adaptive radiation, the phenotypic novelties that opened new ecological niches; highly interesting are to the students of evolvability the developmental changes that, at various points in the evolution of life, made new directions of phenotypic variation developmentally possible, or that increased the potential of phenotypic variability of a population of organisms.

The problem of the degrees of novelty

A third problem that I will leave aside is of a more abstract nature but should be mentioned for the sake of perspective. A distinction should be made between the question of the definition of novelties as described earlier and the question of the degrees of novelty or the hierarchisation of novelty in evolution. If novelty is defined in terms of uniqueness, unpredictability, or modification of the space of possibilities, then debates about the proper definitions of novelty presented earlier can be interpreted as focused only on a subset of what is novel in evolution.

The concept of evolutionary novelty, although it is used to refer to new entities across levels of organisation (genes, cell types, metabolic capacities etc.) has been mostly used and appropriated to refer to new morphological characters. Now, other literatures focus on novel properties of life without using the term novelty. The perspective of organisation focuses on life not as evolving but as primarily defined by autonomy (Moreno & Mossio, 2015; Varela, 1979). One object of focus is however the transitions between different degrees of autonomy, especially at the level of cells. The literature on major transitions in evolution focuses primarily on transitions such as the origin of the eukaryote cell or the transitions from unicellularity to multicellularity (Smith & Szathmary, 1997; Szathmáry, 2015). In a sense, the literature on morphological or developmental novelty possesses criteria to establish degrees of novelty since the concepts of constraints and evolvability can be quantified (e.g. Bedau, 1992; Cheverud, 1984; Wagner, 2008). However, the idea of a hierarchy of novelty at a more general level might be impossible to operationalise and might not be interesting. Even so, the point remains that the literature on phenotypic novelty focuses only on a subset of what is novel in evolution and that therefore, I will focus in this thesis on only a subset of what is novel in evolution.

PHILOSOPHICAL AND HISTORICAL APPROACHES TO THE PROBLEM OF THE ORIGIN OF EVOLUTIONARY NOVELTIES

My main focus is on problems related to the origin of evolutionary novelties and to their scientific explanation. However, I should admit at this point that no single overarching problem nor a single method has guided my investigation. If there is a single guiding principle to my research, it is reactive: because the study of the origin of novelty has often been conceived in terms of the origin of form, I focused on functional approaches to novelty; because most philosophical and theoretical work on novelty is focused on animals, I turned my attention to plants; because many historical investigations of research on novelty have been conducted as part of the history of evo-devo, I focused on history of functional approaches to novelty and more generally on research on novelty in the Modern Synthesis era. Each reactive research choice has brought a different set of problems. Therefore, in this research, I vindicate a use of different styles and methods of philosophical and historical analysis. This pluralism is not a principled choice but proceeds from the subject chosen itself.

The functional-historical approach and the evo-devo approach to novelty

The opposition between the Modern Synthesis and evo-devo in relation to novelty is sometimes expressed in the following way: The Modern Synthesis, centred on, or even reduced to, population genetics, provided statistical explanations of evolutionary change and adaptation, while evo-devo provides a mechanistic explanation of changes in form (Amundson, 2005; Carroll, 2008; Laland et al., 2015; Müller, 2007a; Pigliucci, 2007; Raff, 1996). Some evo-devo practitioners and defenders vindicate a separation between the study of function and adaptation, and the study of form and changes of form, and they identity the problem of novelty with the latter (Amundson, 2005; Carroll, 2008; Müller, 2007a; Raff, 1996), . However, the origin of a novelty is the *historical* emergence of a new *character*, which involves one or several forms (in the case of muscles for example) and one or several *functions. The identification of the explanation of novelty* with the mechanistic explanation of form is not a universally accepted conceptual step. To the profound objections to his theory, described earlier, Darwin's main response was a functional and historical solution. There actually is an asymmetry here between formal approaches and functional approaches to novelty. While some evo-devo scientists and philosophers conceive novelty as the problem of form or the problem of change of form (Amundson, 2005; Carroll, 2008; Müller, 2007a; Raff, 1996), the functional approach to novelty is not symmetrically analytical; for the latter, the problem of novelty inseparably involves form and function.

Several types of philosophical approaches to the explanation of complex scientific phenomena have been undertaken:

The philosophy of mechanism for example can be conceived as descriptive and analytical. It describes and analyses scientific explanations in terms of the search for mechanisms. Secondly, there are several approaches that can be considered normative. For example, the confrontational strategy consisting in evaluating whether a particular scientific explanation, theory, or a field of scientific enquiry, fits the normative standards of some philosophical theory of scientific explanation, reasoning, and evidence. Belonging to this type are the analysis of natural selection as tautological (e.g. Popper, 1976), the critique against methods in some research in evolutionary psychology (e.g. Dupré, 2001; Griffiths, 1996), and the analysis of flaws in randomised clinical trials (e.g. Cartwright, 2007; Cartwright & Munro, 2010). Applied to research on novelty, it could consist in evaluating actual research and explanations of novelty according to criteria of explanatory adequacy imported from general philosophy of science.[3]

Another kind of normative approach can be called the conceptual strategy. It amounts to relying on some form of conceptual analysis evaluate a scientific theory, Jerry Fodor and Thomas Nagel critiques of Darwinism may be interpreted this way (Fodor, 2007; Richards, 2012). Yet another normative strategy is a form of bottom-up approach, abstracting normative standard from the observation of scientific practice in the field under consideration. Because the origin of evolutionary novelties is a complex phenomenon and because biology is a domain of specialised science, much scientific research addressing the problem will be partial, focusing on different research questions that can be seen as parts of the wider problem of the origin of novelty (Love, 2008).

It is important to note that these strategies can be used by scientists themselves to either criticise past or competing theories and explanations or to elaborate and justify their own theories and explanations. They engage in these strategies often without explicit reference to work in philosophy of science, or more rarely, they can make explicit use of philosophy of science. One example of the latter is the use of philosophical concepts of Karl Popper by some proponents of the cladistics method in systematics (Hull, 1988). It is also the case of some practitioners of evo-devo who have been entertaining a dialogue and have sometimes directly collaborated with philosophers of science and who explicitly use concepts from

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[3] The idea of confrontation has also been used to describe an approach seeking to test theories of scientific change by applying them to historical or contemporary scientific case studies (see below).

this discipline to elaborate or clarify their own theories (Minelli & Pradeu, 2014; Müller & Pigliucci, 2010; Wagner, 2000, 2014).

My approach will not be primarily normative. I focus on the functional-historical conception and the evo-devo conception of novelty without presupposing whether the explanations they each produce are competing, or partial and integrable into more complete explanations, or complementary, focusing on different types of phenomena. I will try to understand to what extent the distinction between these conceptions of novelty is justified, and what the reasons – theoretical, methodological, empirical, historical, sociological - of their distinction are. My approach is close to what Jutta Schickore (2011) has called an hermeneutic approach in history and philosophy of science. As opposed to a normative stance intending to determine the criteria of adequacy of a scientific explanation and whether specific scientific explanations meet these criteria, and as opposed to a confrontational stance intending to test philosophical theories of science on historical case studies, the hermeneutic stance is an interpretative process of progressive adjustment of provisional analytic concepts used to make sense of particular forms of scientific practice or particular scientific historical episodes. My approach is hermeneutic in that the concepts of form and function and the functional-historical and evo-devo conceptions of novelty, among others, are provisional concepts to be refined in order to understand research on evolutionary novelty in the last eighty years or so.

Plants and the generalisation of theories of novelty

The empirical research on novelties in plants is booming, but the conceptual and philosophical work as well as the general theories about novelty are elaborated with mostly the animal kingdom in mind. As stated before, the renewal of attention on the concept of evolutionary novelty in the last three decades is tied to the rise of the evo-devo movement (Müller & Newman, 2005). The founders of this movement were mostly developmental biologists, either with a molecular focus or a morphological focus, whose empirical work was generally based on animal species (Morange, 2011). The contemporary work on evolutionary novelties is still predominantly based on research on animal species.

A comprehensive quantitative survey to back this claim is still needed, however a look at theoretical writings and review articles on evolutionary novelty gives an unambiguous picture (Hall & Kerney, 2012; HallgrÍmsson et al., 2012; Moczek, 2008; Müller & Pigliucci, 2010; G. P. Wagner, 2014).

In his review article, Mockzek (2008) refers to many examples, mostly from research on arthropods (butterflies, beetles, flies, fireflies …) but not one from research on plant species. In their review article on novelty, Hall and Kerney (2012) review six examples, four from vertebrate species and two from invertebrate species (worms). Hallgrimsson et al. (2012) develop a general definition of novelty, relying on four examples, none of them including plant species. Meanwhile, Wagner (2014) develops a general theory of novelty, devoting five chapters to examples of novelty, with one on new cell types, three on different novelties in vertebrates, and one on the evolution of floral organ.

The problem of theoretical generalisation, understood as the problem of the scope of applicability of a theory or a finding, is pervasive in biology (Darden, 1996); and relative significance controversies, that is, controversies about these scopes of applicability, arise at every level in biology (Beatty, 1995). The problem occurs even at a small phylogenetic scale because of the small number of model organisms compared to the large number of extinct and extant species. It should become even more complicated when generalisations expand to different kingdoms.

The turn towards history

In many historical narratives of research on novelty in the last decades, the rise of evo-devo is presented as the crucial event.[4] This is because these

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[4] Problems and questions actually arise from the complexity of evo-devo’s nature and historical roots and the multiplicity of conceptual and historical interpretations rather than from a lack of scholarship. In agreement with the dominant view of evo-devo centred on developmental genetics, there is a dominant narrative of the history of evo-devo centred on the progressive discovery of developmental regulatory genes. Several conceptual tools have been used by different authors to offer alternative narratives. For example, the idea of a romantic, an enthusiastic and an academic phase in the history of evo-devo used by Wagner, Laubichler and Chiu (Gunter P. Wagner, 2007; Günter P. Wagner, Chiu, & Laubichler, 2000); the distinction between the perspective of problems and the perspective of tools proposed by Alan Love (2005) and also used by Gerd Müller (2007) ; the Bachelardian concept of “epistemological obstacle” used by Michel Morange (2011).

narratives have often been written from the point of view of evo-devo, either by practitioners or by historians or philosophers with a sympathetic outlook. Indeed, the involvement of scientists with the history of their field is as striking in the case of evo-devo as it was in the case of the Modern Synthesis. In analysing the relation of evo-devo practitioners to history, Manfred Laublicher and Jane Maienschein offer the following reading:

> “This historical approach gives a unique perspective on, and informs, current developments; in that way, historical awareness can actually improve scientific practice. Practitioners of evolutionary developmental biology have long recognized this fact, and there is probably no other group of scientists that is currently as deeply engaged in discussions about the history of their field. The ambiguous status of evolutionary developmental biology as a new “synthesis” and the diversity of its multiple research agendas certainly contribute to this interest in history, as does the deeply historical character of its main scientific problems.” (2007, p.25)

Some historians or historians-philosophers of science have embraced the endeavour of scientists and promoted a form of partisan history. For example, Ronald Amundson has offered a history of biology from the point of view of evo-devo (Amundson, 2005). In that case, the historian-philosopher takes part in the same historical project as the scientists, picking his side and joining in on the battlefield. Others have warned against being enrolled or even used by scientists as a risk the historian should try to avoid (Cain, 2009). This focus on history could be understood in the context of the struggle of a new discipline for power and recognition. The search for eminent predecessors can be seen as a way to anchor the discipline in a tradition, to show that the new discipline is not an anomaly is the history of biology. Georges Canguilhem, for example, has noted this use of history: “scientists, when they explore new or controversial fields, need to find themselves prestigious predecessors to be heard by their peers” (Canguilhem & Delaporte, 1994).

A focus on a functional-historical approach to novelty prompts another perspective on the history of research on novelty and a reappraisal of the question of research on novelty in the Modern Synthesis era.

OUTLINE OF THE THESIS

Chapter 1 focuses on different characterisations of the problem of the origin of novelty in contemporary biology and attempts to tease apart the conceptual, theoretical, disciplinary and historical reasons for these differences. Since practitioners of evolutionary developmental biology have defined this problem of the origin of novelty as central to their endeavour and have produced substantial amount of definitional, theoretical and empirical work, the characterisations of the problem produced in this literature are a natural place to start the investigation. The problem of novelty plays an important part in the definition of the identity of evo-devo as distinct from, or alternatively, as competing with, the Modern Synthesis. According to an influential group of evo-devo practitioners, novelty is outside of the scope of the Modern Synthesis as a theoretical framework because of the latter's neglect of development as an evolutionary factor and because of the distinction between novelty and adaptation, identified as its central *explanandum*.

I single out another approach to the problem of novelty that I call the functional-historical approach. I identify its roots, its contemporary manifestations and its evolving characterisation of the problem of novelty. I stress its continuity between the Modern Synthesis era and the contemporary period. I then focus on the reasons for its rejection or neglect by evo-devo practitioners. One important reason is the distinction between novelty and adaptation. I distinguish several forms of the distinction found in the evo-devo literature by relating it to the biological and philosophical problem of the creativity of natural selection.

The importance of the functional-historical approach to novelty and the historical variations of the conception of the relation between novelty and adaptation call for a reappraisal of research on novelty during the Modern Synthesis era. Chapters 2 and 3 are mainly devoted to this task. In chapter 2, I investigate the position of novelty in the landscape of concepts and research central to the Modern Synthesis. I identity four essential concepts, each involving several disciplines and research programs: species and speciation, origin of higher taxa, increase in complexity and adaptation. Focusing on different research programs and different uses of the same concepts reveals a plural picture that is eluded in some contemporary representations of the Modern Synthesis. For example, the concept of preadaptation is used by George Gaylord Simpson within the ecological framework of the theory of adaptive radiations. In contrast, a different version of the concept is used by functional morphologists to study the origin of evolutionary novelties. The focus on both zoological and botanical research reveals important contrasts. For example, the relation of experimental taxonomy to novelty is not identical in zoology and in botany. Furthermore, the problem of the origin of the angiosperm flower, related to research on the origin of the angiosperm as a taxon involves methodological problems and research strategies that are different from those found in research on animal novelties.

In chapter 3, I address debates in the historiography of the Modern Synthesis more directly. I identify three central characteristics of the dominant view of the Modern Synthesis, its gene-centrism, the exclusion of development and the consensual nature of the Synthesis, especially of the late Synthesis. A focus on research related to the problem of novelty in the Modern Synthesis era can shed light on debates about the interpretation of the Modern Synthesis. The idea that development was fully excluded from the Modern Synthesis has already been nuanced by some historians (Davis, Dietrich, & Jacobs, 2009; Love, 2009). Here, I focus on Bernhard Rensch and George Ledyard Stebbins, two well-known architects of the Modern Synthesis. I analyse their research and theorisation on development and novelty, which are neglected part of their work, and further challenge some received views on the Modern Synthesis. Another path to an alternative view on the Modern Synthesis is opened by focusing on Ernst Mayr’s theory of genetic revolutions as a speculative theory of the rapid origin of phenotypic novelties. Although Mayr’s theory has been widely commented on and criticised, its relation to the problem of the origin of novelties, explicitly theorised by Mayr has not been thoroughly studied. Focusing on the conceptual, theoretical and empirical background to Mayr’s theory sheds new light on controversies within the late Modern Synthesis.

In chapter 4, I focus on the relationship of novelty to the concepts of homology. The close relationship between the two concepts will have been presented in chapter 1 and illustrated by the debate on the origin of the angiosperm flower in the Modern Synthesis era. The contemporary relationship of developmental genetics to homology bears on the question of the origin of the flower and on general theories of the origin of novelties. Some of the most influential researchers working on the problem of novelty rely on character-based definitions of novelty (Müller & Newman, 2005; Müller & Wagner, 1991; G. P. Wagner, 1989, 2014). These definitions are crucially dependent on the biological concept of homology based on developmental genetics. Although research on novelty is dependent on phylogenetic systematics, the biological concept of homology conflicts with the use of the concept in phylogenetic systematics. I will show that the progress in plant developmental genetics has shed new light on the problems of the origin of the angiosperm flower and of homologies among plant characters. This, I argue, has prompted Günter Wagner to recently apply his general developmental genetic theory of the origin of novelty to this problem. I will examine Wagner's application of his theory and show that it raises questions regarding generalisations in evo-devo.

This historical and philosophical endeavour to document and make sense of functional-historical approaches to novelty and their relation to evo-devo approaches can be related to contemporary calls for (Breuker et al., 2006; Brigandt and Love, 2012; Hallgrímsson et al., 2012) and practice of (e.g. Budd, 2006; Galis, 1996; Niklas, 2000; D.B. Wake, 2009) a functional evo-devo. The dominance of a structuralist perspective in evo-devo, focusing on changes in form without a concern for functional questions, is an uncontroversial fact (Brigandt and Love, 2012, p. 423). Criticisms of this bias and attempts at integrating structural and functional considerations in evo-devo have recently been formulated. This thesis can be viewed as a historical and philosophical contribution to this project by providing elements of a history of functional approaches to novelty and by showing continuities as well as evolutions between research projects of the Modern Synthesis era and some contemporary projects in constructional, evolutionary and functional morphology as well as evo-devo.

CHAPTER 1: TWO APPROACHES TO THE PROBLEM OF NOVELTY

INTRODUCTION

The issue of the existence of a multiplicity of definitions of novelty and the debates about the appropriate definition can be related to and partly diffused by the existence of different research programs addressing different questions related to the phenomenon of qualitatively new variations in evolution (Brigandt & Love, 2012). That there should exist different formulations of the problem of novelty and different ways to characterise it in the biological literature should not be a surprise considering the complexity of the phenomenon alone. However, many questions remain regarding the reasons for these differences in formulation of the problem and regarding the relations between these formulations.

This chapter will involve different levels of investigation. At a first level, the focus will be on the formulation and characterisation of the problem of novelty: What is the problem of the origin of novelty? How is it distinguished from other problems such as the origin of adaptations? How should it be decomposed? What are the research questions that need to be addressed? And what are the biological disciplines that need to be involved?

I will contrast the formulation and characterisation of the problem by evo-devo practitioners and the formulation of the problem according to what I will call the functional-historical approach. Therefore, another level of investigation will resort to understanding the relationship between the two approaches. Is it that the evo-devo and functional-historical appraoch are addressing different problems?

Different types of novelties? To what extent can they be considered complementary explanations?

Outline of the chapter

In the first section I will address the evo-devo characterisation of the problem of novelty. Since the concept of novelty is embedded in theoretical controversies, I will first provide some context on the matter and on the situation of novelty in the debates. In the second section I will turn to the functional-historical approach by focusing on its formulation and use by Charles Darwin, Anton Dohrn and Walter Bock. I will then discuss some of its contemporary developments. In the third section I will focus on some causes of the relative separation between the evo-devo and the functional-historical approach. In the last section I will come back to the distinction between novelty and adaptation and compare how it is put to use in an evo-devo and a functional-historical explanation of novelty.

I – CHARACTERISATION OF THE PROBLEM OF NOVELTY: THE VIEW OF EVO-DEVO

The problem of the origin of evolutionary novelties has been revived and appropriated by practitioners of evo-devo since the beginning of the 1980s. Some of these practitioners have made considerable efforts both to define the concept (HallgrÍmsson et al., 2012; Müller, 2010; Müller & Newman, 2005; Müller & Wagner, 1991; Wagner, 2014; West-Eberhard, 2003), determine the research questions involved in the problem (Laubichler, 2007; Love, 2005, 2008; Müller & Newman, 2005; Wagner, 2000), and to empirically study and explain cases of novelty.[5] Therefore, when trying to characterise the problem of novelty in contemporary biology, this literature in evo-devo appears as an appropriate starting point.

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[5] Empirical case studies are too numerous to refer here, examples of research on particular novelties will be provided along the thesis.

In this literature, the characterisation of the problem of novelty is often associated with a criticism of the Modern Synthesis, the still dominant theoretical framework in evolutionary biology which was elaborated around the middle of the 20th century. For the present purpose, the Modern Synthesis theoretical framework can be defined with a small set of tenets, as it usually is in the contemporary literature (Amundson, 2005; de Ricqlès & Padian, 2009; Futuyma, 2015; Kutschera & Niklas, 2004; Laland et al., 2015; Müller & Pigliucci, 2010; Reif, Junker, & Hossfeld, 2000):

(1) The central unit of evolution is the population of organisms, and not individual organisms (centrality of population genetics).
(2) The source of variation is inheritable genetic mutations that are not directed by the needs of the organisms, but that are not necessarily random in other respects. Mutations of small phenotypic effect have a more important role in evolution than mutations of large effect, which are usually lethal or deleterious.
(3) Changes in the genetic and phenotypic compositions of populations are caused by natural selection, genetic drift, mutations, genetic recombination and migrations.
(4) Among these factors, natural selection acting on individuals in populations is the main cause of adaptation of organisms to their environment.
(5) Species are gradually formed by the splitting of populations and the emergence of reproductive isolation between the sub-populations via several mechanisms.
(6) The phenomena of macroevolution, that is, the large-scale patterns of evolution and the origin of higher taxa (families, orders, classes, phyla) and of their specific characters (novelties) can be explained by the accumulated action of factors of microevolution described in (3).

The history of the formation of the Modern Synthesis and the question of its theoretical content will be dealt with in more detail in chapters 2 and 3. From the inception of evo-devo (Bonner, 1982), to its maturation phase (Hall, 1999; Müller & Newman, 2005b, 2005a; Newman & Müller, 2000; Raff, 2000; Wagner, 2000; Wagner, Chiu, & Laubichler, 2000), and until recent years (Müller & Pigliucci, 2010; A. Wagner, 2014; G. P. Wagner, 2014), the problem of novelty has often

been negatively characterised as that which is not and cannot be explained within the Modern Synthesis framework. More precisely, two claims are recurrent:
A) The problem of novelty has been put aside by the Modern Synthesis:

> "Evolutionary innovations are outside the scope of any current research program. Through its contribution to the solution of that question, [evo-devo] genuinely expands the explanatory range of evolutionary theory" (Wagner et al., 2000, p.822);[6]

B) The Modern Synthesis did not have the theoretical means to explain novelty.

> "It has become *possible* to address phenomena of evolution that were *untreatable by the [Modern Synthesis]*, and to cast them as "how" questions, such as How did body plans originate? How did homoplasies arise? *How did novelties evolve*? How do organisms change phenotypes in response to different environments?" (Pigliucci et al., 2010, p.12-13)

My focus here is on the characterisation of the problem of novelty; the definitional and normative debates about the present and future theoretical framework of evolutionary biology have a much wider range, and a detailed analysis of these debates is beyond the scope of this chapter. However, because the reference to the failures or limitations of Modern Synthesis concepts and research programs plays such an important part in the characterisation of the problem of novelty by evo-devo practitioners, some contextualisation is required.

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[6] Here are a few other examples: "... the majority of the new work concerns problems of evolution *that had been sidelined in the MS* and are now coming to the fore ever more strongly, such as *the specific mechanisms responsible for major changes of organismal form*, the role of plasticity and environmental factors, or the importance of epigenetic modes of inheritance." ((Pigliucci, Müller, & others, 2010, p.12). "I will make the argument that one of the main benefits of a deeper understanding of homology is that it enables an empirical research program on the major transitions in evolution, in particular the origin of evolutionary novelties. I argue that the origin of novel characters and novel body plans is one of the most important but least researched questions in evolutionary biology."(Wagner, 2014, p. 3)

Overview of the contemporary debate on the content and structure of evolutionary biology

From the 1970s onwards, a series of theories and research programs on phenomena absent from or marginal in the Modern Synthesis has been growing aside from this dominant framework in evolutionary biology. As a consequence, some have expressed a call to replace the framework of the Modern Synthesis with a “new synthesis” (Stephen J. Gould, 1987) or more recently with an evo-devo synthesis (Müller, 2007), or an “Extended Synthesis” (Laland et al., 2014, 2015; Müller & Pigliucci, 2010; Pigliucci, 2009). Central behind the idea of a new synthesis was the theory of punctuated equilibrium (Eldredge & Gould, 1972), the first major attack against the Modern Synthesis.[7] Punctuated equilibrium is a theory of macroevolution opposed to one of the central tenets of the Modern Synthesis: extrapolationism (Mayr, 1942; Simpson, 1953), that is, the idea that macroevolution obeys the same principles as microevolution and thus can be deduced from the study of microevolution by population genetics. Behind the more recent call for an Extended Synthesis is a much more diverse constellation of theories. It is thus more difficult to determine which tenets of the Modern Synthesis, if any, are challenged by these new developments.

A constellation of disciplines and research programs

One way to represent changes in evolutionary biology is to focus on the evolution of disciplines and research programs. To illustrate this evolution we can rely on the analysis of Massimo Pigliucci (2009) who offered the following representation of the expansion of evolutionary biology.[8]

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[7] See (Gayon, 1990) for a review of criticisms against the Modern Synthesis until the end of the 1980s.

[8] Pigliucci’s representation is one among several others (e.g. Kutschera & Niklas, 2004; de Ricqlès & Padian, 2009; Müller & Pigliucci, 2010; Laland et al., 2015; Huneman, 2014; Love, 2010) but as I stated earlier, my goal is not to review these representations or to argue for one in particular.

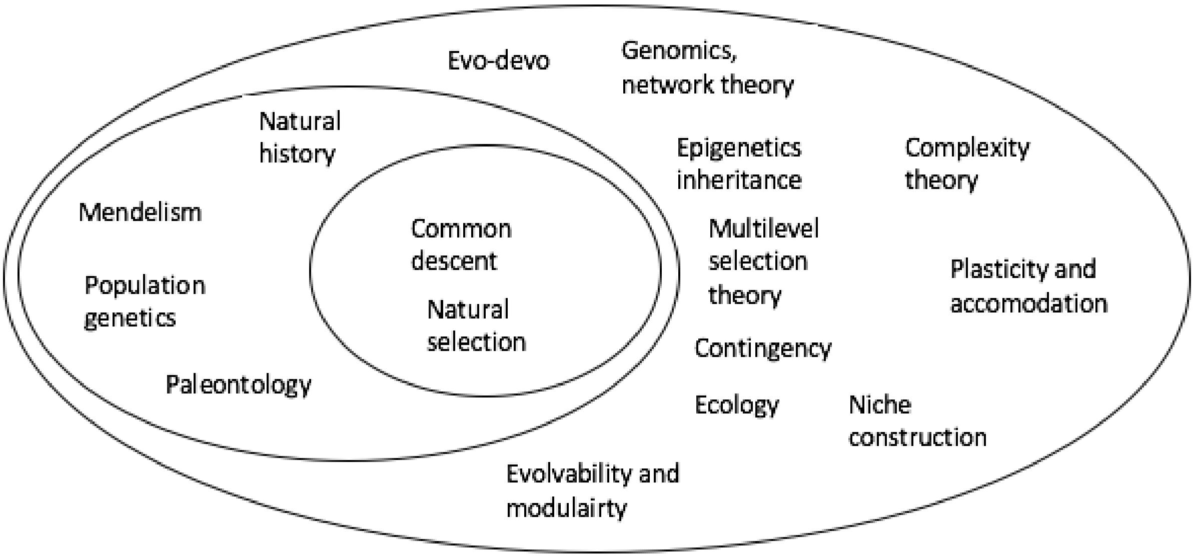

Figure 1. Representation of the evolution of evolutionary biology since Darwin. The small circle contains the two fundamental principles proposed by Darwin. The middle circle contains the components of the Modern Synthesis. In the largest circle, are, in addition to the previous elements, the theories and phenomena absent or marginal in the Modern Synthesis (redrawn after Pigliucci, 2009).

Pigliucci notes that this diagram contains “ideas, phenomena studied and fields of inquiry” (Pigliucci, 2009, p. 226). The outer circle reflects (parts of) the contemporary research landscape. This expansion does not in itself have unequivocal consequences in terms of the theoretical content and structure of evolutionary theory in biology. There are at least four reasons for this indeterminacy: research pluralism, multiple interpretations, relative significance and theoretical or explanatory pluralism. By research pluralism, I mean the multiplicity of approaches and theoretical perspectives contained in the different fields of enquiry. This is especially true of evo-devo and will be addressed in more detail in the next section. Because this pluralism characterises many of the new fields of inquiry, the relationship between them and the dominant theoretical framework is not straightforward. Multiple interpretations refer to the different possible ways to integrate the same phenomenon within a wider theoretical framework. This can be illustrated by a recent formulation of an Extended Synthesis (Laland et al., 2015, see also 2014). Laland and colleagues rely on the importance of developmental bias, developmental plasticity, inclusive inheritance and niche construction to vindicate an Extended Synthesis. According to them, what differentiates the Extended Synthesis is the interpretation of these phenomena as ultimate causes, having an effect on the course of evolution, while the Modern Synthesis interprets them as only proximate causes, relevant for functional biology but not for evolutionary biology (Mayr, 1961; Laland, Sterelny, Odling-Smee, Hoppitt, & Uller, 2011).[9] Relative significance (Beatty, 1995, 1997) refers to the fact that biological sciences are rarely a search for universal laws; many debates in evolutionary biology for example are not about whether a theory correctly describes all possible cases of evolution but about the proportion of cases of evolution that it correctly describes. Some theories can be recognised as unorthodox and the existence of the process they describe acknowledged but they can still be no threat to the Modern Synthesis because they are considered only marginal. For example the occurrence of sudden speciation by a single mutation is not contested, especially in plants (e.g. Niklas, 1997), and the debate rather regards whether it should be considered as a major factor in evolution. Finally, by theoretical or explanatory pluralism, I refer to the combination of different causal factors in the same explanation (Mitchell, 2003). The problem is then to determine the explanatory weight of each factor. A classic example is the determination of the relative contribution of selection and drift in a sequence of microevolution.

Conservatism, expansionism or revolution

In order to give an overview, three positions can be distinguished in ongoing debates: conservative, expansionist and revolutionary. For the strict conservative, the supposedly new theories are either already included in the Modern Synthesis or genuinely new but too marginal empirically to grant a change in the framework. The revolutionary discards one or several central principles of the Modern Synthesis. Among these principles, it is natural selection that is the main target of attacks. Its predominant role in evolution has been questioned from several standpoints: by Gould and others placing contingency over natural selection (Gould, 2000); by self-organisation theorists (Kauffman, 1993; Newman, Forgacs, & Muller, 2006); by developmental or evo-devo biologists insisting on the role of developmental constraints (Schwenk & Wagner, 2003); even by population geneticists attributing a greater role to alternative factors such as drift (M. Lynch, 2007a, 2007b).

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[9] I will come back to the proximate causes/ultimate causes distinction in relation to the problem of novelty in the next part of this chapter.

However, very few protagonists of the debate present themselves as revolutionaries or as strict conservatives. One of the central issues concerns the meaning that is given to the term expansion. There is more than one way to be an expansionist. On the one side, most defenders of the Modern Synthesis would argue for an accommodating expansionism in which new theories fit into already formulated problems and explanations as complements or exceptions (Laland et al., 2014) . On the other side, proponents of the "new" or the "extended" synthesis argue for a quarrelsome expansionism. In this view, expanding the framework means formulating and addressing problems of evolutionary biology that have not been properly formulated and addressed by the Modern Synthesis, thus considering the latter as only a partial framework. For example, the theory of punctuated equilibrium states that macroevolution is not properly addressed by the Modern Synthesis. Another example is the distinction between the problem of adaptation and the problem of form (Amundson, 1994, 2005). According to this "structuralist" perspective, the Modern Synthesis addresses the problem of the arising of adaptations, this being attested by the central role of population genetics and ecology; but it leaves aside the problem of the production and change of form, as attested by the absence of embryology in the Modern Synthesis.

The old and the new in evo-devo

I now return to the problem of novelty as it is formulated by practitioners of evo-devo. The characterisation of the problem of the origin of novelties as outside of the scope of the Modern Synthesis is better understood if replaced in the context of a general characterisation of evo-devo in terms of different types of contributions to biology, some of which are integrated to pre-existing research programs while others involve the creation of new research programs.[10] While it

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[10] The terms evo-devo and devo-evo have been used by some practitioners and theorists to draw a distinction within research programs associating evolution and development. The problem is that there is little agreement on the definition of the two terms and their relations. Some state that they are complementary research programs (e.g. Müller, 2007). On the other hand, Brian Hall sees them as conflicting interpretations of the field (Hall, 2000), or as synonyms (Hall, 2003). The difficulty with the meaning of the distinction of between evo-devo and devo-evo can partly be explained by the causes of indeterminacy mentioned earlier (research pluralism, multiple interpretations, relative significance and

is difficult to determine the proportion or evo-devo practitioners who adhere to this representation of their field, it has been forcefully vindicated by influential figures (Gilbert, 2003; Laubichler, 2007; Müller, 2007; Wagner, 2000, 2001; Wagner, Chiu, & Laubichler, 2000). One clear formulation is provided by Günter Wagner and colleagues (Wagner, Chiu, & Laubichler, 2000; see also Laubichler, 2007). Among the contributions of evo-devo to existing research programs, they include:

_ The evolution of development. This is the study of the evolution of developmental characters, using the same framework as for the evolution of genes and phenotypes. It integrates into this existing research program by adding one type of entity. The evolution of some of these developmental characters, such as developmental pathways, involving DNA, RNA and transcription factor proteins, is decoupled from the evolution of the phenotypic characters they determine. Homological characters can be generated with developmental pathways that underwent divergent evolution while the characters stayed the same. This pervasive phenomenon has been called “developmental system drift” (Haag & True, 2001, 2018).

_ The assessment of homologies. As stated in the introduction, homology is a relation of identity between characters in different organisms explained by common descent.[11] The assessment of homologies is a program initiated in comparative anatomy before the Darwinian revolution (Amundson, 2005; Panchen, 1994). Gene expression patterns add a level at which to establish homologies, as well as a level of evidence to assess relations of homology between characters, although, as the phenomenon of developmental system drift alone shows, there does not exist a simple relation between homology at the level of morphological characters and homology at the level of developmental pathways. This has led some to develop a hierarchical view of homology (Abouheif, 1997; Hall, 1994).

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explanatory pluralism). Because of this confusion of meanings and because the distinction seems to have faded from the more recent literature, I will not rely on it here.

[11] Several types of homology can actually be distinguished. These types, and the impact of competing theories of homology on the problem of novelty will be covered in detail in chapter 4.

_ The genotype-phenotype map of adaptation. The two main disciplines involved in the quantitative study of adaptation, population genetics and quantitative genetics, focus on genes and phenotypic traits, respectively, leaving aside the question of development, that is, the question of the processes of production of phenotypes. Populations genetics focuses on the dynamics of gene frequencies in populations. Quantitative genetics focuses on the dynamics of different values of quantitative phenotypic traits, assumed to be controlled by many genes. Evo-devo provides information on the developmental genes involved in quantitative phenotypic differences within species or between closely related species, such as species of *Drosophila* or stickleback fishes (Chan et al., 2010; Hohenlohe et al., 2010; Jones et al., 2012; Peichel et al., 2001; Taylor & McPhail, 2000).

As opposed to the three contributions of evo-devo just reviewed, the study of developmental constraints[12] and of the origin of evolutionary novelties are the research programs that are introduced by evo-devo. Regarding novelty, several justifications of its situation outside of the scope of previous research programs have been given by different authors.

Evo-devo and the origin of novelties as a new research question

Why is the problem of novelty outside the scope of existing research programs?

In section IV of this chapter, I will argue that the following characterisations of the problem of novelty, especially 2) and 3), can be challenged, partly on the basis of clarifications of different meanings of the concepts and function, adaptation and novelty. For now I will present these different characterisations.

1) A problem distinct from the problem of adaptation

A first way to single out novelty is to distinguish it from adaptation as two distinct problems (Amundson, 2005; Brigandt & Love, 2012; Love, 2013; Müller &

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[12] There are many definitions of developmental constraints, and perhaps the most widely used is “a bias on the production of variant phenotypes caused by the structure, character, composition, or dynamics of the developmental system” (Smith et al., 1985). I will not focus directly on developmental constraints here.

Newman, 2005; Wagner, 2014). Adaptation, understood in its “engineering” meaning, denotes the good design of organisms or of their characters. The study of how organisms appear designed to perform certain function does not depend on an evolutionary view of life and was already undertaken by Aristotle and many others after him. Within an evolutionary framework, the question is transformed into how this is design produced through evolution, or more exactly this evolutionary problem is added to the first descriptive problem. In contrast, novelty is not a problem of design but a problem of differences between organisms. The problem of how new characters arise is distinct from the problem of how these characters become better designed to perform certain functions. It can be said that there is also a pre-evolutionary version of the problem of novelty: just like the non-evolutionary counterpart to the origin of adaptation is the study of design or functional biology, the non-evolutionary counterpart to the origin of novelty is the comparative study of commonalities and differences between organisms, that is, comparative anatomy, morphology or physiology.

2) Different processes and their different outcomes

While a distinction between novelty and adaptation in terms of problems does not imply any claim on the causal factors involved, a distinction between *variation* and *innovation*, as different processes, and *adaptation* and *novelty* as their respective outcomes implies distinct causal factors at play (Müller & Newman, 2005; Peterson & Müller, 2013, 2016). The argument goes as follows: adaptations are the result of the action of natural selection on existing characters presenting heritable variations. So there has to be a pre-existing character in order for natural selection to act on small variations of this same character in a population to lead to an adaptation. Novelties cannot be the result of this process precisely because they are new characters. They are the starting points of the process of variation leading to adaptations but they cannot be the result of this same process. The process of innovation is thus different from the process of variation.

3) A different balance of explanatory force

Another way to conceive the specificity of novelty is through the concept of explanatory force, taken by Günter Wagner from Ronald Amundson (1989). This concept can be related to the notion of explanatory pluralism described earlier. The distinction is formulated in epistemic and relative terms rather than in causal and absolute terms: it is not that natural selection has not causal role in the generation of novelty, it is that population genetic processes are only marginally explanatory significant in cases of novelty, whereas they are more significant than developmental processes in other cases of variation or stasis such as the maintenance of the 1:1 sex ratio in populations.

> "The question we need to answer is this: in what kind of situations do developmental mechanisms contribute more to the explanation of an evolutionary process than population genetic mechanisms? Or, alternatively: what are the characteristics of situations where population genetics contributes more to an explanation than developmental genetics?" (Wagner, 2000, p. 96)

In the case of the stable 1:1 sex ratio, there are many different mechanisms that can bias the sex of the offspring in different species. What explains the stability of the sex ratio across species are not the particular mechanisms occurring in different cases but the frequency dependent selection that favors the sex that is underrepresented in the population. In contrast, in cases of novelty, such as the origin of eyespot patterns on butterfly wings, the explanatory force is found in the properties of the cells that form the organiser of the eyespot and in the co-optation of a complex of regulatory genes that are responsible for the formation of the anterior-posterior compartmentalization of the larva.

Characterisation of the problem of novelty

The way in which Wagner and colleagues (2000) conceive the different research questions implied by the problem of novelty can be presented by focusing on the disciplines that they consider necessary to tackle the problem.

1) *Comparative anatomy* or morphology is needed to define the characters that are to be explained. Establishing relations of homology

between characters in different species is essential if one relies on a definition of novelty as a non-homologue. As stated in the introduction, this definition of novelty is related to a debate about the nature of homology that will be addressed in chapter 4. This debate can be left aside for now. Regardless of the concept of novelty that one subscribes to, comparative anatomy is essential to elaborate hypotheses of character transformation. Debates on the origin of particular novelties are sometimes partly debates about which ancestral character is homologous to the novelty. This will be illustrated in the next chapter with research on the origin of the angiosperm flower.

2) *Phylogenetic systematics* is needed to establish evolutionary patterns. While comparative anatomy establishes non evolutionary relationships between characters, phylogenetic systematics establishes pattern of evolution of taxa and their characters. Thus, it is necessary either as a prerequisite for the establishment of hypotheses of character transformation or origination, or as a test of hypotheses. Again the role of phylogenetic systematics will be addressed in more details in chapters 2 and 4.
3) *Evolutionary genetics* provides information on the selective forces acting on developmental genes. Wagner and colleagues include evolutionary genetics although as show in the last section Wagner does not attribute much explanatory power to it.
4) *Paleontology* provides information on reconstruct sequences of character evolution.
5) *Developmental biology* provides the mechanistic explanation of the origin of characters.

Although the first four disciplines provide ancillary information, the central discipline involved in the explanation of novelty is developmental biology. The main component research questions are framed in developmental terms:

_ “What is the developmental mechanism that accounts for the derived character (state)?”
_ “Does the developmental mechanism for the derived character (-state) map to the same node on the phylogeny as the derived character (-state)?”

_ "What are the developmental changes that occurred at the origin of the derived character (-state)?"
_ "Are the genetic differences sufficient to cause the derived character (-state)?" (Wagner, Chiu, & Laubichler, 2000, p. 827‑828)

There are many epistemic difficulties arising from these research questions (Love, 2005; Wagner, Chiu, & Laubichler, 2000). I will however not address this issue here. My focus is on the characterisations of the problem of novelty and the differences in their content and the reasons why multiple characterisations exist. Considering the claims of some evo-devo practitioners mentioned earlier, there should not exist other approaches to the problem since the origin of novelty is said to be absent of any research program except the evo-devo program.

In the next section I will focus on what I will call the functional-historical approach to novelty. In section III I will focus on the causes of the divide between the functional-historical approach and the evo-devo approach. In section IV I will come back to the relation between adaptation and novelty.

II – THE FUNCTIONAL-HISTORICAL APPROACH TO NOVELTY

Three stages in the functional-historical approach

The functional-historical explanation is multi-disciplinary in nature like the evo-devo approach, but whereas the latter is centred on developmental processes, the former is focused on physiology, functional morphology and behaviour. This distinction between the evo-devo approach and a functional-historical approach relates to the venerable question of which concept, between form and function, should have the primacy as an organising principle of life and of the sciences of life (Russell, 1916). consequently, such a presentation could have started with George Cuvier or even Aristotle. However, my focus is on approaches to novelty. Therefore I will narrow my focus on functional theories of novelty. I will first present the approach as used by Charles Darwin, Anton Dohrn and Walter Bock before reflecting on its characterization of the problem of novelty and justifying the use of the expression functional-historical (rather than simply functional, or adaptationist or adaptive-historical). The functional-historical approach can be presented in three stages:

_ The origin of the functional-historical approach is found in Charles Darwin's and Anton Dohrn's tackling of the problem of the origin of novelties and their respective concepts of conversion of function and succession of functions (*Funktionswechsel*).

_ The functional-historical approach in the late Modern Synthesis illustrated by Ernst Mayr, Walter Bock and Gerd Von Wahlert: Mayr's influential paper on the emergence of evolutionary novelty can be seen as a combination of Darwin's conversion of function and Bock's and Von Wahlert's ideas in functional morphology with a stress on the role of behaviour as the "pacemaker" of evolution.

_ The third phase corresponds to some contemporary developments in functional and evolutionary morphology.

Darwin and Dohrn, conversion and succession of functions

The concept of conversion of function is developed by Darwin in the first edition of the *Origin of species* (Darwin, 1859, chapter 6) and is expanded and given more importance in the sixth edition in reaction to criticisms formulated by St. George Mivart, in particular regarding "the incompetency of natural selection to account for the incipient stages of useful structures" (Darwin, 1872, p. 176; see Mivart, 1871, chapter 2). Darwin first introduced the idea as an answer to the difficulty that "organs of extreme perfection and complication" represent. He notes: "We should be extremely cautious in concluding that an organ could not have been formed by transitional gradations of some kind". Conversion of function is one type of mechanism, among others, that can explain both the transitional gradations towards the production of new organs and the selective significance of incipient stages :

> “The illustration of the swimbladder in fishes is a good one, because it shows us clearly the highly important fact that an organ originally constructed for one purpose, namely flotation, may be converted into one for a wholly different purpose, namely respiration.” (Darwin, 1859, chapter 6)

Although Darwin does not give a detailed definition of the principle, the common idea in all the examples that he provides is that at least some characters perform more than one function. These different functions can be either equally important for the organism, or there can be a dominant function and another or several accessory functions. The change in a character or the creation of new characters can then occur in different ways:

_ A multifunctional organ divides into several new organs, each performing one of the original functions.
_ Two structures perform the same functions, and one or both of these structures undergo change by specializing in one of the initial functions.
_ One structure has a dominant function and an accessory function, and the change occurs through the development of the second function.

The expression conversion of function seems to best fit the last case, but all three cases answer the problem of the incipient stages of new organs: natural selection can act even at this early stage because the alternative function is already present. To illustrate the last type, beside the transition from swim bladder to lung in fishes[13], Darwin gives an example from barnacles (cirripedes). The branchiae of the sessile cirripedes are homologous to the ovigerous frena of the pedunculated cirripedes, which are folds of skin that hold the egg via an adhesive secretion. In sessile cirripedes, the egg rests at the bottom of the sack, protected by a more enclosed shell. The pedunculated cirripedes have no branchiae and breathe through the whole skin including the frena. Darwin postulates the

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[13] This example of the conversion of the swimbladder into a lung is emblematic. It is reused for example by Simpson (1953) and by Mayr in his article on novelty (1960). Stephen Jay Gould has stressed that Darwin’s explanation is “not only wrong, but backwards” (Gould, 2002, p. 1224). The hypothesis favoured by Gould (that lung is the ancestral and swimbladder the derived condition) was actually already the dominant one in the Modern Synthesis era, as noted by Mayr and Simpson (Simpson, 1953, p. 192, note 11; Mayr, 1960, p. 352). The case is still debated today. The main competing hypothesis is the independent derivation of both organs from a respiratory pharynx (Lambertz and Perry, 2015; Perry and Sander, 2004).

progressive origin of branchiae from ovigerous frena by growth of their size and suppression of the secreting glands, with respiration becoming the primary function.

Anton Dohrn developed the concept of succession of function in relation to his theory of the evolution of vertebrates from annelids. The main difference between Darwin's concept and Dohrn's is the higher degree of systematisation of the latter.[14]

> "The transformation of an organ takes place by reason of the succession of the functions which one and the same organ possesses. Each function is a resultant of several components, of which one is the principal or primary function, while the others are the subsidiary or secondary functions. The weakening of the principal function and the strengthening of a subsidiary function alters the total function; the subsidiary function gradually becomes the chief function, the total function becomes quite different, and the consequence of the whole process is the transformation of the organ (Dohrn 1875, p.60 cited by Russel, 1916, p. 276).

This principle is applied by Dohrn to many organs in the hypothesised transition from annelids to vertebrates . The principle of succession grants a functional approach to phylogenetics and evolutionary morphology that Dohrn opposes to purely morphological approaches (Ghiselin, 2003; Nyhart, 2002).

> "In the principle of succession of functions a key arises, the assistance of which, in the application of all other embryological, palaeontological , comparative anatomical and physiological methods of investigation, would appear to move the solution of intricate problems towards clarification. Hitherto it was the most dangerous precipice in genealogical investigations, that they proceeded on a one-sided morphological basis, without remembering physiological elements, except occasionally and through the very generally expressed term 'adaptation'. The concept of succession of functions is purely physiological. It contains the elements out of which perhaps an evolutionary history of functions will gradually arise. But for that very reason it will also be of great use for morphology – and for the evolutionary history of structures, which, finally are only the content and the

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[14] On the relation between the concepts of Darwin and Dohrn, see Caianiello (2015).

> process of functions projected as form, and cannot even be conceived without functions." (Dohrn, 1875, p. 70; Dohrn and Ghiselin, 1994, p. 74)

This functional approach will not have many successors until the late Modern Synthesis period (Dohrn & Ghiselin, 1994; Levit, Hossfeld, & Olsson, 2004; Sewertzoff, 1931; Waisbren, 1988).

The second phase of the functional-historical approach

Walter Bock: the evolution of the avian medial brace as an illustration

In the Modern Synthesis era, the principle of conversion of function was referred to with the term of preadaptation. In chapter 2, I will focus more on the history of the concept of preadaptation and argue that it had different meanings and was put to different uses in the Modern Synthesis era. Walter Bock' s version of the concept was close to the spirit of Darwin's principle. In the article in which he introduced his version of the concept of preadaptation[15], Walter Bock relied on the origin of a secondary jaw articulation in some groups of birds as an illustration (Bock, 1959). Bock noted that this rarely described articulation between the medial process (bony outgrowth) of the articular bone and a ventral process of the basitemporal plate, was present in some birds such as the black skimmer and the herring gull but absent in others such as the boat-tailed grackle, which has prominent bone processes but no articulation. The structure formed by the two processes, both in birds with the articulation and in birds without it, is called the medial brace. In species with a developed medial brace (that is, with prominent abutting bony processes), including those without the articulation, this structure limits the movement of the jaw through the contact between the bone

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[15] In an earlier paper, Bock (1959: 201) defined preadaptation as: "A structure is said to be preadapted for a new function if its present form which enables it to discharge its original function also enables it to assume the new function whenever need for this function arises." While this definition is basically correct, it was formulated with a loose and rather erroneous concept of function so that it is necessary to redefine preadaptation within the framework of concepts developed in this paper. We would define preadaptation as follows: A feature is said to be preadapted when its present forms and functions (both utilized and non-utilized ones) allow one of the faculties (either currently utilized or nonutilized) to acquire a new biological role and hence establish a new synergical relationship with the umwelt whenever the need (= appearance of the selection force) for this new adaptation (the faculty) should arise." (Bock & von Wahlert, 1965, p. 292). I will come back to this double definition in the next section.

processes when the jaw is open. Other species of birds do not have a developed medial brace; in these species, the bony processes are small and there is no contact of the bones when the jaw is open. In all species, these processes serve as attachment points for jaw muscles. The question addressed by Bock is thus twofold: how did the medial brace originate? And how did the basitemporal articulation of the medial brace originate? Bock hypothesised a transformation series from small bony processes to larger ones producing the medial brace. He additionally hypothesised that the basitemporal articulation originated in some species through epigenetic induction during ontogeny because of the closer contact between the processes.

The most important point here is the method that Bock used to arrive at these hypotheses. Bock sketches this method in the following way:

> “Study of the evolution of a structure must not cease with the establishment of correct sequences of the structural modifications. This is a necessary step, but it is as important or even more important to determine the ancestral structural form and the selection forces guiding the evolution of the structure. In discussions of the origin of a new structure, it is also necessary to know the "prehistory" of its several component parts.” (Bock, 1959, pp. 195–196)

The study of functional morphology, behaviour and putative selective forces is essential in Bock’s elaboration of the evolutionary sequence of origination of the structures (medial brace and basitemporal articulation). Bock notes that there is a correlation between the presence of the medial brace and feeding behaviours involving increased forces on the jaw. For example, the black skimmer, which has the most developed medial brace among the known birds, feeds through flying low with its mandible in the water and faces strong pressures on the jaw when a fish is caught this way (in particular, a stress on the articular-quadrate hinge). Bock then infers that “[e]volution of the medial brace begins when a bird ‘acquires’ a more ‘active’ method of feeding” (p.196). Bock argues that active methods of feeding initiate two distinct selection pressures: one for increased support of the mandible and one for increased muscular strength of the bill. The initial evolutionary trend was the increase in jaw musculature. This muscular increase implied an elongation of bony processes to which the muscles are attached. The bony processes grew until they were large enough to be in contact when the bird's bill is open:

> "The structures are now in position - preadapted - to be acted upon by the selection forces for additional support of the mandible. The preadapted stage is difficult to recognize, but it may be present in the herons, especially the night-herons (Nycticorax), and the cuckoos. At this stage in the evolution of the medial brace, the sole requirement is that the bones be in contact with one another only when the bill is opened." (p.197)

In some birds with active feeding behaviours exerting especially important forces, such as skimming, the mandibular support conferred by the medial brace was positively selected. This second selection pressure led to the further development of the medial brace until the close proximity of the processes favoured the origination of an articulation. Bock does not go into details on mechanism of origin of selection but insists that it did not initially required specific genetic changes. He refers to Schmallhausen's theory of stabilizing selection (Schmalhausen, 1949): the progressive increase in genetic control of initially environmentally or epigenetically induced phenotypic traits.

Bock's hypothesis was rapidly challenged on functional grounds (Zusi, 1962). This does not affect the interest of Bock's explanation as an exemplar of the functional-historical approach to the origin of novelty. Two important features of Bock's approach are to be distinguished: 1) The functional-historical explanation of the origin of an evolutionary novelty; and 2) the method of relying of functional and selective factors to reconstruct character transformation and phylogenetic histories. The two dimensions (explanation of the origin and evolution of character and phylogenetic reconstruction) are intertwined in one single research endeavour. In chapter 2, I will focus on a similar situation with research on the origin and evolution of the angiosperm flower in the Modern Synthesis era. However, the validity of the functional-historical explanation is not dependent on the validity of the method of using selective factors for phylogenetic reconstruction. The latter will be criticised by proponents of cladistics in the 1970s and 1980s (Bock, 1981; Cracraft, 1981; Eldredge & Cracraft, 1980; Richards, 2009) .

Ernst Mayr on the emergence of evolutionary novelties

Mayr's account of the origin of novelties in his influential paper 'The emergence of evolutionary novelties" (Mayr, 1960) is structured around an opposition between gradualism and saltationism:

> "The exact definition of an "evolutionary novelty" faces the same insuperable difficulty as the definition of the species. As long as we believe in gradual evolution, we must be prepared to encounter immediate evolutionary stages. Equivalent to the cases in which it is impossible to decide whether a population is not yet a species or already a species, will be cases of doubt as to whether a structure is already or not yet an evolutionary novelty. The study of this difficult transition from the quantitative to the qualitative is precisely one of the objects of this paper. Unwillingness to face such a difficult situation is one of the reasons so many authors have adopted a saltationist interpretation." (Mayr, 1960, p. 351)

Mayr (1960) himself seems to formulate the problem in population genetics terms:

> "The problem of the emergence of evolutionary novelties then consists in having to explain how a sufficient number of small gene mutations can be accumulated until the new structure has become sufficiently large to have selective value."

But he immediately adds: "Or is there an explanation which avoids this troublesome threshold problem?" (p. 360).

Mayr's account is actually largely influenced by Darwin's treatment of the question. Mayr's main process of the origin of novelty is change (or conversion) of function. He proposes two other processes: novelty as a pleiotropic by-product of a changing genotype, and novelty as a result of an intensification of function, but he states that change of function is "by far the main principle in the interpretation of the origin of new structures" (p. 360).

The initiating conditions of a conversion of function are, according to Mayr, either a change in the environment, a change in behaviour, or a change in the structural environment, that is, the structural organisation of the organism. Possibly Mayr's most original contribution is the stress on the role behavioural novelties or behavioural exploration in driving the change of morphological structures.

The functional-historical approach to novelty and concepts of function

Now that the approach has been presented, I will explain the use of the term functional-historical. In a sense, the functional-historical approach as illustrated by Darwin, Bock and Mayr, is adaptationist. Bock and Von Wahlert make it clear:

> “A definition of biological adaptation is inadequate unless it can be used as the foundation for an explanation of the mechanisms underlying the evolution of new adaptations and the adaptive origin of new major groups of organisms. These are not independent parts of evolutionary mechanisms; indeed, the solution of the latter question is completely dependent upon the solution of the former. The evolutionary principles for the emergence of novelties may be built upon the concept of adaptation advanced in this study by a synthesis of ideas such as those advanced by Mayr (1958, 1960, 1962, and 1963) and Bock (1959, 1963a) and with the concepts of population genetics such as those summarized by Lerner[16] (1954, 1958).” (Bock & von Wahlert, 1965, p. 294)

The resolution of the problem of novelty depends on adaptation. However, because the functional-historical approach involves several concepts of function, it should not be equated to a naïve adaptationism stating that all the functions of the organism are the product of selection. Regarding the concepts of function used in this approach, Bock and Von Wahlert’s changing definition of preadaptation is instructive:

> “In an earlier paper, Bock (1959: 201) defined preadaptation as: "A structure is said to be preadapted for a new function if its present form which enables it to discharge its original function also enables it to assume the new function whenever need for this function arises." While this definition is basically correct, it was formulated with a loose and rather erroneous concept of function so that it is necessary to redefine preadaptation within the framework of concepts

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[16] See chapter 3

> developed in this paper. We would define preadaptation as follows: A feature is said to be preadapted when its present forms and functions (both utilized and non-utilized ones) allow one of the faculties (either currently utilized or nonutilized) to acquire a new biological role and hence establish a new synergical relationship with the umwelt whenever the need (= appearance of the selection force) for this new adaptation (the faculty) should arise." (Bock & von Wahlert, 1965)

Since Bock and Von Wahlert's terminology is rather idiosyncratic, I will rely here on the terminology of Wouters (2003), who built on Bock and Von Wahlert's account to distinguish four different concepts of function in biology[17]. Bock and Von Wahlert actually focus on two distinct concepts of function: function as activity, function as biological role. The distinction between function as activity and function as causal role is intended to distinguish between the functions that can be performed by a character or a set of characters and the functions that actually play a role in the survival or functional organisation of the organism. For example rabbit legs can perform running, jumping, kicking, scratching etc., these are their activities, and actually the activities of characters extend to all their physical and chemical properties. A correlate of this concept of function is that it makes no sense to consider form completely separately. Any form has functions in the sense of activities. The actual biological roles of rabbit legs can be running to escape predators, or scratching to get rid of parasites. All activities are not causal roles. One of the points of Bock and Von Wahlert was to stress that tests of function in laboratories are not informative enough on the actual biological roles of the characters. Bock and Von Wahlert focus primarily on morphological characters involved in locomotion or feeding but the idea can be extended to other characters such as organs like the lungs or the heart.

Related to the idea of conversion of function is the idea that characters can have a primary and secondary biological roles. For example, in Darwin's example of the barnacle ovigerous frena, the performance of respiration by the skin is not

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[17] My point here is to show the non-naïve use of functions employed by the functional-historical approach. I will not engage directly with the philosophical literature on function (Godfrey-Smith, 1994; Griffiths, 1994; Huneman, 2013; Nagel, 1977; A. Wouters, 2005; A. G. Wouters, 2003)

simply an activity but a secondary biological role. It is hypothesised that this biological role progressively trumps the role of holding the eggs. Another possibility is when an activity becomes a biological role. The point here is to make clear that the concepts of functions used in the functional historical approach do not amount to a selectionist concept of function of the form: the function of the character is that for which it or was selected.

The functional-historical approach and historical contingency

The approach is not only functional but also historical, first because there is an attention to the different functions adopted by characters through evolutionary time, but also because there is a place left for random events:

> "Nor are all the functions, including all past and present ones, the only factors determining the form of a feature. It is not correct to assume that the form of a feature may be explained completely by correlating it with all past and present functions. An accidental component, one usually associated with the origin of the feature or with the major shifts in its evolution, is also involved. The basis for this accidental component stems largely from the chance factor in genetical changes such as mutations, chromosomal aberrations, and recombinations of all sorts. The accidental component forms the basis for the principle of multiple pathways of adaptation[18] (Bock, 1959; Bock and Miller, 1959; Mayr, 1960 and 1962). Moreover, this accidental component is just as important in understanding the evolution of a single pathway of adaptive evolution." (Bock & von Wahlert, 1965, p. 275)

To the mutations evoked here can be added epigenetic events such as the one occurring in Bock's hypothesis of the evolution of the avian basitemporal articulation. The functional-historical approach involves contingency in both meanings distinguished by John Beatty: unpredictability and dependence on initial conditions[19].

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[18] This principle will be covered again in the next chapter.

[19] "a historically contingent sequence of events is one in which the prior states are necessary or strongly necessary (causal-dependence version), but insufficient (unpredictability version) to bring about the outcome." (Beatty, 2006, p. 340).

The third phase

There has been a development of functional and evolutionary morphology prior to and then in parallel with evo-devo, from the 1950s until today. Several evolutions are particularly significant:

1) Integration of criticism from anti-adaptationism, of cladistics and other methods to test hypothesis of evolution
2) Constructional morphology and internal selection
3) Integration of new methods and technologies in morphology
4) Specialisation into different fields
5) Integration of different approaches and types of data, among which developmental data

An important question of interpretation regards the degree of continuity between the approach of Mayr, and especially Bock and Von Wahlert, who focus on adaptation to the external environment and have no problem affiliating themselves to the Modern Synthesis and more recent developments in functional morphology illustrated by George Lauder (1981, 1986, 1990; Lauder & Liem, 1989; Lauder & Thomason, 1995), David Wake (Lombard & Wake, 1976, 1977; Wake, 1982, 1991), Marvalee Wake (1992), Frieston Galis (1996) and many others. Walter Bock and Carl Gans[20] are particularly representative of the continuity between the late Modern Synthesis era and the contemporary period, by their reliance on the concept of preadaptation or protoadaptiation and by their instrumental role in the constitution or an “Integrative biology” centred around functional morphology. However, Marvalee Wake (1992) and Alan Love (2003, 2006) for example, focusing on the more recent developments, have stressed the greater reflexivity about methods, the higher standards of hypothesis testing, the change of focus of some functional morphologists from the role of the external environment to the role of internal structural and functional constraints. I will address some of these questions.

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[20] See next chapter.

Anti-adaptationism and exaptation

The locus classicus of the critique against adaptationism is Gould and Lewontin “Spandrel” paper (1979). However, I will focus on the Gould and Vrba’s article introducing the concept of exaptation which pursues the critique against adaptationism and is more related to the functional historical approach. The concept of exaptation is elaborated against the concept of preadaptation. However, the ambiguity of their approach can be revealed by the following passage:

> “Why has this conflation of historical genesis with current utility attracted so little attention heretofore? Every biologist surely recognizes that some useful characters did not arise by selection for their current roles; why have we not honored that knowledge with a name? Does our failure to do so simply underscore the unimportance of the subject? Or might this absent term, in Foucault's sense, reflect a conceptual structure that excluded it? And, finally, does the potential need for such a term at this time indicate that the conceptual structure itself may be altering?” (Gould & Vrba, 1982, p. 6)

Now, preadaptation denotes exactly what Gould and Vrba refer to. The problem is that Gould and Vrba want to promote two different ideas: historical discontinuity and non-adaptation. And their concept of exaptation reflects this by denoting both cases where a non-adaptive or neutral character is co-opted for a certain function and cases where an adaptive trait is co-opted for a different function. In order to promote the conceptual innovation brought by the notion of exaptation, Gould and Vrba stress the unfortunate connotations of the term preadaptation (Gould & Vrba, 1982; Gould, 2002, p. 1231). However, the ideas put forward by Gould and Vrba are fully contained in the approach to novelty developed in the late Modern Synthesis era and analysed in the last chapter. First, it should be noted that the co-optation of originally non-adaptive characters was the original meaning of preadaptation when it was coined by Lucien Cuénot (see chapter 2). Thus, preadaptation was first coined to denote the exact same phenomena for which Gould and Vrba say a that a term is missing. Second, this non-adaptive origin of novelty was accepted as one possible type of origin by Mayr (Mayr, 1960) and Bock and Von Wahlert (Bock & von Wahlert, 1965, p. 293). It is however true that the idea of a co-optation of anon-adaptive trait is not contained in Bock and Von Wahlert's concept of preadaptation.

The near equivalence between the concepts of preadaptation and exaptation has already been noted (Casinos, 2017; Endler, 1986, p. 46; Grandcolas, 2015). Some have argued that the term 'exaptation' is plagued by nearly as many flaws as the term 'preadaptation' (Casinos, 2017; Cattani, 2008). Exaptation does not seem to have replaced preadaptation in biological literatures[21] (Budd, 2006; Cattani, 2008), but it has had more influence in the philosophical literature (Dennett, 1998) and among anti-adaptationist biologists. Gould and Vrba's stress on the discontinuity of their approach with previous ones, coupled with the success of the term 'exaptation', may have played a role in the neglect of the functional approach to novelty and the popularity of the idea that the problem of novelty was not addressed during the Modern Synthesis era.

Gould and Vrba are right in pointing out that the term preadaptation contributes to perpetuating the conflation of two meanings of adaptation: A) adaptation as the result of a process of transformation of a character, involving mutations and natural selection (selectionist adaptation); B) adaptation as a judgment regarding the fitness of a character for a certain function, regardless of whether this state is the result of a process of transformation under natural selection (engineering adaptation). Rather than favouring the replacement of preadaptation with exaptation, Futuyma presents the two concepts as complementary (Futuyma, 2005, p.261). This is actually what Gould and Vrba propose as well, except that they argue for the replacement of 'preadaptation' with 'preaptation':

> "…what we now incorrectly call "preadaptation" is merely a category of exaptation considered before the fact. If feathers evolved for thermoregulation, they become ex- aptations for flight once birds take off. If, however, with the hindsight of history, we choose to look at feathers while they still encase the running, dinosaurian ancestors of birds, then they are only potential exaptations for flight, or preaptations (that is, aptus-or fit-before their actual cooptation). The term

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[21] For example: "I do not see the need to replace the unambiguous term 'preadaptation ' with the term 'exaptation ' (Gould & Vrba, 1982), and thus retain the older term, while recognising that it has no teleological implications." (Budd, 2006, p. 618)

> "preadaptation" should be dropped in favor of "preaptation." Preaptations are potential, but unrealized, exaptations; they resolve Mivart's major challenge to Darwin." (Gould & Vrba, 1982, p. 11)

However, Bock and Von Wahlert's multiple concepts of function show that this confusion of the meanings of adaptation does not apply to them.

Constructional morphology and internal selection

In the 1970s and 1980s there were several reactions to the explanation of the evolution of phenotypic characters through the functional relations of the organism to the environment and the external selection pressures acting on the latter. A stress was put on the organism as a structural whole composed of interrelated parts and on the idea that this structural organisation itself, regardless of the changes and particularities of environment was the essential entity to focus on in order to understand evolutionary change. For example, George Lauder distinguished between the equilibrium approach focusing on the influence of external selection pressures on morphological change[22], and the transformational approach, for which "Historical patterns of structural change are analyzed as a consequence of intrinsic organizational properties of structural systems" (Lauder, 1981, p. 431).

However, it would be inaccurate to interpret this approach as a switch from a focus on function to a focus on form. It is rather a switch from a focus on functional relations with the environment to internal functional relations between parts of the organism, and from external selection to internal selection. Here is for example how a constructional morphologist expresses this position:

> "Those constructional morphologists who, like myself, emphasize the bioconstruction primacy prior to the environment, join Gould and Lewontin (1979) in their attack against the "adaptationist program". However, in contrast to their criticisms, we do not argue the role of selection. Their misconception of selection

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[22] "Three aspects of equilibrium analysis relate directly to the study of historical hypotheses in morphology: (1) the inference of historical selective forces to explain morphological change, (2) the use of morphological series as a reflection of the actual historical pattern of structural change, and (3) the explanation of adaptive radiations in terms of key innovations." (Lauder, 1981, p. 431)

> [...] follows from the traditional Darwinian view, that only special environmental conditions are capable of selection. However, if you concede that the matter and energy consuming and converting part of the organismic machinery contributes to fitness as well as matter and energy acquisition organs, it must necessarily be exposed to selection as strongly. More than that, it is the coherent unity of the organismic construction that determines how subsystems can respond to selective forces. It sets the framework for possible morphological, physiological, and behavioural changes during the optimization and economization process [...] driven by selection." (Vogel, 1991, p. 63)

The relative importance of environment-specific selection pressures and internal selection pressures depending on the structural organisation may depend on the type of character considered. Regardless there is a continuity with the principles of the functional-historical approach. This can be illustrated by the approach of Graham Budd who singles out the principles of "functional continuity", "asymmetrical dependency[23]", "redundancy" and "preadaptation" to study the evolution of the structural organisation of organisms (Budd, 2006).

An important question regards the extension of the principle of conversion of function: what are the types of novelty that the principle can contribute to produce and what are the types that cannot be explained by it? Bill Wimsatt, referring to different body plans, for example, the exoskeleton of arthropods and the endoskeleton of chordates, states that "[t]his kind of change in functional organization runs so deep that there is no adaptive - even no meaningful - transition from one to the other" (2013, p. 36). He then concludes:

> "This puts the contrast between role function and selection function in a new light. It is not just that people investigating role functions are not interested in a selectionist account of their origin. They could well be at a suitable distance. Rather, the problem is that there is no differential selectionist account moving

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[23] "In the terminology of this review, the unnecessary component is the least constrained, and by hypothesis will be the component of the system to evolve first once the system is in place, although the last to be emplaced into the system. In other words, the unnecessary component exercises a functional constraint on the necessary component, whereas the converse is not true. No matter how tightly integrated and interdependent a system might seem, it will still have many points of weakness – some of them very subtle – upon which selective pressures can act to cause change." (Budd, 2006, p. 616)

> from any form that is anywhere close to the form under consideration to the alternative modes of organization considered in a comparative morphological analysis." (Wimsatt, 2013, p. 36)

This question of the novelties for which a conversion of function is impossible should, in principle, be distinguished from the question of how many cases of novelties actually involve a conversion of function. This second question relates on the one hand to the issue of testing hypotheses of character evolution and on the other hand to the issue of relative significance. Regarding the issue of testing, all cases for which hypotheses of conversion of function can be formulated are not actual instances of conversion of function.

Ultimate and proximate causes

The functional-historical approach does not fit with Mayr's distinction of proximate and ultimate causes if this distinction is understood in the following way, expressed by George Lauder:

> "Mayr has emphasized the distinction between functional biology, concerned primarily with understanding how organisms work and proximate causation, and evolutionary biology, committed particularly to studying historical pathways and ultimate causation. A major theme to emerge from a consideration of five areas of interplay discussed below is that clear areas of overlap exist between these two approaches that may provide new insights into organismal diversity and the mechanisms that have produced it. Research into the evolution of function increasingly exemplifies aspects of both "types" of biology." (Lauder, 1990, p. 320)

It can be argued that if this is how Mayr's position in his article on cause and effect in biology should be interpreted, then there is a contradiction between this theoretical position and Mayr's own account of the emergence of evolutionary novelties because in the latter, Mayr himself implements a perspective that combines the two approaches of functional and evolutionary biology.

A double movement of specialisation and integration

Another evolution of the functional-historical approach is a double movement of increased specialisation and of integration. In a review, Marvalee Wake notes the specialisation into functional morphology, biomechanics, ecomorphology, developmental morphology; while evolutionary morphology or integrative biology refer to the reunion of these disciplines under a common project (Wake, 1992). Walter Bock and Carl Gans[24] can be seen as figures of continuity since the former contributed to the development of ecomorphology and the latter to the development of integrative biology (Adler, 2011).

Evo-devo biologists and the functional approach

Some evo-devo practitioners focusing on developmental genetics rather than morphology can be said to adopt a functionalist framework. For example, Sean B. Carroll, when explaining the origin of novelties, refers to Darwin's explanation and offers multifunctionality and redundancy as crucial explanatory factors because they create "the opportunity for the evolution of specialization through the division of labor" (Carroll, 2005, chapter 7). Carroll insists on the continuity between organs. Rather than offering an alternative explanation to the functionalist framework, Carroll argues that evo-devo has offered new tools to support it:

> "The erroneous notion of the anti-evolution camp has been that the intermediate stages in the evolution of structures must be useless – the old saw of "What use is half a leg or half an eye?" Following this preposterous "logic", the conclusion is that structures must be forged perfectly in one instant – that evolution didn't happen. This view clutches desperately at Darwin's own explicit discussion of difficulties with the theory of natural selection in the *Origin*, yet it always fails to grasp or cite Darwin's brilliant resolution of the matter. The crucial insight he had was that the same organ often performs wholly distinct functions, and that two distinct organs may also simultaneously contribute to the same function." (Carroll, 2005, p. 170)

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[24] More on Gans in chapter 2.

However, few evo-devo biologists seem to endorse the functional-historical approach, and many instead subscribe to the opposition between the study of form and the study of function forcefully expressed by Ronald Amundson (Amundson, 2005).

III – CAUSES OF THE NEGLECT OF THE FUNCTIONAL-HISTORICAL APPROACH

The reduction to population genetics

The neglect of the functional-historical approach to evolutionary change and novelty partially comes from a conflation of the distinction between structuralism and functionalism and the distinction between the population genetic perspective and the organismal perspective (e.g. Amundson, 2005; Laubichler, 2007; Wagner, 2014; Walsh, 2013). It is true that the Modern Synthesis introduced the population genetic approach, but a functional approach to evolution and novelty was also perpetuated by some during the Modern Synthesis era. Consider this description by Denis Walsh:

> “The modern synthesis conception is grounded in a commitment to sub-organismal mechanism. It locates the source of adaptive evolution in the actions of genes/replicators and proceeds by elucidating the activities of genes/replicators in the production of phenotypes, both novel and recurrent. Phenotypes vary in their contribution to organismal survival and reproduction according to the replicators that produce them. Consequently, some genes/replicators systematically leave more of their copies in future generations than others. In this way, populations change in their genetic/ replicator structure, and concomitantly they change in the phenotypic character of the organisms they comprise: hence the bias in form and function. The ultimate source of evolutionary novelties, on this view, is random mutation. Adaptive evolution proceeds by the gradual accretion (and recombination) of very small, lucky mutations.” (Walsh, 2013, p. 59)

The problem with this characterisation of the Modern Synthesis approach to novelty is that it does not capture the actual level at which explanations of novelty such as Mayr's or Bock's are situated. The usual attribution to Mayr, without qualifications[25], of the gene-based approach described by Walsh reveals the neglect of the functional-historical approach. Admittedly, the latter is not a creation of the Modern Synthesis (Darwin introduced it) and it is not specific to the Modern Synthesis. Still, this approach has historically an important place in the Modern Synthesis, if only in its later phase. This also relates to problems with the historiography and definition of the Modern Synthesis, which will be addressed in the next two chapters, along with a historical analysis of the functional-historical approach.

Objections to the functional definition

The recent theoretical literature on novelty has focused extensively on the problem of the proper definition of an evolutionary novelty. In that context, the functional definition of novelty, often attributed to Mayr (1960), has been criticised and rejected. Here is how Mayr formulates the definition:

> "Our discussion will gain in precision if I state at the very beginning what I include in the category "evolutionary novelties." *I include any newly arisen character, structural or otherwise, that differs more than quantitatively from the character that gave rise to it.* Consequently, not every change of the phenotype qualifies, because change of size or of pigmentation would be a change of phenotype not necessarily qualifying as "emergence of an evolutionary novelty." What particular changes of the phenotype, then, would qualify? Certainly any change that would permit an organism to perform a new function. Tentatively, one might restrict the designation "evolutionary novelty" to any newly acquired structure or property which permits the assumption of a new function. This working definition must remain tentative until it is determined how often it is impossible to decide whether or not a given function is truly "new." (Mayr, 1960, p. 351, emphasis added)

Some defenders of the evo-devo approach to novelty have discarded the functional-historical approach to novelty altogether more on the basis of a critique of the functional *definition* of novelty than on the basis of a critique of the

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functional-historical *explanatory approach* (Müller & Wagner, 1991). The critique of the definition has led to a neglect of the functional approach. Now, the latter is independent of the former. Since these criticisms of the functional definition are in, my opinion, valid and have been influential, I will review them, all the while stressing the independence of the functional-historical account from the functional definition.

Restriction to key innovations.

An efficient way to detect the appearance of a new function is to look for adaptive radiations. These diversifications following the colonization of new habitats are sometimes initiated by the appearance of a new function allowing the colonization. For example, the acquisition of avian flight linked to the emergence of wings led to the radiation of birds. According to Pigliucci (2008, p. 888), defining novelty by the acquisition of a new function “links novelties directly to the ecology of the organism, imposing the stringent criterion that a novelty be connected to the adaptive radiation of a whole group”. But there is no one-to-one relation between novelty and adaptive radiation. “Novel features can appear without playing a role in adaptive radiations (ex□ the transfer of jaw bones in the ear in early mammal history), and traits can play an important role in adaptive radiations while not being novelties in an interesting way” (*Ibid.*). One example of this latter case is the differentiation of teeth in mammals which played a crucial role in their evolutionary success but is only based on quantitative changes of shape (Hunter & Jernvall, 1995).

In Mayr’s defence, he himself uses the example of the transfer of jaw bones into the ear in mammals to illustrate one of the processes of emergence of novelties. And Mayr does not mention adaptive radiation as a criterion in his article of 1960. Novelties do not always play a role in adaptive radiations, but neither do new functions.

Displacement of the problem on function.

The problem of distinguishing between quantitative and qualitative difference can be reformulated about function. This is shown by the ambiguity about the relation between novelties and adaptive radiations. Just as a new function was the criterion to distinguish qualitative from quantitative variation, adaptive radiations are a way to distinguish between the functions that are new and those that are not, that is, a function is new when it leads to an adaptive radiation. This is problematic as it leads back to the first objection: It restricts novelties to key innovations. This problem was acknowledged by Mayr himself: “This working definition must remain tentative until it is determined how often it is impossible to decide whether or not a given function is truly "new" (Mayr, 1960, p. 351).

No distinction between morphological differences.

By including all traits associated with a new function, Mayr discards the intuitive distinction between quantitative and qualitative structural or morphological variation. This is because, as stated earlier, a quantitative change can lead to a new function. For example, in finches of the Galapagos (*Geopsizidae*), a simple change of shape in the beak can be associated to the new function of cracking open big seeds, leading to new eating habits (in *G. magnirostris*) (Grant & Grant, 2006; Lack, 1947). And the quantitative differences in beak size and shape in the different species of finches are produced by a quantitative change in the expression of a signalling protein. Now, it seems that this intuitive distinction between quantitative and qualitative structural change, however insufficient, should not be discarded but rather refined by a scientific definition of novelty.[26]

Circularity or infinite regress

The objection of circularity appears when Mayr’s definition of novelty is confronted with the main principle that he proposes to explain the origin of novelty: the functional shift (e.g. Müller & Wagner, 1991, p. 231). According to this principle, the formation of a novel structure is caused by the assumption of a new function by an existing structure, leading to a new selection pressure that will guide the transformation of this structure. Thus there is a tension between Mayr’s definition of novelty and his explanation of novelty. On the one hand novelties are defined as traits allowing the realization of new functions, on the

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[26] As noted earlier, this distinction is stressed by Mayr himself.

other hand these very new functions are the *starting point* of the arising of novelties. To be fair to Mayr, the problem of circularity is not internal to his explanation of the arising of novelty. It comes from a literal interpretation of his definition of novelty, which he himself describes as a “working definition”.

The principle of functional shift is not itself circular: new functions are primary to changes in the structures, they drive these changes through new selective pressures. It can then be asked: if the transformation into the novel structure is caused by a change of function of the initial structure, what caused the initial structure to appear? The mechanisms of functional shift seem to produce an infinite regress.

The neglect of the functional-historical approach is not universal

The neglect of functional morphology and ecology is not shared by all evo-devo biologists who focus on novelty (Breuker et al., 2006; Galis, 1996; Gilbert, 2003; Hallgrímsson et al., 2012; D. B. Wake, 1982; M. H. Wake, 2015) nor by all philosophers of biology who focus on this topic (Brigandt, 2010; Brigandt & Love, 2012; Love, 2003, 2005, 2006; Pigliucci, 2008). Alan Love, in particular, has repeatedly stressed the role of morphology in evo-devo and for the explanation of innovation and novelties. He distinguished two roles for morphology:

> “Therefore, morphology plays two essential roles in explaining the origin of qualitative variation at particular phylogenetic junctures without which the criteria of explanatory adequacy for innovation and novelty cannot be met. The first is the conceptualization and operational identification of the targets of explanation (complex morphological features) in the establishment of non-homology and phylogenetic juncture for the pattern component of explanations. The second is the elucidation of causal interactions at higher levels of organization.” (Love, 2006, p. 327)

While Love stresses the essential contribution of morphology, as a group of disciplines, to the explanation of the origin of novelties, I single out the functional historical approach as a tradition of explanation of the origin of novelty. Actually, Love (2003) has also singled out the revival of functional and evolutionary morphology from the 1950s. A difference, however, is that Love (2003, 2006) defends rather strongly the idea of an exclusion of morphology from the Modern Synthesis, while I would argue that the case of Mayr and Bock and Von Wahlert, among others, undermines the idea, at least regarding the later phase of the Modern Synthesis. This is partly due to differences in interpretation of the chronology and theoretical content of the Modern Synthesis, a subject that will be dealt with in chapters 2 and 3. This is also due to an overtly genetic interpretation of Mayr's conception of novelty. Love states that:

> "Importantly, Mayr recognizes that the primary loci for discussions of innovation and novelty were the disciplines of comparative anatomy and paleontology but he ultimately reduces the project of explaining the emergence of evolutionary novelties to population genetics in sync with the Modern Synthesis theoretical framework." (Love, 2003, p. 321)

He refers to Mayr's formulation of the problem:

> "The problem of the emergence of evolutionary novelties then consists in having to explain how a sufficient number of small gene mutations can be accumulated until the new structure has become sufficiently large to have selective value" (Mayr, 1960, p. 357)

But, as shown by his immediate next sentence: "Or is there an explanation which avoids this troublesome threshold problem?" (Mayr, 1960, p. 357), and by the rest of his article, Mayr's account does not ultimately reduce the problem of novelty to population genetics. Mayr's diverse views on novelty, and their potential contradictions, will be dealt with in more details in chapter 2 and 3.

Massimo Pigliucci (2008) has noted the limitation of the developmentally focused approaches to novelty (Müller & Wagner, 1991) and he has stressed the role of ecology. They do not include ecology, turning the novelty problem into a purely developmental problem. They stress too much the discontinuous nature of novelty, undermining the fact that nature often uses "tinkering".

> “Evolutionary novelties are new traits or behaviors, or novel combinations of previously existing traits or behaviors, arising during the evolution of a lineage, and that perform a new function within the ecology of that lineage. [This] definition (1) makes explicit the fact that often novelties are not absolute discontinuities but can be built on previously existing parts, (2) indicates that they are a phenomenon that affects the evolution of certain lineages without implying that all derived characters are in fact novelties, and (3) requires some kind of ecological function to eventually be coupled with the novelty, although it does not imply a necessary link between novelties and adaptive radiations.” (Pigliucci, 2008)

According to Pigliucci, the prospects of an explanation of evolutionary novelties by evo-devo are meagre, because evo-devo has been focused much more on development than on evolution and is concentrated on the molecular underpinnings of quantitative traits rather than on the underpinnings of the formation of complex new traits. This trend is confirmed by recent quantitative analysis of research in the field (Diogo, 2016, 2018).

IV – NOVELTY AND ADAPTATION

I will now come back to the distinction between novelty and adaptation to confront the view of some evo-devo practitioners with the view of the functional-historical approach. Müller, Newman and Peterson repeatedly distinguished variation and innovation as distinct processes and novelty and adaptation as their respective outcome (Müller, 2010; Müller & Newman, 2005; Peterson & Müller, 2013, 2016). Here is one of their schematic representation of the relation between the two processes. In this most recent version, the term adaptation replaces variation to designate the first process and the term adaptive trait replaces adaptation to designate its outcome, but the spirit of the conceptual distinction remains the same:

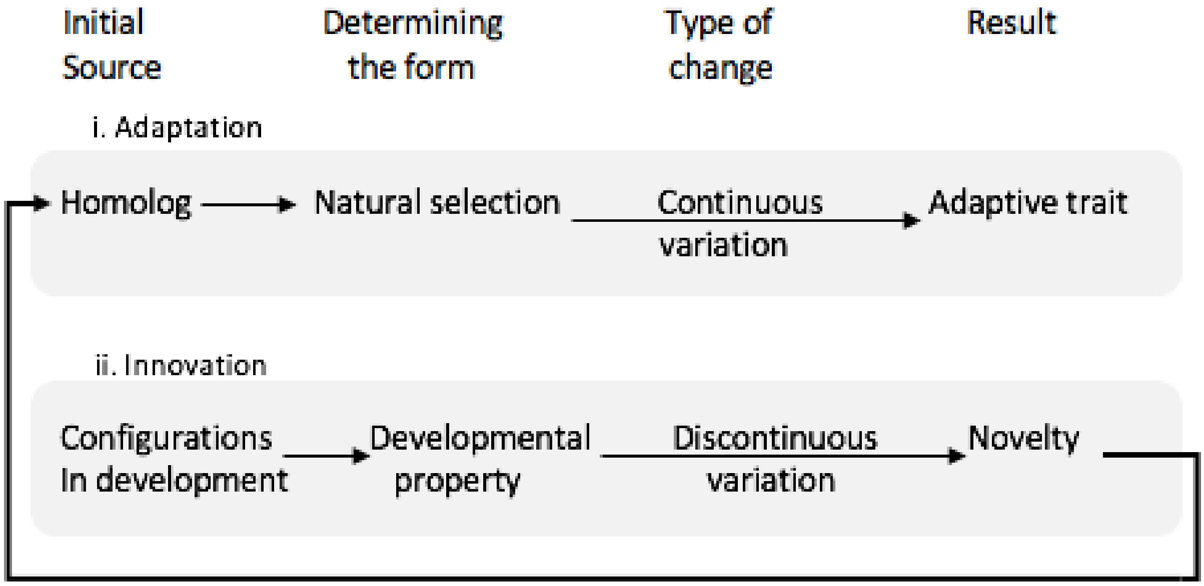

Fig. 2 Distinction between adaptation and innovation (redrawn after Peterson & Müller, 2016)

They explain the diagram in the following way:

> “**i** Adaptation. A preexisting element is the starting source for adaptive change. Natural selection acting on heritable variation determines the form of the phenotype. This works through continuous variation, with small changes in each generation resulting in an adaptive trait present in the population. **ii** Innovation. The initial source for innovation is the configuration of the developmental system, including both epigenetic and genetic factors. Epigenetic in this case refers to traits and processes above the gene level, such as environmental factors, tissue interactions, biomechanical forces, etc. A developmental property, such as cartilage induction by compression, determines the form that occurs from the developmental configuration. In the case of novelties, this form appears as discontinuous variation of the phenotype compared to previous generations. The resulting novelty, a new homologue, can undergo further adaptation.” (Peterson & Müller, 2016)

It is important to acknowledge that this discontinuous view of evolution is not shared by all practitioners of evo-devo. I have stressed that the work of some evolutionary developmental biologists can be placed within the functional-historical approach; in the same way some of them criticise the discontinuous view promoted by Müller, Newman an Peterson (Hall & Kerney, 2012; Minelli, 2015; Moczek, 2008; Shubin, Tabin, & Carroll, 2009). This is for example the case with Alessandro Minelli, who explicitly criticises the distinction between the process of innovation and the process of variation and states:

> “The better we know a process, the less we are able to identify its exact origins, these instead being determined by arbitrary choice. In science, and especially in biological disciplines with a strong historical dimension such as evolutionary biology and developmental biology, we should frame questions in terms of transitions rather than origins.” (Minelli, 2015)

In order to understand how this distinction is applied to cases of novelties, I will focus on an example experimentally studied by Gerd Müller, the origin of the syndesmosis tibiofibularis in birds (Müller, 1990). A comparison with Walter Bock’s explanation of the basitemporal articulation in some birds presented earlier will illuminate similarities and differences in explanatory styles.

Illustration: the origin of novelties in the avian hind limb skeleton

The syndesmosis tibiofibularis is a cartilaginous or bony crest that links the tibia and the fibula in birds’ legs. Müller’s work on this structure was inspired by the experimental work of Armand Hampé who placed a piece of mica between the tibia and the fibula of developing chicks. In birds, the distal part of the fibula is shortened compared to the tibia and it has no connection with the tarsal joint. The proximal part of the fibula is larger and contains an attachment point of the iliofibularis muscle. In Hampé’s developed chicken, the tibia and fibula were of equal length. Müller reproduced the experiment with the same result, he observed other anatomical changes beside the reduction of the fibula, in particular the absence of the syndesmoisi tibiofibularis. Müller and Streicher formulated the hypothesis that as the fibula was reduced during evolution of archosaur, dinosaur and birds, the increased mechanical pressures caused by the iliofibularis muscle on the fibula led to the formation of the syndesmosis tibiofibularis.

> “In the scenario outlined, three major, but morphologically unspecific, adaptive trends (improvement of archosaur gait, trend towards bipedality in dinosaurs, and

> weight reduction in the evolution of flight) are canalized towards the bird-specific limb morphology by a set of functional and developmental factors (such as cell number of early rudiments, differential growth, fusion processes, mechanical stimulation of cartilage and bone formation, lability of early rudiments etc.). The syndesmosis tibiofibularis and the mechanisms of its formation are found to have played an important role in this process, allowing strong distal fibula reduction together with the maintenance of its proximal participation in the knee joint." (Müller & Streicher, 1989, p. 336)

Müller and Streicher relied on ontogenetic evidence and showed that the development of the syndesmosis tibiofibularis depends on a process of ossification caused by mechanical pressures (Müller & Streicher, 1989; Streicher & Müller, 1992). Gerd Müller (1990), relying on this example and other of similar nature, developed a "side-effect" theory of the origin of novelty that he later summarised in the following way:

> "If selection acts on body proportions and skeletal proportions, the ensuing biomechanical changes and the reactive potential of skeletogenic tissues will automatically generate new elements. This effect is neither the direct result of a mutation or "new genes" for that specific character nor the result of selection "for" that character but rather a developmental by-product of general selection regimes, affecting growth rates for instance, that trigger a specific developmental response at certain threshold points of the affected developmental system. This response is "unforeseen" and the ensuing character could be called "neutral," because it may exist for prolonged periods of time purely for developmental reasons without selective advantage." (Müller, 2002, p. 59)

Comparison of the types of explanations developed by Walter Bock and Gerd Müller

Müller and Streicher's explanation of the origin of the syndesmosis tibiofibularis is very close in spirit to Bock's explanation of the origin of the avian basitemporal articulation. Müller's case is a pressure induced ossification of a tendon, Bock's case is a pressure-induced formation of a diarthrosis between two bony processes. In the two explanations there is a reliance on postulated adaptive trends based on data from comparative anatomy, functional morphology, behaviour and ecology. In the two explanations, there is a combination of continuous modification of anatomical parts under different selection pressures, and of a discontinuous change caused by the reactive properties of developing tissues.

A first difference is that Müller and Streicher rely on multiple threads of ontological evidence, both descriptive and experimental, while Bock's use of an epigenetic mechanism is not backed by direct evidence but on general principles of reactivity of developing tissues and on a reference to the work of Schmalhausen. However, I do not see how this reliance on experiment could conflict with Bock's approach; in fact, this is another level of evidence that could be added to Bock's explanation. Another difference, is the timescale of the evolutionary sequence considered. While Bock focuses on a novelty within birds and relies on the study of different extant birds, Müller and Streicher focus on transition between archosaur, dinosaurs and birds and rely on palaeontological data. Overall, one the one hand, the variety of sources of evidence and the quality of the evidence is greater in Müller and Streicher' s work, on the other hand, while Bock is focused of a few characters and a reduced time scale, in contrast, the time scale and number of evolutionary events hypothesised by Müller and Streicher make their work more ambitious but also speculative. More importantly, the general styles of the two explanations are very similar.

The comparison between Müller's and Bock's types of explanation seems relevant to issues regarding differences of epistemic values between scientists, or influence of disciplinary homes on the choice of criteria for an adequate explanation. Surprisingly, there seems to be a contrast between the claim from evo-devo practitioners, including Müller, that novelty is only studied by evo-devo and was outside of any research program, and the actual structures of Bock's and Müller's explanations of cases of novelty. Moreover, Müller and Streicher's study answers the four research questions about novelty defined in section I of this chapter, but their investigation goes beyond these four questions.[27] The same

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[27] "1) What specific developmental mechanisms are responsible for a new derived character state that has been identified as an evolutionary novelty? 2) Did the developmental mechanisms that are responsible for the derived character state originate at the same time as this character state? 3) What were the exact developmental mechanisms responsible for the initial changes in the character state? 4) Are the observed genetic differences between these two developmental systems sufficient to account for the observed phenotypic differences?" (Laubichler, 2007)

can be said about the disciplines involved in their work.[28] They rely on developmental biology, systematics, comparative anatomy and palaeontology. But they also rely on functional morphology to infer adaptive trends[29]. They write:

> "In this scenario different adaptive demands are met by a variety of developmental mechanisms that in turn channel the further ability of the system to be modified. Depending on the availability of developmental mechanisms at specific stages of the evolutionary process entirely different pathways may be taken to meet similar adaptive problems." (Müller & Streicher, 1989, p. 337)

The explanation of the origin of the syndesmosis is embedded in a sequence that involved adaptive trends and these trends, such as the reduction of the fibula are used as one source of evidence for the hypothesis.

Can the difference between Bock and Müller be seen as purely semantic? Conceiving the whole sequence of events as the origin of a novelty, or as a sequence of adaptation-novelty-adaptation makes little difference if, on one side, Müller and Peterson accept that the study of evolution prior to and after the emergence of the novelty is necessary to provide the context and the initiating conditions of this emergence; and if on the other side Bock acknowledges that the emergence of the basitemporal articulation or of the syndesmosis are not simple cases of continuous adaptations. Looking at the practices of explanation shows commonality of explanatory goals and strategies beyond the opposition of concepts.

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[28] "1) developmental biology, which provides insights into the proximate mechanisms of character development; 2) evolutionary genetics, which provides insights into the forces acting on the developmental genes; 3) systematics, which provides us with the comparative methods for testing the evolutionary assertions; 4) comparative anatomy, which helps us to coherently define the characters and the character states we seek to understand; and 5) paleontology, which provides us with information about the sequence of phenotypic transformations that led to the character" (Wagner, Chiu, & Laubichler, 2000, p. 829)

[29] Echoing Bock's prescription: "Study of the evolution of a structure must not cease with the establishment of correct sequences of the structural modifications. This is a necessary step, but it is as important or even more important to determine the ancestral structural form and the selection forces guiding the evolution of the structure. In discussions of the origin of a new structure, it is also necessary to know the "prehistory" of its several component parts." (Bock, 1959, pp. 195–196)

However, I think there are conceptual problems in the formulation of the relation between novelty an adaptation adopted by Müller, Newman or Peterson.

V – NOVELTY, VARIATION, AND THE CREATIVITY OF NATURAL SELECTION

There are at least three problems with the distinction between novelty and adaptation formulated by Müller and colleagues:

1) Their distinction presupposes a mechanism for the origin of novelty: a novelty arises through discontinuous variation.

2) It associates natural selection to quantitative variation of existing characters[30] and qualitative discontinuous variation with absence of selection or neutrality[31].

3) It confuses the problem of the generation of variation and the problem the generation of novelty.

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[30] "Given the sensitivity of skeletogenesis to mechanical stimulation and its dependence on environmental conditions, it is legitimate to consider potential evolutionary roles of these interdependencies. One straightforward inference is that this kind of reactivity of the skeletogenic system provides a source of phenotypic plasticity. Natural selection would be able to operate on variations of size and shape of skeletal elements induced by environmental change. Such a role of an environment-dependent developmental mechanism is in line with the standard evolutionary theory and its emphasis on variation and selection." (Müller, 2002, p. 58)

[31] "However, there is a second and possibly distinct evolutionary role of mechanosensitive skeletogenesis: the de novo formation of skeletal elements from responsive tissues. In this case, the starting point would be selection acting not on the new element itself (because it would not yet exist) but on other characteristics, such as size, shape, or proportions of body parts. Continuous selection on these parameters, for instance the relative size of limbs and their skeletal support, will alter the biomechanical conditions in the affected region and result in new pressure and tension loads in the involved tissues. If these tissues have a chondrogenic capacity, they will respond by producing cartilage matrix and begin cartilage cell differentiation at certain threshold levels of mechanical load. A new skeletal element will result. This new element could remain selectively neutral for long periods of time, its continuous existence merely depending on the maintenance of the same biomechanical conditions in every subsequent generation. But eventually it can become itself subject to selection and will thus be stabilized and integrated in the developmental-genetic machinery." (Müller, 2002, p. 58)

Regarding 1), by modelling their idealised process of innovation on the cases of novelty that they study, Müller and colleagues do not leave room for continuous mechanisms of origination of novelty.[32]

Regarding 2), Müller seems to imply that quantitative variation is affected by natural selection while epigenetically induced new structures can remain neutral:

> "This new element could remain selectively neutral for long periods of time, its continuous existence merely depending on the maintenance of the same biomechanical conditions in every subsequent generation. But eventually it can become itself subject to selection and will thus be stabilized and integrated in the developmental-genetic machinery." (Müller, 2002, p. 58)

However, this distinction does not seem warranted. Quantitative variations can also be neutral, for example some allometric trends can be the product of drift rather than selection. Furthermore, epigenetically formed new structures are likely to have an significant effect on the fitness of the organism.

I will address problem 3) at more length in the next two sections.

The generation of variation and the sorting of variation

An often made and valid distinction between the perspective of population genetics and the perspective of evo-devo is in terms of types of explanation. Population genetics and quantitative genetics offer statistical explanations of evolutionary change or stasis in terms of factors acting on gene frequencies or phenotypic values in populations. Evo-devo offers mechanistic explanations of

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[32] This is manifest in Müller's recent endeavour to match types of novelties with mechanisms of origin:

Type of novelties	**Mechanisms**
Type I novelties (Bauplans)	epigenetic mechanisms (e.g. Newman & Müller, 2000)
Type II novelties (non homologous new traits)	epigenetic mechanisms and phenotypic plasticity
Type III novelties (homologous new traits)	"variational paradigm" = genetic changes of the QTL (*quantitative trait loci*) type

(after Müller, 2010)

evolutionary change or stasis in terms of developmental mechanisms acting on phenotypes.

One problematic aspect of the distinction between variation and innovation as processes (Müller & Newman, 2005; Peterson & Müller, 2016) is that it suggests that population genetics can explain the process of quantitative variation leading to adaptation but not the process of qualitative variation producing novelty. But population genetics cannot explain either of these processes, that is, the problem of the generation of variation is outside the scope of population genetics for quantitative variation as well as for qualitative variation. Douglas Futuyma thus notes:

> "Some evolutionary biologists, especially population geneticists, are inclined to dismiss [evo-devo] altogether. But that would be a great mistake, I believe, for the argument that evolutionary theory lacks but needs a theory of the origin of phenotypic variation is convincing—even obvious." (Futuyma, 2015, p. 68)

How phenotypic variations, quantitative and qualitative, are generated is a problem for developmental biology. The mechanistic explanation of the generation of variation complements the statistical explanations of population genetics in both cases.

Two meanings of adaptations

Müller and Peterson define adaptation in the following way:

> "Adaptation. A preexisting element is the starting source for adaptive change. Natural selection acting on heritable variation determines the form of the phenotype. This works through continuous variation, with small changes in each generation resulting in an adaptive trait present in the population." (Peterson & Müller, 2016)

The validity of the argument about the active role of selection in producing adaptation and not novelty is partly contingent on the definition of adaptation adopted. Two meanings of adaptations have to be distinguished (Lloyd, 2017):

_ The *selected-product* definition of adaptation. Under this definition, any trait whose presence in a population is a result of a process of selection is an adaptation. This type of adaptation can be illustrated by the classic case of the population of pepper moths composed of black and white individuals. If initially the trees on which the moths rest are light-coloured, the white individuals are better hidden from predators and their frequency in the population is higher than that of the black individuals. If the trees darken, the black moths will become fitter and their frequency will increase in the population. Under this definition of adaptation, the pigmentation of the black moths is said to be an adaptation because it has been positively selected, even though the black variant was present at the beginning of the process.

_ The *engineering* definition of adaptation. Under this definition, an adaptation is the result of a process of change where new phenotypes are produced that constitute a better fit with the environment than phenotypes previously existing in the population. This can be illustrated by the progressive adaptation of Darwin’s finches to different ecological niches and in particular of their beak shape and size to specific feeding habits, such as cracking nuts in one case or picking insects in another. The definition of Peterson and Müller cited earlier matches the engineering rather than the selected-product definition of adaptation since it implies of the occurrence of “small changes in each generation” (Peterson & Müller, 2016) which are selected and result in an adaptive phenotype that was not present at the beginning of the process.

We can relate this discussion to the debate about the creativity of natural selection (Endler, 1986; Forber, 2005; Godfrey-Smith, 2009; Neander, 1988, 1995; Sober, 1995; Stegmann, 2010). Some authors argue that natural selection can only play a role in distribution explanations, that is, in cases of selected-product adaptations, where the variants are present at the beginning of the process and natural selection has a role in changing the relative frequencies of the variants over time - their distribution in the population (Endler, 1986; Sober, 1995). Others argue that natural selection has a positive role in cases of engineering adaptations, or more generally in origin explanations (where the trait involved can be an engineering adaptation or a novelty) (Forber, 2005; Godfrey-Smith, 2009; Neander, 1988, 1995).

Thus, Müller and Peterson appear to be on the side of those who attribute a creative power to natural selection since they argue that natural selection can shape (engineering) adaptations by acting on continuous variations. Does their argumentation match that of those who defend the creativity of selection? Actually, the latter do not argue that natural selection "determines the form of the phenotype" (Peterson & Müller, 2016), but rather that natural selection has a creative role by increasing the chances of the occurrence of the adaptive phenotype (e.g. Godfrey-Smith, 2009, pp. 42-43). It increases these chances by contributing to raise the frequency of variants that have a closer access to this phenotype. This reasoning applies regardless of whether the variation is continuous or discontinuous. And it can in principle apply to the case of the basitemporal articulation or the syndesmosis tibiofibularis. To schematise, by increasing the frequency of birds with smaller fibula thus decreasing support against the mechanical force exerted by the iliofibularis muscle, natural selection makes the origination of the syndesmosis more probable. Natural selection is not more able to determine the "form" of an engineering adaptation than that of the syndesmosis, but it can increase the probability of their occurrence in the same way.

There are counterexamples to this positive role of natural selection. I will use a hypothetical example here for the sake of simplicity.[33] Let us imagine a population of finches feeding on nuts in which the frequency of individuals with larger beaks more suited to cracking nuts increases under natural selection. Let us further assume that in this case the variants with smaller beaks have access to a mutation (or an epigenetic event) that determines the production of an even larger beak more adapted to cracking nuts. The occurrence of this mutation, or epigenetic event, is much more probable in the offspring of variants with smaller beaks than it is in the offspring of variants with larger beaks. Thus, by selecting against smaller beaks, natural selection makes the occurrence of the more

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[33] Godfrey-Smith (2009, p. 50-52) provides other types of counterexamples.

adapted beak less likely, it does not have a creative role as far as this phenotype is concerned. However, the examples of the syndesmosis and of the basitemporal articulation do not belong to this type of cases. In both examples, natural selection makes the occurrence of the new phenotype more probable.

To summarise, there is a contrast between the characterisation of the problem of novelty by some evo-devo practitioners and the actual explanatory practices of actual cases of novelty.[34] The functional-historical explanation of Walter Bock, affiliated with the Modern Synthesis[35], is close in style to the explanation of the evo-devo practitioners Müller and Streicher. However, the difference in definition of novelty is not purely semantic and innocuous as it confuses the distinction between the generation of variation and the sorting of variation with the distinction between the generation of adaptation and the generation of novelty.

CONCLUSION

Through the investigation of the characterisation of the problem of novelty in evo-devo and its characterisation within the functional-historical approach, several reasons of the existence of these distinct characterisations have been identified. Some evo-devo practitioners claim that they have introduced the origin of novelty as a new research problem in evolutionary biology. This is justified in different ways depending on authors, either by distinguishing the problem of novelty from the problem of adaptation; by defining variation and innovation as distinct processes; or by relying on the epistemic concept of explanatory force. Evo-devo characterisations of the problem of novelty are centred around identifying the developmental mechanism responsible for the production of the phenotypic character investigated, determining if the developmental mechanism originated at the same time as the phenotypic character, determining the type of

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[34] Admittedly more case studies are needed to generalise to be able this statement. Müller's position may have hardened over the years, as suggested by this recent comment from Douglas Futuyma "Müller gives lip service to the complementarity of the [Modern Synthesis] and developmental mechanism, but in effect treats them as alternative explanations." (Futuyma, 2015, p. 58)

[35] This affiliation will be addressed in more details in the next chapter.

developmental change that occurred when the phenotypic character originated. The null hypothesis is that the change was genetic but research for changes at other organisational levels are undertaken. Developmental biology alone is not sufficient for this endeavour and tackling these research questions requires the help of phylogenetic systematics, comparative anatomy, palaeontology and evolutionary genetics. The role of the last discipline seems however minimal. The role of disciplines like functional morphology, biomechanics, physiology or ecology in solving the problem of novelty is rarely denied but the dominant idea among theoreteticians of evo-devo seems to be that the developmental endeavour can be conducted separately.

The functional-historical approach to novelty can be compared to the evo-devo approach using the venerable form-function dichotomy. This dichotomy can however be misleading because, while some evo-devo researchers or philosophers argue for a study of the evolution of form independently from function (Amundson, 2005; Raff, 1996), one the other hand the functional-historical approach is not a study of function independently of form, instead it partly relies on the idea that the evolution of form and function should not be studied separately.

The functional-historical approach, illustrated by Darwin's principle of conversion of functions, but not limited to it, is characterised by the use of different forms of functions, activities and biological roles, and by the attention to different types of contingency, unpredictability and dependence on past conditions, which entails that the characters of organisms and their transformations cannot be explained solely either by their current function, nor past function, nor even the series past and present functions.

The comparison of Bock's explanation of the origin of the avian basitemporal articulation and Müller 's and Streicher's explanation of the avian syndesmosis tibiofibularis revealed very similar explanatory strategies, regardless of the latter's far richer use of descriptive and experimental ontological evidence. This prompted a stress on a distinction between theoretical positions and debates on one side and explanatory practices on the other. This might stem from a conceptual confusion. Müller (and Peterson and Newman) stress that natural selection cannot explain the generation of novelty. But natural selection cannot explain the generation of variation either. The generation of variation, continuous or discontinuous, novel or not, is provided by developmental biology. This does not mean that an explanation of character change or of the emergence of a novel character in evolution is completely explained by developmental biology alone. This is demonstrated by Müller and Streicher‘s own explanation, which appeals to concepts from functional morphology and ecology as well as to developmental concepts.

What conclusions can then be drawn from this confrontation between an evo-devo and functional-historical characterization of the problem of novelty?

First, the claims of proponents of evo-devo that novelty was neglected during the Modern Synthesis and that the Modern Synthesis did not have the conceptual and empirical tools to tackle novelty are undermined by the developments of the functional-historical approach to novelty. However, this conclusion about the relation of the Modern Synthesis to novelty can only be preliminary since there is no strict identity between the functional-historical approach to novelty and the Modern Synthesis. The functional-historical approach to novelty was championed and developed by architects and sympathisers of the Modern Synthesis like Ernst Mayr, Walter Bock, Gerd von Wahlert and others, but is only a part of the Synthesis. More needs to be said about the history and content of the Modern Synthesis to fully assess its relation to the problem of novelty. This will be addressed further in the next two chapters.

Second, the historical study of the functional-historical approach revealed continuities between approaches to novelty from the Modern Synthesis era and evo-devo approaches to novelty. Some biologists and philosophers have presented the Modern Synthesis and evo-devo as two irreconcilable theoretical perspectives (Amundson, 2005; Laubichler, 2010; Müller, 2007), or as two scientific endeavours each concerned with one of two distinct and non-overlapping sets of phenomena (Craig, 2014). These views appear at odds with study of the evolution of the functional-historical approach between what I have called its second and its third phases, which revealed how developmental, morphological or phylogenetic considerations were already present and got progressively refined and more tightly integrated into this approach. Some scientific movements like transformation morphology or strands of constructional morphology and integrative biology, are representative of this complexification and enrichment of the functional-historical approach to novelty. Importantly, as we have seen, some trends in evo-devo can also be included in this list. And even among practitioners of evo-devo who forcibly separate their field from the Modern Synthesis and who define the problem of novelty as the exclusive task of evo-devo, one can find a contrast between this proclaimed distance separating theoretical perspectives and the actual proximity of explanatory practices.

Third, the possibility of producing generalisations about the disciplines, models and sources of evidence needed for the explanation of all types of novelty is far from guaranteed. Some types of characters are more functionally integrated and constrained than others, some are under strong selection pressures and some not, some are submitted to extreme developmental constraints and other are less developmentally constrained. The question of the appropriate explanatory resources is partly contextual. This idea of types of characters or the related idea of types of model organisms is a key to understanding the diverse nature of the landscape of research on novelty.

Fourth, some of the uses that certain evo-devo practitioners and theoreticians make of the distinction between novelty and adaptation are conceptually flawed. It is not only the generation of novelty that cannot be explained by population genetics but the generation of variation in general, quantitative as well as qualitative, non-novel as well as novel. Furthermore, for some representatives of the functional-historical approach of the Modern Synthesis era, novelty is not so much neglected but rather consciously weaved together with adaptation, as illustrated by Mayr’s following statement:

> “The problem of the emergence of evolutionary novelties then consists in having to explain how a sufficient number of small gene mutations can be accumulated until the new structure has become sufficiently large to have selective value. Or is there an explanation which avoids this troublesome threshold problem? *This has been discussed by a number of authors, usually under the heading ‘the origin of adaptations’*" (Mayr, 1960, p. 357)

This weaving is also made clear in the statement by Bock and Von Wahlert cited earlier.[36] This invites a broader reconsideration of the place of novelty in the conceptual and research landscape of the Modern Synthesis.

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[36] "A definition of biological adaptation is inadequate unless it can be used as the foundation for an explanation of the mechanisms underlying the evolution of new adaptations and the adaptive origin of new major groups of organisms. These are not independent parts of evolutionary mechanisms; indeed, the solution of the latter question is completely dependent upon the solution of the former. The evolutionary principles for the emergence of novelties may be built upon the concept of adaptation advanced in this study by a synthesis of ideas such as those advanced by Mayr (1958, 1960, 1962, and 1963) and Bock (1959, 1963a) and with the concepts of population genetics such as those summarized by Lerner(1954, 1958)." (Bock & von Wahlert, 1965, p. 294)

CHAPTER 2 – NOVELTY IN THE MODERN SYNTHESIS ERA. Part 1: NOVELTY IN THE CONCEPT AND RESEARCH SPACE OF THE MODERN SYNTHESIS

INTRODUCTION

The history of research on evolutionary novelty has been the central subject of only a few historical works (Love, 2015, 2005, 2003). This subject is however frequently addressed among other themes in publications centred on the history of evo-devo (Amundson, 2005; Hossfeld and Olsson, 2003; Laubichler and Maienschein, 2007; Love, 2015, 2009, 2007; Love and Raff, 2003; Olsson et al., 2010; Raff and Love, 2004). Historical works dealing with how the problem of novelty was conceptualized and tackled during the Modern Synthesis period have focused more on the research and theories of "outsiders" than on research programs falling under the dominant framework.

This historical literature dominantly concurs with and gives weight to the idea frequently found in the theoretical evo-devo and Extended Synthesis literature: namely, that the problem of novelty has been neglected by the Modern Synthesis. More precisely, as shown in chapter 1, two theses are recurrent: A) The problem of the origin of novelties, among other problems, has been neglected during the Modern Synthesis era, and is neglected by the Modern Synthesis as a theoretical framework.[37] B) The theoretical and empirical tools necessary to solve the problem of the origin of novelty were not available during the Modern Synthesis

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[37] See for example: "Evolutionary innovations are outside the scope of any current research program. Through its contribution to the solution of that question, [evo-devo] genuinely expands the explanatory range of evolutionary theory" (Wagner et al., 2000, p.822); or: "... the majority of the new work concerns problems of evolution *that had been sidelined in the MS* and are now coming to the fore ever more strongly, such as *the specific mechanisms responsible for major changes of organismal form*, the role of plasticity and environmental factors, or the importance of epigenetic modes of inheritance." (Müller and Pigliucci, 2010, emphasis added)

era, and they are not available to the Modern Synthesis as a theoretical framework.[38]

Because the major part of the historical research on novelty in the Modern Synthesis era has been done from the point of view of evo-devo, the attention has been directed at research that prefigured the framework of evo-devo. A consequence of this focus is that research on novelty that did not include or emphasised developmental biology was relatively neglected. Furthermore, the power of the historical narrative of a separation between evolution and development during the Modern Synthesis era (Amundson, 2005; Gilbert, 1994; Gilbert et al., 1996; Hamburger, 1990; Sapp, 2003) has prevented a thorough search for research associating the two by architects and biologists associated with the Modern Synthesis.

Clarifications on the Modern Synthesis

A few words of clarification are needed about what is referred to here as the "Modern Synthesis". Regarding terminology, Betty Smocovitis (1996, p. 54; see also Reif et al., 2000) has drawn distinctions between the "evolutionary synthesis", referring to the historical movement; the "synthetic theory", referring to the theory produced as a result; and the "modern synthesis" referring to the original characterization by Huxley (1942) of what he saw as new developments in biology.[39] Despite the usefulness of these distinctions, the recent literature in biology and philosophy of biology has come to use the expression "Modern Synthesis" to refer both to the theoretical structure supposedly still dominant today, and to the historical movement that produced this structure in the middle of the 20th century. Because I engage primarily with this literature, and for the

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[38] See for example: "It has become *possible* to address phenomena of evolution that were *untreatable by the MS*, and to cast them as "how" questions, such as How did body plans originate? How did homoplasies arise? *How did novelties evolve*? How do organisms change phenotypes in response to different environments?" (Müller and Pigliucci, 2010, pp. 12–13, emphasis added)

[39] The use of the term "modern" was apparently not the import of Huxley alone. In a review of Mayr's *Systematics and the origin of species* (1942), the ornithologist Alden H. Miller writes: "One element of style in writing proves annoying. It is the excessive use of the word "modern". Indeed, through repeated reference to the "modern worker," he creates an illusion of a caste of modernists arrogantly assigning to themselves a favored position in their science. Mayr would of course regret such a spurious impression." (Miller, 1943, p. 290)

sake of convenience, I will conform to it and use “Modern Synthesis” to refer to the theoretical structure and “Modern Synthesis era” to refer to the historical period.

Even though the details of the chronology of the Modern Synthesis era are still a matter of debate (Cain, 2009; Reif et al., 2000), this issue will not impair my investigation of research on novelty during that era, and will thus be left aside. For the sake of clarity, I will follow the chronology provided by Reif et al. (2000). They distinguish four phases:

> “(1) *Roots* (1920 and before): Mendelian genetics, mutation theory, chromosome theory of inheritance etc. (2) *Preparation* (1920s and early 1930s): empirical and mathematical analysis of natural populations, biogeography of demes, populations and other low taxonomic units. (3) *Formation* = process of the Synthesis (early 1930 s to 1950): harmonization of population genetics, systematics, comparative morphology and paleontology, extrapolation of the five microevolutionary factors: mutation, recombination, selection, isolation and drift to macroevolution. (4) *Reception* (after 1950): application of the Synthetic Theory in modern research projects of population biology, ecology, systematics, biogeography, comparative morphology and paleontology.” (Reif et al., 2000, p. 76)

My focus will be restricted to the third and fourth phases. I will argue in this chapter that important theoretical and empirical advances and debates related to novelty occurred during the last phase, and that a neglect of this last phase has led to a reductive representation of research on novelty during the Modern Synthesis era. Therefore, I will not refer to this last phase as the “reception” phase but more neutrally as the “late Modern Synthesis”. Regarding the end of that late phase, it is usually placed between 1970 and 1980, a time when the first major attacks against the Modern Synthesis appeared (the neutral theory of evolution and punctuated equilibria). Since I will focus partly on George’s Ledyard Stebbins’ *Flowering plants* (1974), I will place the end of that period after 1974.

The theoretical content of the Modern Synthesis

The question of the theoretical content of the Modern Synthesis is still a matter of debate to this day. A notable pattern in the positions on this question is that authors who are sympathetic to the Modern Synthesis tend to describe it as difficult to reduce to a small number of theoretical claims, or as a fluctuating theoretical entity that has never been fully stable but has kept adjusting and integrating new elements (Futuyma, 2015; Mayr, 1992; Wray et al., 2014). On the contrary, authors who are positioned against the Modern Synthesis often have much less reservation about identifying and summarizing its content.[40] Since this is still a heated theoretical debate, there are reasons to interpret the two opposed attitudes as strategic. Under this lens, the fluid conception of the Modern Synthesis appears as a strategic device that allows its defenders to evade criticisms and to more easily accommodate new concepts and findings.[41] Conversely, the reduction of the Modern Synthesis to a limited number of dogmas appears as a way to clearly define the target in order to attack and overthrow it.

We are thus confronted with diverging views of the content of the Modern Synthesis and with an added layer of complexity brought by the ongoing state of scientific controversy and its constitutive social and strategic dimensions. It is however reasonable to assume that historians of biology are less under the influence of these dimensions, that is, at least those historians who do not endorse a partisan conception of history. Here again, there is no unanimous view, but many historians have expressed the difficulty to reduce the Modern Synthesis to a limited set of theses[42], or to a single theory[43]. Some have argued that it is

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[40] Cain (2009) analyses this particular case, and other in the recent history of biology, such as the critique of G.G. Simpson by Gould in the 1970s, in terms of “ritual patricide”. The ritual dimension refers to the social function of such theoretical attacks. After the original act of patricide, the repetition of the attacks has a role in reinforcing the cohesion of the group (such as the Extended Synthesis group, or the defenders of punctuated Equilibrium group). This process is not exclusively taking place in minority, or non-dominant scientific groups. Gould (Gould, 1982a) noted the same kind of ritualized attacks about the relation of the Modern Synthesis towards Richard Goldschmidt, and more generally of dominant scientific groups towards heretics.

[41] See for example Stoltfuz (2017), for an analysis of this type.

[42] “The evolutionary synthesis was a very complex process; its historical development cannot be encompassed accurately by any single thesis. The synthesis occurred on many levels. [. . .] [It] was more than a simple application of new concepts in genetics to other facets of evolutionary biology, as earlier accounts have suggested” (Provine 1980, p. 405).

[43] “It is very difficult to define the Modern Synthesis as a ‘theory’ . . . it is indeed questionable whether

better described as a “moving target” (Burian, 1988, p. 250; Smocovitis, 1996). I concur with these analyses. It is however necessary and useful to address the dominant views on the Modern Synthesis in order to refine or criticise them.

Are these considerations affecting the conditions of possibility of a historical study of research on novelty during the Modern Synthesis era? They would make this study difficult if the method employed was to establish the stable and coherent theoretical content of the Modern Synthesis and then deduce from it the approach of the Modern Synthesis to novelty. It is however possible and preferable to investigate research related to the problem of novelty in the Modern Synthesis era without a pre-established alleged content of the Modern Synthesis channeling investigation. The constraint that will be applied to this historical research will be less stringent and artificial: I will focus less on the work of researchers obviously considered outsiders in the Modern Synthesis era and more on work unanimously considered as instrumental or related to the Modern Synthesis as a scientific movement. Thus, I will give particular attention to the work of Bernhard Rensch, Ernst Mayr and George Ledyard Stebbins and George Gaylord Simpson. I will also focus on several less prominent figures such as Isadore Michael Lerner, John Gordon Torrey, Walter Bock, Carl Gans and others, whose work was recognized and used by some of the more central figures. Finally I will try to also focus on figures opposed or indifferent to the Modern Synthesis in order to clarify the theoretical oppositions or the differences in research focus.

Outline of the chapter

My goal in this chapter and the next is to provide elements for an intellectual history of research on evolutionary novelty, to study the concepts and methods produced to tackle this research problem and to show how these concepts and methods shaped the problem in return. My aim is not to produce a new general history of the Modern Synthesis, or of Evo-devo. However, I intend

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the Modern Synthesis should be considered as one single theory” (Gayon 1990, p. 3). Designations of the Modern Synthesis as a single theory are actually rare in the contemporary literature, even among those who are not sympathetic to it. For example, Amundson (2005) uses the terms “approach”, “perspective”, “viewpoints” to qualify the Modern Synthesis. Cf. (2014) for a detailed analysis.

to argue that a focus on research on novelty in the Modern Synthesis era can provide evidence to challenge some widely held views about the Synthesis. This will be addressed more directly in the next chapter where I will focus first on research relating development and evolution by Rensch (1947, 1959) and Stebbins (1974a), which relates to the historical narrative of an exclusion of development by the Modern Synthesis movement. Second, I will focus on controversies in the late Modern Synthesis era, which relates to the thesis of a late hardening of the Modern Synthesis (Gould, 2002; Smocovitis, 1999).

The present chapter will be focused on the situation of novelty among concepts and research programs during the Modern Synthesis era. First, I will focus on the relation of novelty to mutationism and saltationism in order to assess Ernst Mayr's claim that novelty was neglected during the Modern Synthesis because it was associated with these theories (Mayr, 1960, p. 350). Another reason for the apparent lack of explicit attention to the problem of novelty is the awkward position it holds in the conceptual space relatively to four major preoccupations of the Modern Synthesis: 1) the diversification of species, 2) the origin of higher taxa (genera, families, orders, etc.), 3) the increase in complexity or levels of organization of organisms, 4) the adaptation of organisms to their environment. The problem of novelty is conceptually distinct from these four other problems. However, it entertains a close relation with each of them. The process of speciation may act at least as a condition for the origin or the maintenance of novelties. Higher taxa are defined by a series of diagnostic characters, thus inquiring about their origin involves explaining the evolutionary emergence of these characters. The problem of the increase of complexity overlaps with the problem of the origin of novelties. Certain types of novelties produce a change in complexity or level of organisation. The increase in level of organisation can also be conceived as a subset of the category of adaptation. Finally, the relation between novelty and adaptation is a complex and debated one that I have analysed in chapter 1.Some trends in the Modern Synthesis weaved the two problems together. In this chapter, I will focus on the different uses of the concepts of preadaptation which reveals different ways of relating adaptation and novelty coexisting within the Synthesis. It is thus essential for a history of research on novelty in the Modern Synthesis era to focus in more detail on how these four problems were addressed and how they related to the problem of novelty. I will focus in turn on speciation, complexity, higher taxa and adaptation.[44]

I – THE CONCEPT OF NOVELTY ASSOCIATED WITH MUTATIONISM

The idea of a neglect of the problem of novelty is formulated as early as 1960, by Ersnt Mayr himself, one of the architects of the Modern Synthesis, in the most influential theoretical paper on novelty of that era:

> “There are fashionable problems and there are neglected problems in any field of research. The problem of the emergence of evolutionary novelties has undoubtedly been greatly neglected during the past two or three decades, in spite of its importance in the theory of evolution.”(Mayr, 1960, p. 350)

Mayr explains the neglect of the problem of novelty since the 1930s by the association of the concept with mutationism:

> “Indeed, most of the evolutionary literature of recent decades has been devoted to the description and documentation of the gradual nature of all kinds of evolutionary changes. Hence the emphasis on allometry, on clines (in space and time), on polygenic systems, on genetic and developmental homeostasis, and on other manifestations of gradual change and of factors favoring it. This period, somehow, did not provide quite the right intellectual climate for the question "How does an evolutionary novelty emerge?" This question seemed, to antimutationist ears, to demand a mutationist answer. As a result, the problem of the emergence of evolutionary novelties has been almost completely neglected during the past two or three decades.” (Mayr, 1960, p. 350)

Although mutationist and saltationist theories of novelty are not the central subject of this chapter, this remark by Mayr calls for some explanation. Saltationism can be preliminary defined as a family of theories centred on the idea of evolution through jumps, that is the sudden origin of new characters,

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[44] As I just mentioned and as it will appear throughout the chapter, the frontiers between these concepts are porous, and their separate treatment in this chapter should not be read as a plea for strict separation but primarily as a matter of convenience.

species or types, as opposed to their gradual evolution over many generations. Mutationism, as it is used here by Mayr, is arguably a form of saltationism attributing the evolutionary jumps to specific types of genetic mutations.[45] Mayr does not elaborate on why the concept of novelty is associated to mutationism, but two conceptual reasons can initially be offered: first, the emergence of new characters was one of the phenomena that mutationists thought the gradualist and selectionist Darwinian theory could not explain. Second, the mutationist explanation of novelty gives a clear identity to the phenomenon: it is a single event clearly circumscribed in time and it has its own specific cause: large mutations. Meanwhile, in a gradualist and selectionist framework the causes that produce novelties, in short (small) mutations and selection, are not specific to the phenomenon since they also cause quantitative variation, and the origin of novelty is a less clearly temporally circumscribed process, threatened of being diluted in a continuum of change.

A clarification of saltationist and mutationist theories of novelty is important to understand Modern Synthesis research on the topic because they usually were the explicit opponents. In several works that adopt the problem of the origin of novelties as a central topic (Mayr, 1960; Rensch, 1959; Schaeffer and Hecht, 1965; Stebbins, 1974), what is at stake is generally to show that an explanation of novelty compatible with the Modern Synthesis is possible. These presentations of the problem are structured around two couples: microevolution and macroevolution, and mutationism, or saltationism, and gradualism. The distinction between microevolution and macroevolution is accepted and not questioned[46], the goal is then to show how a gradualist explanation of the transition from one to the other is possible, as opposed to a saltationist explanation. These broad dichotomies are accurate but they can also exacerbate the oppositions and obscure the exact nature of the debates. Modern Synthesis dogma is sometimes wrongly represented as the rejection of all but infinitesimal mutations. Three concepts are of particular importance: homeotic mutations, macromutations and systemic mutations. I will first clarify the positions of Modern Synthesis thinkers towards these three types of mutations and then show that the

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[45] For historical studies of these theories see for example Bowler (1992) and Levit et al. (2008)

[46] Stebbins (1974b) for example writes about different points of view to reconcile.

centre of the debates is the question of the origin of higher taxonomical categories.

Homeotic mutations, macromutations and systemic mutations

The phenomenon of homeosis, the presence of a displaced character, appearing in an abnormal part of the organism, has been long known. It was studied in details by William Bateson, who coined the term "homoeosis"[47] that he defined as a type of variation "which consists in the assumption by one member of a Meristic series, of the forms or characters proper to other members of the series" (Bateson, 1894, p. 84).[48] The idea that homeotic mutants had a genetic determination was first offered by Calvin Bridges and Thomas Hunt Morgan in 1915 when the first mutant in *Drosophila* was discovered[49] (Gehring, 1998; Lewis, 1994). This mutant had a duplicated thorax and was thus called "bithorax". It emerged spontaneously in the laboratory, and a lineage of bithorax was produced and conserved. It would play a central role decades later in the beginning of new discoveries in developmental genetics (cf. chapter 4). Other homeotic mutants were soon discovered; in *The material basis of evolution,* Richard Goldschmidt describes five known types of homeotic mutants in *Drosophila* (Goldschmidt, 1940, pp. 326–328). The phenomenon of homeotic mutations was acknowledged by architects of the Modern Synthesis.[50] When they targeted the mutationist school, it was not the existence of homeotic mutations that was their focus.

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[47] The orthography now in use is "homeosis".

[48] The link between Bateson's concept of homoeosis and the genetic concept of homeosis is actually not straightforward. In the *Materials for the study of variation*, Bateson focused on discontinuous variations in nature as a key to understand evolution. He distinguished two kinds of discontinuous variations: "substantial variation", affecting the substance of organisms and thus producing changes of size, proportions, colour, colour patterns etc.; and "meristic variations" affecting the parts composing the structure of organisms. Among meristic variations are, on the one hand, the strict additions or deletions of parts, such as the reduction of the number of joints in the tarsus of the cockroach, or the increase in number of parts to the flower of the tulip; and on the other hand, cases of homoeosis. In this category, Bateson includes the replacement of one part by another along the anteroposterior axis, but also changes in bilateral asymmetry such as in the flat-fish where in some individuals, the characters normally present on one side are switched to the other side.

[49] Between Bateson's work and the study of *Drosophila* mutants by geneticists, homeosis was studied by the *Entwicklungsmechanik* tradition (see Schmitt, 2004 for a historical account)

[50] Simpson for example, recognized the existence and interesting nature of homeotic mutants although he restrains their importance: "Homoeotic mutants have special interest because (at full penetrance) they have spectacular phenotypic results, but their limitation by the system in which they occur is obvious. They do not produce new structures but only change the places where structures occur.

A second distinguishable concept, broader than homeotic mutations, is macromutation. While homeotic mutations refer to the displacement or duplication of an existing character, macromutations include this phenomenon but they can also refer to the sudden creation of a new character or the sudden qualitative modification of an existing character. The existence of macromutations was not denied by proponents of the Modern Synthesis (Dietrich, 1995, 2000; Futuyma, 2015). For example Fisher referred to large mutations to explain the discrete variation of colour patterns of the wings of butterflies. A switch to a new colour pattern could be produced by a macromutation and then modified incrementally in later generations by allele substitution (Fisher, 1930). Furthermore, phenomena such as polyploidy and hybridization were recognized as potential causes of large phenotypic changes (Haldane, 1932, pp. 104–105; Stebbins, 1950).

A third hypothetical phenomenon is described by Goldschmidt as “systemic mutations”. Rather than involving a single gene or a small number of genes with large phenotypic effects, systematic mutations affects the patterns of organisation and interactions of genes on a chromosome. Thus, a systemic mutation can arise without the occurrence of a genetic mutation in the strict sense.

> “A repatterning of a chromosome may have exactly the same effect as an accumulation of mutations. And even more, a complete repatterning might produce a new chemical system which as such; i.e., as a unit, has a definite and completely divergent action upon development, an action which can be conceived of as surpassing the combined actions of numerous individual changes by establishing a completely new chemical system. Model: two different pictures produced with the same set of mosaic blocks, the new picture "emerging" only when all blocks are in their proper place.” (Goldschmidt, 1940, p. 203)

As suggested by the analogy drawn in the last sentence, although the large phenotypic effects of systematic mutations appeared suddenly, the chromosomal repatterning itself could take many generations before becoming manifest in the

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"(Simpson, 1953, p. 84). See Davis et al. (2009) for an extended account of the reception of research on homeotic mutants by architects of the Modern Synthesis.

phenotype. This concept of systemic mutations is the product of the evolution of Goldschmidt's views in physiological genetics. From his studies of sex determination in the moth genus *Lymantria* and from the production of intersex specimens, Goldschmidt (1928) developed a view of genes as proteins acting as catalysts in networks of chemical reactions, especially during development. Thus, the nature of genes and quantity of genetic material genes would determine the nature and rate of the reactions and ultimately the phenotypic products. And variations in quantities and rates caused by mutations would affect the phenotypic result. The idea of systemic mutations originated in a departure from this initial view of genes. Goldschmidt was influenced by experimental studies of Herman Muller and others on position effects, especially in *Drosophila*, showing phenotypic effects of gene rearrangements comparable to those of mutations. (see Dobzhansky Theodosius, 1936 for a review). While these results questioned the classical view of genes as independent beads on a string, Muller insisted that these rearrangements could not have effects of the magnitude of proper mutations. Goldschmidt went further and made the chromosome, and not the gene, the proper unit of physiological genetics. The arrangement of genes on a chromosome produces a chemical system and a series of changes in genetic positions could produce a repatterning of the whole system that Goldschmidt called a systemic mutation (Goldschmidt, 1940, 1938). Of the three types of mutations reviewed here, systemic mutations were the only type that was nearly unanimously rejected by participants in the Modern Synthesis.[51]

To summarize, the possibility and existence of homeotic mutations as well as of mutations with large phenotypic effects were recognised by most Modern Synthesis biologists and were not points of contention in themselves. Only systemic mutations were not accepted. I now turn to the actual locus of debate regarding these mutations: their role in macroevolution.

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[51] See Dietrich (1995) for a review their reactions.

The central debate against mutationism and saltationism: the mode of origin of higher taxa

The German geneticist Richard Goldschmidt and the German paleontologist Otto Schindewolf were the most prominent proponents of saltationist theories in the Modern Synthesis era and the main interlocutors of the Modern Synthesis architects. When introduced, the saltationist school of the Modern Synthesis era is usually reduced to a handful of individuals. For example, Mayr (1963, p. 586) describes it as composed of a geneticist, Goldschmidt (1940, 1948, 1952), a palaeontologist Schindewolf (1950), and of zoologists, Jeannel (1950), Cuénot (1951) and Cannon (1958). In another description (Schaeffer and Hecht, 1965), the morphologists Good (1956) and Russel (1962) are added. The group of biologists who sympathised with mutationist views surely extended beyond those few individuals, although it is quite difficult to estimate their number[52]. For the sake of brevity, I will limit my focus to Goldschmidt and Schindewolf. It is, however, not the object of this chapter to analyse in detail Goldschmidt's and Schindewolf's views on the origin of novelty.[53]

The main source of debate between Schindewolf and Goldschmidt on one side, and proponents of the Modern Synthesis on the other, was not the question of the existence of large mutations, but the question of their importance in macroevolution, more precisely their capacity to suddenly produce new species or new higher taxonomical categories.[54] This question occupies a particularly

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[52] This statement by the paleontologist Everett C. Olson, although not only about mutationists, is revealing regarding the difficulty of this estimate: ""There exists, as well, a generally silent group of students engaged in biological pursuits who tend to disagree with much of the current thought [the Modern Synthesis] but say and write little because they are not particularly interested, do not see that controversy over evolution is of any particular importance, or are so strongly in disagreement that it seems futile to undertake the monumental task of controverting the immense body of information and theory that exists in the formulation of modern thinking. It is, of course, difficult to judge the size and composition of this silent segment, but there is no doubt that the numbers are not inconsiderable. Wrong or right as such opinion may be, its existence is important and cannot be ignored or eliminated as a force in the study of evolution." (Olson, 1960, p. 523)

[53] A rather vast literature already exists on Goldschmidt's synthesis of evolution and development (see Allen, 1974; Davis et al., 2009; Dietrich, 2000, 1995; Gould, 1982; Schmitt, 2000) and to a lesser extent on Schindewolf's work (Eldredge, 1992; Grene, 1958; Laubichler and Niklas, 2009; Levit et al., 2008; Reif, 1986).

[54] This judgement is determined by the object of our attention: evolutionary novelty. Schindewolf's and especially Goldschmidt's challenges are not limited to the origin of higher taxa. For example, Michael Dietrich lists five different challenges posed by Goldschmidt: "The responses of the neo-Darwinians addressed five major challenges presented by Goldschmidt. These challenges concerned (1) the validity of the theory of the gene; (2) the nature of mutation, and its role in evolution; (3) the origin of isolating

prominent place in the works of George Gaylord Simpson (1953, 1944) and Bernhard Rensch (1959, 1947). That this hypothesis is clearly distinct from the question of the existence of macromutations' producing new characters or qualitative differences in characters, is expressed for example by Simpson, who offered an extensive critique:

> "The issue is not, or certainly not only, whether large or small mutations are normally involved in evolutionary processes, as some discussants seem to think (e.g., Davis, 1949). It is rather whether a real or possible mutation, of any size, can give rise to a higher taxonomic category in one step and whether single mutations can occur and have occurred producing differences, genotypic and phenotypic, corresponding to those between families, orders, classes, etc." (Simpson, 1953, pp. 98–99)

Schindewolf's concept of typogenesis and Goldschmid's concept of hopeful monster both refer to this phenomenon of a sudden origin of a higher category. Schindewolf developed a complex theory of macroevolution combining saltation and orthogenesis. Typogenesis was the first phase of the evolution of types, which is an anatomical and morphological concept but can be related to higher taxonomical categories such as orders and classes. The second and third phases are typostasis and typoloyse, the stasis and then senescence of the type. Schindewolf called the entire cycle a typostrophe. To explain the sudden origin of types, Schindewolf appealed to alterations of the early stages of ontogeny with large scale effects. For example, for Schindewolf the fossil *Archeopterix* represents the exact point of transition from reptiles to birds. It represents the sudden occurrence of a new type possessing several new characters making flight possible (Schindewolf, 1993). An essential characteristic of typogenesis is that it is a nested historical process in correspondence with the taxonomical ranks of the Linnean hierarchy. That is to say, according to Schindewolf, the process of origin of types follows the descending hierarchy, the typogenesis of a class such as birds is an event that precedes typogeneses of smaller magnitude that suddenly produce orders within that class, and are themselves followed by typogeneses of even smaller magnitude.

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mechanisms necessary for species formation; (4) the concept of species and incipient species, as well as what Ernst Mayr calls population thinking; and (5) the tempo of evolution" (Dietrich, 1995).

Goldschmidt' s hopeful monster is to be distinguished from the hypothesis of systemic mutations. As Goldschmidt himself notes, the production of a hopeful monster can be conceived both on the basis of classical genetics via mutations of large effects or on the basis of Goldschmidt's alternative conception of genetics via systemic mutations (e.g. Goldschmidt, 1940, p. 252). That is, the idea of hopeful monsters is not dependant on the validity of systemic mutations. The magnitude of change implied in hopeful monsters, that is, in short, the number of new phenotypic characters involved and the amplitude of their divergence from the ancestral characters, is variable. Consider the following illustration given by Goldschmidt:

> "A monstrosity appearing in a single genetic step might permit the occupation of a new environmental niche and thus produce a new type in one step. A Manx cat with a hereditary concrescence of the tail vertebrae, or a comparable mouse or rat mutant, is just a monster. But a mutant of Archaeopteryx producing the same monstrosity was a hopeful monster because the resulting fanlike arrangement of the tail feathers was a great improvement in the mechanics of flying." (Goldschmidt, 1940, p. 391)

This example seems to show that a hopeful monster can involve simply the sudden emergence of a single character, or a large change in a single character.

But, like Schindewolf, Goldschmidt holds the hierarchical view of the origin of higher taxa:

> "The phyla existing today can be followed farthest back into remote geological time. Classes are a little younger, still younger are the orders, and so on until we come to the recent species which appear only in the latest geological epochs. Thus logic as well as historical fact tells us that the big categories existed first, and that in time they split in the form of the genealogical tree into lower and still lower categories." (Goldschmidt, 1952, p. 92)

Thus, the logical taxonomic hierarchy is matched by the historical process. Furthermore, these logical and historical dimensions are matched by the mechanistic dimensions of macromutations (or systemic mutations). Minor cases of hopeful monsters can involve a qualitative change in a single character, but where high taxonomical categories are concerned, hopeful monster can involve a new body plan or many new characters[55].

The opposition of Simpson[56] to the views of Schindewolf and Goldschmidt about the origin of higher categories is at least threefold:

_ Simpson objected to the hierarchical nature of taxonomy reflecting the historical process. Characters defining higher taxa do not evolve simultaneously but successively, and in a contingent fashion according to a process called "mosaic evolution" (de Beer, 1954) or "heterobathmy" (Takhtajan, 1959) and that Goldschmidt ironically named the "'crazy-quilt' method" (1952, p. 92).

_ Simpson also objected to the mechanistic dimension of saltation. He denied the possibility of hopeful monsters of larger magnitude, involving a new body plan or many new characters arising simultaneously (e.g. Simpson, 1953, p. 194). However, as stated earlier, he did not reject large mutations affecting a single character, as in Goldschmidt' hypothetical examples of the Manx cat and *Archaeopteryx*. Simpson himself uses the concept of "key mutations", possibly of large effect[57]. These large mutations had the status of exceptions, not impossibilities, as Simpson insisted that "change by very small steps is the rule not only for metrical characters, as would be expected, but also *frequently* for qualitative characters and the appearance of new structures and tissues, which might be expected to originate by large mutations" (Simpson, 1953, p. 105, emphasis added).

_ Additionally, like Dobzhansky and Sewall Wright, Simpson objected to Goldschmidt's lack of consideration for population genetic processes (cf. Davis

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[55] For example: "it may then be assumed that major departures of the rank of higher categories are attained initially by single large mutational changes producing at once the essentials of the new type" (Goldschmidt, 1952, p. 94)

[56] Detailing the different reactions of Modern Synthesis participants would be beyond the scope of this chapter, thus I will here mainly take Simpson as an example.

[57] Simpson's use of these concepts and the relation of his theory to evolutionary novelty will be tackled in part IV of this chapter.

et al., 2009; Dietrich, 2000, 1995). In his words: ‘‘the appearance of a mutant individual is not evolution’’ (Simpson, 1944, p. 53).

Considering that this debate was mostly focused on the mode and rate of origin of higher taxonomical categories and that this phenomenon is closely related to the origin of evolutionary novelty, it appears to come into conflict with Ernst Mayr’s claim that novelty was neglected during the Modern Synthesis. If one of the main goals of at least some of the protagonists of the Modern Synthesis was to argue for the gradual origin of higher taxonomical categories through the action of natural selection combined with other factors, then the argument for a gradual origin of evolutionary novelties had to be part of the agenda. After having clarified the nature of the debate between the Modern Synthesis and saltationists, we now have to search the work of Modern Synthesis thinkers and practitioners themselves for other reasons of Mayr’s claim that novelty was neglected. Furthermore, if the focus on the origin of higher taxonomical categories was central, then we have to clarify the exact relation between this problem and the problem of the origin of novelty.

II – NOVELTY, SPECIES AND SPECIATION

Novelty and speciation

In his article on the emergence of evolutionary novelties of 1960, Mayr notes the conceptual distinction between the origin of novelties and the origin of new taxa:

> “The origin of new taxa, from species to higher categories, will be considered as lying outside the scope of this discussion. Even though, admittedly, the origin of new higher categories is often correlated with the emergence of a new structure or other character, the natures of the two problems are sufficiently different to necessitate separate treatment.” (Mayr, 1960, pp. 356–7).

Regarding the difference between the origin of new species and the origin of novelties, Mayr does not go into more details in this article, but some of his other writing can be used for clarification (1963, 1947, 1942). According to Mayr, the process of origin of a new species, namely speciation, poses the problem of reproductive isolation within a population. It is a process of transformation of one population into two reproductively isolated populations. It does not necessarily imply the upcoming of novelties. However, the ambiguity of the relation between speciation and the origin of novelty is still stressed by George Gaylord Simpson in 1953, in one of the late classic texts of the Modern Synthesis, *The major features of evolution*:

> “Usages vary considerably, but most students understand by the word "speciation" one or both of two processes: (1) the origin of genetic isolation between two populations (or groups of populations), and (2) the origin of new characters and their distribution or differentiation among and within populations (a process that begins far below the level of genetic isolation and continues above it).” (Simpson, 1953, p. 380)

Simpson goes on to give his own view of speciation, based on the first of the two processes, genetic (or reproductive) isolation, a view similar to Mayr’s and the dominant view of the late Modern Synthesis era:

> “It now seems clearer to think of speciation as, literally, the origin of species and particularly the origin of genetical or horizontal species. On this basis, speciation is the process of differentiation within populations and of the rise of genetic isolation between populations formerly part of the same species. Subsequent divergence is not, strictly speaking, speciation but an aspect of phyletic evolution. Of course this frequently has its roots in differentiation within populations and hence is not absolutely distinct from speciation. This merely again exemplifies the fact that what we are analyzing is integral and that its elements do not have absolute distinctions.” (Simpson, 1953, p. 380)

What Simpson is saying here is that the emergence of new characters occurs during phyletic evolution, that is during the phenotypic evolution of single species. This origin does not coincide with speciation, which is a process of splitting of two populations[58], although his last sentence makes clear that the distinction is not

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[58] In *The major features of evolution*, Simpson argues for the replacement of the term “speciation” by the term “splitting” for more clarity. (Simpson, 1953, p. 380)

absolute and that incipient stages of new characters can occur during speciation. As suggested by Simpson's quotes, the relation between the problem of the origin of new species and the problem of the origin of new characters has evolved during the period of elaboration of the Modern Synthesis. To frame the matter schematically, it can be said that previous to the Modern Synthesis era the two problems were more closely related than during that era; or, to use pattern-oriented terms, the concepts of diversity – the existence of a multiplicity of species – and of the concept of disparity – the phenotypic differences between species – were pulled apart during the Modern Synthesis. And arguably more attention was given to the problem of speciation than to the problem of the origin of new characters.

The distinction of the two problems is dependent on the surge of interest for processes of speciation between the 1930s and the 1950s, illustrated for example by the important role played by the Society for the Study of Speciation (Cain, 2009b; Milam, 2009), and on the development of the biological concept of species and of theories of geographical and ecological speciation. A detailed history of the relation between the two problems from Darwin to the late Modern Synthesis era would require an independent chapter at least (see Wilkins, 2009; Zachos, 2016). I will focus here on the critique of Darwin's conception of species and speciation and on the principles of experimental taxonomy.

The critique of Darwin and the biological species concept

The elaboration of the biological concept of species was closely related to a critique of Darwin's concept of species by its main proponents, Dobzhansky (1937, 1935) and Mayr (1959, 1942). Therefore, to explain the impact of the first trend on the relation between novelty and speciation, I will briefly review the motives and arguments of this critique of Darwin and how they connect to the relation between speciation and novelty. Two questions are of particular interest here: What are the differences between the morphological and biological species concept in relation to the conceptualisation of novelty? More precisely, how does a move towards the biological species concept further separate the problem of speciation and the problem of novelty? It should be noted here that the question of Darwin's view of species is still a heated debate to this day (e.g. Mallet, 2010;

Stamos, 2013; Zachos, 2016). My point here is to present the view that Modern Synthesis thinkers had of Darwin's conception of species. This is not the place to attempt a detailed assessment of this view.

Darwin argued against the view of species as essences that was dominant in his time. According to Darwin, variation within population of organisms produces new varieties that progressively turn into species. How then to explain the formation of species and the existence of morphological gaps between them? Darwin relied primarily on the "divergence of character" under the influence of natural selection (Darwin, 1859 chapter IV). In an area where many organisms are living, those that diverge to occupy specific ecological niches not accessed by the rest will suffer less competition. Therefore natural selection will favour this divergence leading to the formation of new specialized varieties. The morphological gaps between existing species comes from the extinction of the varieties that did not diverge and were outcompeted (see e.g. Kohn, 2009). Thus, the main principle that drives the production of varieties as well as the production of species is continuous phenotypic change explained by the tendency of natural selection to favour divergence.

The biological species concept and allopatric speciation

It has been said that the confusion in contemporary scholarship on Darwin's view of species is due to the fact that most scholars tend to recover their own views in Darwin's work[59] (Stamos, 2013). This problem fails to apply to Dobzhansky and especially to Mayr:

> "...Darwin failed to solve the problem indicated by the title of his work. Although he demonstrated the modification of species in the time dimension, he never seriously attempted a rigorous analysis of the problem of the multiplication of species, of the splitting of species into two. I have examined the reasons for this failure [...] and found that among them Darwin's lack of understanding of the nature of species was foremost." (Mayr 1963, p. 12).

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[59] Stamos insightfully compares his assessment to the one made by Albert Schweitzer about scholarship on Jesus at the beginning of the 20th century.

Dobzhansky and Mayr objected both to Darwin’s definition of species and to his preferred explanation of their origin. Darwin had focused on phenotypic divergence in the formation of species; because this divergence is gradual and because gaps are caused by extinction of less fit intermediate varieties, Darwin did not see a difference of nature between varieties and species. He had thus not fully perceived the singularity of species, grounded in the existence of isolating mechanisms.

Here is how Dobzhansky defined a species:

> “a species is a group of individuals fully fertile inter se, but barred from interbreeding with other similar groups by its physiological properties (producing either incompatibility of parents, or sterility of the hybrids, or both)” (Dobzhansky, 1935, p. 353)

Mayr adopted the same definition which he called the “biological species definition” (Mayr, 1942, p. 119). What Dobzhansky (1937) called isolating mechanisms provided at the same time a way to define species as a category, a criterion to identify species taxa, and they were also an essential part in the explanation of the origin of species. Regarding the identification of species, Mayr in particular insisted on problems with morphological criteria, such as sibling species, which are not differentiated phenotypically but do not interbreed (e.g. Mayr, 1942, p. 151), and polytypic species, single species with multiple phenotypically divergent but intergrading or potentially intergrading subspecies (Mayr, 1942, p. 111). Regarding the origin of species, the formation of isolating mechanisms was now considered the essential part of the process. Mayr developed the theory of speciation through allopatry, the view that geographic isolation was necessary for the initial formation of genetic, physiological or ethological isolating mechanisms through divergence (Mayr, 1942, pp. 154–185).

It is important to note that, even though the biological species concept and allopatric speciation arguably became progressively dominant, there was no consensus regarding the definition of species as a category, the identification of distinction between species taxa, and the processes of speciation. Mayr himself recognised the limits of the biological species concept to provide diagnostic criteria and its failure to apply to asexual organisms and freely hybridising organisms such as some plants (Mayr, 1942, pp. 121–122). The concept was criticised for example by Julian Huxley (1942) or C. D. Darlington, who argued that "[t]here are many kinds of species and many kinds of discontinuities between species" (in Huxley, 1940, p. 158). However, the essential point here is that during the Modern Synthesis era, there was an increased focused on processes of speciation and that this process was, at least conceptually, decoupled from the process of gradual origin of new characters, and rather centred on the formation of isolating mechanisms.

The distinction between the problem of speciation and the problem of variation

Darwin was included among those who had neglected isolating mechanisms and the reality of species but he was not the only target. Population geneticists focused mainly on genetic dynamics within populations and its models were mostly based on infinite populations. Experimental geneticists like Thomas Hunt Morgan, focused on the generation and transmission of genetic variations. The main question about evolution for Morgan was whether natural selection was a creative force acting on the direction of variation, or whether, as he thought, natural selection was just a negative force and mutations had the creative role (Allen, 1980; Beatty, 2016; Stoltzfus and Cable, 2014). Far from defending the reduction of evolution to the problem of the production and selection of variations, Dobzhansky, followed by Mayr and other students of speciation, insisted on the species and speciation as a different level of biological reality not captured by this production and selection of variations:

> "Mutations and chromosomal changes are constantly arising at a finite rate, presumably in all organisms. But in nature we do not find a single greatly variable population of living beings which becomes more and more variable as time goes on; instead, the organic world is segregated into more than a million separate species, each of which possesses its own limited supply of variability which it does not share with the others [...] The origin of species [...] constitutes a problem which is logically distinct from that of the origin of hereditary variation" (Dobzhansky, 1937, p. 119).

Thus, the study of speciation reintroduced a focus on discontinuity in the biological world. Since the problem of the production of new characters was viewed as an extrapolation of the problem of the production and selection of variations, the distinction between the problem of speciation and the problem of variation was by extension a distinction between the problem of speciation and the problem of novelty.

Experimental taxonomy in botany

A conceptual change thus occurred regarding species and speciation. Equally important, a change in research practices and interests occurred at the same time. This general change in practices and concepts has been called by some of its actors the "new systematics" (Huxley, 1940; Mayr, 1942, pp. 6–7). Following Cain (2009b, p. 628), the new systematics can be decomposed in three elements: the rise of speciation studies, the development of experimental taxonomy, and the general move from a focus on objects to a focus on processes of evolution. Here I will focus briefly on experimental taxonomy in botany[60] because it was more developed than in zoology (Cain, 2009), and because it had arguably a more interesting and ambiguous relationship to the problem of novelty.

Jens Clausen, David Keck and William Hiesey, arguably the most important representatives of experimental taxonomy in botany, along with Ernest Babcock, defined their approach in the following way:

> "The threefold objective of the experimental taxonomy programme is an understanding of the various kinds and degrees of kinship between plants, of the relations between plants and their environment, and of the evolutionary processes that have produced the diversity between plants and their fitness to the environment." (Clausen et al., 1948)

Regarding the first objective, the experimental way of distinguishing between species associated with the biological species concept was seen as an

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[60] As noted by Hagen (1984, p. 250) several appellations have been used for the body of research referred to here: synthetic taxonomy, genecology, genonomy, population systematics, biosystematics, and experimental taxonomy. I follow Hagen and others (e.g. Cain, 2009; Smocovitis, 2009) in using experimental taxonomy.

improvement on the museum-style method of recognition based on the morphology of specimens, although the two were combined rather than opposed (see Hagen, 1984). The criterion of breeding behaviour of the biological species concept offered a clear way to empirically test hypotheses in systematics. In botany, it was especially interesting for what was called “critical” genera, that is, groups of related polyploid species difficult to classify. Hybridisation experiments between these species were the most reliable way to test hypotheses of phylogenetic relationships between these species. They were undertaken for example by Babcock and Stebbins on the genus *Iris*, by Clausen, Keck and Hiesey on *Layia* and *Madia*. Furthermore, the discovery in 1937 (Blakeslee and Avery, 1937), that colchicine, an alkaloid produced by the roots of plants of the genus *Colchicum*, could induce polyploidy in plants led to its use by horticulturalists to produce new species, but also by taxonomists to test hypotheses regarding phylogeny and evolution of plant species.

Two pathways through which polyploidy can produce a new species in nature were distinguished: autopolyploidy and allopolyploidy (Kihara and Ono, 1926):
1) Autopolyploidy is polyploidy derived from individuals of a single species. There are two ways in which autopolyploidy can occur: the non-reduction of gametes during meiosis produces diploid gametes (2n). The fusion of these games can then produce tetraploid (4n) or triploid (3n) offsprings which can isolate from the original population and form new species either through asexual reproduction or by mating with each other. The second way in which autopolyploidy can occur is during somatic development: a failure of sister chromatids to separate during mitosis can lead to tetraploidy (4n). It was found that it was the type of polyploidy occurring in mutants of the evening primrose discovered by Hugo de Vries (Gates, 1924). This was the main type of polyploidy produced artificially through treatment with colchicine (Eigsti and Dustin, 1955; Stebbins, 1951). 2) Allopolyploidy, or amphiploidy, occurs when the polyploid organisms are derived from to different species through hybridisation. The polyploidy event can occur during hybridisation, if a zygote is formed with unreduced gametes of individuals or different species, or after the hybridisation event, if there is a meiotic disturbance in the offspring of a hybrid.

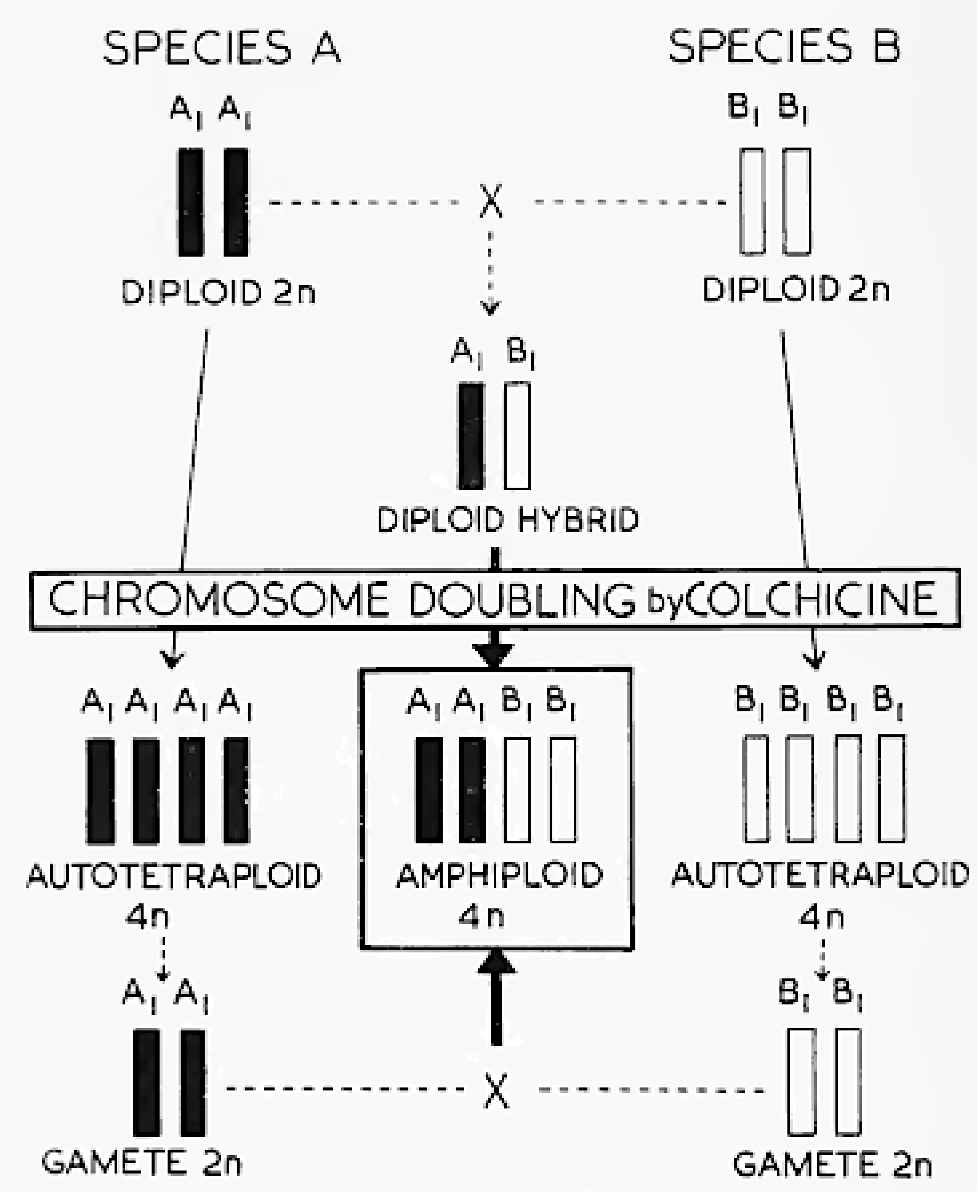

Fig. 3: Three ways to produce polyploids with colchicine: A) Autotetraploids from the doubling of somatic chromosomes. B) Amphiploids (or alloploids) by doubling of the chromosomes of a hybrid between two species. C) Amphiploids by hybridisation of autotetraploids of different species produced with colchicine (after Eigsti & Dustin, 1955, p. 278).

Before detailed knowledge of polyploidy was acquired, this succession of hybridisation and polyploidy was hypothesised to explain the evolution of some plant taxa, for example the chrysanthemum family in which species had chromosome number that were multiple of nine (18, 36, 54, 72, 90) (Winge, 1917). This evolutionary hypotheses scenario was later produced experimentally by Clausen and Goodspeed with tobacco species (Clausen and Goodspeed, 1925). Other researchers used colchicine to experimentally produce hypothesized evolutionary events. It was applied in particular to study the origin of crop species, many of which were known to be polyploids, for example to the origin of hexaploid wheats, of oats, of new world cottons and many others[61]. The relative frequency of different types of polyploidy in nature, and especially the frequency of the type of polyploidy produced experimentally, was however a debated matter (Harlan and deWet, 1975).

Regarding the second objective of understanding the relations between plants and their environment, one of the major questions addressed was the distinction between genetically induced and environmentally induced variation. This question was studied through transplant experiments, either by transplanting a species into the environment of the related one and vice versa, a method used from the 1920s by Frederic Clements and Harvey Hall, or by transplanting plants from several different environments into a single controlled garden, a method perfected by the Swedish botanist Göte Turesson (see Hagen, 1984).

Regarding the third objective, the study of evolutionary processes that produced diversity, part of the focus of transplant experiments was on forms and genetic underpinnings of adaptation to local environments, for example the adaptations to different soils or the conservation of ecotypic forms after transplantations. There was also a great attention to the processes of polyploidy, hybridisation, apomixes and their combination in evolution. George Leydard Stebbins, working in collaboration with Babcock on polyploidy and apoximis in *Crepis* (Stebbins and Babcock, 1939) or with Anderson on the role of hybridisation in evolution (Anderson and Stebbins, 1954), was at the forefront of research on what he called "cataclysmic evolution" in plants (Stebbins, 1951), that is abrupt speciation and possibly phenotypic change through polyploidy events. Because of the intense research on such processes and their frequency in plants, evolutionary taxonomy in botany, much more than its zoological counterpart, was expanding beyond the domain of speciation and species level variations and towards the origin of higher taxa of lower ranks, especially genera. The case of research on polyploidy and hybridisation also shows the interpenetration of the first and third objectives of experimental taxonomy. The same research was both contributing to taxonomic knowledge and to knowledge of evolutionary processes.

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[61] See for example Eigsti and Dustin (1955) for review and references.

To summarize the relation between novelty and species and speciation studies during the Modern Synthesis era, the increased interest in speciation and its genetic, geographical and ecological conditions conceptually separated speciation, centred on isolating mechanisms, from the process of genetic and phenotypic variation and by extension, of novelty. The Modern Synthesis era saw the rise of experimental taxonomy, a multi-disciplinary and multi-purpose endeavour, which focused both on speciation and variation as processes but was mostly limited, at least in animal studies, to species-level and below species-level variations and adaptations, which were mostly quantitative and did not qualify as novelties. However, experimental taxonomy in botany has a special status because it was more developed than in zoology and because the experimental study of polyploidy and hybridisation entered the realm of the origin of higher taxa, and, more indirectly, of the origin of novelty.

III – NOVELTY AND HIGHER TAXA

Novelty and the origin of higher taxa

With experimental taxonomy in botany, there was, to a certain extent, a blur in the division between the study of speciation and species-level variations and the study of higher taxa and more large-scale variations. However, this division was commonly accepted, as shown in these disciplinary distinctions made by Simpson:

> “The experimentalists are mainly concerned with evolutionary processes and events in subdivisions of species. The neontological systematists work for the most part around the level of species, on larger subdivisions of species, on species as a whole, or on closely related groups of species. The biological paleontologists and others who might be called historical biologists (representing a subscience that has no accepted name) are less concerned with species and more with groups from genera upward.” (Simpson, 1953, p. 338)

Regarding the relation between the origin of higher taxa (groups from genera upwards) and the origin of novelties, it is worth going back to the views expressed by Ernst Mayr. In his article on “The emergence of evolutionary novelties”, Mayr chooses to separate the two problems:

> “The origin of new taxa, from species to higher categories, will be considered as lying outside the scope of this discussion. Even though, admittedly, the origin of new higher categories is often correlated with the emergence of a new structure or other character, the natures of the two problems are sufficiently different to necessitate separate treatment.” (Mayr, 1960, pp. 356–7).

Thus, there is enough difference between the origin of novelty and the origin of higher taxonomic categories to require a separate treatment, but there is nonetheless a correlation between them. However, a few years later, Mayr expresses a different judgment:

> “It is evident that the origin of a new type, the origin of new morphological and other biological characteristics, and the origin of the higher categories are three problems that cannot be separated from each other. Indeed, they are merely three different aspects of the same problem. Whatever contribution is made to one of the three problems is also a contribution to the other two.” (Mayr, 1963, p. 589).

One way to explain the ambiguity is to argue that novelty and higher taxonomic categories are overlapping but non-identical problems. Some novelties are associated with the origin of higher taxonomic categories while others can be proper to a single species or a small number of species. Conversely the origin of a higher taxonomic category often implies a series of novelties, but it is a broader process that also requires speciation events.

Precisely because the origin of a higher taxa, especially of taxa of high ranks (families, orders and above), usually involve the origin of several novelties, historical research focused on the evolutionary history of particular taxa often tackles the question of the origin of their diagnostic characters. Thus, research on novelty of the Modern Synthesis era is to be found in research focusing on the origin of higher taxa as well as on research more explicitly on some phenotypic character. Surveys of animal research on novelty in the Modern Synthesis era have shown the sustained presence, if not abundance, of this research and revealed that this research falls within the disciplines of paleontology, morphology and comparative embryology. (Love, 2009, 2005; Love and Raff, 2003; Raff and Love, 2004). Rather than focusing on the same material, I will turn to the state of research on the origin of higher taxa in botany in order to provide a comparative view of the two domains. I will more precisely focus on the origin of angiosperms (and angiosperm novelties) since it was the most studied group.

The origin of angiosperms

As noted by George Ledyard Stebbins (1974a, p. 340), plants are superior to animals in terms of the possibilities of crossing between related species and even related genera and of subsequent genetic analysis. This partly explains the greater advancement of experimental taxonomy in botany than in zoology. At the same time, the fossil record, which allows tracking of evolutionary change, is much more abundant for animals than for plants, especially for angiosperms. This poor fossil record brings a disadvantage for the study of large-scale evolution. A look at research on the evolution of higher categories in plants is significant because it reveals a different power balance in this domain than in the domain of animal studies. While the Modern Synthesis perspective had reached a dominating position in animal evolution at least from the 1950s, the situation in plant evolution was more contested, as illustrated by this statement from Stebbins:

> "The reason that no botanist in the 1930s and 1940s did for botany what Simpson and Rensch did for zoology is perhaps that the only people who thought above the species level were the morphologists and the anatomists. They were dominated by people like Arber, Bower, and Bailey, who regarded adaptation and selection as teleology and were strongly opposed to truly Darwinian concepts. […] Their hypotheses did not deal with the processes that produced change, but rather with the descriptive morphology of the types that were supposed to have been present. It was pure phylogeny, based upon supposed morphological homologies." (Stebbins, 1980, pp. 150–151)

When Stebbins published his own book-length account of the origin and evolution of the angiosperms (Stebbins, 1974a), a review by the British botanist David Mabberley stated:

> “[...] cutting a swathe through the jungle of botanical conjecture and hypothesis, the author leaves a trail of battered and bruised theories. Among the injured are the ideas of Arber (and thus Goethe), Corner, Eames, Holttum, Melville, Sporne, van Steenis, Zimmermann.... Bews, Fedorov, Sattler and Takhtajan”.

And later concluded:

> “If Professor Stebbins is right in his genetic uniformitarianism, then this book will be seen, when sufficient evidence has been gathered, to be that of a prophet; if wrong it will be seen as yet another, almost colonial, imposition of temperate ideas on the tropical.” (Mabberley, 1976, p. 529)

As expressed by Mabberley, a flurry of evolutionary hypotheses coexisted and the Modern Synthetic adaptationist and uniformiatarian view was not in a dominant position.

Regarding angiosperm systematics, many different classifications still coexisted during the Modern Synthesis era. One can distinguish between artificial classifications, based on a small selection of characters, such as the Linnean sexual system based on the number of stamens and pistils; natural classifications, focused on overall similarity and based on numerous, mostly morphological, characters, such systems organized in a series of nested classes (e.g. genus, family, order etc.) and allowing more predictions and generalisations than artificial systems; and historical or phylogenetic classifications, whose purpose is to reconstitute the evolutionary history and relationships between taxa (Briggs and Walters, 2016; Constance, 1955; Singh, 2016).

Many plant biologists doubted the possibility of phylogenetic taxonomies. A minority considered that it should be the main goal of taxonomy (Constance, 1955; Winsor, 1995). For example, this debate applied to taxonomy in general was the main subject of the discussions of the Taxonomic Principles committee of the Association for the Study of Systematics in Relation to General Biology, which led to the publication in 1940 of the influential volume *The new systematics*. As Winsor (1995, p. 227) notes:

> “Most of the botanists asserted that taxonomy was a practical matter to be kept distinct from phylogenetic speculation, and most of the zoologists insisted that taxonomists must strive to represent evolution if they wished to be scientific”.

The reasons for the scepticism about the phylogenetic approach to taxonomy were multiple: a) the different proposed phylogenetic systems relied on speculations to a large extent; b) the poverty of the fossil record meant that few transitional forms between extent plant taxa were found; c) phylogenetic systems thus usually directly linked extant forms in transformation series, but the origin of extant forms from other extant forms was improbable in many cases; d) the uncertainty regarding the direction of evolutionary trends, that is, regarding which character is primitive and which is derived; e) the contradictions between phylogenetic series based on different types of evidence (different morphological characters, or embryological, biochemical, physiological evidence); f) the debates about different possible relations of homology between characters in different taxa; g) the reduction of the utility of taxonomy by sacrificing its other goals to the single goal of establishing phylogenetic relations (after Constance, 1955, pp. 412–413; see Garay, 1960; Davis and Heywood, 1963; Briggs and Walters, 2016).

The difficulties of the phylogenetic approach did not prevent plant biologists from both sides, defenders and opponents of phylogeny, to hypothesize many sequences of character transformation, or typological series. A closer look at these character sequences shows that the simple opposition between natural and phylogenetic classifications is too coarse. For example, the influential classification of the German botanists Adolf Engler (1844-1930) and Karl Prantl (1849-1893) has been considered as the beginning of phylogenetic classifications (Singh, 2016), but it was composed of linear sequences of plant groups according to a principle of increasing complexity, which appears as a relatively naïve phylogenetic principle and has been refuted in many cases due to the importance of reduction in plant evolution (Singh, 2016, p. 313).

Here, a distinction should be made between phylogeny as an ideal and as a classification practice. Botanists who doubted the phylogenetic ideal could still produce local evolutionary sequences as robust as botanists upholding this phylogenetic ideal. The German botanist Walter Zimmerman, although he was on the phylogenetic side, favoured “character phylogeny” (*Merkmalsphylogenetik)*, the hypothesizing of evolutionary series of single characters, which he contrasted with “species phylogeny” (*Sippenphylogenetik)*, the actual phylogeny of plant species or groups, the latter being much more difficult to investigate (Zimmermann, 1934). Zimmermann distinguished six processes responsible for plant morphological change through evolution (represented in figure 3 below): 1) overtopping, 2) planation, 3) fusion (a – in leaf, and b- in stems), 4) reduction and 5) incurvation (Zimmermann, 1965, p. 76).

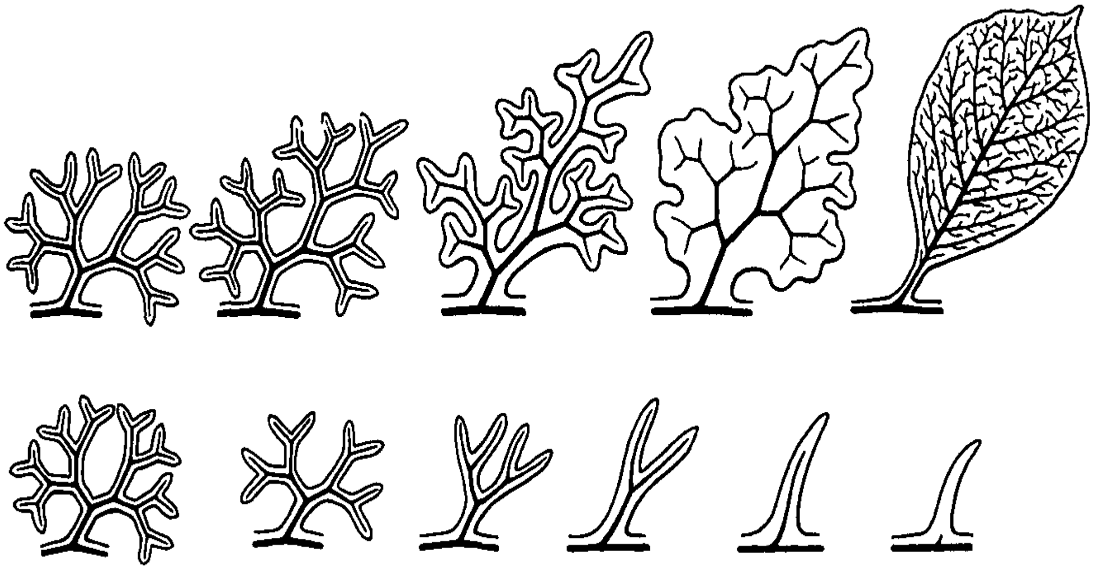

Fig. 4: Examples of character phylogenies. Transformation of the leaf through overtopping, planation, fusion and reduction. Above: in *Magnolia*. Below: in conifers (After Zimmermann, 1965).

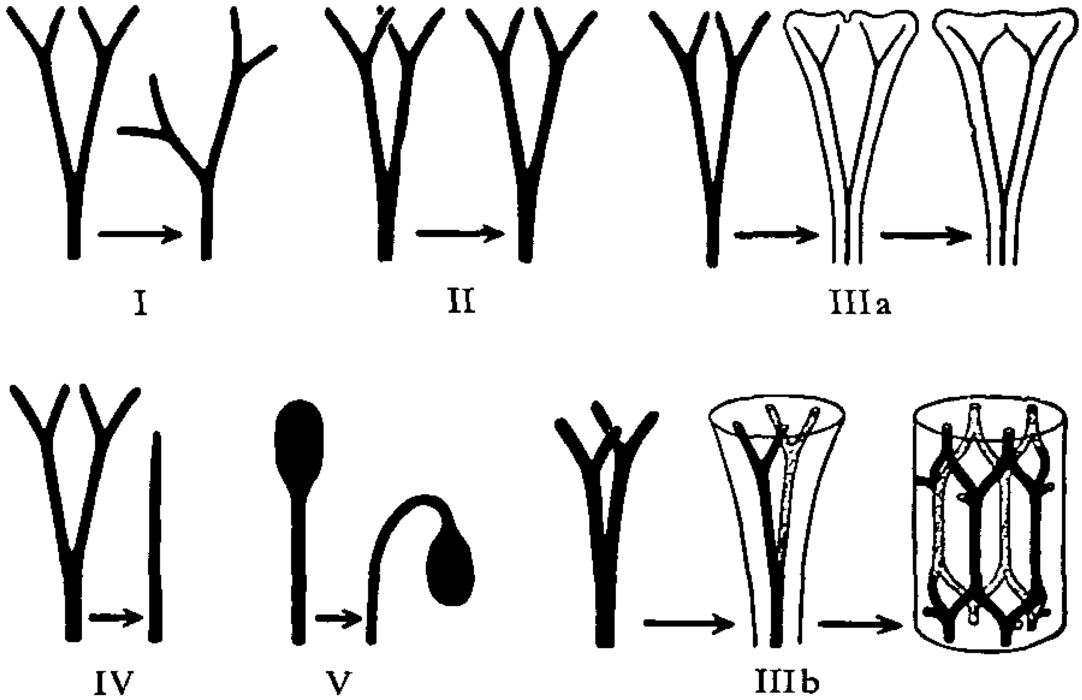

Fig. 5: processes of character transformation in vascular plants (After Zimmermann, 1965).

More generally, in a review of plant taxonomy, Davis and Heywood (1963, p. 35-37) list 29 generally accepted evolutionary trends, often based on morphological character series. Many other of these putative transformation series or “character phylogenies” were however, highly contested (Constance, 1955). Other plant morphologists, like Agnes Arber, were skeptical about the phylogenetic approach and preferred producing logical, non-evolutionary and non-directional morphological series. Arber established relations between characters from a developmental and dynamic perspective. (Arber, 1950, 1937; Classen-Bockhoff, 2001; Rutishauser and Isler, 2001; Vergara-Silva, 2003). Thus, while Stebbins is right in describing Arber as skeptical of natural selection, his description of her method as “pure phylogeny” (Stebbins, 1980, pp. 151, cited earlier) is misleading. In any case, most hypotheses of character evolution were also based on inferences from comparative morphology of extant angiosperm species rather than on inferences from the fossil record.

Differences in emphasis

As suggested earlier, the origin of particular higher taxonomical categories is a problem that can be divided into several component research questions. An essential point for my investigation is to determine how much of the research on the origin of higher taxa was involving research on the origin of evolutionary novelties associated with these higher taxa. Some research on the origin of the angiosperms has an ecological and biogeographical focus with little reference to evolutionary novelties. For example, here is how the paleoecologist Daniel Axelrod divided the problem of the origin of the angiosperms:

> “The problem has several facets, which may be viewed in terms of the following questions: (1) What were their ancestors? (2) What is their antiquity? (3) What was the general nature and area of the environment in which they originated? (4) Did they actually assume dominance with "bewildering suddenness" during the Cretaceous?” (Axelrod, 1952, p. 29)

As stressed by Axelrod, there was little agreement on any of the four questions. For example, regarding the first question, there were debates between the hypotheses of a monophyletic origin and of a polyphyletic origin of the angiosperms; between the hypotheses of a similarity of the first angiosperms with some extant group or of their dissimilarity to any extant group; a prominent debate was about the growth habit of the ancestral angiosperms. About the second question, the major debate was whether the angiosperms originated shortly before the first known fossils, dating from the early Cretaceous, or long before, in the Mesozoic.

In order to assess research within the Modern Synthesis framework, a significant document to consider is the first volume of the publication derived from the Darwin centennial celebration at the university of Chicago (Tax, 1960). Of the twenty contributions, two are focused mainly on plant evolution, that of Axelrod on ‘The evolution of flowering plants”(Axelrod, 1960), which again adopts the same biogeographical and ecological perspective, and that of Stebbins, “The comparative evolution of genetic systems” (Stebbins, 1960), which focuses mainly, but not exclusively, on the evolution of alternation of generations in plants, concentrating on the genetic and chromosomal level and with a selectionist outlook. This suggests that, for Modern Synthesis scientists, the question of the origin and evolution of angiosperms (and of plants more generally) was decoupled from the question of the origin of angiosperm novelties. It is certain that the latter was not dominant research subject. The case of Stebbins, however, forces us to nuance this diagnosis. In *Variation and evolution in plants* (1950 chapter 13), Stebbins treated the question of large scale evolutionary trends in plant morphology. He later published a book-length account of the evolution of flowering plants combining the perspective of Axelrod and of G.G. Simpson with a focus on morphological and developmental evolution (Stebbins, 1974a). Stebbins's approach will be covered in more detail in the next chapter.

Stebbins (1980, pp. 150–151, cited earlier) makes a distinction between the Modern Synthesis approach, which was interested in "the processes that produced change" and the approach of morphologists like Agnes Arber, Irving Bailey and Frederick Bower, who were only interested in phylogeny and morphological homology. As I said, this dichotomy is confusing. There should be a distinction between the logical perspective of some comparative morphologists like Arber, focused on homologies and sceptic of the phylogenetic approach, and the perspective of the taxonomists and morphologists who pursued this phylogenetic approach. Regarding the latter, what was the relation between their work and the question of the origin of novelty? Even if Stebbins' dichotomy is too coarse, it can be reframed to apply to both comparative morphologists like Arber, and phylogenetic taxonomists: according to Stebbins, both were interested only in patterns (typological or phylogenetic), while only the Modern Synthesis perspective was concerned with processes of evolutionary change. I think that, again under this interpretation, Stebbins's opposition between the pattern and the process perspectives is too strong. Walter Zimmermann is a case in point, as his work is both a contribution to phylogenetic systematics and a development of theories of character transformation grounded in processes at different levels: the descriptive processes of morphological transformation described earlier are, in his framework, grounded in genetic processes (mutations), in developmental physiology and in the action of natural selection (Zimmermann, 1965; Classen-Bockhoff, 2001). More generally, research with phylogeny as a primary objective was often involved with processes of transformation on which to ground the phylogenetic patterns. The establishment of phylogenetic relationships is based on different lines of evidence (fossil, morphological, anatomical, cytological, biochemical, developmental). Transformation series have to be established at these different levels, especially at level the morphological and developmental characters. These hypothesized transformations series have to be justified by formulating explanations which are involved with evolutionary processes. Thus, at least, some of the research primarily concerned with the phylogeny of the angiosperm pertains to the domain of research on the origin of angiosperm novelties. I will illustrate this in the next section with the example of the relation between the phylogeny of the angiosperm as a taxon and the origin and evolution of the angiosperm flower.

The origin of the angiosperm flower

There was historically a strong association between the origin and evolution of the angiosperm taxon and the origin and evolution of the angiosperm flower because the use of floral characters in classification and phylogeny had been dominant for two centuries and was still dominant (Constance, 1955). Regarding the definition and origin of the flower, Foster and Gifford noted:

> “As angiosperms are commonly designated the flowering plants, it might be assumed that there is rather general agreement about the scientific concept of a flower. Unfortunately, this is not the case, and the literature on floral organography, ontogeny, and structure displays widely divergent viewpoints of the fundamental nature of the flower as well as on the interpretation of its component organs (sepals, petals, stamens, and carpels). One of the basic difficulties lies in our complete ignorance of the evolutionary history of the flower […]; it becomes largely a matter of conjecture whether it is justifiable to draw comparisons between modern angiospermous flowers and the spore-producing structures of other tracheophytes [vascular land-plants]. If such comparisons are attempted, it is quite possible to reach either a very broad or a very restricted concept or definition of a flower.” (Foster and Gifford, 1974, p. 593)

Although Foster and Gifford’s view is especially pessimistic, it reflects the multiplicity of competing theories regarding the homologies between flower organs and other plant organs and regarding the origin of the flower.

Three main groups of hypotheses regarding the origin and nature of the ancestral angiosperm flower were competing during the late Modern Synthesis era.

_ The first group of hypotheses is grounded in the classical homology between flower organs and leaves, which goes back to Goethe. According to that homology, the flower is a determinate shoot with appendages, and the latter (sepals, petals, stamens, carpel) are modified leaves. The prominent modern formulation of this view is the strobilus theory of Arber and Parkin (1907). A strobilus or cone is a group of sporophylls (leaves bearing the organs that produce spores) borne terminally on a shoot. Strobili are found in several plant groups other than angiosperms. They can be unisexual (with only megasporophylls or microsporophylls) as in the Cycyads, or bisexual, as in the fossil group Bennettitales. Conifers possess compound unisexual strobili. Under that view the ancestral flower was derived from a bisexual cone and was “a radially symmetrical flower with an elongated axis bearing numerous, indefinite in number, separate, leaflike members arranged in regular spirals, or cycles, or pairs, depending upon the vegetative phyllotaxy” (Constance, 1955, p. 422).

_ The second group of theories interpret the flower as derived not from a single bisexual axis but from the condensation of two unisexual cones, or by derivation from the compound cones of some gymnosperms. However, this second group also adopts the homology between the flower and a vegetative shoot, and between floral organs and leaves (e.g. Wettstein, 1908; Melville, 1960).

_ The third group, in contrast, denied the view of the flower as a modified vegetative shoot. Different sources of evidence were used by different researchers such as phyllotaxy, and developmental evidence. For example, Satina and Blakeslee, who used chimera of the species *Datura* induced by colchicine treatment to study the fate of cells in development, relied on their developmental evidence to question the homology of all floral organs to leaves. Colchicine treatment of the seeds leads to the random polyploidy of some plant cells and because these polyploid cells are distinguishable, it allowed Satina, Blakeslee and Avery to trace cell lineages during the development of the plant. They used the technique to demonstrate the existence of three distinct germ layers in the shoot meristem (Satina et al., 1940). Satina and Blakeslee later demonstrated that like leaves, sepals and petals originate from meristematic material of the central germ layer, whereas stamens and carpels originate from the innermost germ layer. They argued that this evidence weakened the claim of homology between leaves and all floral organs and thus the strobilus theory of flower origin. (Satina and Blakeslee, 1943, 1941).

Thus, firstly, the example of research on the origin of the angiosperm flower shows that the frontier between phylogenetic research on the angiosperms and evolutionary research on the origin of angiosperm novelties was quite porous. The example of Satina and Blakeslee illustrates the bridge between developmental, evolutionary and phylogenetic research. Secondly, the multiplicity of different hypotheses shows the limitation of the evidence and the lack of a common theoretical framework.

IV– NOVELTY, COMPLEXITY AND LEVELS OF ORGANISATION

The position of the problem of novelty in the Modern Synthesis era can be approached from a different angle by referring to the frequently used distinction between increase in complexity, or in level of organization, and diversification. This broad distinction is related to several conceptual dichotomies important at the time: between general adaptation and special adaptation, grade and clade, anagenesis and cladogenesis. As Schaeffer and Hecht argue in their introduction to the proceedings of the Symposium on “The origin of higher levels of organization” (Schaeffer and Hecht, 1965), several key authors of the Modern Synthesis era (Simpson, Huxley, Schmalhausen, Rensch, Mayr) distinguish between the process that produces superior levels of organization and the one that leads to the diversification of species. There was however no clear unanimous understanding of the former process. This can be illustrated by the various meanings of the concepts of anagenesis and cladogenesis.

The concepts of anagenesis and cladogenesis are particularly interesting because they had conflicting meanings that revealed disagreements or ambiguities in the way Modern Synthesis scientists conceived evolution. The terms were first used together by Rensch in the first German edition of *Evolution above the species level* (Rensch, 1947). Here is how Rensch distinguishes the two distinct processes in the English translation of the second edition:

> "Though it has rightly been argued that the 'lower' species may be 'perfectly' adapted to their special habitats, the existence of a 'lower' and a 'higher' has not been denied. There is no doubt that most of our Recent types of mammals are 'higher' than their smaller Jurassic and Cretaceous ancestors, and that Recent insects represent a higher form of organization than their annelid ancestors. However, as a 'higher' level may be caused by increased complexity, improved rationalization, or greater versatility in reacting to environmental stimuli, the problem of progressive evolution, observed in so many phylogenetic branches, needs a consideration of its own. I have proposed referring to it as anagenesis, whereas the normal branching of lines of descent should be distinguished as kladogenesis." (Rensch, 1959, p. 281)

Rensch makes several important distinctions here. First, anagenesis is not identical to adaptation as a process: less anagenetically advanced species can be as well adapted to their habitat as more advanced species.[62] Still, Rensch insists that anagenesis is the product of natural selection, and not of autonomous principles, as many who discussed the phenomenon argued, such as Lamarck or, more recently, Daqué and Beurlen. Thus, anagenesis is only one form of adaptation among others. Second, anagenesis includes increase in complexity but is not limited to it (the components of anagenesis will be discussed further below). Third, anagenesis and cladognesis should not be considered as alternative processes, the latter refers for Rensch to the diversification of life through phylogenetic branching. It includes both the splitting of lineages and their genetic and phenotypic change. Anagenesis should be considered as one form of change occurring during cladagenesis:

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[62] Relatedly, there is no identity or necessary link between survival and spread on one side, and anagenesis on the other: "When we accept Charles Darwin's statement (1859, chapter 11) that all 'recent species have proved their superiority over their extinct ancestors by their survival', we should remember that this superiority does not necessarily mean a result of progressive evolution". (Rensch, 1959, p. 285)

> “As at any phylogenetic level anagenesis is only one of several evolutionary possibilities, it is comprehensible that sometimes regressions will occur and that sometimes the anagenetic level will remain unaltered”. (Rensch, 1959, p. 300)

Rensch distinguishes six types of anagenesis: (1) Increase in complexity. This process mainly resides in differentiation of parts. Differentiation is progressive when the specialisation of parts allows for improvements in the performed functions or for the assumption of new functions. Rensch insists on the principle of “the origin of new organs as a consequence of a strictly quantitative increase of certain tissues causing new growth gradients”, and cites as examples “the origin of parapodial appendages of polychaetes, the formation of wings in insects, the fins of primeval fishes, feathers and hairs, the neural groove, the optic cups, the semicircular ducts of the optic labyrinth, the basilar papilla of the internal ear, the neopallium of the vertebrate brain” (1959, pp. 289–290). However, this should not lead us to believe that Rensch includes in anagenesis any new morphological or physiological character; all the examples used are related to the essential functions of locomotion, respiration, thermoregulation, perception and cognition. (2) Rationalisation of structures and functions. This is the improvement of efficiency by diminution of the number of parts or by centralisation. (3) The increase in complexity and rationalisation of nervous systems are treated separately but they can be seen as illustrations of the two previous processes. (4) The increase in plasticity of structures and functions. (5) “Improvement permitting further improvement”. Rensch here contrasts this process with adaptation leading to overspecialisation and possibly blind alleys, fatal when changes in environmental conditions occur. This further specifies the distinction of anagenesis with evolutionary novelty: many new characters can be included in anagenesis but many others only increase specialisation. In the English edition of 1959, Rensch equates his idea with Simpson’s (1949) “progress in adaptatbility” and Julian Huxley’s (1954) “nonrestrictive improvement”. (6) The increase of autonomy and independence from the environment.

As I noted in part II of this chapter, Simpson favours a distinction between speciation or the splitting of lineages, and phenotypic evolution, which occurs within lineages and which he calls phyletic evolution; he equates the first with cladogenesis and the second with anagenesis (Simpson, 1949, pp. 178–179).

The different conceptions that Rensch and Simpson have of anagenesis and cladogenesis are manifest in Simpson's review of the first German edition of Rensch's *Evolution above the species level*. What is of significance is that Simpson does not see this as simply a case of different meanings conventionally attributed to the same terms, but argues that the use Rensch makes of the terms reveals some inconsistency in his vision of evolution[63]. About Rensch's version of cladogenesis, Simpson writes:

> "Rensch moreover includes and emphasizes under "cladogenesis" the various phenomena involved in progressive specialization and, particularly, the origin of new organs and new basic structural types or 'Bauplane' Now, it would appear that this is not correctly conceived as an aspect of cladogenesis, 'Stammverzweigung,' unless the new organ or new basic type (and hence a new higher taxonomic category) appeared at the time of the branching, as a phenomenon of the branching itself and not as a progressive development within a continuous line of descent." (Simpson, 1949, p. 179)

Simpson then writes about anagenesis:

> "In general, anagenesis is considered as progressive change in structures and groups already established as such (similar to what I have called "phyletic evolution"), and yet the distinction from progressive specialization or from progressive development of new groups is far from clear (to me, at least), and indeed Rensch has given nearly identical examples (e.g. rise of mammals and their basic structures from reptiles and theirs) for both cladogenesis and anagenesis." (Simpson, 1949, p. 179)

I think that the criticisms that Simpson formulates against Rensch are based on an ambiguity and a misunderstanding. The ambiguity is that of the concept of progressive evolution. The misunderstanding applies to Simpson's belief that, like him, Rensch views cladogenesis and anagenesis as alternative processes, whereas, as noted earlier, for Rensch anagenesis is one form of cladogenesis. The two interpretation problems are manifest in the following diagram included

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[63] "In some respects, however, the concepts involved in Rensch's classification of these evolutionary aspects do not seem entirely clear and they may even be partly inconsistent with some of his main conclusions as to forces and processes in evolution." (Simpson, 1949, p. 179)

by Simpson, even though he notes that the concepts are “analogous but not identical” (Simpson, 1949, p. 178):

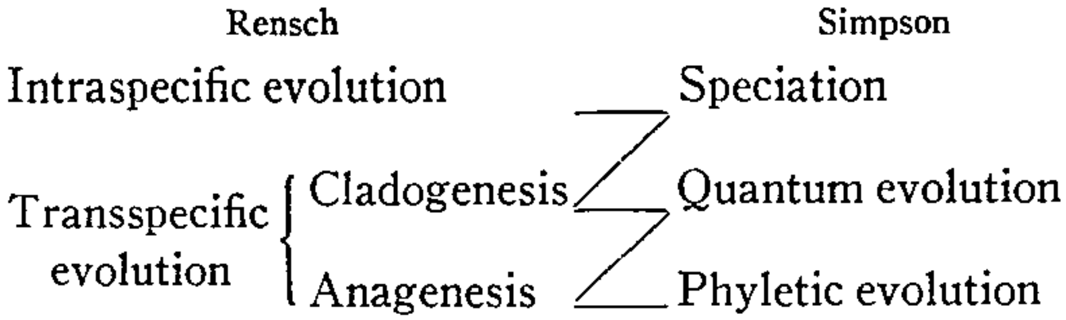

Fig. 6: Comparisaon of Rensch’s and Simpson’s processes of evolution (after Simpson, 1949, p. 179)

Regarding anagenesis as progressive evolution, Simpson uses the concept in its temporal sense, as opposed to rapid or saltational evolution, and he assumes that Rensch does the same. Meanwhile, Rensch actually uses progressive evolution in its qualitative sense, as an increase in complexity or rationalisation or the other forms of anagenesis described earlier. Because of the misunderstanding and the ambiguity, here is the contradiction that Simpson perceives in Rensch’s framework: on the one hand, he notes that Rensch, like himself, believes, contrary to Schindewolf and Goldschmidt, in the gradual formation of “groups”, that is, of higher taxa with characteristic structural plans. The phase of formation of groups is just as gradual as their phase of specialisation. On the other hand, Rensch assigns the formation of new organs and especially of new “Bauplane” (structural plans) to cladogenesis, suggesting that this formation coincides with branching and is thus sudden or even saltational.

The misunderstanding between Simpson and Rensch can be interpreted as a difference of perspective. Simpson argues that Rensch has the perspective of a neozoologist while he himself has the perspective of a paleozoologist. I think that in this case, the following interpretation is more accurate: Simpson conceives cladogenesis and anagenesis within the context of the problem of the tempo and mode of evolution, whereas Rensch conceives cladogenesis as pertaining to this problem but anagenesis as pertaining to another one, the problem of qualitative progress in evolution.[64]

The case of anagenesis and cladogenesis can be related to the dual objective of evolutionary systematics in the Modern Synthesis era. Evolutionary systematics intends to classify taxa both according to phylogenetic relationships, in order to accurately represent phylogenetic history; and according to level of organisation or morphological similarity. These levels of organisation are usually represented in ecological terms of niches or adaptive zones, with which morphological characteristics are associated. The combination of these two dimensions is for example defended by Mayr who opposes the cladistic school led by Hennig, which only considers the first dimension valid for systematics:

> "Any theory of classification which pays no attention to the tremendous range of difference between shifts of phyletic lines into minor niches and into entirely new adaptive zones, is bound to produce classifications that are unbalanced and meaningless" (Mayr, 1974, pp. 105–106).

The concepts of clade and grade, formalised by Julian Huxley (1959), each embody one of the dimensions. While clades are groups based on phylogeny, more precisely monophyletic groups, grades are groups that share a level or organisation, for example based on mechanisms of feeding or locomotion. A grade can thus be reached by different lineages through convergent or parallel evolution.

Thus, the primary research context in which the concept of grades was elaborated was the systematic classification of taxa. However, the problem of the transition between grades or levels of organisation was an important research topic during the Modern Synthesis era. This is illustrated for example by the Symposium entitled "The origin of higher levels of organisation" (Schaeffer and Hecht, 1965) which gathered biologists from different disciplines to study

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[64] Simpson's meaning of anagenesis and cladogenesis will progressively become the dominant one. The distinction is still used today although there is again a polysemy of the terms and a debate regarding their usefulness (Allmon, 2017; Vaux et al., 2016).

separately the different factors playing a role in the origin of new grades. The selected factors were: genetic mechanisms, morphogenesis, adaptive mechanisms, ecological factors, natural selection and experimentation (the overlap between the different factors was recognised). I will study some of these origin explanations in more detail in the next part of this chapter. The problem of transitions between grades or levels of organisation thus overlaps with the problem of the origin of novelties because the former often imply several morphological and physiological changes and these changes can include clear origin of novelties but also quantitative changes such as elongations of bones and muscles, loss of organs, changes of shapes.[65]

V – NOVELTY AND ADAPTATION

Adaptive types and adaptive radiations

In the previous chapter, I examined the conceptual relations between novelty and adaptation and the arguments in favour of keeping these two problems separated. Here, I will now examine in more detail how adaptation and novelty were weaved together during the Modern Synthesis era. In a recent article, the paleobiologist Douglas Erwin (2015) summarizes the dominant position on novelty in the Modern Synthesis era with three claims:

1) All the diversification events in the history of life are adaptive radiations.
2) All the adaptive radiations are triggered by ecological opportunities.

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[65] Here is an example of the different types of transformations involved in the transitions between the three grades of sharks (cladodonts, hybodont and modern): “The transition from primitive placoderm to cladodont involved loss of the dermal armor, perhaps in relation to requirements for greater buoyancy, but retention of the cartilaginous (frequency calcified) endo-skeleton. The relatively large semicircular canals may have been carried over from the placoderm ancestry. The cladodont feeding mechanism, including the amphistylic jaw suspension (probably also a retained ancestral character), was obviously efficient for both the cladodont and the hybodont way of life. Possibly the reduced otic region, involving smaller semicircular canals, and surely the tribasal pectoral fins of the hybodont level, represent expressions of increased maneuverability. In modern sharks, the protrusible palatoquadrate, the calcified centra, and the fused pelvic plates were among the final refinements in feeding and locomotion.” (Schaeffer, 1965, p. 320)

3) The rate of morphological diversification between taxa is faster at the beginning of the history of a clade but slows down with the decrease of ecological opportunities.

Adaptive radiations can be defined as the rapid diversification of a lineage into new species associated with the ecological and phenotypic divergence of these species and where this divergence corresponds to a process of adaptation to the different habitats involved. The theory of adaptive radiations gained momentum in the later phase of the Modern Synthesis, through the impulsion of Lack (1947), Dobzhansky (1951) and especially Simpson (1953). It was at the time illustrated by a few empirically well studied cases, especially from island fauna, such as the Galapagos finches (Lack, 1947) and the Hawaii honeycreepers (Amadon, 1950). Douglas Erwin later argues that the progressive documentation of different adaptive radiations in the last decades has shown that they are actually not sufficient to produce the past and present diversity of life forms:

> “The most striking observation [...] is the absence of evolutionary novelty associated with classic adaptive radiations. Indeed, by their nature, adaptive radiations concern the adaptive exploitation of ecological opportunities via variation on existing adaptive themes, but not the formation of the themes themselves. While the fossil record documents adaptive radiations that encompass greater morphological diversity than Darwin’s finches, mockingbirds or Anolis lizards, including the spread of insects and angiosperms, and the Mesozoic radiation of mammals, the origins of morphological novelties often seem to involve a different process.”(Erwin, 2015, p. 933)

The argument formulated by Erwin can be summarised in the following fashion: The Modern Synthesis represented evolution as a series of adaptive radiations. Now, it appears that adaptive radiations are not associated with evolutionary novelties, they are only associated with variations on existing adaptive themes. The process of production of novelty is situated outside of sequences of adaptive radiation and has not been covered by the Modern Synthesis. It is pertinent here to ask what Modern Synthesis thinkers and researchers would have thought of Erwin’s argument. And what did Simpson and others have to say about what happened between adaptive radiations? I shall then focus on whether the formation of what Erwin calls “adaptive themes” was tackled by Modern Synthesis researchers. Was the question of the formation of adaptive themes left unaddressed? If not, what strategies were used to address this problem and what degree of importance was attributed to it? There are three possibilities here:

1) MS biologists were focused only on adaptive radiations as episodes of diversification of species and specialisation in different directions from a generalist adaptive theme, and the formation of the adaptive themes themselves, and thus of evolutionary novelties, was left as an unexplained blind spot.
2) MS biologists produced explanations of the transitions between adaptive themes but rejected the two-stage view of phenotypic evolution in favour of a continuous view: phenotypic changes, and thus novelties, occur as much during radiations as during transitions between adaptive themes.
3) MS biologists produced explanations of the transition between adaptive themes and embraced, at least partly, the two-stage view of phenotypic evolution, locating essential phenotypic changes (and thus novelties) at these transitions.

It appears that whereas Simpson's view is best described by proposition 2), other Modern Synthesis participants or sympathisers were closer to proposition 3). While fleshing out the whole theory of adaptive radiations is a task that would lead us away from evolutionary novelties, the concept of *preadaptation* is a cornerstone of the relationships between the Modern Synthesis' adaptive view of evolution and evolutionary novelties. It was used by Simpson to articulate his views, without having novelty as a direct explanatory target, but also by others, such as Ernst Mayr and functional morphologists, as a causal principle more directly targeted at explaining the origin of novelties. I will thus briefly describe some concepts essential to Simpson's view of adaptive radiations and then focus on the development of the concept of preadaptation and its varying relationship to novelty.

Adaptive types and adaptive zones

The concept of adaptive themes that Douglas Erwin describes as the starting points of adaptive radiations, which proceed via variation on these themes, is not literally present in Simpson's theory, but two of his essential concepts are related to it: adaptive types and adaptive zones:

> "*Adaptive types* may be defined in part and in some cases in geographic or physical environmental terms, but it is essential to remember that what we are talking about here is not a geographic, physical, or even in the broadest sense environmental zone but an *adaptive zone*, representing a characteristic reaction and mutual relationship between environment and organism, a way of life and not a place where life is led." (Simpson, 1953, pp. 201–202)

Three characteristics are essential to properly understand adaptive types and adaptive zones:

_ They are ecological concepts rather than morphological, anatomical or physiological; they represent ways of life, not phenotypic structures. In contrast, Erwin's concept of adaptive themes is linked to evolutionary novelties and can be deemed close to the concept of *Baupläne*, types of structural organisation, which is a morphological and anatomical concept.

_ Due to convergent evolution towards similar adaptive types, the latter can but do not necessarily coincide with taxonomical units. In that sense, Simpson's adaptive types are very close to Huxley's grades. On the one hand, Simpson states that major adaptive types correspond to taxonomical classes; on the other hand, distantly related species can share an adaptive type while their close relatives belong to different types. For example, the extinct tasmanian wolf (thylacine) is phylogenetically much more closely related to marsupials such as kangaroos than to canidae such as dogs, but its adaptive type is much more similar to that of dogs than that of kangaroos.

_ Adaptive type is a nested and relative concept. Simpson notes that even two birds born in the same nest have different adaptive types, although this level of difference is irrelevant in most research contexts. More generally, adaptive zones can be repeatedly subdivided into subzones and for each case, several possible modes of subdivision are possible.[66]

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[66] "For example, a major zone of rodentlike adaptation might, as one of numerous possible systems of subdivision, include zones one of which is squirrellike, in turn subdivided perhaps into arboreal and

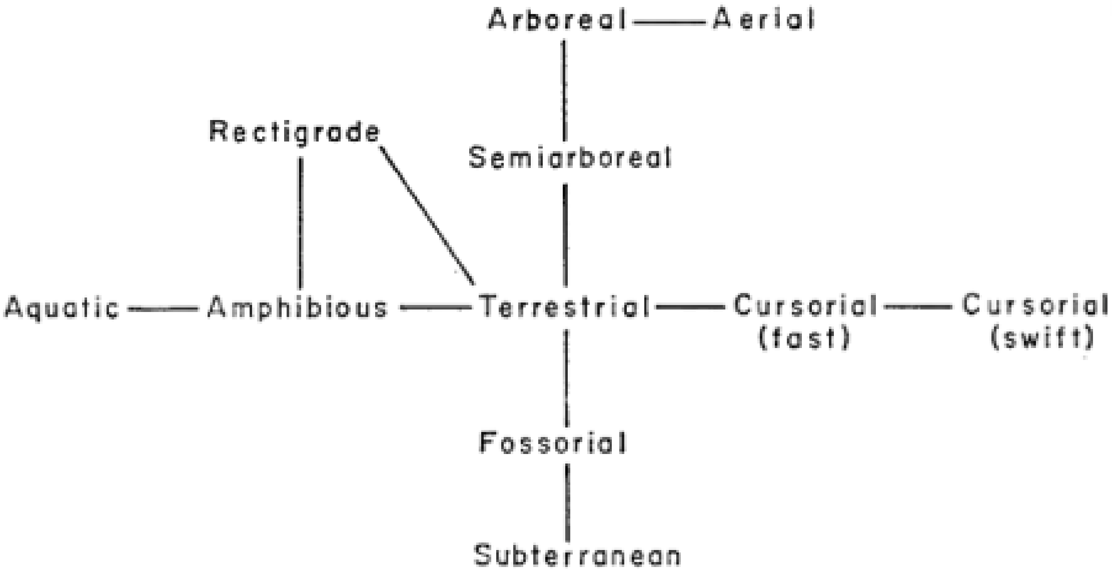

Fig. 7: Major adaptive types in the vertebrates. Lines imply possible transitions but are not exhaustive (After Axelrod, 1960).

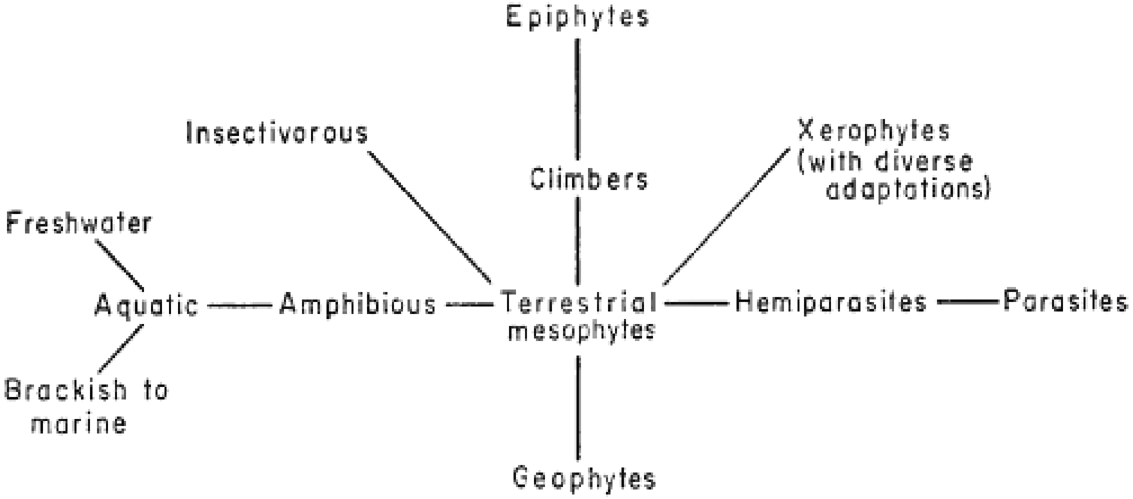

Fig. 8: Major adaptive types in flowering plants (After Axelrod, 1960).

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terrestrial subzones, the latter into nonfossorial and fossorial or maybe noncommunal and communal, and so on down to a sub-subzone representing the particular and special adaptive type of one colony of Cynomys gunnisoni zuniensis (such as the one visible to me as I write these lines) or of one family or individual in that colony." (Simpson, 1953, p. 202)

Adaptive radiation and phyletic evolution

To attribute to Simpson the idea that all diversity is the result of adaptive radiations may seem at odds with his insistence on the role of anagenesis or phyletic evolution.[67] As noted earlier, Simpson insisted on the distinction between splitting, or speciation, and phyletic evolution, stressing the fact that phenotypic evolution occurs mostly during the latter process. The following text from Simpson may help to clarify the matter:

> "The now existing major adaptive types of chordates do not owe their origin to early adaptive radiation in the phylum, which occurred but which involved lesser adaptive differences. The major types, corresponding to the classes in taxonomy, arose partly by radiation and partly by successive occupation of major zones: the Placodermi by succession from Agnatha, the Chondrichthyes and Osteichthyes probably as the most successful branches of a (poorly known) radiation in the Placodermi, the Amphibia by succession from Osteichthyes and the Reptilia by succession from Amphibia, the Aves and Mammalia, finally, as the most successful branches of a radiation in the Reptilia. The complexity of the process and the lack of definite distinction between radiation and succession is, however, shown by the fact that even when the relationship as between classes is successional the particular lineage that made the adaptive shift is one of many involved in lower-level radiation." (Simpson, 1953, p. 225)

Thus, first, contrary to what was suggested by Douglas Erwin, in Simpson's framework adaptive radiations are not the only process producing phenotypic change, as change can be produced by the succession of different types. However, Simpson recognises the lack of conceptual precision and clear delimitation between these processes. It can be said that while an adaptive radiation at a lower taxonomic level, such as the radiation of finches on the Galapagos islands, can be clearly defined and delimited, an adaptive radiation at the level of a phylum or class is a much more complex, hard to track and loosely defined process. Second, at least for high-level radiations stretching over ten million years or more, there is no inconsistency in the idea that phenotypic change occurs through phyletic evolution within an adaptive radiation (and not during the

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[67] See earlier, parts II and IV of this chapter.

splitting events involved in the radiation). Third, While Simpson distinguishes between adaptive types and variations within adaptive types, he rejects the two-staged view of phenotypic evolution suggested by Douglas Erwin. Instead, as stated previously in section II of this chapter, Simpson favours a “mosaic” view of evolution. There is no inconsistency between the concept of adaptive type and the mosaic view since the former is a flexible and multi-level concept.

Now that these clarifications on the theory of adaptive radiation have been given, I can turn to the concept of preadaptation. I will look first at its origin and then turn towards its different uses during the Modern Synthesis era.

Preadaptation and novelty

The logic of what I have called the functional-historical approach to novelty and its origin in Darwin and Dohrn has been analysed in chapter 1. Here I will focus on the development of this approach in the Modern Synthesis era. The interest of focusing on the concept of preadaptation is that it is put to divergent uses by different Modern Synthesis biologists, which makes clear the distinction between different research questions. While George Gaylord Simpson makes use of it as an explanatory concept of the transitions between adaptive zones, some functional morphologists (e.g. Bock, von Wahlert, Gans) and zoologists (e.g. Mayr), include preadaptation in explanations of the origin of phenotypic novelties. The neglect of these differences in research questions and in uses of preadaptation might explain some of the sweeping generalisations on novelty in the Modern Synthesis era. Before moving to Modern Synthesis uses of preadaptation, I will focus on the creation and use of the concept by Lucien Cuénot.

Cuénot’s concept of preadaptation

The term “preadaptation” itself was coined by the French biologist Lucien Cuénot (1901). Cuénot was dissatisfied with the idea of the creative role of natural selection and insisted on the role of chance and nonadaptatation in the origin of functional characters, for example of defensive mechanisms in insects, which he studied extensively. Cuénot hypothesized that in these cases initially non-adaptive traits, such as the excretion of saliva during a stress reaction, can become defence mechanisms via random mutations, such as when a mutation adds a toxic compound to the saliva. Cuénot later gave the following general definition of preadaptation:

> "I called preadaptive or prophetic characters, or shortly preadaptations, neutral or semi-useful characters that appear in one species and that are susceptible of becoming clear adaptations if that species moves into a new habitat or acquires new behaviours, these latter changes being made possible precisely by the existence of the preadaptations." (Cuénot, 1914, my translation).

Another example given by Cuénot is the genus of cave-dwelling crustacea *Niphargus*, whose members lack eyes and pigment. Cuénot argued that the loss of eyes is not an adaptation to the cave habitat but that it preexisted the move to caves, giving as evidence the presence of some species of *Niphargus* in surface waters. The mechanism for the loss of eyes is thus unknown but *Niphargus* was preadapted for a move to caves. The related example of the blind cavefish was frequently used in early discussions of preadaptation (cf. Hubbs, 1938; Simpson, 1953). Although Cuénot's theoretical outlook was complex and evolving (Grimoult, 2001), he was associated with mutationism (e.g. Fisher and Stock, 1915; Mayr, 1963). Furthermore, preadaptation was used by Goldschmit and Schindewolf to refer to the property of some hopeful monsters of being immediately adapted to a new environment[68].

Simpson's use of preadaptation

By the middle of century, in *The major features of evolution,* Simpson notes that preadaptation has taken up a variety of different meanings. He writes

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[68] For example: "I need only quote Schindewolf (1936), the most progressive investigator known to me, who showed that the material presented by paleontology leads to exactly the same conclusions as derived in my writings, to which he refers. He elaborates the thesis that macroevolution on a higher level takes place in an explosive way within a short geological time, followed by a slower series of orthogenetic perfections, as exemplified in the oft-quoted evolutionary series. *He realizes that the conception of preadaptation accounts completely for this type of evolution.*" (Goldschmidt, 1940, p.395, emphasis added)

that Cuénot's definition is the strictest one[69] but it refers to only one of nine types of phenomena associated with the concept. For that reason, and because of the mutationist connotation associated with the concept, Simpson prefers coining the expression "prospective adaptations" to refer to this large class of phenomena:

> "Prospective adaptation is not a quite distinct sort of adaptation or even a clear-cut analytical category of adaptations. It is an aspect of adaptation in general or, if you prefer, a direction of looking at adaptation: it is the possession of characteristics making possible a change in adaptation and on which the new adaptation is built. Probably all organisms except the most extremely narrowly specialized, and perhaps even those, do have characteristics that would permit some adaptive change." (Simpson, 1953, p. 189)

The concept of prospective adaptation fits into Simpson's view of evolution as changes in the interrelationships between organisms and environments. Evolution does not only consist in the progressive fine-tuning of organisms to their adaptive zone, it is also made of transitions between these adaptive zones, or of creation of new adaptive zones. These transitions are caused by an interplay of factors: some are physical, such as a climatic change or the migration of a population, some are behavioural or ecological, such as the adoption of a new feeding habit, some are genetic or mutational, such as the appearance of a new form of tooth. To make sense of changes of adaptive zone without physical changes of the environment, Simpson develops the concepts of "prospective functions" and "realized functions" attributed both to the organism and the environment, as shown in the diagram below:

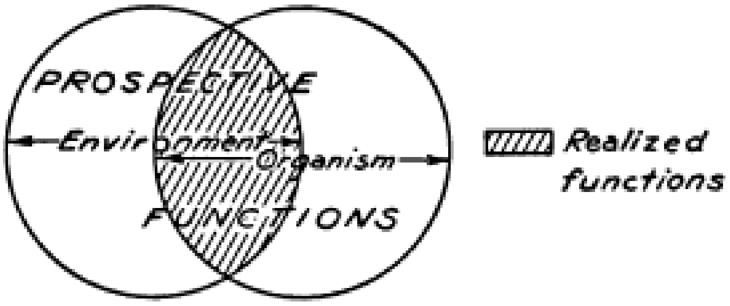

Fig. 9: Diagram of the realisation of functions (after Simpson, 1953, p.185)

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[69] "A character nonadaptive or inadaptive in an ancestral group may be adaptive in a descendant group. This is preadaptation in the strictest sense of the word." (Simpson, 1953, p. 192)

The diagram could suggest a rather static picture, with organisms progressively filling pre-existing niches, or prospective functions, of the environment. But Simpson stresses the fluctuating nature of the relationship between organism and environment, that changes in realized functions lead to changes in the set of prospective functions[70]. Within this conceptual framework, prospective adaptations are traits that allow the transitions from prospective to realized functions.

The two main conceptual divisions within Simpson's list of prospective adaptations are the one between those that involve genetic changes and those that do not, and the one between those that were adaptive in the previous condition and those that were non-adaptive in the previous condition (Cuénot's preadaptation). Among the prospective adaptations that do not involve genetic changes, Simpson includes:

a) an adaptation that allows the transition from a broader to a narrower habit, such as the transition from a polyphagous to a monophagous species.
b) An adaptation to an ecological niche that permits the transfer to another niche, for example plants with adaptations to desert soils are preadapted to the epiphytic condition (growing on the surface of other plants).
c) An adaptation that assumes a new function, such as the broad digging foot of the platypus that is used for swimming.
Among the prospective adaptations that involve some genetic changes, Simpson includes:
d) Mutations causing phenotypic variations in the direction of an existing adaptive trend.

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[70] "The extent of realization of functions tends constantly, although usually slowly, to change. Prospective functions have a certain short-range stability, but also tend to change; in fact, change in their realization normally changes their overall extent and nature" (Simpson, 1953, p. 185).
Here are two illustrations of this process: "When radiation does occur in a zone, it usually happens that this entails not merely an occupation but also a considerable expansion of the zone and changes in many of its features. Although the land carnivore zone of today has developed from that of the Paleocene, it is tremendously broader and so different that it does not even include any animals adaptively very similar to the earliest carnivores-the smaller bears are perhaps as nearly similar as any, and they are a late group, not a survival. Another rather frequent development, not sharply distinguished from the last, is spread from the occupied zone into others more or less different, as exemplified by the pinnipeds among carnivores." (Simpson, 1953, pp. 349–350)

e) Mutations creating a new adaptive trend; Simpson uses the expression "*key mutation"* to describe the phenomenon and gives the example of the origin of claws in taeniodonts (an extinct early group of non-placental mammals) that, according to Bryan Patterson initiated the differentiation of stylinodontine taeniodonts. In this case, "a single orthodox mutation resulting in the development of claws is believed to have been the starting point of the new adaptive shift represented by the Stylinodontinae" (Patterson, 1949). The acquisition of the claw is a key change because the digging behaviour associated with this character initiated a switch into a new adaptive zone.

f) A trait that becomes adapted to a new environment by intensification, such as adaptations to extreme cold in the penguin *Aptenodytes forsteri* that are intensifications of traits found in its relatives.

g) A trait that acquires a new function by intensification or continuation, for example incisors in the seal *Leptonychotes weddelli* are used to cut breathing holes in the ice and are larger than incisors found in close relatives.

h) A "structure adaptive in one way in an ancestral group may be transformed to serve quite a different function in a descendant group". The examples that Simpson gives for this category are the ones most likely to qualify as evolutionary novelties: "transformation of the reptile walking limb to the bird flying wing or of the mammalian walking limb to the bat flying wing or the cetacean swimming paddle; transformation of reptilian jaw articulating bones to mammalian auditory ossicles; transformation of breathing lung to hydrostatic bladder in fishes and later incorporation of the bladder in the auditory apparatus; and many others" (Simpson, 1953, pp. 191–192).

Thus, Simpson has a very inclusive and loose definition of prospective adaptations. His most questionable inclusion is that of simple favorable mutations (d). Furthermore, Simpson mixes cases where the focus is on a single character (c, e, g, h), and cases where the focus is on the adaptation of whole organisms to environments, which implies the involvement of several different characters (a, b, f). Some are cases of change of function of a character (c, e, g ,h), while others are cases of intensification of the same function (f). Finally, some cases arguably only involve quantitative morphological change (c, e, g), while others involve qualitative change (h). At the same time, Simpson's concept is strongly determined by his framework of adaptive radiation. One of his main concerns is whether preadaptations in the sense of Cuénot ever occur or whether they are adaptive all along. Whereas Darwin relied on his principle of conversion of function to defend gradualism, Simpson accepts that new characters are initially created by mutations and that these can be of large effect. He insists however that to be fixated these changes need to be adaptive “from the start” (p. 195). He allows exceptions to this rule, relying on Sewall Wright’s shifting balance theory to explain them, but insists that “the phase during which they are nonadaptive or inadaptive must usually if not always be very short in terms of geological time” (p.195).

Key mutations, key innovations and ecological opportunities

Most importantly, as stated before, Simpson’s main concern is to show how preadaptations can explain the transition between, or creation of, adaptive zones. Some of these transitions may involve the origin of evolutionary novelties, the two main candidates being “key mutations” (e), and transformed structures (h), but some other transitions do not imply novelties. Importantly, although he does not explicitly make this distinction, Simpson is more focused on the preadaptation of organisms to new habitats than in the preadaptation of phenotypic characters to new functions.[71] While Darwin devised the concept of conversion of function partly to explain how ecological evolution can drive morphological evolution and produce evolutionary novelties, Simpson does not have the latter as a direct explanatory target. For Simpson, the central research question in relation to which the concept of preadaptation is developed is: how do *ecological opportunities,* allowing to enter into new adaptive zones, occur?

This focus on ecological opportunities allowing for switches into new adaptive zones was shared by several other researchers of the time. Close to Simpson’s key mutations was the concept of key innovation, introduced by Alden Miller and defined as "key adjustments in the morphological and physiological mechanism which are essential to the origin of new major groups"(Miller, 1949). With Simpson’s key mutation, there is a focus on the genetic nature of the change produced as well as its ecological consequence. In comparison, the concept of

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[71] This distinction is stressed by Mayr (1960, pp. 364–365).

key innovation does not imply a specific mechanism of origin. Furthermore, Simpson's key mutations as well as his general concept of prospective adaptation is primarily focused on the access to new adaptive zones and not on the subsequent radiation. A character can be a prospective adaptation whether or not the switch to the new zone led to a bursting radiation. For example, the stylinodontine taeniodonts did not diversify into many species. Key innovations as defined by Miller had a similar meaning, the focus was on the characters deemed crucial in the formation of new taxonomic groups; whether the group was very successful in terms of number of species was not a determining factor.

However, the meaning of the concept progressively changed towards the end of the Modern Synthesis era influenced by an increasing number of studies focusing on key characters hypothesised to have been instrumental in rapid adaptive radiations. A key innovation became not a character initiating the formation of a new group but a character initiating a radiation involving the rapid formation of many species (Alfaro, 2014; Galis, 2001). The most influential of these early studies of key innovations was the work of Karel Liem on the relation of the cichlid fish pharyngeal jaws to the explosive radiations of this fish in different lakes (Liem, 1973).

Even though the work of Liem is also focused on the genetic and developmental mechanisms of the origination of the cichlid specific pharyngeal jaw, the common main focus of Simpson's work and of studies of key innovations is on the evolutionary effects of the chosen characters, whether ecological opportunity or evolutionary success, rather than on the causes and process of origin of new characters. I will now turn to another research program making use of the concept of preadaptation with a focus on origin rather than evolutionary fate. Simpson's ecological framework and studies of key innovations are often referred to when picturing the Modern Synthesis' approach to novelty. In contrast, the following research program centred on functional morphology has been neglected.

The development of preadaptation by functional morphologists

Recent depictions of research on novelty in the Modern Synthesis tradition usually combine claims of the neglect of novelty and of the absence of theoretical and empirical tools to tackle the problem, with a cursory presentation and dismissal of the ideas and research presented in Mayr's 1960 paper "The emergence of evolutionary novelties" (e.g. Müller and Newman, 2005a, 2005b; Müller and Wagner, 1991). What is rarely noticed is that Mayr's contribution is not a single and short-lived attempt at cobbling together hypotheses to tackle a neglected problem. On the contrary, Mayr's article coincides with the rise of a research program combining functional and evolutionary morphology and ecology, and refining and applying to case studies the concepts presented by Mayr. This program produced new conceptual and empirical developments of the idea of preadaptation. It can be situated within the framework of the ecological theory of adaptive radiations laid out by Simpson but it is not a simple application of Simpson's ideas to case studies.[72] This development is original in its shift in emphasis compared to Simpson (Bock, 1959, p. 194): from the ecological opportunities offered by the prospective adaptations to the mechanisms of emergence of phenotypic novelty through the interactions between prospective adaptations and environment. There is also a shift in the degree of generality, from the formulation of general mechanisms to the explanation of particular evolutionary sequences:

> "The major problem associated with the question of the adaptive origin of higher taxa lies, I believe, not with the known mechanisms of evolutionary change but with the description and analysis of the events involved in the origin and development of new groups. This facet of the problem has not received the attention it deserves from supporters of the synthetic theory of evolution; indeed, most analyses of the origin of new groups are very vague and weak in their discussion of the sequence of events involved." (Bock, 1965, p. 274)

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[72] The representation that these researchers had of their relationship to the Modern Synthesis is well expressed in the reaction of two of them, Walter Bock and Gerd Von Wahlert, to a paper by Marjorie Grene comparing Simpson's and Schindewolf's theories: "The basic ideas used by most morphologists today are in complete agreement the synthetic theory of evolution, if not based completely upon it. The synthetic theory is not founded upon the determination of ignoring structure, it is concerned with examining and understanding structure as structure as well as its genetical and development bases. It is, thus our belief that by accepting Schindewolf's position as typically representative for all morphologists, Grene was deceived about the true relationship between morphology and the synthetic theory and was unable to understand Simpson's inquiries into the genetical bases of structure and of macroevolutionary changes" (Bock and von Wahlert, 1963, p. 142)

The shift in emphasis is linked to differences in the biological disciplines of the researchers involved. The concept of preadaptation is developed mainly by morphologists. Most prominent among those who both developed the concept theoretically and used it in case studies were Walter Bock, Gerd von Wahlert and Carl Gans. Bock and von Wahlert speak of a “current revival of morphology” that “is heralded by a flourish of studies in functional anatomy with the general result being a renewed focus of interest in the problem of organic form.” (1965, p.269). What characterizes this revived morphology is an integration of form, function and environment, although Bock and von Wahlert note that “the traditional considerations of pure morphological description and of the phylogenetic change of morphological form are not ignored” (Bock and von Wahlert, 1965, p. 269). The fact that this research program in morphology is placing itself fully under the framework of the Modern Synthesis is at odds with the repeated claim that morphology did not contribute to the Modern Synthesis (Coleman, 1980; Ghiselin, 1980). This judgment may be caused by the restriction of the definition of morphology to a descriptive and comparative science and by the absence of focus on the late phase of the Synthesis (after 1950).[73]

It is actually quite limiting to define these researchers as solely morphologists. This is especially true of Carl Gans (1923-2009), a herpetologist with a background in mechanical engineering, who made contributions in the fields systematics, functional and evolutionary morphology, biomechanics and physiology and was a pioneer of integrative biology (Gans, 1974; Adler, 2011). Walter Bock (born in 1933) is an ornithologist, close to Ernst Mayr, who combined from early on empirical work in avian functional and evolutionary morphology and systematics, and theoretical work in evolutionary biology. Gerd von Wahlert (1925-2016) was an ichthyologist and general biologist, less influential than Gans and Bock partly because he mostly published in German.

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[73] “How much, if anything, morphology contributed to the modern synthesis is partly a matter of how one defines that term. In the strict sense, morphology is a purely formal discipline and had very little to contribute. Morphology may also be considered a kind of data, and when it becomes functional a better case can be made for its role in evolutionary studies. Be that as it may, the incorporation of morphology into the synthesis was a later development.” (Ghiselin, 2006)

For the sake of brevity, I will concentrate on the work of these few individuals, although they were not the only ones to apply a functional approach to the study of evolutionary novelties in that period.[74] For example, there were related developments of the approach of functional morphology in invertebrate paleontology, such as the method of "paradigms" aimed at inferring the functions of fossil characters from their structures and thus their ways of life (Rudwick, 1964). This research program was primarily focused on functional analysis independently of evolutionary considerations, but it was also applied to trace the evolution of echinoderms or brachiopods (Nichols, 1967; Rudwick, 1970)[75]. This functional approach in paleontology was first advocated by Stephen Jay Gould (Gould, 1970) before his later turn against adaptationism (Gould and Lewontin, 1979; see Rudwick, 2017, 2018). Although I will not provide an extensive review here, I will give a few other examples of the use of functional morphology to infer the evolution of higher taxa and new characters. These studies did not all use the concepts of preadaptation and functional shift in their explanations but manifest a common trend in methods and theoretical commitments: the origin of the heat-sensing pit organ of pit vipers (Dullemeijer, 1959); the evolution of the head in a teleost fish (Liem, 1967); of tail autotomy in salamanders (Wake and Dresner, 1967); the origin of the mammalian lower jaw (Crompton and Parkyn, 1963); of the jaw of bolyerine snakes (Frazzetta, 1975, 1970); the origin of the coelom (Gutmann, 1966; see Gudo, 2002); of wings and flight in insects (Flower, 1964; Wigglesworth, 1973, 1963); of the insect ovipositor (Scudder, 1964, 1961); of the protrusile tongue in salamanders (Lombard and Wake, 1977, 1976; see Griesemer, 2013); the evolution of characters in arthropods, such as those associated with locomotion (Manton, 1972, 1977); the evolution of some mollusks (Yonge, 1969); of some crustacea (Fryer, 1968); of ceratopsian dinosaurs (Ostrom, 1966).

How is the concept of preadaptation developed by these functional morphologists different from Simpson 's concept? How does it apply to the explanation of the

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[74] There are many other important figures in this movement in functional morphology in the late Modern Synthesis era. My choice here is informed by the use of the concept of preadaptation and by space restrictions. Particularly important on the theoretical front are Pieter Dullemeijer (Dullemeijer, 1980, 1959) and Wolfgang Gutmann (Gutmann, 1966; see Gudo, 2002).

[75] See Rudwick (2018, 2017) for a historical account of this research program.

origin of novelties? Bock is critical of the looseness and confusion in Simpson's use of preadaptation (Bock, 1959, p. 201). While Simpson does not make any direct reference to Darwin's conversion of functions or Dohrn's succession of function, in his own formulation of preadaptation, Bock makes this filiation explicit:

> "The definition of preadaptation that I shall adopt is close to Dohrn's original one and to the one implied by most authors. A structure is said to be preadapted for a new function if its present form which enables it to discharge its original function also enables it to assume the new function whenever need for this function arises." (Bock, 1959, p.201)

As it was shown in chapter 1 with Bock's study of the origin of the avian medial brace, the concept of preadaptation is used by these researchers as a guiding principle in the understanding and explanation of the origin of evolutionary novelties. However, their range of explanatory strategies and concepts was rich and should not be reduced to the preadaptation. Several critiques of Modern Synthesis approaches to novelty (Bonner, 1982, pp. 282–283; Gould and Vrba, 1982; Müller and Wagner, 1991) have focused on problems with the concept of preadaptation, its complex origins, polysemy and teleological connotations, and have neglected the contributions of this research program in functional morphology by not focusing on the detail of their explanations.

The articulation of selection and contingency

Two essential elements of these functional explanations of the origin of novelties are the action of selection pressures and the role of historical contingency. The evolution of new structures is conceived as the interaction of adaptive and non-adaptive factors. At least four important features of these explanations should be stressed:

a) The role of epigenetic mechanisms in the emergence of novelties.
b) The multiplicity of historical events and selection pressures leading to transitions in morphology and ecology.
c) The multiplicity of evolutionary pathways to adaptations.

d) The role of behaviour and behavioural explorations and innovations in the origin of novelties.

I will address each in turn.

a) Epigenetic mechanisms

The role of epigenetic mechanisms has been illustrated by Bock's example of the avian basitemporal articulation. Bock will later call the epigenetic mechanisms he appealed to in the example of the avian medial brace "somatic adjustments" and he will stress their essential role in the emergence of novelties (Bock, 1979, p. 26). The progressive genetic assimilation of the process is a possibility but not a central part of the explanation[76]. More generally, the explanations of the origin of novelties within this tradition of functional morphology rarely involve a genetic component. These explanations involve units (tissues, morphological characters, behaviours etc. …) and causes (selection pressures, mechanical forces, tissue interactions etc. …) pertaining to higher levels of reality. The explicit endorsement of the Modern Synthesis perspective by Bock and Van Wahlert and more generally the compatibility of the research program with the Modern Synthesis comes from a commitment to the role of natural selection and the rejection of orthogenesis, saltationism and Lamarckism rather than from a use of population genetic explanations or a commitment to random genetic mutations of small effect as the sole pertinent causal unit of change.

A few explanations explicitly refer to epigenetic mechanisms. Other explanations are best described as agnostic regarding the genetic and epigenetic mechanisms involved in the evolutionary change. This is for example the case with Gans's explanation of the origin of the snake jaw (Gans, 1961). Gans distinguishes three research questions: "(i) What was the change that established the selective

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[76] This is not developed by Bock in his early papers. Bock later clearly stated that genetic assimilation was, according to him' not a necessary part of the process: "Sometimes these phenotypic changes do acquire a direct genetic basis as shown over a century ago by Baldwin (1896), and discussed ever since by evolutionists as the Baldwin Effect. But I suspect that more frequently phenotypic changes resulting from physiological adaptation never, or only very slowly acquire a direct genetic basis. For example, many groups of birds possess an articulation between the medial process of the mandible and the base of the brain case (Bock 1960) or, between the mandibular ramus and the ectethmoid plate as in the Australian honey-eaters (Passeriformes: Meliphagidae; Bock & Morioka 1970)." (Bock, 2002, p.69)

advantage for a fundamentally different feeding mechanism snakes? (Or possibly: What change was possible because a different feeding apparatus arose?); (ii) How did such a mechanism evolve?; (iii) What ophidian modifications may be viewed as secondary reflections of the functional and structural shift?" (Gans, 1961, p. 217). Regarding the mechanism, Gans locates the crucial process in the liberation of the mandible through the suppression of the mandibular symphysis. The entities involved are bones, nerves and muscles as well as feeding behaviours, and the explanation focuses on the functional and mechanical conditions of the phenotypic shift.

b) Multiple historical events

The historical dimension is essential to explanations involving preadaptation. The concept implies that the formation of a character is not explained by its current function(s) and involved a historical shift. The historical dimension is essential and becomes in general more complex when the focus is transferred form the origin of a single novelty to the origin of a higher taxon. As noted earlier, Bock (1965, p. 274) stated that the weakness of the Modern Synthetic treatment of the origin of taxa is not in the evolutionary mechanisms proposed but on the details of the historical events for each particular taxon. The origin of some new taxon cannot be explained by single shift between adaptive zones, but involve a complex history possibly involving multiple changes in ecological conditions. This is illustrated by Bock's hypothesis on the origin of diagnostic characters of birds through a series of functional shifts (climbing, leaping between trees, parachuting, gliding, active flight) involving multiple successive or simultaneous selection pressures rather than a single switch between two broad adaptive zones (Bock, 1965).[77]

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[77] "The avian tibiotarsus and tarsometatarsus and the reversed pubis evolved in connection with bipedal locomotion; the reversal of the hallux with arboreal life; feathers, warm-bloodedness, and perfection of sight and hearing with a later stage in arboreal life; the wing and flight feathers, balance, and the beginnings of the rigid trunk with the stages of leaping, parachuting, and gliding. The enlarged sternum and its keel, flight muscles, the final fusion of the synsacrum and other parts of the skeleton, loss of teeth and many other features appeared only in a late gliding stage, or after active flight was achieved." (Bock, 1965, p. 178)

c) The multiplicity of evolutionary pathways

Another form of contingency playing a role in the functional-historical approach is the existence of multiple evolutionary pathways (Bock, 1959; Bock and Miller, 1959; Bock and von Wahlert, 1965). This is stressed for example by Bock in the example of the medial brace:

> "There are several ways to counteract strong forces on the quadrate hinge. In some families, the condyles of the quadrate hinge are completely adequate to withstand the disrupting forces; in others, the jaw muscles and ligaments inserting on the mandible may be sufficient to protect the quadrate hinge. A discussion of these other methods of preventing the disarticulation of the mandible would lead us too far from the central problems of this paper, hence I shall quite arbitrarily accept the development of the medial brace as the only adaptive response to the selection force for additional support of the mandible." (Bock, 1959, p. 196)

d) The role of ecology and behavior

The rise of the research program in functional morphology was related to a surging interest in behaviour and in the relation between behaviour and evolution (Corning, 2013), illustrated for example by the 1958 volume edited by G.G. Simpson and Anne Roe entitled *Behavior and evolution*. While some, like Romer or Colbert, focused on the complex physiological and morphological underpinnings of behaviour and on the dependence of the latter on the two former, Mayr insisted, after Konrad Lorenz, that behaviours often precede the evolution of the correlated morphological structures (Mayr, 1958). Mayr developed the idea in his article on evolutionary novelties[78], later defining behaviour as the "pacemaker" in evolution (Mayr, 1976, p. 106, see also 1974).

This approach is shared by Bock, Von Wahlert, Gans and others (Bartholomew, 1964; Bock, 1959; Gans, 1963; Wahlert, 1965). Wahlert for example argues that:

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[78] "It is now quite evident that every habit and behavior has some structural basis but that the evolutionary changes that result from adaptive shifts are often initiated by a change in behavior, to be followed secondarily by a change in structure (Mayr, 1958). It is very often the new habit which sets up the selection pressure that shifts the mean of the curve of structural variation." (Mayr, 1960, p. 371)

> "The actual evolutionary effect of […] environmental factors is in part determined by the organisms exposed to them. A population of hares may be threatened by wolves invading their habitat. The hares may cope with this danger by trying to outrun the wolves; this would establish a selection force favoring and resulting in an increase of speed. Or the hares may try to out-maneuver the wolves or to escape by rushing into holes; either method would induce the operation of a quite different selection force, although the ecological factor remains the same." (Wahlert, 1965, p. 296)

A note on Baldwin effect, stabilizing selection and genetic assimilation

The dominant contemporary view regarding the relation of the Modern Synthesis to behaviour seems to be that the latter was neglected and that its role in evolution was considered minor. This view may stem from a limited focus on the "Baldwin effect".[79] A focus on the research program that I just described should refute that appreciation, at least for a part of the late Modern Synthesis. Furthermore, the Badwin effect itself was not rejected (Simpson, 1953, p. 183; see Corning, 2013). There is a close relation between this research program and the concepts of Baldwin effect, Schmallhausen's stabilizing selection and Waddington's genetic assimilation. I will not cover these concepts in detail for lack of space, and because they were less directly applied to the problem of the origin of novelties. The Baldwin effect in particular, is more focused on genetic stabilization than on novelty and change[80]. It is focused on the physiological or behavioural initiation of new traits followed by natural selection for their genetic determination. Examples of the Baldwin effect studied during the Modern Synthesis era are new bird songs, the new preferences for different food sources and plants (e.g. Simpson, 1953).

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[79] For example: "The irony is that the great palaeontologist, George Gaylord Simpson (1953) who coined the term ["Baldwin effect"] did so in order to disparage it. He and many others who forged the new synthesis did not think that behaviour played an important role in evolution. This became the standard line of neo-Darwinists." (Bateson, 2004)

CONCLUSION

The weaving together of novelty and adaptation in the functional-historical approach prompted me to embark on a reassessment of the place of novelty in the Modern Synthesis era. A guiding principle was that one should not conclude that novelty was not addressed or neglected from the fact that it was not clearly singled out and isolated as an independent problem.

Two main general conclusions emerge at the end of this chapter:
_ First, for all the research themes covered (species and speciation, higher taxa, levels of organisation and adaptation) there are some research programs which address, more or less directly, the problem of the origin of novelties.
_ Second, one cannot summarise in a simple, straightforward way the position of the Modern Synthesis on the problem of novelty, either in terms of whether it was neglected or not, or in terms of the Synthesis' explanation of novelty. There are multiple answers regarding both aspects.

To support the first conclusion, one can refer to experimental taxonomy in botany, to the close connection between research on the origin of the angiosperm and research on the origin of the flower, to the overlap between the question of the origin of new grades and the question of the origin of novelty, and finally to the use of the concept of preadaptation by functional morphologists in the explanation of the origin of novelty.

To support the second conclusion, one can rely on several contrasts: first, the rise of speciation studies and of the biological species concept separated the process of the origin of new character and the process of speciation, however some experimental plant taxonomists, especially by focusing on hybridization and polyploidy, combined the study of speciation and the study of novelty. Second, among botanists focusing on the origin of the angiosperm, some do adopt an ecological and biogeographical focus with little interest for angiosperm novelties, others consider the problems or the origin of angiosperm taxa and angiosperm novelty as inseparable; and this distinction does not coincide with the one between Modern Synthesis proponents and opponents. Finally, while G. G. Simpson adopts and ecological standpoint, and is interested not in how novelties originate, but rather in how novelties, among other factors, can allow organisms to seize ecological opportunities and switch between adaptive zones, some functional morphologists, who claim their allegiance to the Modern Synthesis, focus on the problem of the origin of novelty within the theoretical framework of the Synthesis.

CHAPTER 3 – NOVELTY IN THE MODERN SYNTHESIS ERA. Part 2: THE PLACE OF DEVELOPMENT AND CONTROVERSIES

INTRODUCTION

In the last chapter, I focused on concepts and research programs central to the Modern Synthesis which are closely, and sometimes ambiguously, related to the problems of evolutionary novelty. In this chapter, I will address more directly debates regarding the historical representations of the Modern Synthesis and focus on elements in the history of research on novelty that can directly contribute to these debates. More precisely I will focus on three dominant representations of the Modern Synthesis: 1) It is centred on population genetics; 2) It did not integrate development in its framework; 3) It arrived at a consensual theoretical framework and this consensus hardened in the late phase.

The population genetics view of the Modern Synthesis

The Modern Synthesis is nearly unanimously associated with reconciliation of the Mendelian particulate theory of heredity with Darwin's theory of gradual evolutionary change under natural selection thanks to the elaboration of population genetics led by Ronald Fisher, John Haldane and Sewall Wright (Gayon, 1998; Provine, 1978, 2001). The debate regards the relation of the Modern Synthesis to population genetics: should it be interpreted as the application of the principles and results of populations genetics to other biological disciplines, or should it be interpreted as a synthesis of contributions from different disciplines, population genetics being only one of them?

The major part of the literature calling for an Extended Synthesis or an evo-devo synthesis adopts the first interpretation of the Modern Synthesis (Amundson, 2005; Craig, 2014; Laland et al., 2014; Laubichler, 2010, p. 201; Müller & Newman, 2005; Müller & Pigliucci, 2010, pp. 13–14; Stoltzfus, 2017). The competing interpretation is defended for example by Stephen Jay Gould (2002, pp. 532–541) or Ernst Mayr (1980). This second interpretation denies that the Modern Synthesis can be viewed as an alignment on genetics, or as Stephen Jay Gould phrases it, "a whipping of older disciplines into line" (Gould, 2002, p. 532). According to this alternative view, the naturalist disciplines were constitutive in the formation of the synthesis and not secondary. Gould sees Theodosuis Dobzhansky as the one who initiated the synthesis by reinstating the diversity of species as the central problem of evolutionary theory. Mayr expressed this view very strikingly[81]:

> "Actually, nothing in the supposedly evolutionary writings of T.H. Morgan, R.A. Fisher, and J.B.S. Haldane explained the multiplication of species, the origin of higher taxa, and the origin of evolutionary novelties. Their interpretation concerned the gene level in a single gene pool." (Mayr and Provine, 1980, p. 11)

Many of the materials presented in the last chapter can be used as evidence in favour of this second interpretation.

The exclusion of development from the Modern Synthesis

Few historical works about research on novelty have focused on continuities between the Modern Synthesis and contemporary eras. Historical works on evo-devo, both by scientists and by professional historians have emphasised the continuity between their contemporary problems and methods and old research traditions in experimental embryology (*Entwicklungsmechanik*), comparative embryology and comparative morphology (Amundson, 2005, 2007; Gilbert, Opitz, & Raff, 1996; Laubichler & Maienschein, 2007; Love & Raff, 2003; R. Raff, 1996; R. A. Raff & Love, 2004). This continuity is rather presented as a resurrection since these old research traditions were excluded by the rise of

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[81] Ironically, very similar statements can be found in some of the recent writings of proponents of an Extended Synthesis with the only difference that the name of Mayr himself (and maybe those of other architects of the Modern Synthesis) would be added to the list.

classical genetics and of the Modern Synthesis (Allen, 1980, 1986; Amundson, 2005; Gilbert, Opitz, & Raff, 1996; Hamburger, 1980). The history of the mutual exclusion of evolution and development at the beginning of the 20th century and during the Modern Synthesis era has been investigated by many. Some of the historical works on individuals who tried to build bridges between evolution and development have corroborated the thesis of the mutual exclusion because these individuals were outsiders (Burian, Gayon, & Zallen, 1991; Dietrich, 1995, 2003; Gilbert, 1994; Peterson, 2011). A minority of authors have argued for a revision or tempering of the mutual exclusion thesis (Davis, Dietrich, & Jacobs, 2009; Love, 2009). Others have focused on the exclusion of other disciplines from the Synthesis (morphology, macroevolutionary theory), implying or explicitly arguing that development should not be singled out as the sole excluded dimension (Coleman, 1980; Ghiselin, 1980; Gould, 2002; Love, 2003, 2005, 2006).

In narrations of the mutual exclusion of evolutionary biology and embryology during the Modern Synthesis era, a considerably stronger emphasis has been put on the rejection of embryology by architects of the Modern Synthesis than on the rejection of evolutionary concerns by embryologists. The model of the relation between development and evolution that was the most influential among developmental biologists at the beginning of the 20th century was Haeckel's recapitulation theory. Haeckel had argued that the evolutionary history of living beings was inscribed in the individual organism's development so that the stages of development of an organism from a certain species corresponded to the stages of the evolutionary history leading to that species. According to Hamburger (1980), developmental biologists considered it an important endeavor to refute the recapitulation theory well into the 1930s (De Beer, 1951; Smit, 1962). This refutation was driven by the growing body of experimental studies in embryology. With the rejection of the recapitulation theory came a decrease in the interest in the link between development and evolution. Hamburger's thesis is that the distance of the embryologists from the concerns of the Modern Synthesis came not from a stagnation of their discipline but on the contrary from different advances of a mechanical and experimental perspective in embryology (see also Maienschein, 2007).

Even the most virulent proponents of the idea of an exclusion of development during the Modern Synthesis era have recognized points of contact (e.g. Amundson, 2005, pp. 189–197). Ronald Amundson singled out the work of Sewall Wright, Oxford morphologists (Edwin Goodrich, Julian Huxley and Gavin de Beer[82]), Conrad Waddington, Ivan Schmallhausen and Richard Goldschmidt. The roles of Goldschmidt[83], Schmallhausen[84] and Waddington[85] have especially attracted the attention of scholars. Alan Love focused on lesser known figures, comparative embryologist Norman John Berrill, morphologist D.Dwight Davies and palaeontologist William K. Gregory (Love, 2003, 2005, 2006, 2007). In the domain of plant biology, much fewer historical works have focused on the relation between the Modern Synthesis and developmental biology. The studies of historical traditions related to contemporary plant evo-devo concentrate on figures with no or very little relation to the Modern Synthesis, such as British

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[82] On Oxford morphologists, see also Waisbren (1988). Among them, Gavin de Beer has attracted the most attention. He is credited in particular for developing the study of heterochrony (Brigandt, 2006; De Beer, 1951).

[83] Richard Goldschmidt was more clearly marginalized because he was characterized as a mutationist, although his work on physiological genetics was unanimously respected (Cf. this chapter, I.2) and cited references).

[84] On Schmalhausen and his relation to the Synthesis,, see for example Gilbert (1994), Levit et al. (2006), Olson et al. (2010).

[85] See for example Gilbert (1994), Peterson (2011). The relation between Waddington and the architects of the Modern Synthesis was complex. The position of Waddington as an outsider has been more emphasized than his influence on evolutionary biology on some of the central figures of the Modern Synthesis, and more generally on the evolutionary biology of this era . For example, Peterson (2011) insists on the disagreements between Waddington and Mayr. He focuses on a specific incident of particular interest for the subject of this chapter: prior to the 1959 Darwin centennial conference in Chicago, papers were circulated among the participants. Waddington was particularly interested in Mayr's paper, which was to become the influential "The emergence of evolutionary novelties" (Mayr, 1960). In his commentary of Mayr's paper, Waddington wrote: "the major argument in favour of [saltation in] evolution is nowadays in embryology and that this requires rather special discussion" (Waddington to Mayr, 22 June 1959, cited by Peterson, 2011, p.315). As noted by Peterson, Mayr did not reply to Waddington's comments. Peterson goes on to write: "But it is clear from earlier correspondence that Mayr regarded much of European embryology as "riddled with metaphysical concepts" (Mayr to Waddington, 20 July 1959, CHW-UEL, MS 3035.3). Mayr's feelings may have extended to Waddington's philosophy as well, especially considering some of the misgivings expressed above." (Peterson, 2011, p. 315). However, Peterson does not mention the influence of Waddington on the idea of the homeostasis of the genotype, adopted by Mayr and others, and on Mayr's theory of genetic revolutions. The latter explicitly stated the influence of Waddington on his theorizing (e.g. Mayr, 1963, Chapter 19). Peterson also insists on the way Waddington was sidelined by the 1959 centennial conference. It is true, that Waddington was not a member of the panel entitled "the evolution of life" where the state of evolutionary theory was discussed. However, one of the 16 themes discussed clearly referred to concepts developed by Waddington: "6. The relations of developmental (epigenetic) and physiological processes to selection and evolution are proving to be very important: e.g., stabilization (canalization) of developmental processes, partial simulation of Lamarckian evolution by genetic assimilation and other evolutionary "feedback" mechanisms. The role of pedomorphism and recapitulation in evolution." (Tax and Callender, 1960, p. 108).

botanist Agnes Arber (Classen-Bockhoff, 2001; Vergara-Silva, 2003) and figures in the German tradition such as Goethe and 20th century plant morphologists Wilhelm Troll and Walter Zimmerman (Classen-Bockhoff, 2001; Kaplan, 2001; Vergara-Silva, 2003).

One can find sources even closer to the "centre" of the Modern Synthesis that can question, or at least nuance, the accepted history of a mutual exclusion of developmental and evolutionary biology during the Modern Synthesis era. Indeed, a close study of the interplay between development and evolution can be found in the works of two authors that are considered as "architects" of the Modern Synthesis (Mayr and Provine, 1980). These works are Bernhard Rensch's *Evolution above the species level* (1959) and Stebbins' *Flowering plants* (1974). Both of these works are partly based on the original research of the authors, but they are mostly synthetic works that rely on a wide range of sources and thus give an overview of research trends of the period and not only of isolated, marginal research.

The consensual view of the Modern Synthesis

The literature that is critical of the Modern Synthesis framework often summarises it in a small set of tenets: the centrality of population genetics, gradualism, externalism (natural selection determines the direction of evolution), gene centrism and extrapolation of microevolution to macroevolution (e.g. Amundson, 2005; Laland et al., 2015; Müller & Pigliucci, 2010). This view that the Modern Synthesis can be defined as an unambiguous and consensual theoretical framework appears shared by some historians who have stressed the spirit of consensus that existed between architects of the Synthesis, especially in the late phase. For example, focusing specifically on the 1959 Darwin centenary celebration at the university of Chicago, Betty Smocovitis writes:

> "By the late 1950s, the group including Wright, Dobzhansky, Mayr, Stebbins, Simpson, and, of course, Huxley had worked out many of their differences and had carved out well-defined locations for themselves in evolutionary studies; little was left to spontaneous disagreement." (Smocovitis, 1999, p. 298)

In the same spirit but with a more critical tone, Stephen Jay Gould has argued for a “hardening” of the Synthesis in the late phase, relying as evidence on the 1959 conference and on evolutions in the works of Dobzhansky, Simpson and Mayr (Gould, 1983, 2002).

Other historians have stressed the importance of the social dimension for the analysis of the Modern Synthesis (Cain, 2009; Hull, 2008). For example, David Hull noted that:

> “Scientists are much more interested in the content of science than anything that might count as the social structure of science, but social structure does make a difference. The founders of the synthetic theory of evolution were not really all that much in agreement with each other about the fundamentals of the synthetic theory of evolution - in fact, synthetic theory was not very synthetic - but they agreed to mute their disagreements. They did not go after each other in print.” (Hull, 2008)

The importance of the social dimension should prompt us to be wary of claims of unity and consensus by the actors of the Synthesis and look more closely at implicit dissensions and inconsistencies between scientists and even between parts of the work of each scientist. For example, it would be hasty to deduce too much about the content and status of the Synthesis from a celebration such as the one in Chicago in 1959. Other historians have insisted clearly on the pluralism on the Modern Synthesis[86] (Beatty, 1992; Provine, 1992). A few historians have focused on controversies within the late Synthesis (Beatty, 1987; Gayon, 1998; Rao & Nanjundiah, 2011).

How is the question of controversies within the Modern Synthesis related to the history of research on novelty? The reductive, gene-centric and consensual, view of the Modern Synthesis has served and continues to serve several purposes in the context of theoretical controversies in biology. In the case of evolutionary novelty, this view has favoured the oversight of different approaches to the

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[86] "There were about as many different versions of the evolutionary synthesis as there were major evolutionary biologists associated with it" (Provine, 1992, p. 169). "We cannot let the 'constriction' and 'hardening' of the synthesis blind us to the diversity of possible evolutionary agents being discussed in the fifties, sixties and seventies and to the incredible room still left for controversy about these actual modes of evolution" (Beatty, 1992, p. 188).

problem of novelty pursued during the Modern Synthesis. It has also favoured the partial misinterpretation of certain approaches. For example, the solution of the problem of novelty in terms of functional shift, illustrated by Mayr, Bock and others[87], should not be interpreted in terms of gene-centred gradualism, but rather in an organism-centred perspective integrating ecology, ethology and functional morphology.[88] Asking whether there existed coexisting or competing perspectives within the Modern Synthesis can thus help us with the interpretation of concepts and theories that were devised during this period to address the problem of novelty.

Outline of the chapter

In the first section, I will address the question of the relation between development and evolution by focusing on how this relation is conceived, and articulated to the problem of novelty, by Bernard Rensch and George Ledyard Stebbins.

In the second section, I will address the question of consensus and controversies in the Modern Synthesis by focusing on some debates of the late phase. I will try to show how I. Michael Lerner's theory of heterozygosis-based homeostasis and especially Mayr's theory of genetic revolutions controversially affect the problem of novelty.

I – RESEARCH RELATING DEVELOPMENT AND EVOLUTION WITHIN THE MODERN SYNTHESIS

Bernhard Rensch's *Evolution above the species level*

There are several reasons why Bernhard Rensch (1900-1990) is a particularly important figure in this history of research on novelty in the Modern Synthesis era and in the history of the relation between development and

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[87] See chapter 2, part V.

[88] On the different framings of the problem of novelty depending on different theoretical assumptions, cf. Chapter 1.

evolution. First, in many historical accounts, Bernhard Rensch is included among the "architects" of the Modern Synthesis (e.g. Futuyma, 2015; Levit et al., 2008b; Mayr and Provine, 1998; Reif et al., 2000). Second, his major work, *Evolution above the species level,* which appeared in German in 1947, and in a second edition in 1954 that was translated in English in 1959, contains significant chapters on the problem of the origin of novelties (1959, pp. 126–239 and 266–280) and another one on the different types of alterations of ontogeny during evolution (1959, pp. 239–266).[89] Third, although Rensch was not primarily an embryologist himself, his work uses a wide array of research in experimental and comparative embryology to offer a synthetic treatment of the different possible alterations of development during evolution and their respective potential effects on the production of novelties. And fourth, despite his status, the work of Rensch has been much less studied by historians or philosophers of biology than the work of other architects.[90]

There has been a recent movement among historians towards a restitution of the international nature of the Synthesis, with a special focus on German and Russian contributors. For example, Levit et al. (Levit, Simunek, & Hossfeld, 2008) and Reif et al. (Reif, Junker, & Hossfeld, 2000) credit Erwin Baur (1875–1933), Walter Zimmermann (1892–1980), Nikolai V. Timofeev-Ressovsky (1900–1981) and Gerhard Heberer (1901–1973) along with Bernhard Rensch for the shaping of the Modern Synthesis in Germany. However, it seems that, at the time of the Modern Synthesis, among these German biologists only Bernhard Rensch was considered as an architect by other architects based in Anglo-Saxon countries. For example, in the foreword to the 1959 English edition of *Evolution above the species level*, Theodosius Dobzhansky writes:

> "Together with an attempt by Huxley (1942) which fell rather short of synthesis, we have had the works of Mayr (1942) stemming from zoological and of Stebbins (1950) stemming from botanical systematics and genetics, of Simpson (1944,

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[89] These chapters have been expanded in the 1959 English edition, but there was no significant change in content, in particular in Rensch's view of the relation between evolution and development. I will rely on the 1959 English edition.

[90] The literature on Rensch focuses more on his general philosophy than on his biological work and contribution to the Modern Synthesis. (Delisle, 2008, 2009; Levit et al., 2008b).

> further developed in 1953) from paleontology, of Schmalhausen (1946 in Russian, 1949 in English) from comparative morphology, of Darlington (1939) and White (1945, 1954) from cytology and genetics, and of Rensch (the two German editions in 1947 and 1954) from systematics, comparative morphology and paleontology." (Rensch, 1959, p. v).

A decade earlier, in his review of the first German edition of Rensch's major book, Simpson[91] presented Rensch as "one of the great authorities on speciation in a narrow sense, on what he calls 'intraspecific evolution'", and he noted that his work on speciation is "known to all students of evolution" (Simpson, 1949, p. 178).[92] In *The major features of evolution* (1953), Simpson refers to Rensch's work on 20 different occasions, mainly to the first German edition of *Evolution above the species level.* In another review of the first German edition in the *Quarterly review of biology*, the geneticist Bentley Glass places Rensch's book at the level of the landmarks of the Modern Synthesis by Huxley, Mayr and Simpson, which were unknown to Rensch when he wrote it. Concerning the section on the different forms of alteration of ontogeny during evolution, Glass notes the proximity between Rensch's work and Gavin de Beer's *Embryos and ancestors*, which was also unknown to Rensch (Glass, 1949).

Thus, the central status of Rensch during the Synthesis is not the product of a retrospective historical effort. Rensch was included in the canon of the Synthesis very early on, his work was known and acknowledged by other architects of the Synthesis. He was for example one of the 20 contributors to the volume that emerged from from the 1959 Darwin centennial conference in Chicago. More specifically, Rensch's study of the relation of the different types of evolutionary modifications of developmental processes has not gone ignored or neglected.

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[91] In the preface to *The major features of evolution* (1953), Simpson also includes Rensch's book in his list of synthetic works of major importance: "A number of important summarizing and reviewing volumes in the new spirit of evolutionary theory have also appeared in the last ten years, outstanding among them those by Huxley (1942), Mayr (1942), Heberer (1943), Rensch (1947), Schmalhausen (1949), Stebbins (1950), Carter (1951), and Dobzhansky (1951)." (Simpson, 1953, p. x)

[92] Mayr for example acknowledged Rensch's influence on him: "Rensch cited from the literature and from his own research numerous examples of natural populations that were on the borderline between subspecific and specific rank, and he pointed out that all of these crucial populations were geographically isolated. My own work', Mayr concluded, 'was a continuation of the work of Rensch". (Mayr, 1976, p. 118)."

For example, Mayr explicitly praises this part of Rensch's work in his *Animal Species and evolution*:

> "Rensch [...] has given the best modern discussion of the manifestations of evolution at the various stages of the ontogenetic cycle. He describes the manifold ways in which evolution can affect development and considers critically the various evolutionary theories based on ontogenetic phenomena." (Mayr, 1963, p. 607)

His specific analyses of the origin of new organs and new structures have also been praised, if not fully endorsed by other architects of the Modern Synthesis. Here is for example what Simpson wrote in *The major features of evolution*:

> "Rensch (1947) has treated the origin of new organs and new "structural plans," an essential aspect of the origin of high categories, under "cladogenesis" or phyletic branching. (His discussion of the subject is perhaps the best in print, but seems to me weakened by this approach[93].)" (Simpson, 1953, pp. 354–355)

Alterations of ontogeny and evolution

In his study of developmental alterations during evolution, one of the main goals of Rensch is to show that these alterations do not reveal a directionality brought about by the properties of developmental systems. Rensch seeks to evaluate the degree of validity of the "Biogenetic rule", Ernst Heackel's idea that ontogeny recapitulates phylogeny; and the degree of validity of "Van Baer's rule", Karl Ernst Van Baer's first law stating that the more general characters of a taxonomic group arise earlier in development than the more specialised characters (characters common to the phylum will occur before those common to the class, order, family etc.). In his study of the different types of alterations of ontogeny during evolution, Rensch reuses the typology developed by Nikolai Sewertzoff (1931; Levit, Hossfeld, & Olsson, 2004; Olsson, Levit, & Hossfeld, 2010), modifying some of Sewertzoff's definitions[94]: archallaxis refers to the

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[93] See Chapter 2, part IV for an analysis of Rensch's and Simpson's conflicting views on anagenesis and cladogenesis.

[94] For a summary of Sewertzoff's original definitions, see Olsson et al. (2010).

changes in early stages of ontogeny; deviations are changes in the middle and late stages of ontogeny; anabolia are additions of ontogenetic stages; abbreviations are suppressions of ontogenetic stages, caenogenesis refers to changes in ontogenetic stages that do not result in changes in the adult. Each process can occur at the level of the developing organism or at the level of an organ, thus, for example, Rensch distinguishes organ archallaxis and total archallaxis (p.242). He presents his approach in the following way:

> “We shall consider some examples typical of each of the categories mentioned and try to determine the regularity of these phylogenetic phenomena in the course of ontogeny. We shall also determine which of these alterations is most frequently met with and which of them is most likely to initiate the evolution of new organs, new structures and new types of organization.” (Rensch, 1959, p. 241)

Throughout his analysis, Rensch demonstrates a clear conscience of and affinity for the idea that evolution occurs through the modifications of developmental systems. According to Rensch, the study of these modifications with the tools of experimental and comparative embryology is key to explaining each singular case of the arising of a new structural pattern or a new phenotypic character. Rensch stresses however that very few general laws or rules can be extracted from the study of developmental alterations. One of Rensch’s main conclusions is that because many types of alterations of development can lead to the same type of new character, developmental biology does not provide *explanatory laws* of evolutionary change. This does not mean that developmental biology provides no explanation of evolutionary change at all, only that developmental explanations cannot be generalised to high taxonomical levels (Rensch, 1959, pp. 265–266). In that regard, Rensch’s approach is similar to Gavin de Beer’s approach in *Embryos and ancestors* (De Beer, 1951).

Regarding the methods of investigation of ontogenetic changes, Rensch relies on a combination of comparative and experimental embryology:

> “In most transpecific alterations an adequate analysis of the genetic background is impossible, because hybrids of species and genera usually are inviable or

> infertile. Thus, we must rely on comparative studies of ontogenetic development. Transplantations and explantation experiments, however, provide sound clues towards the proper evaluation of the potencies, affinities, and induction effects of single cells and organ buds, from which one may draw some conclusions regarding the genetic causes of archallactic alterations." (Rensch, 1959, p. 242)

Like others before him (De Beer, 1930; Schindewolf, 1936), Rensch refers to a flurry of cases from descriptive and comparative embryology to illustrate several developmental phenomena such as proterogenesis (also called paedomorphosis or neoteny), "the shift of juvenile characters towards adult stages" (p.260), which undermines the theory of recapitulation. More importantly, he takes a large part of his evidence from experimental embryologists, especially from work on xenoplastic transplantations. He relies in particular on the works of Leopold von Ubisch (1923, 1933) and Fritz Baltzer (1950a, 1950b), both former students of Theodor Boveri, like Hans Spemann, but who, more than Spemann, were interested in the relations of genetics to development (Gehring, 1998, p. 87; Sander, 1994). Rensch also relies on early experimental work of Johannes Holtfreter (1934). The latter, a student of Hans Spemann, was "the world's foremost experimental embryologist in the decades between 1930 and 1960" (Gerhart, 1998, p. 3). He was a central figure in the transfer of Spemann's study of embryonic induction and of the organizer from the level of tissues to the cellular and biochemical level (Gerhart, 1998; Hamburger, 1988; Holtfreter, 1991; Steinberg & Gilbert, 2004). However, the majority of works that Rensch relies on pertain to what was already called in the mid-century "classical experimental embryology" (Oppenheimer, 1955).

For example, against Von Baer's first law, Rensch relies on the experimental work of Leopold Von Ubisch on sea urchins to show that phenotypic differences between closely related species can be caused by archallaxis. Ubisch transplanted the four micromeres of *Parechinus miliaris* taken at the sixteen-cell stage, into half of a blastula of *Echynocyamus pusillus*. These micromeres normally develop into skeletal spicules after several cell divisions. After transplantation, they develop into spicules characteristic of the donor species *Parechinus*. Rensch introduces the example by stating that in echinoderms, "the development of many specific and generic traits has been found to occur at early phases of ontogeny" (1959, p. 243). Rensch's interpretation of this case as an example of archallaxis is questionable. For Rensch, the experiment demonstrates the early determination of the skeletal identity of the micromeres and thus a change in early development between related species. An important point is that this interpretation of the experiment in terms of developmental evolution is Rensch's own import. In contrast, the research questions pursued by Von Ubisch were related to the mechanisms and types of induction involved in the formation of the skeletal spicules. There was for example a debate on the relative influence of nuclear and cytoplasmic factors (Horstadius, 1939; Ubisch, 1939). Rensch also provides clearer examples of archallaxis between closely related species without important differences in the adult phenotype, such as the related species of worms *Tubifex rivulorum* and *pachydrilus lineatus*, studied by Andreas Penners, which differ in their type of cleavage and in most later stages of development (Penners, 1922, 1930).

Is transspecific evolution directed?

Rensch concludes his investigation of ontogenetic alterations in evolution by the following judgment:

> "Reviewing the various types of ontogenetic alterations arising in the course of phylogeny, we have to state that the primary undirected evolution, initiated by random mutation, is quite obvious also in the transspecifc differentiation of ontogenetic development, as in many groups of animals almost any possible alteration of ontogeny can develop, provided that it remains biologically tolerable […]. This means that once more there is no reason to assume special autonomous factors of evolution causing a certain direction of ontogenetic alterations, and that mutations and selection provide sufficient explanations of the phenomena in question." (Rensch, 1959, pp. 263–264)

Rensch's verdict could be misinterpreted as claiming that genetic mutations are the only pertinent level of analysis to explain evolutionary change and that developmental mechanisms do not contribute to this explanation. But to properly understand Rensch's position, it is important to be aware of the contrast class against which it is formulated. Rensch argues against two central ideas: recapitulation theory and Von Baer's first law on the one hand, and orthogenesis on the other. Regarding the former, Rensch argues against the validity of these universal laws linking development and evolution, this does not mean that he argues against the relevance of developmental mechanisms to explain particular cases of evolutionary change. Regarding the latter, it is important to distinguish it from the contemporary concepts of physical, developmental or phylogenetic constraints. One problem of interpretation is that orthogenesis was popular in the first part of the twentieth century and more than twenty different versions were in existence (Levit, Meister, & Hossfeld, 2008; Levit & Olsson, 2006). However, from Rensch's own review of orthogenetic theories (Rensch, 1959, pp. 57–59), it is clear that it is against a strong version that he argues, orthogenesis understood as an "autonomous evolutionary factor" determining the directionality of evolution over large scale trends.

Against orthogenesis, Rensch's argumentation is twofold: on the one end Rensch stresses the opportunism in evolution: cases where there is a clear absence of directionality; on the other hand, Rensch recognises the existence of trends that show directionality, he focuses on rules of allometry, the correlated changes in parts of organisms and seeks to explain them in developmental and selectionist terms rather than in orthogenetic terms.

Rensch's verdict on ontogenetic alterations can be seen as an illustration of opportunism. Rensch also relies on examples in which all the possible states of a trait have evolved. Thus, in the case of hibernation in butterflies, only four possibilities can be realized: either hibernation as an egg, as a caterpillar, a pupa or as an adult. All of these four possibilities are realized in different species. Rensch also uses morphological examples such as the many shapes of Gastropoda shells or antelope horns. These examples are primarily directed against orthogenesis, but in some cases, Rensch also clearly states that they show the limitation of the action of selection:

> "Of course, these horns serve an important purpose as a weapon and as a means of species recognition, but there can hardly be any selective force necessitating the appearance of the particular characteristics of the surface, of bending and twisting etc." (p. 60).

Allometry and the factors of transspecific alterations

Related to his focus on allometry and directional trends, Rensch develops many concepts and hypotheses that contribute to an integrated and holistic view of organisms and their evolution.

> “Do random mutations and natural selection add one character to the other, or is a certain state of harmonious animal construction being maintained throughout the stages of transformation? Numerous facts suggest that the latter assumption is true” (Rensch, 1959, p. 127)

Among Rensch’s integrative concepts and hypotheses[95], one that directly relates to the origin of evolutionary novelties is the principle of “compensation of body material[96]” (Rensch, 1959, p. 181). This is a developmental hypothesis to explain negative allometry by the existence of a competition for developmental material. Rensch refers to early experiments of amputations and regenerations conducted for example by Edmund Wilson or Hans Prizbram (see Laubichler & Maienschein, 2007) but notes that:

> “most of these experiments were made on single animals, or at best on a few, no statistical tests of the results were made, and other possible causes, such as traumatic, hormonal, and nervous stimuli, did not receive sufficient attention in the experiments”(Rensch, 1959, p. 181)

Thus, Rensch asked one of his students, Hubert Wilbert, to conduct such experiment on a large scale using the stick insect (*Carausius morosus*) (Wilbert, 1953). Wilbert conducted ablations of one hind leg on larvae and measured the

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[95] Also stressed by Rensch, but with a less direct relation to the problem of novelty, are the mutual induction of tissues and the general effects of hormones such as prolactin and thyroxin during development.

[96] The principle of material compensation has been originally formulated by Goethe and then by Goeffroy Saint-Hilaire who named it “loi de balancement” (balancing law). It was acknowledged by Darwin, although he remained more neutral than Rensch on the role of natural selection in the principle: "For I hardly see any way of distinguishing between the effects, on the one hand, of a part being largely developed through natural selection and another and adjoining part being reduced by this same process or by disuse, and, on the other hand, the actual withdrawal of nutriment from one part owing to the excess of growth in another and adjoining part" (Darwin, 1859, p. 147). For contemporary studies of material compensation see for example Klingenberg and Nijhout (1998).

correlated effects of their regeneration on the growth of other organs (contralateral leg and ovaries), controlling for other causes. He found significant effects on the growth of the correlated organs, which Rensch interprets as material compensation. Rensch also refers to similar experiments and interpretation by Tschumi (1954) on amphibians. He concludes:

> “The above examples prove that processes of material compensation do occur, and hence we should account for this fact and its consequences in phylogeny, though we must not forget that all evaluation of phyletic transformation and its causes is based on extrapolation, and this should be done with care.” (Rensch, 1959, p. 183)

Rensch indeed applies the principle to some evolutionary changes. In particular, it play an essential role in Rensch’s explanation of the evolution of vestigial organs. To the question of why vestigial organs continue to be present over long periods of time in many cases, such as the vestigial hind limbs of whales, Rensch answers:

> “The hereditary character is still preserved and hind limbs would develop if increased growth of other parts of the body did not cause a retardation in their development by way of material compensation. Selection directly affects the hind limbs only slightly if at all, because otherwise they would completely disappear.” (Rensch, 1959, p. 225)

Relying on the developmental work of Sewertzoff (1931) and Maran (1927) among others, Rensch further notes that in some reptiles (such as lizards *Chalcides ocellatus* and *Ophimorus tridactylus* with vestigial limbs), whales, and insects (such as species of the beetle *Poecilus* with reduced wings), the distal parts (phalanges, distal wing veins) are the first to be reduced. Because these parts differentiate last in development, they are the first to be affect by the lack of material used by other increased organs.

George Ledyard Stebbins's *Flowering plants*

The focus on Rensch and Stebbins is intended to provide evidence and analysis of research on the problem of evolutionary novelty involving developmental resources inside the Modern Synthesis circle. *Flowering plants*, published by Stebbins in 1974, is a late work and could arguably be placed after the Modern Synthesis era. Using this book to illustrate Modern synthesis research on novelty would not be pertinent if it was the product of a late change in Stebbins's methods and research interests. It is however not the case. *Flowering plants* is the expansion and update on subjects that were already treated in chapter 13 of *Variation and evolution in plants,* published in 1950. There are at least three reasons to focus on the former rather than the latter: it is more extensive and Stebbins's methods and theories are presented in more details; it engages with the evolutionary, systematic and developmental literatures of the late Modern Synthesis era; finally, it has been much less studied by historians and philosophers of biology.

The importance of the study of comparative and experimental embryology for the study of plant macroevolution.

As it was stressed in the last chapter, the origin, evolution and systematics of the angiosperms attracted a lot of attention before and during the Modern Synthesis era. How does Stebbins relate to the numerous existing theories regarding evolutionary trends in the angiosperms? And how different is his approach?

> "One of my major objectives is to find out to what extent both phylogeny itself and the methods of gaining new information about evolutionary history will be modified if botanists shift their major emphasis away from traditional taxonomy and idealistic morphology, and towards population and developmental genetics, comparative developmental physiology, and an ecological viewpoint that places primary emphasis upon interactions between populations and their environment." (Stebbins, 1974a, pp. viii–ix)

According to Stebbins himself, the two main originalities of his approach are his application of Simpson's theory of adaptive radiations to flowering plants and his use of experimental and comparative embryology and developmental genetics to understand evolutionary trends.[97] As shown in the last chapter, the adaptationist approach was actually rare among botanists studying large scale plant evolution. Regarding the importance of embryology to understand plant evolution and systematics, Stebbins was not alone in relying on comparative embryological data to establish phylogenetic patterns (Constance, 1955; Davis, 1967). More importantly, Stebbins stressed the importance of development to understand the evolutionary process and developed concepts of developmental availability, constraint and irreversibility:[98]

> "The bridge between gene action as understood by developmental geneticists and an understanding of the genetic basis of morphological trends that is needed by the evolutionist must be provided by studies of morphogenesis. The basic postulate for such studies, as mentioned above, is that morphological characteristics are determined by complex sequences of gene actions that are controlled by many genes, acting upon the cells of developing tissues. On the basis of this postulate, evidence must be sought that will permit evolutionists to decide *what kinds of changes are accomplished with relative ease, what changes are more difficult from the point of view of gene action, what changes can be reversed with relative ease, and which ones are intrinsically irreversible or nearly so.* " (p.102, emphasis added)

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[97] During the discussions at the Darwin centennial conference in Chicago, Stebbins already stated the importance of a knowledge of the details of development to understand the origin of evolutionary novelties:"When we find out how those forty-six strings of DNA effected all the differentiation of cells, tissues, and organs, all the forward steps and feedbacks, eventually ending in this beautiful form we all admire, then we shall be better able to argue about the selective basis of adaptations, the emergence of novelties, or any other type of change." (Tax and Callender, 1960, p. 143)

[98] An illustration of the role that Stebbins attributes to development can be found in the criticism that he formulates against Walter Zimmerman's approach to plant evolution (described in the last chapter): "The concepts of overtopping ('Uebergipfelung'), webbing, and anastomosis of vascular strands are […] useful for describing the ways in which adult structures became modified. They do not however, even begin to analyze the causal factors involved, or to associate these changes with modified gene action that could be the result of new mutations and gene recombinations. A first step in the direction of such an analysis would be to describe and compare carefully the developmental patterns that give rise to each of the different kinds of adult structures, in terms of the distribution and activity of meristematic regions, cell division as compared to cell enlargement, polarized growth of both cells and tissues, and the times and methods of procambial cell differentiation. Such descriptive studies should be followed by altering development experimentally through changing the balance of growth substances" (Stebbins, 1974a, pp. 144–145) (Webbing and anastomosis, the formation of connections between branching structures, belong to Zimmerman's category of fusions).

The combination of Stebbins's ecological and adaptive framework, and of his focus on the role of development in plant evolution can be illustrated by his treatment of the concept of transfer of function. Within his adaptive framework, Stebbins makes use of the concept that Darwin called conversion of function and Mayr functional shift, and which he calls "transfer of function" (p.64) or "transference of function" (p.79). Stebbins applies the concept to explain shifts from one pollinator to another: the transitions is made possible by a stage of "double function" in which two different vectors are pollinating the flower. Stebbins also uses the concept to speculatively explain some evolutionary trends in which organs originally having a function of protection of the developing ovule adopt a function of dispersal of the mature seeds and the function of protection is adopted by another organ. Stebbins identifies evolutionary trends that he interprets as serial repetition of this same pattern, and thus calls the phenomenon "cycles of transference of function" (p.83; see Stebbins, 1970).

In botany, the concept of transference of function was actually introduced by E.J.H. Corner (Corner, 1958; see Baum & Donoghue, 2002) who defined it in the following way: "a property which occurs in an organ, tissue, or cell-layer in one case may occur in other parts of the body in other cases. The property is the same, but its site of development has shifted" (Corner, 1958, p. 33). After a survey of examples, Corner later summarises his central idea:

> "It is considered that many evolutionary changes in plants, including the division of labour and neoteny, result from restricting the site of development of a hereditary property or by moving it to another part of the plant-body." (Corner, 1958, p. 40)

Stebbins refers to Corner and notes that several of the latter's examples pertain to the same category as his own examples. However, Stebbins argues that Corner confuses the matter by including within the category of transference of function phenomena of different natures. This is illustrated by Corner's example of the transition from apacarpous ovary to the syncarpous ovary. In flower with multiple separated carpels (apocarpous), each carpel contains an ovary; in the syncarpous condition, the carpels are fused and enclose a single ovary with different ovules and placentas (points of attachment of ovules). For Corner, this transition involves an intercalary growth, and there is a transference of function between the two types of ovaries.[99] Here is how Stebbins analyses Corner's example:

> "Apart from the problems that this interpretation raises regarding homologies, this example is inappropriate because it does not involve transference of function at all, according to the ecological meaning in which the concept was originally used by Darwin, as well as by Dohrn, Mayr, and many others, including myself. It illustrates, rather, a reorganization of the developmental pattern, so that ovules that retain their original function acquire a new position of origin. The position at which ovules appear is not a property or characteristic of the carpel or the ovary, but of the developmental pattern that produces it. If we are to understand better the complex interrelations between structures, function, and development that exist in higher plants, we must define our concepts more clearly than Corner has done." (Stebbins, 1974a, p. 84)

Stebbins accuses Corner of conflating two different uses of the term function, an ecological use and a developmental use. Indeed, in the example of the syncarpous ovary, Corner is saying that the function of producing the ovary with all its morphological component parts (placentas, ovules, vascular supply etc.) is "transferred to the new intercalation" (Corner, 1958, p. 35). To employ a term now in use, but that is not used by Stebbins, Corner confuses a complex form of heterotopy, the development of a morphological character in a new location, which is a developmental concept, with a transfer of function (such as protection of ovule and dispersal of seeds) which belongs to ecology.

This does not mean that there is no interplay between developmental processes and ecological processes and that the two dimensions should be separate. This can be stressed by coming back to Bock's example of the avian medial brace.

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[99] Here is Corner's own formulation: "The syncarpous ovary has always been a problem, now beset with many artificial theories. In essence it is an intercalary growth at the base of the free or apocarpous carpel-primordia, which thus become elevated on the new "ovary-box". This seems a new feature, but it is merely concerted internodal growth. However, the point is that most of the properties of the apocarpous ovary become transferred to the new intercalation, namely the placentas with the ovules, the vascular supply, the postfertilization development of the carpel-wall and the method of dehiscence." (Corner, 1958, p. 35)

The development of the basitemporal articulation is a developmental process explained by Bock in terms of epigenetic mechanisms, however this developmental process fits into the explanation of the evolution of the medial brace which involves factors belonging to ecology, ethology and functional morphology. Similarly, in Darwin's hypothesis that a conversion of function can be initiated when two structures perform the same function, this redundancy of structures can be the product of a duplication fully explained in developmental terms. This reminder should help us understand Stebbins's position. He is not claiming that the study of developmental processes and the study of ecological evolution should be separate, he is stating that the two levels of analysis should not be conflated. Corner conflated the production of organs by developmental processes and the performance of functions by these organs.

The example of the syncarpous ovary, however, poses the question of the relative explanatory weights of developmental processes and ecological processes in general and in the case of plant character evolution in particular. In several of their zoological examples, Darwin, Mayr or Bock attribute an important explanatory weight to ecological and functional factors. For example, in Darwin's case of the transition from the ovigerous frena to branchiae in barnacles, no major developmental shift needs to be postulated. Bock's avian medial brace is an intermediate example since the formation of the basitemporal articulation is a significant developmental shift, but ecological factors are instrumental in the larger transformation. In the case of the transition from the apocarpous ovaries to the syncarpous ovary, the explanatory weight seems to be attributed fully to the properties of developmental processes. Stebbins makes the epistemological comment that the study of transfer of function in an ecological sense is much more difficult in plants than in animals because of the greater difficulty to recognize selection pressures (in particular selection pressures on the structure of plant reproductive organs and seed), and because of the greater plasticity of plants. Furthermore, although he does not state it explicitly in this case, Stebbins' analysis of Corner example show that the former recognises the important explanatory weight of developmental processes in plant character transformations. This point will be further illustrated in the next section.

Stebbins's use of developmental biology to study plant novelties

As noted earlier, in *Flowering plants*, Stebbins argues for the essential role of the study of morphogenetic processes to understand changes in plant form (e.g. Stebbins, 1974a, p. 104). Stebbins stresses the importance of the study of developmental genetics and singles out regulatory genes in the determination and change of morphological characters:

> "genes that determine morphological characters most probably code either for regulators or control systems that affect the action of other genes, or for structural proteins that can function properly only in conjunction with other proteins that are coded by different genes" (Stebbins, 1974a, p. 104)

Stebbins conducted research on developmental genetics in the 1950s and 1960s. In particular he did cytogenetic studies on the development of stomatal complexes (pores on leaves and stems serving for gas exchange) (Stebbins, 1956; Stebbins and Khush, 1961; Stebbins and Shah, 1960), and developmental genetic studies of the effect of mutations in barley (Gupta and Stebbins, 1969; Stebbins and Yagil, 1966, 1966; Wijewantha and Stebbins, 1964; Zeiger and Stebbins, 1972).

The fact that significant morphological differences in plants can be caused by a limited number or even single genetic mutations has been recognised from very early on (Gottlieb, 1984). The relations between single genetic mutations and large morphological and architectural differences both within species and between species of plants, as well as morphological abnormalities, has been widely studied during the 20th century, as reviewed for example by Gottlieb (1984). However, there were few studies of the developmental mechanisms at different levels involved between the genetic factors and the anatomical and morphological characters (Meyerowitz, Smyth, & Bowman, 1989). In that regards, some of the developmental work of Stebbins, especially his work with Ezra Yagil on the hooded barley, is pioneering. Stebbins and Yagil focused of the genetic and epigenetic causes of the morphological differences between the awned barley and the hooded barley. In the latter, two additional florets are growing on the lemma of the main floret.

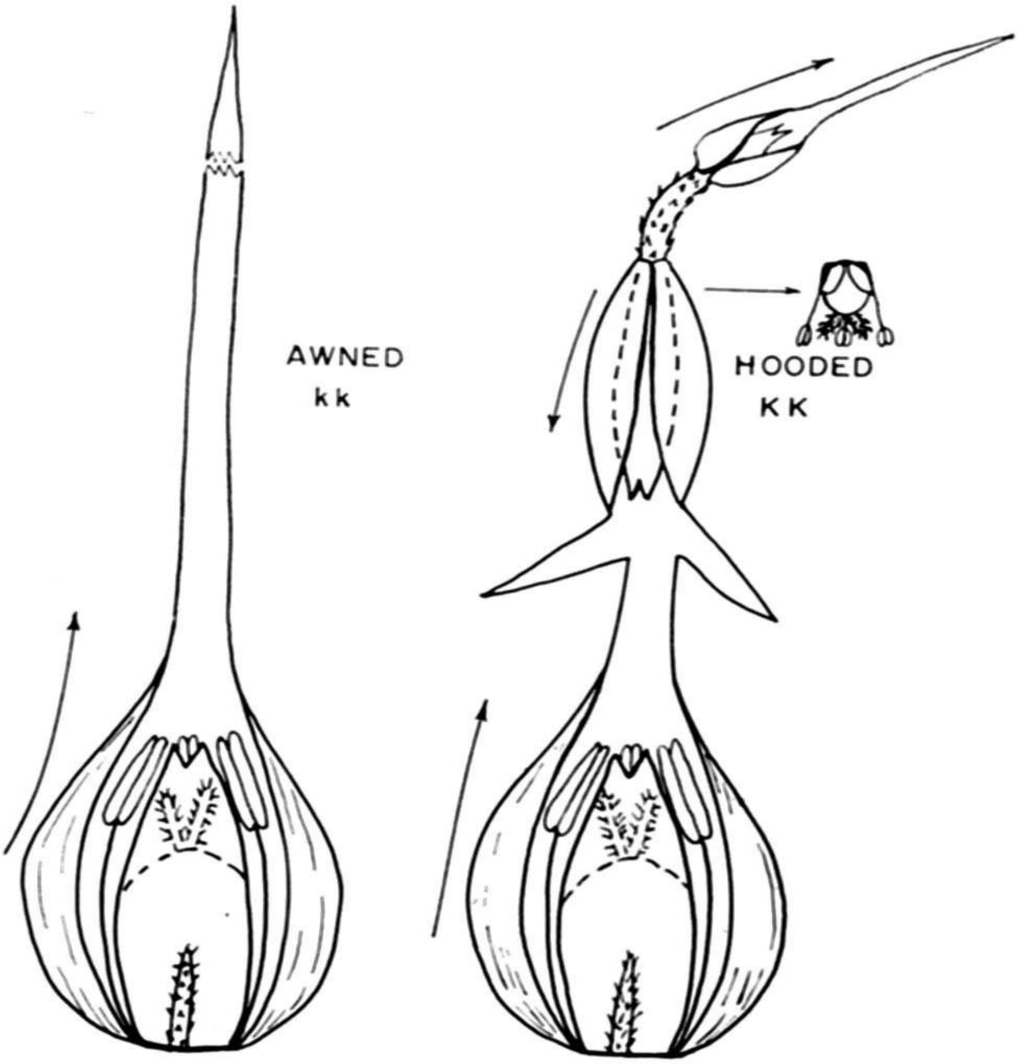

Fig.10: Differences between awned and hooded barley showing differences in axis of polarization of the florets. (after Stebbins & Yagil, 1966).

Stebbins and Yagil show that the morphological difference is linked to the mutation of a single gene. The cascade of epigenetic effects starts with an increase of cell proliferation in the distal part of the lemma and a prolonged meristematic state. This is correlated with a change in the direction cell of proliferation. This leads to the formation of a meristematic “cushion”, similar to the primordia of normal florets, from which the inverted floret develops. To summarise, Stebbins and Yagil interpret this morphological change in terms of change of cell division patterns caused by a single gene.

Regarding the role of developmental processes in understanding morphological change and evolutionary trends, Stebbins stresses the importance of other related processes at the cellular level:

_ The influence of meristematic capital on the number of parts in a floral whorl, a process experimentally studied for example by Torrey using indole acid to increase cell proliferation (Torrey, 1955, 1957).
_ The role of intercalary meristems and their control by growth substance such as auxin:

> "The development, intensification, and redistribution within the plant of intercalary meristems form some of the most important kinds of developmental changes, with respect to both the differentiation of angiosperms from other groups of seed plants and the differentiation of the various groups of angiosperms from one another." (Stebbins, 1974a, p. 110)

The role of intercalary meristem in morphological change and evolution of plant novelties is illustrated for example by the transition from apocarpy to syncarpy.

Developmental data of different kinds play a crucial role in Stebbins's formulation of his own hypothesis regarding the origin and evolution of the angiosperm as a taxon, and the origin and evolutionary trends of the flower. It would be beyond the scope of this chapter to analyse in details Stebbins' own position. As we saw in the last chapter (section III), Stebbins is probably less original than he claims in his plea for the study of development in order to understand plant macroevolution. He is more original, at the time, with his attempt to apply the framework of adaptive radiations to plant macroevolution. However, his conception of development and of its role in plant evolution is outstandingly integrative, from developmental genetics to epigenetic mechanisms at different levels.

II – CONTROVERSIES WITHIN THE MODERN SYNTHESIS AND THEIR RELATION TO THE PROBLEM OF NOVELTY

I will develop three arguments in this section:

1) I will argue against the consensual conception of the Modern Synthesis by focusing on controversies that occurred in the later phase of the Synthesis: the classical-balance controversy, the beanbag-interaction controversy and more generally an opposition between atomism and holism. Despite existing studies on these controversies (Beatty, 1987; Crow, 2009; Rao and Nanjundiah, 2011), they are usually not taken into account by defenders of the consensual and gene-centred views of the Modern Synthesis.
2) Even though these controversies have been studied, the link between them and the problem of novelty has not been explored in detail. Lerner's concept of genetic homeostasis and especially Mayr's concept of genetic revolutions have a direct bearing on the question of the tempo and mode of occurrence of phenotypic novelties. While the dominant view held that phenotypic change occurred gradually through phyletic evolution, the concept of genetic revolutions opens the door to a theory of rapid production of phenotypic novelty during speciation, even though this theory was not fully developed by Mayr or others.
3) While open controversies represent explicit dissent, there is also an implicit pluralism in the corpus of the later phase of the Modern Synthesis that has not been an object of close focus. The pluralism of the Modern Synthesis has been stressed by several historians (Beatty, 1992; Cain, 2009; Dietrich, 1995; Provine, 1988); their focus, however, was often centred on the early phase. The interpretation of the later phase has been dominated by Gould's idea of a hardening of the synthesis (Gould, 2002; Smocovitis, 1999). The theory of genetic revolutions is an example of this pluralism, it is implicit because its controversial potential has not been fully explored by Mayr or other Modern Synthesis proponents. Gould's thesis (strengthened adaptationism, extrapolationism and individualism regarding the level of selection) is based on textual evidence that can

hardly be contested. But if one embraces the opposite approach and focuses on what is dissonant with that hardening, a more pluralistic and potentially incoherent picture emerges. Here I will focus primarily on genetic revolutions, the functional theory of the origin of novelties and group selectionist overtones in Mayr and Dobzhansky.

The many faces of the opposition between geneticists and naturalists

In order to oppose the gene-centred view of the Synthesis, Mayr mobilised a distinction between geneticists and naturalists:

> "As Laudan[100] stresses, no victory of one paradigm over another was involved, as in Kuhn's theory of scientific revolutions, but rather an exchange of the most viable components of the previously competing research traditions. For this reason to state that the synthesis was merely an acceptance by the naturalists of the of the newer findings of genetics ignores the numerous concepts that geneticists took over from the naturalists: population thinking, the multidimensionality of the polytypic species, the biological species concept (with the species defined as a reproductively and ecologically autonomous entity), *the role of behaviour and change of function in the origin of evolutionary novelties*, and so on."(Mayr and Provine, 1980, p. 40, emphasis added)

The relationship presented here is one of complementarity and mutual enlightenment between geneticists and naturalists. The picture it offers appears in line with the consensual view of the Modern Synthesis. However, as with several other dichotomies developed by Mayr (Beatty, 1994; Witteveen, 2016), the one between geneticists and naturalists has gone through different meanings and uses over the years. Despite the reductive nature of this dichotomy, it can be a point of entry to restore controversies within the Modern Synthesis.

The distinction between geneticists and naturalists has mostly been developed by Ernst Mayr (e.g. Mayr, 1992, 1982, 1959; Mayr and Provine, 1998) both as an interpretative key to structure the history of biology in the 19th and 20th centuries and as a strategic tool to counter the supremacy of genetics in the Modern

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[100] Laudan (1977)

Synthesis[101]. However, the use of this opposition is not limited to Mayr. It was in particular adopted as a strategic tool by other biologists such as Dobzhansky (Dobzhansky, 1980) (cf. Beatty, 1990; Gould, 2002; Milam, 2010; Smocovitis, 1996), and it has been used as an interpretative key by other historians (e.g. Bowler, 1992, p. 217). It was closely related to, and sometimes conflated with an opposition between reductionism and holism or organicism in biology (Milam, 2010). The study of this distinction may be a good path to move beyond the unified view of the Modern Synthesis stated earlier and recover some of the controversies taking place within it.

A crucial angle from which to analyse the opposition between geneticists and naturalists is the strategic or social angle and I will describe three strategic reasons for the development of the opposition by Mayr and others. But although it is necessary to have the strategic dimension in mind, it is also manifest that several topics of research cannot be understood with a purely genetic-centred reading of the Synthesis. To the ones cited by Mayr (population thinking, polytypic species, biological species concept, functional approach to novelties), we can add the ones that we analysed in the last chapter: speciation, the origin of higher taxa and the increase in complexity.

One can find at least three contexts in which the distinction between geneticists and naturalists was deployed as a conceptual and strategic tool in controversies within the Modern Synthesis:

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[101] Mayr has theorised and defended in several places (1963, 1982b) his use of simplifying dichotomies or categorical statement in science and history of science. In the preface to *The growth of biological thought,* he attributed it a strategic role in bringing out the truth, using an analogy with Hegel's dialectics: "I agree with Passmore (1965) that histories should even be polemical. Such histories will arouse contradiction and they will challenge the reader to come up with a refutation. By a dialectical process, this will speed up a synthesis of perspective." (Mayr,1982b, p. 9). This should of course grant caution about unreflectingly reusing Mayr's historical dichotomies. However, two remarks can be offered in defence of this use: firstly, the dichotomy has been used by other historians. Secondly, Mayr's sweeping statements are usually criticised for reducing or hiding debates and controversies rather than for artificially creating them (e.g. Witteveen, 2015, 2016). Thus, it is very probable that controversies within the Modern Synthesis were more complex and more numerous than the one described by Mayr's dichotomy. Now, this is not a major problem for my argument, considering that the goal in this section is to move away from the reductive unified view of the Synthesis and restore controversies and oppositions.

_ A conflict for power and recognition against the domination of genetics, already visible for example in *Systematics and the origin of species* (1942).
_ A controversy between two distinct views of genetics ("classical" and "newer", or "atomistic" and "holistic" genetics, in Mayr's words) that developed from the 1950s.
_ A historiographic fight against an account of the Synthesis centred on population genetics, especially formulated by William Provine, from the 1970s (Provine, 1978, 2001).[102]

The second controversy appears not to fit within the general category of oppositions between geneticists and naturalists. Although, as indicated by its name, it was primarily a debate internal to population and evolutionary genetics, it involved Dobzhansky and Mayr as some of its main protagonists and they partly sided with the holistic school of genetics because it fitted their naturalists' concerns. Thus, it still has its place within the category. Here I will principally focus on this second context for several reasons. First, it developed in the later phase of the Modern Synthesis, at a period that dominant historical accounts describe as the reaching of a consensus or the hardening of the Synthesis, this controversy thus provides evidence to question or at least nuance these dominant accounts. Second, this controversy is related to the formulation of Mayr's theory of genetic revolutions, a theory that has a direct bearing on how the problem of novelty was tackled during the Modern Synthesis era.

A fourth context should be mentioned in relation to the opposition between geneticists and naturalists, the fight against the rise and domination of molecular biology in the 1960s. Here a different opposition was elaborated, mainly by Dobzhansky, Mayr and Simpson (Dobzhansky, 1964; Mayr, 1961; Simpson, 1964), between reductionist molecular biology and anti-reductionist organism-centred, museum and field based biology. This opposition is closely related to the

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[102] For example, in a letter to George Gaylord Simpson, Mayr wrote, "as far as the conference on the 'Synthesis' is concerned—confidentially—I want to counteract the present historiography which gives just about all the credit to the geneticists. They shall have all the credit they deserve, but not more." Mayr to Simpson, 27 Aug 1973, GSP, Series I: Correspondence, Folder Ernst Mayr #3. On this historiographic conflict and more generally on Mayr's central role in stimulating the production of historical accounts of the Modern Synthesis, see (Cain, 2009; Haffer, 2007; Smocovitis 2007).

one between geneticists and naturalists.[103] I will however not focus on this controversy because molecular biology is not usually considered as an integral part of the Modern Synthesis, thus focusing on this fight does not exactly shine a light on controversies internal to the Modern Synthesis. Furthermore, this opposition has received several historical and philosophical accounts (Beatty, 1990, 1994; Milam, 2010).

The idea of different forms of oppositions between geneticists and naturalists during the Modern Synthesis apparently stands in conflict with the view of the Modern Synthesis as a reconciliation of these two groups. Indeed, as noted for example by Bowler (1992, p. 216), the opposition between the geneticists and naturalists was focused up until the 1930s on the importance of natural selection itself in evolution. For example, in their comprehensive survey of animal variation, Robson and Richards (1936) give a large place to non-adaptive variation and favour Lamarckism over selectionism for adaptive characters. This is opposition fades as the naturalists progressively accept selectionism during the 1930s and 1940s. However, right as this reconciliation and synthesis spirit in evolutionary biology is celebrated, a tension arises regarding the respective contributions of the different groups or disciplines. This is expressed by Mayr at the very beginning of *Systematics and the origin of species* (1942):

> "There was a tendency among laboratory workers to think rather contemptuously of the museum man, who spent his time counting hairs or drawing bristles, and whose final aim seemed to be merely the correct naming of his specimens. A welcome improvement in the mutual understanding between geneticists and systematists has occurred in recent years, largely owing to the efforts of such men as Rensch and Kinsey among the taxonomists, Timofeeff-Ressovsky and Dobzhansky among the geneticists, and Huxley and Diver among the general biologists. *It was realized by these workers that only some of the problems of the origin of species can be solved by the geneticist, while other*

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[103] Milam has recently stressed the proximity and even the blending of the two oppositions: "in 1959 Mayr was more interested in defending evolution against the influence of geneticists than he was in defending the broader community of organismic biologists against molecular biology. This would slowly change, although these two defensive lines can be difficult to tease apart because they were engaged in the same battle to maintain the position of museum- and field-based biology in a rapidly changing world" (Milam, 2010, p. 289).

> *aspects are more accessible to such branches of biology as ecology and biogeography, paleontology, and taxonomy*. A satisfactory understanding of intricate evolutionary phenomena can be attained only through the cooperation of all these disciplines, and systematics is willing and able to contribute its share." (Mayr, 1942, p. 3, emphasis added)

This tension, while never eliminated, will take a new turn in the 1950s and 1960s. Since this new turn has its origin in a series of controversies within genetics, it may be misleading to define it as another episode of the confrontation between geneticists and naturalists. In this case, the arguments of the naturalists were renewed and fuelled by new developments coming from different branches of genetics itself. Thus, if one had to characterise the episodes and ideas that will be the subject of the next section with one opposition, the one between atomism and holism would be better suited, although, as it will hopefully become clear, no single opposition would be sufficient.

Different forms of holism in the late Modern Synthesis

"Classical" and "newer" populations genetics

In *The genetic basis of evolutionary change*, Richard Lewontin refers to the classical-balance controversy in evolutionary genetics and brilliantly analyses its inception and evolution between the 1950s and the 1970s. But as noted by Joel Felsenstein (1975), Lewontin weaves together different themes that could be better interpreted as different controversies: the classical-balance, beanbag-interaction and selection-neutrality questions. Here, my focus will be on the two first controversies, because the selection-neutrality unfolded only from the mid-1960s and has attracted more recent attention than the first two, the neutral theory of evolution being considered as the first or one of the first attacks against the Modern Synthesis (e.g. Dietrich, 1994; Stoltzfus, 2012). Mayr distinguished the "classical population genetics" of Fisher, Wright and Haldane and the "newer population genetics". As representative of this new trend, he listed Dobzhansky's "balance theory," Isadore Michael Lerner's "genetic homeostasis," and Kenneth Mather's work on quantitative inheritance ("genetic inertia"). Mayr later designated Lerner as the leader of the holists. The following quote is revelatory of how this opposition relates to the relationships between geneticists and naturalists:

> “Every naturalist, I suppose, has a feeling that a purely reductionist approach fails to explain the holistic aspects of organisms and of evolution. Some geneticists, in the 1940s and 1950s, came to the same conclusion, even though by a very different route. Dobzhansky had sympathies in this direction, but even more so his students Wallace, Brncic, and Vetukhiv. K. Mather's experiments led to similar conclusions, but M. Lerner became the leader of this school of holistic thinking (Lerner 1954). I felt that he had demonstrated convincingly the importance of nonadditive genes and of the genetic homeostastis of the genotype as a whole. In Cold Spring Harbor it was Bruce Wallace's work with irradiated populations that opened my eyes to the existence of a remarkable cohesion of the genotype.” (Mayr, 1992, p. 14)

Partly like Lewontin, Mayr seems to include several debates into his dichotomy between classical and newer population genetics.

The classical-balance controversy

Under the *classical view* of genetics, natural selection favours the allele with the highest fitness at each genetic locus, thus, the effect of selection is a progressive elimination of less fit alleles. Because there is usually no absolute dominance at a genetic locus, selection will favour homozygotes with the fittest allele over heterozygotes. Thus, the frequency of homozygotes with the optimal allele for each locus will increase and the population will tend towards homozygosis at all loci. There cannot be a total elimination of genetic diversity, but this diversity is “either neutral, or transient, or morbid” (Dobzhansky, 1955, p. 3). Under the *balance view*, the notion of the allele with the highest fitness, the optimal allele, is questioned. This is partly due to the variability of environments which leads to any allele being more beneficial in some conditions but less in others. Thus, homozygotes will be generally less fit than heterozygotes because of their overspecialisation. Because of the superior fitness of heterozygotes, a population will contain and maintain a high degree of variability at most loci.

The main proponents of this debate were Herman Jospeh Muller, who defended the classical view, and Theodosius Dobzhansky who defended the balance view. The reasons for which the debate did not resolve easily are multiple: the difficulty of collecting and assessing evidence (e.g. high heterosigosity in *Drosophila* was mostly based on chromosomal inversions rather than on alleles at gene loci), the social implications of the debate, especially its relation to eugenics, the strong personalities of the protagonists. Here is not the place to go over these reasons in detail[104], it is sufficient for my purpose to note that this controversy was not superficial and involved deep theoretical issues such as the mode of action and the levels of selection. This will be further addressed later in this section.

Isadore Michael Lerner: heterozygosity and homeostasis

In his presentation and defence of the balance view, Dobzhansky makes several references to Isadore Michael Lerner. For example, Dobzhansky refers to the mechanism of "obligate heterozygosity" as contributing to the balance view. Lerner defines obligate heterozygosity as the requirement of a certain amount of heterozygosis to allow the normal development of organisms (Lerner, 1954, p. 6). Lerner is important for my investigation because of his influence in the later phase of the Modern Synthesis, as attested for example by Mayr, and because he appears to be the missing link between Conrad Waddington and Ivan Schmallhausen's developmental perspective on one side, and Mayr and Dobzhansky's organismic and holistic perspective on the other side. Lerner was a Russian geneticist who had emigrated to Vancouver in 1927 and then spent his career at Berkeley working on poultry breeding and later on species competition. His work *Genetic homeostasis*, published in 1954, draws a link between the classical-balance controversy and genetic and evolutionary concepts with holistic connotations such as the coadaptation of the genome, developmental canalisation and genetic inertia or homeostasis.

In a series of publications, Conrad Waddington developed the idea of developmental canalisation (Waddington, 1942, 1948). Considering that

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[104] For an analysis of these reasons, especially of the social implications of the controversy, see Beatty (1987)

environmental stresses or genetic mutations can disrupt developmental pathways and have deleterious effects on the phenotypic outcome of development, Waddington suggested that natural selection favoured genetic combinations that limited the possibilities of disruption of developmental reactions. To explain this developmental canalisation, Waddington referred to feedback mechanisms and other cybernetic concepts but he did not provide a genetic theory of developmental canalisation. Lerner refers to Waddington's definition of canalisation, asserts its importance in evolution and provides a potential, albeit speculative[105], genetic mechanism for it, based on heterozygosity. Lerner distinguishes an additive version of the mechanism, where heterozygosity at certain specific loci is needed for canalisation, and a non-additive version, where canalisation does not depend on heterozygosity at specific loci but on a certain overall rate of heterozygosity at the level of the of the group of genes involved in a developmental reaction, or at the genome level. Lerner provides the following abstract and simplified model of the non-additive version:

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[105] "mere designation of a phenomenon by the term 'buffering of development' does not imply real understanding of the process; this must await the time when the physiology of gene action and of normal ontogeny is reduced to precise physico-chemical terms. In Landauer's (1952) words, 'It is important that we should not deceive ourselves. Our knowledge concerning the hereditary forces governing normal embryonic development is practically nil.' Only when such great voids have been filled can generalizations of the type attempted here rest on a sound foundation." (Lerner, 1954, p. 114)

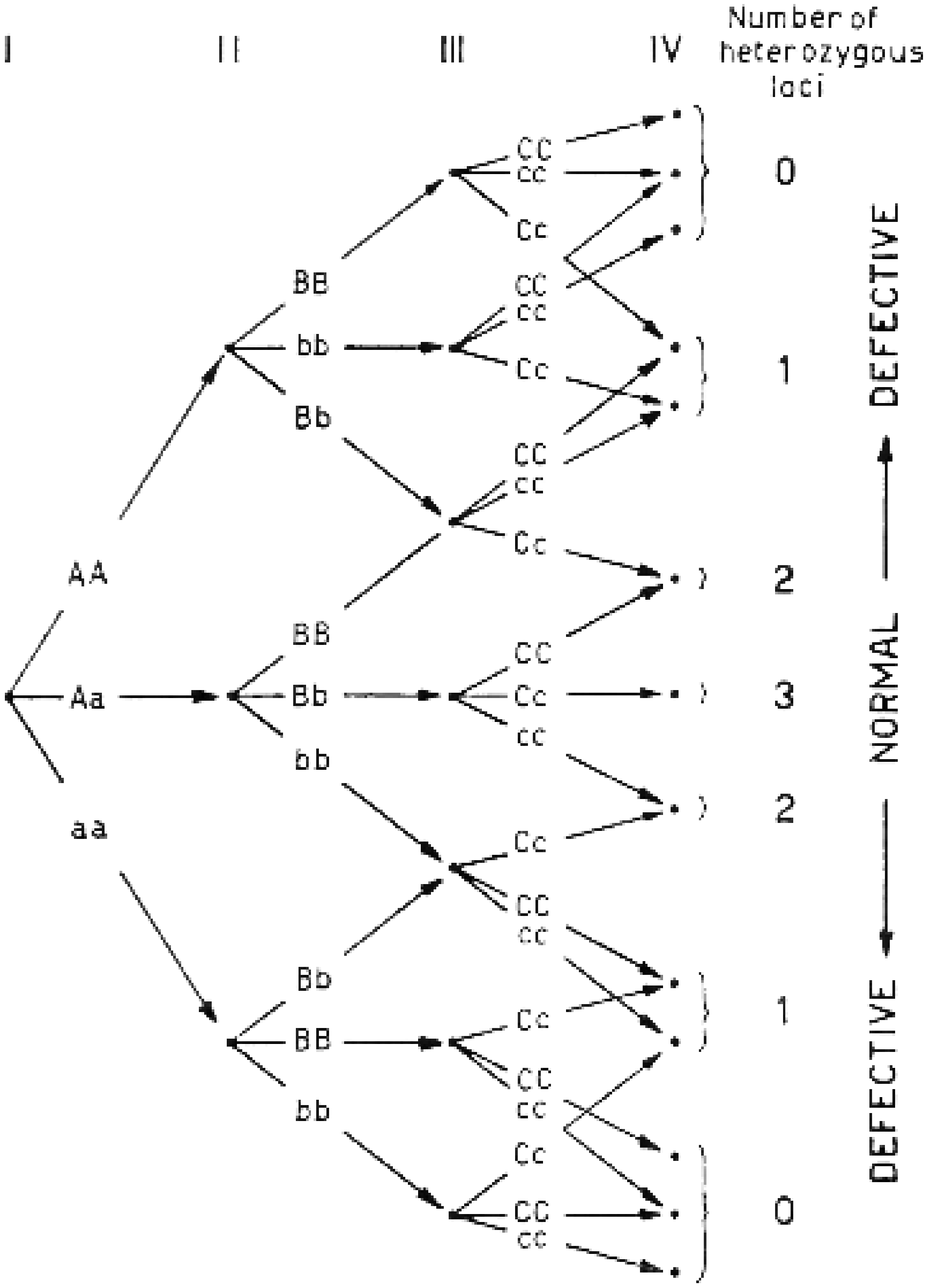

Fig. 11: “Non-specific control of buffering by heterozygous gene pairs. Roman numerals represent stages of development between which the products of gene pairs Aa, Bb and Cc enter into play. The arrows represent developmental paths taken by each genotype. At the extreme right the range of normal phenotypic expression is indicated.” (Lerner, 1954, p. 67)

Lerner notes that there is no conclusive evidence for either version of the mechanism and that the reality is probably a combination of the two versions. [106]

While the concept of *developmental homeostasis*[107] applies to the individual level, Lerner also develops the concept of *genetic homeostasis*, which is a population level concept and which he defines as “the tendency of a Mendelian population as a whole to retain its genetic composition arrived at by previous evolutionary history” (Lerner, 1954, p. 81). The main source of evidence for this phenomenon is found in examples of the tendency of a population under artificial selection for an extreme phenotype to return to its initial condition after the artificial selection has stopped. To explain this phenomenon, Lerner appeals to two mechanisms involving heterozygosity:

> “It is suggested here that heterozygosity has a dual function in the life of Mendelian populations. On the one hand, it provides a mechanism for maintaining genetic reserves and potential plasticity, and on the other it permits a large proportion of individuals to exhibit combinations of phenotypic properties near the optimum. Underlying both processes is the superior buffering ability of heterozygotes as compared with homozygotes.” (Lerner, 1954, p. 108)

Lerner explains genetic homeostasis as either a by-product of developmental canalisation based on obligate heterozygocity at the individual level, or as a consequence of the greater adaptability to different environments of a highly heterozygote population. In short, the selection for an extreme phenotype tend to increase homozygocity and thus decrease overall canalisation and fitness. Natural selection thus acts towards a return to the more heterozygous state. To illustrate Lerner’s ideas, one can refer for example to the work of Carl Huether on the species *linanthus androsaceus* (Huether, 1969, 1968) . The flowers of this species, and of the whole Polemoniaceae family, are mostly pentamerous (five petals); however a very small percentage of plants have flowers with more or less

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[106] “On the one hand, the usual lethality of deletions, and the specificity of genes acting on biosynthetic pathways of lower organisms, predispose one to view the first model with favour. On the other hand, the complete overlapping of phenotypes for polygenic traits when their genotypes are different supports the second one. It is most likely that both types of gene action occur.” (Lerner, 1954, p. 68).

[107] Lerner uses the concepts of canalization, homeostasis and buffering alternatively and without significant changes in meaning. Even in contemporary developmental biology, these terms are generally synonymous (Hall, 2005; Hallgrímsson et al., 2002).

petals. To show that this condition was not produced by developmental accidents in a genetically homogenous population but by the presence of genetic variability that is mostly canalised, Huether selected for increased and decreased numbers of petals over five generations and successfully obtained lines with a high level of plants with more than five petals, and, to a lesser extent, lines with a high level of plant with less than five petals. Huether refers to Waddington's concept of canalisation but not directly to Lerner, and he offers two possible interpretations of the combination of stable phenotype and high genetic variability in the natural state, assuming their adaptive significance: either 1) canalisation is a superior way to maintain the stable phenotype, or 2) the genetic variability has an adaptive value. In the first hypothesis, which could be called "non-lernerian", canalisation is adaptive but not based of variability or heterozygosity, these are by-products of canalisation, they are not adaptive but are not selected against because of canalisation. In the second "lernerian" hypothesis, the heterozygosity is adaptive, either because it is the basis of canalisation or for another reason. Stebbins (Stebbins, 1974a, pp. 20–21) goes further than Huether and favours the second hypothesis, directly citing Lerner.

The evolutionary developmental biologist Brian K. Hall has recently devoted an article to Lerner's book (Hall, 2005). Hall introduces Lerner's propositions and gives attention to Conrad Waddington's positive review.[108] But Hall's main interest is in understanding why Lerner's work has gone out of fashion, how could it "not have forged a synthesis of mechanisms uniting genes, individual organisms, populations, environment and selection, or have founded an integrative and holistic biology?" (Hall, 2005, p. 192). Hall is focused on the absence of contemporary legacy of Lerner and thus does not evoke the importance of his influence in the later phase of the Modern Synthesis.[109]

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[108] For example: ''It is refreshing to find a population geneticist who realizes that he cannot avoid talking embryology and who does his best to do so in a sophisticated rather than an elementary fashion'' (Waddington, 1955: p 52)

[109] Several factors can explain why the influence of Lerner's theories declined over the years: only few cases of heterozygote superiority were experimentally observed in the few decades after the publication of Lerner's book. Other mechanisms were shown to be more plausible in explaining the presence of heterozygosis in populations such as frequency-dependent selection and linkage disequilibrium. Explanations of developmental canalisation developed around the robust architecture of gene regulatory networks or the pervasiveness of gene duplications but not around the effects of heterozygosity. Some of these topics will be addressed in the next chapters.

The beanbag-interaction controversy

I now turn to a second controversy that had a strong impact in the later phase of the Modern Synthesis: the confrontation between an atomistic view and an integrative view of the action of genes. While the classical/balance controversy was concerned with the quantity and the role of variability (and heterozygosity) in populations, this controversy focuses on the relation between genes in a genotype during the development of organisms and more generally their whole life cycle. In short, the opposition was between an atomistic view, according to which genes could be studied as independent units, and an integrative or holistic view, according to which the interaction between genes is so important that it cannot be neglected. During the 1950s, geneticists pertaining to what Mayr had termed the "newer" school started questioning the ability of the models of classical population genetics to adequately represent the behaviour of genes. Such criticism is expressed for example by Lerner in *Genetic homeostasis,* as illustrated by the following statement:

> "In any case, if the basis of the ideas suggested here is an acceptable one, it follows that the two-dimensional specifications (time and gene frequency) of evolutionary processes used in the early studies of population genetics, necessary as they were to carry us to our present understanding of evolution, will have to be replaced eventually by much more complex multidimensional ones. Even the first crude stages of quantification of the combinatorial properties of genotypes may be beyond our capacity for statistical manipulation. This fact was undoubtedly realized by the pioneers of population genetics, who as a first approximation confined themselves to the simpler forms of analysis." (Lerner, 1954, p. 120)

What Lerner, Dobzhansky, Wallace and others argued was not that Fisher, Haldane, Wright and other "classical" population geneticists had a naïve atomistic view of the genome, but rather than the simplifying assumptions that they adopted, with models involved one or two gene loci and no interaction with other genes, were useful but limited to represent the behaviour of genotypes composed of a high number of interacting genes.

A full review of the works, concepts and experiments of the "newer" population genetics is not possible here. I will then briefly focus on those most pertinent to the present subject. The concepts of *genetic background* and *genetic environment* refer to the genes with which a specific gene will interact; the genetic background usually refers to the individual level, the individual genotype in which the gene is integrated while the genetic environment refer to the gene pool of the population. The action of a gene and its fitness is not an absolute value but a variable that depends on genetic background and environment. Here again, the criticism addressed to classical population genetics is on the value of simplified models, as illustrated by this recognition from Bruce Wallace and collaborators:

> "Wright (1931), it is true, has pointed out that the behaviour of a gene in a population depends upon its reaction-and the reactions of every one of its alleles-to the entire array of genotypes in which it is found. Since a complete analysis of a complex a system is an obviously impossible experimental or mathematical task, simplifying assumptions must be introduced into the calculations. Until critical experiments have been made, it should be remembered that these mathematical models are working hypotheses awaiting confirmation." (Wallace et al., 1953, p. 273)

The concept of coadapted gene complexes, genotype or gene pool proceeds from this differential effect and fitness of genetic interactions. This is for example illustrated by the adaptive interpretation of chromosomal inversions in *Drosophila*. Chromosomal inversions, if they are heterozygous, prevent the recombination of genetic material between the chromosome on which it is found and its homologous. Dobzhansky, among others, has observed experimental and natural populations of *Drosophila pseudoobscura* with chromosomal inversions (e.g. Dobzhansky, 1950). Heterozygotes offspring for some inversions from parents of the same populations had a superior fitness than homozygotes, while heterozygotes from parents of different populations had a lower fitness than homozygotes. Dobzhansky hypothesized that the chromosomal segments corresponding to the inversions were coadapted gene complexes and that inversions allowed their conservation by preventing recombination.

The controversial nature of the distinction between atomistic and integrative genetics, was amplified, if not created by Ernst Mayr, especially with his 1959 article entitled "Where are we?"(Mayr, 1959). Mayr had been introduced to the concepts of to the "newer" population genetics by Bruce Wallace and James C.

King in 1950 (Provine, 2004), and had found a resonance between them and his naturalist's preoccupations, as noted earlier. Mayr, in 1959 and later, presented the matter not as a problem regarding the powers and limits of populations genetic models, but as the opposition of two conceptions of genetics and of the genotype:

> "For the last 60 years, but one could also say all the way back to Darwin (1859 p. 11, 146; 1868 II:319-335), two traditions of viewing the genotype can be distinguished. According to *the atomistic ("beanbag") view* each gene is independent not only in its actions, but also in the effects of selection on it. Evolutionary stasis of the phenotype, for instance, is explained by the stabilizing selection acting on individual genes. According to *the holistic (integrative) view*, genes perform as teams and large numbers of other genes form the "genetic milieu" (Chetverikov, 1926) of any given gene." (Mayr, 1982a)

Because of these different formulations of the problem, the beanbag/integrative controversy is less clearly defined than the classical/balance controversy, and the latter can arguably be considered as one aspect of the former.

Holism, species and levels of selection

A last aspect of the holism of the late Modern Synthesis is worth mentioning, although it is a complex issue that cannot be covered in detail here: "naïve group selectionism" (Wilson and Wilson, 2007). It can be defined as the belief in adaptations at levels other than the individual organism, especially populations and species, without a clear understanding or formulation of the evolutionary mechanisms necessary to produce these high-level adaptations.[110] Naïve group selectionism was the most obvious in the works of some ecologists, as illustrated by this statement from the 1949 textbook *Principles of animal ecology*:

> "The probability of survival of individual living things, or of populations, increases with the degree with which they harmoniously adjust themselves to each other

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[110] This naïve group selectionism is to be distinguished from later developments of multilevel selection theory.

> and to their environment. This principle is basic to the concept of the balance of nature, orders the subject matter of ecology and evolution, underlies organismic and developmental biology, and is the foundation for all sociology." (Allee et al., 1949, p. 729)

Some of the claims and formulations of proponents of the holistic and balance views of genetics, especially of Dobzhansky and Mayr, also prompt the question of their adhesion to the idea of population-level or species-level selection and adaptation. An illustration of these group selectionist overtones can be found in Dobzhansky's and Mayr's conception of isolating mechanisms as adaptations at the level of the species:

> "[i]solating mechanisms appear to be *ad hoc* contrivances that prevent the exchange of genes between nascent species, rather than incongruities originating in accidental changes in the gene functions" (Dobzhansky, 1951, p. 208).

> "The reproductive isolation of a species is a protective device against the breaking up of its well-integrated, co-adapted gene system. Through organizing diversity into species, a system has been created that permits genetic diversification and the accumulation of favorable genes and gene combinations without any danger of destruction of the basic gene complex." (Mayr 1963, p.423)

Mallet (2010) has argued that the example of isolating mechanisms and others demonstrate that Mayr and Dozhansky endorsed a form of naïve group selectionism. While there are definitely ambiguities in the formulations used by these authors, Mallet is in some cases too prompt to jump from overtones to active endorsement of group selectionism. For example, Mallet speaks of "Dobzhansky's group selectionist reinforcement hypothesis". Now, reinforcement, as formulated by Dobzhansky (1937) only involves individual selection. It was viewed as the second stage of allopatric or peripatric speciation (e.g. Lewontin, 1974, p. 161), when two populations initially isolated come into contact again there can be a reinforcement of incipient isolating mechanisms between the two populations if the hybrids produced have a lower fitness than the non-hybrids. Reinforcement itself cannot warrant Dobzhansky's adhesion to group selectionism.

Mayr's genetic revolutions

Here is where this investigation on controversies within the Modern Synthesis rejoins the problem of novelty most closely: the theory of genetic revolutions, developed by Ernst Mayr as the counterpart to genetic homeostasis, to provide a new mechanism for speciation but also for rapid production of evolutionary novelties. This theoretical development can be seen as the combination of his peripatric theory of speciation with the concepts of the "newer genetics" described earlier. Provine has already stressed that genetic revolutions constituted a change in Mayr's conception of speciation and isolating mechanisms (Provine, 2004). However, he has not analyzed Mayr's proposal of genetic revolutions as a mechanism for the production of evolutionary novelties. I will briefly explain how genetic revolutions constitute a change in Mayr's thinking and then focus on their relation to the origin of novelty.

Relying on his observations of island birds in New Guinea and on the work of Sewall Wright (1931, 1932), Mayr developed in *Systematics and the origin of species* a theory of speciation by rapid evolution of small peripherally isolated populations. Mayr noted the repeated observation of the phenotypic difference between large mainland populations of a species and peripherally isolated populations of the same species, the latter often being more phenotypically uniform. Mayr argued that it was probably due to the "founder principle": the reduced genetic variability, due to their small number, of the first individuals who founded these isolated populations. Additionally, he relied on Wright's genetic models showing higher rates of gene loss and drift, and generally more rapid evolution, in small populations. Mayr later called this theory "peripatric speciation" (Mayr, 1954).

Genetic homeostasis and genetic revolutions

The concept of genetic revolution was introduced in a 1954 article entitled "Change of genetic environment and evolution". Mayr begins the article by referring to the problem of the difference between two types of variation within species: ecotypic variations, between contiguous populations forming an interbreeding series, and what he called, after Schindewolf, "typostrophic" variations that characterise some peripherally isolated populations. On the one hand, ecotypic variations are clinal, that is, they merge into one another, they are dependent on local environments and are of a limited range. Following Goldschmidt (1940), Mayr argues that this type of variation cannot lead to speciation. On the other hand, the type of variation sometimes found in peripheral isolates is "so different from that of contiguous populations that we may be dealing with something entirely new" (Mayr, 1954, p. 160). Thus, Mayr insists, more so than in 1942, on the morphological and ecological novelties found in peripheral populations and provocatively reuses a saltationist term to describe the phenomenon.

Contrary to his work of 1942, where he insisted on the role of drift and on the founder principle to explain speciation and phenotypic difference of peripheral isolates, Mayr now argues that neither drift nor environmental differences are sufficient to explain the phenomenon (Mayr 1954, p. 158). Instead Mayr proposes the mechanism of genetic revolutions as the main explanatory factor. This mechanism is grounded on concepts from the new school of populations genetics recently assimilated by Mayr and described earlier, especially coadapted genetic system, genetic environment and genetic homeostasis. The limited nature of ecotypic variations between populations that interbreed is explained by the presence of gene flow between these populations which prevent the rapid spread of favourable mutations, and by genetic homeostasis explained by the interactions and coadaptation of genes. The problem of variation is thus formulated in terms of the conditions that can allow a breakage or loosening of the genetic homeostasis. Why then are peripherally isolated founder populations providing these conditions? The key idea is that these conditions lead to a change in genetic environment for any of the genes of the founders. The founders switch from a large mainland population to a small number of individuals greatly reduces genetic variability, and this will, according to Mayr, increase homozygosity and expose alleles to negative selection. Moreover, because, according to the holistic view, each gene's action and fitness value depends on the rest of the genes in the genotype and the gene pool, the overall change in genetic composition of the population will instantly change the action and fitness value of each gene.

As noted by Provine (2004), the model provided by Mayr does not come with a lot of details and quantification in terms of population genetics. Mayr insisted that the genetic revolution was a theory of rapid evolutionary change under natural selection and was irritated when it was described as a theory of genetic drift.[111] It seems hard to deny however that Mayr gives an important role to drift in his theory. For example, Mayr talks of the selective pressures of the new environments of the isolates as playing a role, but then states:

> "The amazingly great differences among populations of adjacent islands, e.g. *Tanysiptera carolinae* (Numfor) and *riedelii* (Biak), indicate that the accidents of gene assortment during the "genetic revolution" of the isolated population may be more important than the "directive" force of the similar environment of adjacent islands." (Mayr, 1954, p. 170)

Genetic revolutions and evolutionary novelties

The dominant view regarding phenotypic evolution during the Modern Synthesis era, expressed for example by George Gaylord Simpson[112], was that it occurred mostly during phyletic evolution and not during speciation. With genetic revolutions, Mayr goes against this view by joining speciation and phenotypic novelty.

"It seems to me that many puzzling phenomena, particularly those that concern paleontlogists, are elucidated by a consideration of these [peripherally isolated] populations. This concerns primarily the phenomena of unequal (and particularly very rapid) evolutionary rates, breaks in evolutionary sequences and apparent saltations, and finally the origin of new 'types'." (Mayr, 1954, p. 175)

Contrary to macromutations, systemic mutations or "mutational avalanches", which would not be able to spread in a large population with gene-flow; and

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[111] In a 1961 letter to Phil Sheppard, Mayr wrote: "Frankly, I am a little tired of having my 1954 paper cited as 'a theory of genetic drift' when the major objective of the paper was to prove that the genetic changes in peripherally isolated populations were due to selection and not due to drift". Mayr to P. M. Sheppard, July 19, 1961, Ernst Mayr Papers HUGFP 74.7, box 8, folder 781, General Correspondence, 1952–1987, HU. Cited by Milam (2010).

[112] See chapter 2, II.1)

contrary to ecological changes affecting selection pressures, which are too slow to explain “quantum evolution”, Mayr states that:

> “The genetic reorganization of peripherally isolated populations, on the other hand, does permit evolutionary changes that are many times more rapid than the changes within populations that are part of a continuous system. *Here then is a mechanism that would permit the rapid emergence of macroevolutionary novelties without any conflict with the observed facts of genetics*". (Mayr, 1954, p.176, emphasis added)

The importance of genetic revolutions

How much can be deduced about Mayr’s thinking and about tensions during the Modern Synthesis era from the theory of genetic revolutions depends on the status of this theory in Mayr’s views on evolution and on its impact. If genetic revolutions were only one speculative idea among many others without specific importance for Mayr and without impact on the scientific community, then grounding a historical argument on it would not be warranted. There is enough evidence to the contrary: Mayr recognized the speculative nature of the theory (1982), but he retrospectively considered it to be his most important scientific contribution in several places (e. g. Haffer, 2007; Provine, 2005). For example, Provine (2005) writes: “When, over the course of a 2-day interview, I asked Mayr to tell me his most important contribution to evolutionary biology during his life, he replied without hesitation, ‘genetic revolutions’.” Thus, considering the multiple works in which Mayr developed his theory of genetic revolutions and the high value he attributed to this theory, it is perplexing that contemporary authors cite him as the most, or one of the most, prominent representative of the view of evolution as a gradual shift in allele frequencies.[113]

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[113] Soltfuz (2017) directly attributes to Mayr, Dobzhansky and Simpson the definition of evolution as “shifting gene frequencies”. It is true that the expression originated in Dobzhansy’s *Genetics and the origin of species* (Dobzhansky, 1937). But it is especially controversial to attribute this view to Mayr considering his repeated efforts to counter the population genetic-centred view of the Modern Synthesis and his attachment to his own theory of genetic revolutions that is far from classical population genetic models and that was later criticised by numerous populations geneticists (e.g. Barton and Charlesworth, 1984). Here is one citation of Mayr stating his position on shifting gene frequencies: “The reductionist definition that evolution is a change of gene frequencies is meaningless. Evolution is a matter of phenotypes, structures, developmental pathways, functions, populations, and inter- acting ecosystems. The non-reductionist tradition in evolutionary biology is old, beginning with Darwin's

And the theory, although initially without notable effects, had an important, if belated, influence on palaeontologists (Eldredge, 1971; Eldredge and Gould, 1972) and spurred population genetic studies of speciation (Charlesworth and Rouhani, 1988; H L Carson and Templeton, 1984; Lande, 1980; N H Barton and Charlesworth, 1984) . Although Mayr attempted to clearly distinguish genetic revolutions from a theory of rapid evolutionary change via genetic drift in the 1954 article and later, the fact that many population geneticists interpreted it as a theory of genetic drift (e.g. Barton and Charlesworth, 1984; Crow, 2009) says more about the lack of precise genetic content of the theory as formulated by Mayr than about the distractedness of these geneticists. Thus, Mayr's genetic revolutions should not be considered as a mature theory, but as an influential speculation that opened up new lines of research, maybe similar, in smaller proportions, to the way Goldschmidt's systemic mutations spurred controversy and progress during the earlier phase of the Modern Synthesis (Dietrich, 1995).

Genetic revolutions, drift and saltations

There is actually a proximity between Mayr's genetic revolutions and Goldschmidt's systemic mutations. What distinguished the former from the latter is not their relation to the possibility of rapid phenotypic changes at the individual level, but rather, according to Mayr, his own insistence that this type of phenotypic change could not be understood without integrating population dynamics. Mayr vigorously insisted that genetic revolutions were a population process. One of the many uses of his distinction between typological and population thinking (cf. Witteveen, 2016) may have been to conjure this dangerous closeness of genetic revolutions to saltationist theories. Mayr's proximity to Goldschmidt is particularly striking since they both insisted on their rejection of the classical conception of genetics, characterized by the former as "beanbag genetics" (e.g. Mayr, 1982a) and by the latter as the "string of beads" conception of genetics (e.g. Goldschmidt, 1940, p. 247), and they both defended a holistic view of the genome. Although

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repeated references to the "mysterious laws of correlation," continuing with Chetverikov's concept of the genetic milieu, with Lerner's of genetic homeostasis, and my own of the cohesion of the phenotype. " (Mayr, 1982a) admittedly, Goldschmidt's views became less holistic in the later phase of his career since he moved away from systemic mutations and focused more and more on homeotic mutations. Moreover, the ultimate barrier supposedly setting Mayr apart from saltationists and condemning Goldschmidt, namely population thinking or lack thereof, is weakened if we consider Goldschimdt's late dialogue with Sewall Wright and his attempt at integrating his theory with population genetics (Davis et al., 2009; Dietrich, 1995).

The tension between preadaptation and genetic revolutions

The case of Mayr is particularly interesting because there is a potential tension between Mayr's theory of genetic revolutions and his functional shift account of the origin of morphological novelties. This tension primarily lies between the gradual nature of the origin of novelties through functional shifts and the possibly abrupt nature of phenotypic change during genetic revolutions. Mayr insists that his theory of genetic revolutions is still gradualist because it is a population process. However, this type of gradualism (sudden phenotypic change at the level of individuals but gradual change at the population level), is different from the one that is pictured in Mayr's functional shift account of novelty. In the latter, sudden change at the individual level is not strictly excluded but is deemed less probable than incremental change. The second possible tension is relative to the role attributed to selection in the two processes. On the one hand, the theory of preadaptation if based on the action of successive or simultaneous selection pressures without a role for genetic drift, on the other hand genetic revolutions have been interpreted as involving drift in an important way. This second tension is however more ambiguous since Mayr himself insisted, without much justification, that genetic revolutions did not involve drift.

Mayr recognises the difference between his theory of genetic revolutions and the theory of functional shift in terms of explaining the origin of novelties. Thus, his position regarding the origin of novelties appears *pluralist*:

> "It is evident that too great a stability of the phenotype would be a handicap in a newly arising situation where there is a premium on the development of a new structure. A peripherally isolated population, or any other population in which the

> stabilizing mechanisms are temporarily weakened, may occasionally be in an especially favorable situation with respect to the emergence of evolutionary novelties. *However, in view of the change of function and other mechanisms discussed above, the origin of evolutionary novelties is by no means limited to such peripherally isolated populations*." (Mayr, 1960, p. 377, emphasis added)

However, at the same time Mayr tries to show how the two phenomena can act together:

> "A shift in function exposes the fully formed "preadapted" structure to the new selection pressure. This, in most cases, explains how an incipient structure could be favored by natural selection before reaching a size and elaboration where it would be advantageous in a new role. Mutation pressure, as such, plays a negligible role in the emergence of evolutionary novelties, except possibly on the cellular level. Yet the structure of the gene complex is important: too great a genetic and developmental homeostasis will result in too stabilized a phenotype and will tend to prevent a response to new selection pressures. Any population phenomenon that would tend to counteract excessive stability of the phenotype may favor evolutionary changes." (Mayr, 1960, p. 378)

The ambiguous relation between genetic revolutions and functional shift again shows the speculative nature of Mayr's theories, especially of the former. This partly explains the virulence of the reaction of some population geneticists against genetic revolutions.

A hardening of the Synthesis?

The idea of a hardening of the synthesis has been mostly defended by Gould and by other historians to a lesser extent. The hardened view of the Synthesis has been adopted by a large part of the literature promoting an Extended Synthesis or the framework of evo-devo against the Modern Synthesis framework. Gould grounds his interpretation on evolutions in some of the works of Ernst Mayr, George Gaylord Simpson and Theodosius Dobzhansky, and on an analysis of the Darwin 1959 centennial conferences in Chicago and Philadelphia (e.g. Gould, 2002, pp. 518–585). For the evolution of Dobzhansky's ideas, Gould compares the first and last editions of *Genetics and the origin of* *species* (1937, 1951); for Simpson, he compares *Tempo and mode in evolution* (1944) to *The major features of evolution* (1953); for Mayr, Gould compares *Systematics and the origin of species* (1942) to *Animal species and evolution* (1963).

Gould's main idea is that, at least for these three authors, there was a transition from the recognition of selection as one factor of evolution among others, to the dogma of an all-encompassing power of selection to shape evolution. Gould also argued that the hardening expanded to the other two "legs" of Darwin's tripod, namely the question of the level(s) at which selection operates and the question of the relation between microevolution and macroevolution. Regarding the latter, Gould notes a stronger dogmatism concerning the power of microevolutionary proecces to explain macroevolution. Regarding the levels of selection, Gould identifies a move during the 1960s towards a dogmatic defense of organismic selection as the only valid level, although this move was not led by Dobzhansky, Simpson or Mayr.

Several reasons for the hardening of the Synthesis have been offered by its proponents. Gould considers first the empirical reason: the transition towards a stronger defence of adaptationism was grounded on the accumulation of empirical observations of natural selection in action. He recognises that the case of Dobzhansky gives support to this interpretation[114], but argues that it cannot be a sufficient one or even the main one. Smocovitis offered a political reason: adaptationism coincided much more with the post-World War II values of progress and rationality than genetic drift, associated with stochasticity (cf. Smocovitis, 1992, p. 40). Gould favours a sociological interpretation based on the dynamics of scientific communities. The close proximity, geographical, institutional and affective, of Dobzhansky, Simpson and Mayr (the "New York Mafia" (Gould, 2002, p. 543)), all revolving around Columbia University, contributed to the convergence of their views. In addition, the hierarchical nature

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[114] In the first paper of his series *Genetics of natural populations*, Dobzhansky attributed inversion patterns in the third chromosome of *Drosophila pseudoobscura* to random fluctuations; he then discovered that these fluctuations followed regular and repeatable patterns. The bold title of paper XVII in the series gives a clear idea of Dobzhansky's change of mind: "Proof of operation of natural selection in wild populations of *Drosophila pseudoobscura*" (Dobzhansky and Levene, 1948).

of their scientific community, where few lead and many follow, allowed for the spread and acceptance of these views.

Gould's hardening thesis, especially regarding George Gaylord Simpson, has already been analysed and criticised from a sociological point of view by Cain (2009). Interestingly, the explanation of the hardening of the Synthesis that Gould favours appears similar to Cain's interpretation of Gould's own criticism of Simpson. Cain stresses the influence of social factors, especially of the building of the new paleobiological community, on Gould criticism of Simpson. He argues that as this new scientific community was forming in the 1970s, the critique of Simpson evolved into a "ritual patricide" that played a role in tying the community together and asserting its identity.[115] It is not my purpose here to venture into an overall reassessment of Gould's arguments, mostly because I have not approached here the breadth of sources and experiences on which Gould relies, and secondly because it would move us away from the subject of the chapter. However, it may be fruitful to take stock of the examination of the debates between geneticists and naturalists, atomists and holists and of Mayr's theory of genetic revolution, and to confront some of Gould's claims in the light of it.

To clarify the argumentative line that I would like to pursue against Gould's idea of a hardening of Mayr's position, I will first distinguish it from other possible lines of criticism that I will not engage in. Firstly, one could extend Cain's sociological interpretation to Gould's analysis of Mayr's evolution towards adaptationism. Mayr was not a paleontologist like Gould and Simpson, so the idea of a ritual patricide does not exactly apply to his case; he was however one of the dominant figures of the Modern Synthesis, from which Gould was trying to break, thus what Cain argued about Simpson could be applied to Mayr to a lesser extent. Secondly, Gould's view of a hardening of Mayr's adaptationism between the two books could be disputed by questioning the interpretation that Gould gives of some citations of Mayr[116], or by confronting different citations to the ones that he

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[115] Cain then generalizes his analysis: "In the 1970s, such narratives helped rebels in paleobiology and macroevolution identify what they were breaking away from, just as it later did for the ''evo-devo'' programme and ''four-dimensional'' biology. Giving the idea of synthesis a good kicking frequently operated as a ritualised form of departure" (Cain, 2009b). Cain's analysis also finds a parallel in Michael Dietrich's (1995) analysis of the constructive role or Richard Goldschmidt on the Modern Synthesis.

[116] For example, Gould uses as an illustration of Mayr's adaptationist overconfidence his claim that the search for homologous genes between distant taxa and even between closely related species, is vain (Mayr, 1963, p. 609). Gould writes: "In modern hindsight, this claim provides a particularly compelling

chooses.[117] It is nevertheless hard to contest Gould's overall diagnosis of Mayr's hardened adaptationism.

The point I would like to stress is different from the two previously mentioned and it still stands even if we admit the greater adaptationism of the later Mayr. Despite the pervasive adaptationism, many new developments in Mayr's thinking contribute to build a broader, more pluralistic and maybe more contradictory theoretical picture than the one presented by the earlier Mayr. The holistic view of the genome, the theory of genetic revolutions, the view of species as natural entities (with possibly adaptations at the level of the species), the functional theory of the origin of novelty, among others, contribute to a widening rather than a hardening. Interestingly Gould indirectly recognizes this widening, or even the potential incoherence of Mayr's theories, but he does not draw conclusions from this fact. I will give three examples of this pattern. The first involves peripatric speciation and genetic revolutions, the second involves the origin of evolutionary novelties and the third involves selection at the level of the species.

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example of how hardened adaptationism can suppress interesting questions—for such homologues have now been found in abundance. Their discovery ranks as one of the most important events in modern evolutionary science" (Gould, 2002, p. 539). But what Gould does not say is that this belief was shared beyond the core circle of the Modern Synthesis. It was even shared by Gavin de Beer, one of the most prominent proponents of a synthesis between evolution and development, as late as 1971: "It is now clear that the pride with which it was assumed that the inheritance of homologous structures from a common ancestor explained homology was misplaced; for such inheritance cannot be ascribed to identity of genes. The attempt to find 'homologous' genes, except in closely related species, has been given up as hopeless. What mechanism can it be that results in the production of homologous organs, the same `patterns,' in spite of their not being controlled by the same genes? I asked that question in 1938, and it has not yet been answered" (De Beer, 1971, p. 16)

[117] For example, Gould stresses that in *Systematics and the origin of species*, Mayr uses the category of "nonadaptation". Gould writes: "within this important category of nonadaptation, Mayr includes many prominent phenomena that he would later ascribe to selection." (Gould, 2002, p. 534). However, by "nonadaptation", Mayr essentially refers to characters that he considers as neutral and not maladaptive, such as "combinations of color patterns, spots, and bands, as well as extra bristles and wing veins" (Mayr, 1942, p. 86). Mayr later writes in *Animal species and evolution*: "If a given subspecies of ladybird beetles has more spots on the elytra than another subspecies, it does not necessarily mean that the extra spots are essential for survival in the range of that subspecies. It merely means that the genotype that has evolved in this area as the result of selection develops additional spots on the elytra. When studying geographic variation in the voice of birds, in the plume of birds of paradise, or in the color patterns of parrot and pigeons, one must never ignore the possibility that some of the phenotype is merely the incidental by-product. Yet close analysis often reveals unsuspected adaptive qualities even in minute details of the phenotype" (1963, p. 311). Claiming, as Gould does, that Mayr now ascribes to selection what he then considered as nonadaptive is a shortcut as Mayr is rather postulating a correlation between these traits that he still construes as nonadaptive and other traits that are adaptive.

Regarding the first example, genetic revolutions, here is the analysis given by Gould:

> “In the mid 1990's, Mayr himself (in lift, and personal communications […]), while continuing to explicate and defend his favored themes of 1963, denies any substantial change between the volumes of 1942 and 1963 on questions of adaptation. This difference between current memory and textual record, previously discussed as a general principle (see p. 521), provides a fascinating illustration of how scholars can slowly and unconsciously imbibe a shifting professional consensus, thus imposing a subjective and personal impression of stability upon a virtual transmogrification. *I find this unconscious alteration all the more ironic in Mayr's case because his first category of major change in ideas about speciation—his intellectual move from the dumbbell to the peripatric model—so strongly encourages a widened space for nonadaptationist themes (for many evolutionists have interpreted his notions of genetic revolutions and founder effects in small peripheral isolates as a powerful antidote to the classical panadaptationist model of Fisherian panmixia in large populations).* Yet Mayr never translated the implications of these changes in his own ideas about speciation into doubts about adaptation in his chapters on variation and change within populations.” (Gould, 2002, pp. 536–537, emphasis added)

In this citation, it seems that Gould is himself giving ammunition to his potential contradictors. Indeed, Gould is saying on the one hand that Mayr did not recognise the hardening of his adaptationism between 1942 and 1963, and on the other hand he is stressing that the theory of genetic revolutions, present in 1963 but not in 1942, allows for clearly nonadaptive elaborations. If we follow Gould’s advice and do not rely on Mayr’s late interpretation of his own work but rather focus on the details of the texts, then we are forced to recognise that a potential conflict exists between different parts of Mayr’s book of 1963. This motivates a questioning of Gould’s interpretation: why give priority, or even exclusive attention, to the increased adaptationism while other new and potentially contradictory themes arise in Mayr’s version of the late Modern Synthesis?

The second example is Mayr’s theory of the origin of evolutionary novelties through functional shift. Here is Gould’s analysis:

> “Major subjects, the origin of evolutionary novelty for example, now reside exclusively within an adaptationist framework by purely functional definition: "We may begin by defining evolutionary novelty as any newly acquired structure or property that permits the performance of a new function, which, in turn, will open a new adaptive zone" (p. 602).” (Gould, 2002, p. 539)

Gould is making a case for Mayr’s pervasive adaptationism, thus he cannot be criticized for enumerating the different illustrations of this framework. The problem is that by writing that the origin of novelty “now reside[s]” within the adaptationist framework, Gould suggest that between 1942 and 1963, Mayr moved from a non-adaptationist or non-strictly adaptationist, theory of novelty, to an adaptationist one. Now it is more accurate to say that Mayr did not develop a theory of the origin of novelties in his book of 1942.[118] The theory summarized in *Animal Species and evolution*, and elaborated elsewhere Mayr (1960) and others[119], is best seen as an addition to Mayr’s views on evolution, thus widening his scope.

The third example is the group selectionist overtones present in Mayr’ development of population thinking and of his concept of species. The third part of Gould’s thesis of the hardening of the Synthesis is its increasing dogmatism on the question of the levels of selections, with the insistence on the individual organism being the sole valid level. Gould recognizes that this part of the hardening comes relatively later and not from the figures of the Synthesis who are his main focus (Dobzhansky, Simpson and Mayr) but especially from George Williams (1966). Gould even acknowledges that Mayr’s view of levels of selection does not fit this hardened picture:

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[118] In *Systematics and the origin of species*, Mayr mentions the possible formation of aberrant characters in small founder populations. He attributes this phenomenon to a founder effect and an increased rate of evolution in small populations. The scope of aberrant characters is not exactly determined. It refers mostly to extreme forms of existing characters (such as a very elongated beak in a bird) rather than to novel characters. Regarding the phenomena of macroevolution, Mayr only offers a “very cursory survey” (Mayr, 1942, p. 291) as it is not the main subject of the book. In the conclusion of this survey, he clearly states his conviction of an extrapolation of the principles of microevolution to macroevolution: “In conclusion we may say that all the available evidence indicates that the origin of the higher categories is a process which is nothing but an extrapolation of speciation. All the processes and phenomena of macroevolution and of the origin of the higher categories can be traced back to intraspecific variation, even though the first steps of such processes are usually very minute.” (Mayr, 1942, p. 298)

[119] See chapters 1 and 2.

> "In rereading Mayr's 1963 book with the hindsight of thirty years, however, I was struck by the number of passages and arguments that either speak loosely about explicit advantages to groups and populations (rather than fortuitous beneficial effects arising as side consequences of selection on organisms), or seem to state an explicit claim for selection at the population level." (Gould, 2002, p. 546)

However, Gould does not draw consequences against his hardening thesis from this fact. Gould's indifference seems all the more unjustified that these group selectionist ideas blossomed in the later phase of the Modern Synthesis (Borrello, 2009; Mallet, 2010). Gould could have argued that this trend fits well into his narrative of increased adaptationism but he should have admitted simultaneously that it downplays his general thesis of a hardening of the Synthesis on all fronts.

In conclusion, the many theories developed by Mayr and others between the 1940s and the 1960s and collected in *Animal species and evolution* form a more pluralistic picture than expected, a picture that might not be fully coherent, and that definitely cannot be fully reduced to the supposedly polished and hardened core of adaptationism. The controversies of the late Modern Synthesis (classical/balance, beanbag/interaction, genetic revolutions) raise the question of the place of population genetics in the Modern Synthesis (e.g. Gould, 2002; Lewontin, 1980). Gould insists on the ignorance of Modern Synthesis architects on this matter and on their trust in population geneticists.[120] He further argues that this attitude demonstrates the existence of a shared culture among evolutionists of the time and that it is conducive to a phase of normal science, accumulating illustrations of the accepted principles but leaving aside ambiguous cases and puzzles (Gould, 2002, p. 520). According to Gould, this contributed to a state of orthodoxy in the 50s and 60s. The controversies underlined in this section invite to at least nuance Gould's judgment: there was no consensus in population

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[120] For example: "But if Dobzhansky could integrate the Mendelian experimental world with natural history, what about the supposed centerpiece of mathematical population genetics? Here, by his own repeated, almost gleeful, admission, Dobzhansky remained a near dunce. He did not study, nor could he even understand, the details of this literature. Of his long and fruitful collaboration with Sewall Wright, Dobzhansky simply said that he had followed the principle of "father knows best"—that is, he bypassed Wright's mathematical manipulations and accepted his English explanations on faith. In fact, of all the great second-phase synthesists only G. G. Simpson possessed sufficient mathematical background to read and understand these papers." (Gould, 2002, p. 520)

genetics and there was no blind following of population geneticists by other biologists, as clearly illustrated by Mayr.[121]

Mayr's theory of genetic revolutions particularly stands out in the context of a history of research on novelty. Although it is a speculative effort, it is grounded on genetic and developmental concepts (genetic environment, developmental canalisation, genetic homeostasis etc.) that were widely studied, albeit controversial, in the late Modern Synthesis. It is conceived as a mechanism for the sudden "typostrophic" changes stressed by palaeontologists such as Schindewolf. It potentially clashes with other contemporary theoretical developments on the problem of novelty, even with Mayr's own other theories.

CONCLUSION

The confusion regarding the position of Modern Synthesis participants on novelty partly stems from a neglect of the contrast class, that is, of the theories they were opposed to and tried to refute (saltationism, lamarckism, orthogenesis). As noted by William Provine, The Modern Synthesis was a movement of constriction, ‘‘a vast cut-down of variables considered important in the evolutionary process’’ (Provine, 1992, p. 176). The context of the constriction should be kept in mind and assuming that this constriction applies to any possible variable that is not selection is running a strong risk of anachronism. Rensch and Mayr can be taken as examples here. The position of the Modern Synthesis on novelty is often summarised by opponents in the terms of the extrapolation thesis: the factors of microevolution (natural selection, mutation, migration and drift) are sufficient to explain macroevolution. Applied more precisely to novelty, it means that new characters appear through the accumulation of microevolutionary events (e.g. Amundson, 2005; Bonner, 1982, pp. 279–280; Stoltzfus, 2017). Indeed, in *Evolution above the species level*, Rensch defends the thesis that

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[121] The question of the lack of mastery of theoretical population genetics during the Modern Synthesis era can be related to the problem of "epistemic dependence" (Hardwig, 1985). This is of course no specific to research in evolutionary biology during the Modern Synthesis era and has arguably become more pervasive with the increase in specialisation and interdisciplinary in science over the last few decades.

natural selection and mutations are sufficient to explain macroevolution including the emergence of novelties. However, when one looks more closely at Rensch's work as it was done in this chapter, it becomes clear that Rensch develops many hypotheses regarding the origin of novelties : material compensation, the action of hormones, heterochronies etc. These theories are all formulated at levels of organisation above the genes. Thus, it would not be accurate to summarise Rensch's view of novelty as the action of natural selection on mutations. When Rensch asserts that natural selection and mutations are sufficient to explain macroevolutionary phenomena, what he rejects as unnecessary are not developmental processes but orthogenesis as an internal directional force. This judgment can be applied to several approaches to novelty covered in this chapter and the last, to Stebbins's approach to angiosperm novelties and well as to the work of Walter Bock or some of Ernst Mayr's.

Overall, the materials presented in this chapter and in the previous one undermine the three dominant theses about the Modern Synthesis described in the introduction: that it was mainly focused on the gene level and was an adaptation of biological disciplines to population genetics; that development was excluded from it; that it evolved towards a hardened consensus.

Weighting against the first thesis are several research programs, such as the functional morphologists' approach to novelty or some of Rensch's research, which, despite not referring to the genetic level or population genetics – or not attributing a central place to them - are clearly either identifying with the Modern Synthesis or integrated in its canon. Second is Mayr's evolving but persisting distinction between geneticists and naturalists and his resistance against the geneticist reading of the Synthesis.

Against the thesis of the exclusion of development from the Synthesis, the work of Rensch on material compensation, of Stebbins on the developmental genetics of barley, and of Lerner on homeostasis, constitute not only an abstract recognition of the role of development in evolution but active empirical and theoretical research on this role by architects or influential figures in the Synthesis.

Finally, the thesis of a hardening of the Synthesis is undermined by the vivacity of controversies between classical and new population genetics and by the multiplication of potentially conflicting concepts and theory, as illustrated by Mayr simultaneous defense of preadaptation and genetic revolutions.

CHAPTER 4 – NOVELTY AND HOMOLOGY

INTRODUCTION

The relation between homology and novelty has been addressed partially several times in previous chapters (see especially chapter 1, part I and chapter 2, part III) and the importance of and understanding of homology for the study of novelty should have clearly emerged. The overview of research on the origin of angiosperm and of the flower in the Modern Synthesis era in particular has shown that an important part of the debate centred on which were the correct relations of homology between floral organs and organs in other plant taxa. On these different hypotheses of homology depend the formulations of scenarios of the origin of the flower. The development of cladistic methods, the reliance on molecular phylogenies, and advances in pant developmental genetics have had a significant impact on the problem of the origin of the flower.

Another problem that has emerged relates to the establishment of homologies at different levels of organisation and to the determination of relationships between homologies at different levels of organisation. In the last chapter was evoked the difficulty to establish generalisations regarding the relationships between developmental processes and morphological characters, the same morphological characters in closely related species can develop from different tissues or be induced at different times. For example, homologous bones can originate from cartilage in one species and from a connective tissue in another species (De Beer, 1971; Rensch, 1959). At the genetic level, the discovery of developmental control genes shared across very distantly related species and involved in body axis, segmentation and other pattern formations in all of these species (McGinnis, Garber, Wirz, Kuroiwa, & Gehring, 1984; Quiring, Walldorf, Kloter, & Gehring, 1994; see Gehring, 1998; Morange, 2000, 2011; Rheinberger & Müller-Wille, 2018, chap.8) has raised hopes for a general theory of the developmental genetic basis of homology. However, the importance of developmental system drift has cast doubt on the possibility for such a theory (Haag & True, 2001, 2018).

An influential group of evo-devo researchers base their definition of novelty on the concept of homology. The definition of morphological novelty as "a structure that is neither homologous to any structure in the ancestral species nor homonomous[122] to any other structure of the same organism" (1991, p. 243), developed by Gerd Müller and Günter Wagner, has been widely adopted in the field. This definition is grounded on a developmental concept of homology (Müller & Wagner, 1996; Wagner, 1989a, 1989b). This concept has been developed by Müller and Wagner in recent years (Müller, 2003; Wagner, 2007, 2014, 2015b); Wagner especially has offered it as a general solution to the problems of homology and novelty. The establishment of relations of homology plays a central part in cladistics. Now, Müller, Wagner and their followers on one side, and phylogenetic systematists on the other, do not share the same concept of homology.

Several problems emerge when weaving these different threads together:

_ Although, as stated in chapter 1, phylogenetic systematics has an essential role for research on novelty both as a preamble and as a means of testing theories, the concept of non-homology as it is developed by Wagner and Müller is not used in systematics and potentially conflicts with the concepts of homology used in this discipline.

_ Wagner's recent theory of the developmental basis of homology and novelty relies on a wealth of animal examples at different levels of organisation. Wagner also applies his theories to the example of the origin of the flower. This poses the question of the generalisation of theories of novelty across taxonomic kingdoms.

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[122] Homonomous parts in the same organism, are parts that have similar forms and that constitute series, such as leg pairs in centipedes or fingers in primates.

It also raises the question of the contribution of developmental genetics to the problem of the origin of the flower.

I will address these different questions in turn. Section I briefly introduces the history of the concept of homology and its recent development in systematics. Section II will focus on the relation between the phylogenetic concept of homology and the biological concept of homology and their respective relation to the concept of novelty. Section III will analyse further Wagner's recent alteration of his biological concept of homology. In section IV, I will focus on the origin of the angiosperm flower and on questions raised by the application of Wagner's theory to this example. In section V, I will reflect on this example to address the concept of type and the question of generalization in research on novelty.

I – THE CONCEPT OF HOMOLOGY, ORIGINS AND APPLICATIONS

The concept of homology has its roots in the work of Geoffroy Saint-Hilaire and the French school of comparative anatomy. It was first clearly defined by Richard Owen in the context of species fixism and opposed to the concept of analogy in order to clarify the fluctuating terminology of the time (Amundson, 2005; Panchen, 1994; Schmitt, 2004). He defined a "homologue" as " same organ in different animals under every variety of form and function," as opposed to an "analogue" which was "a part or organ in one animal which has the same function as another part or organ in a different animal" (Owen 1843, p. 379, 374; see also Owen 1848, p. 7). Owen relied on the unity of plan between all of vertebrates. He established a bone per bone correspondence between the skeletons of all groups of vertebrates and devised an abstract "vertebrate archetype" (Owen, 1849) whose parts could be related to the corresponding parts in any vertebrate. The concept of homology was refined by Owen to include three types:

a) "Special homology": a relation of homology between corresponding parts in different species".
b) "General homology": The homology between a part in a species and its corresponding part in the archetype.

c) “Serial homology”: homology between corresponding parts inside an organism.

These concepts were integrated into the theory of evolution. The archetype became the common ancestor and the first two types of homology were explained by a common genealogy. Edwin Ray Lankester, a disciple of Darwin, was the first to give a definition of homology in the context of the theory of evolution:

> “Without doubt the majority of evolutionists would agree that by asserting an organ A in an animal **α** to be homologous with an organ B in an animal **β**, they mean that in some common ancestor **ε** the organs A and B were represented by an organ C, and that **α** and **β** have inherited their organs A and B from **ε**” (Lankester 1870, p. 36).

Lankester also invented the term “homoplasy”. It was distinguished from the concept of analogy in that analogy was a similarity of function regardless of the morphology of the organs, while homoplasy also included a morphological similarity.

These evolutionary concepts of homology and homoplasy are still in use in contemporary evolutionary biology and systematics, and is also applied in molecular biology (Brigandt, 2003). The logic of concepts of homology at the genetic level is very similar to the one at the morphological an anatomical level (Freudenstein, 2005):

_ Different alleles of the same genes can be considered different character states of the same character.
_ Orthology can be equated to special homology. Orthologs are the same gene in different species inherited from a common ancestor. These genes can have undergone different changes.
_ Paralogy can be equated to serial homology. The relation is established between genes that are the result of a gene duplication.

The cladistic school in systematics, starting with the work of Willi Hennig (Hennig, 1966) has vindicated the establishment of phylogenetic relationships, in the strict sense of relationships of common ancestry between taxa, as the main goal of systematics, as opposed to evolutionary taxonomists who combined several goals (see chapter 2, part IV) (Hennig, 1975; Mayr, 1974), and pheneticists who vindicated overall similarity (Sneath & Sokal, 1973; Sokal, 1963).[123] Establishment of relationships of homology between characters is central to the cladistic method. Cladists use hypothesised patterns of identity and transformation series (Brower, 2014; Carine & Scotland, 1999; Grant & Kluge, 2004) between homologous characters in different taxa to infer phylogenetic relationships between these taxa, represented in cladograms. For a given set of species (or higher taxa), they distinguish between the ancestral state of a character (*plesiomorphy*) and the derived state of the character (*apomorphy)*. Ancestral states shared by some taxa are *symplesiomorphies* and derived states shared by some taxa, and only those taxa, are *synapomorphies*.

II – CONTEMPORARY THEORIES OF HOMOLOGY AND THEIR ROLE IN RESEARCH ON NOVELTY

Is a novelty identical to an apomorphy?

The definitions of evolutionary novelties from phylogenetic systematics usually equate novelty to any character used to build cladograms. For example: “the list of identified novelties is endless, virtually equalling the diagnostic characters of all successful higher taxa” (Cracraft, 1990, p.21). Other authors do not restrict novelties to attributes of higher taxa: “*Evolutionary Novelty*. An inherited change from a previously existing character state, the novelty is the transformational homolog of the preexisting character state” (Wiley & Lieberman, 2011, p.13). “All homologs begin their existence as evolutionary novelties.” (*Ibid.*, p.14). Novelties are identified with apomorphies, that is, derived characters (knowing of course that a derived character in one cladogram can be a primitive character in another cladogram). This view is expressed by phylogeneticists (e.g. Cracraft, 1989 ; Wiley & Liebermann, 2011), but also by evolutionary biologists (e.g. Futuyma, 1986) and by evolutionary developmental biologists (e.g. Arthur,

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[123] See Hull (1988) for a philosophical and historical account of the debates.

2000).[124] This shared view on what novelties are would suggest that there is no problem regarding the definition of novelties and that the only remaining problems lay in the explanation of some cases of novelty. But this view is not shared among all biologists, and even if it was, it would leave open the question of how apomorphies are identified and individuated.

Let us first assess the pertinence of the identification of novelty and apomorphy by reviewing the different possible relations between ancestral and derived characters in phylogenetics. If we look at Mammalia for example, following Müller and Wagner (1991), six different forms of relation between primitive and derived characters can be found (Müller & Wagner, 1991, p. 238): loss of trait; change of shape; differentiation of repeated elements; new elements; change of context; combination of plesiomorph elements. The same types of changes can be found at the level of molecular characters (genes used in molecular phylogenies), except for the absence of change of shape and with the addition of the process of acquisition of a foreign element through lateral gene transfer (Freudenstein, 2005). [125]

It appears that the outcomes of these different processes do not satisfy to the same degree the idea of a qualitative difference essential to the intuitive concept of novelty:

_ A *loss of trait* is not a novel structure in itself. It can only bring a new trait indirectly if it is associated with a transformation of its structural environment.
_The status of the *change of shape* may be more complex to assess. In this case, we are still left with the intuitive difference between quantitative and qualitative change. Some changes of shape may appear only quantitative, like the beaks of the Galapagos finches (Abzhanov, Protas, Grant, Grant, & Tabin, 2004), other cases may be more ambiguous. For example, pronotums[126] of treehoppers in the family Membracidae have complex difference in shape not easily analysed in quantitative terms (Moczek, 2008).

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[124] "Novelties and apomorphies are essentially the same." (Arthur, 2000, p. 811)

[125] However, this similarity of processes between molecular and morphological characters does not imply a necessary correlation of the processes at both levels (cf. Freudenstein, 2005).

[126] Superior part of the prothorax in insects.

_The *differentiation of repeated elements* is comparable at the morphological level to a change of shape.

_*New element* is the type that would intuitively qualify more straightforwardly as novelty. Among many examples are feathers (Prum, 1999), the turtle shell (Burke, 1989; Gilbert, Loredo, Brukman, & Burke, 2001; Kuratani, Kuraku, & Nagashima, 2011), the lantern of fireflies (Moczek, 2008).

_ The *change of context* should be understood as morphological context, and not a change in ecological context or functional context. What is implied here is primarily changes in topology, even though these changes can be accompanied by functional changes. A classic example is the transformation of the articular and quadrate jaw bones of amniote ancestors into the malleus and incus ear bones of mammals (Crompton & Parkyn, 1963; Mayr, 1960; Rensch, 1959).

_ The same can be said of the *combination of plesiomorph elements*. One example is the formation of the gynostemium in orchids by the fusion of style and stamens (Rudall & Bateman, 2002), or the transition from the apopetalous to the sympetalous carpel with enclosed ovule (Armbruster, Debevec, & Willson, 2002).

For Müller and Wagner, as well as for many others, especially for some practitioners of evo-devo, the extension of apomorphy is in fact broader than the extension of novelty. Müller and Wagner offer a definition that entails a more restrictive extension of the concept of novelty:

> “A morphological novelty is a structure that is neither homologous to any structure in the ancestral species nor homonomous to any other structure of the same organism” (Müller & Wagner, 1991, p. 243)

According to the authors, the advantages of this alternative definition are the following:

> “The main properties of the definition are that it is independent from descriptive or mechanistic qualifiers, that it excludes merely quantitative or negative traits, and that it allows distinction between meristic variation and true novelties” (Müller & Wagner, 1991, p. 252)

The absence of descriptive and mechanistic qualifiers means that the definition remains neutral regarding the developmental nature of novelties and the processes at their origin. The distinction of meristic variation and novelty is expressed by the exclusion of homonomy. Homonomous traits correspond to serial homologs as defined by Richard Owen, that is, corresponding parts in the same organism, for example leg pairs in centipedes or hairs in mammals. The definition avoids considering a new leg pair or new hairs as real novelties.

As the authors acknowledge, this definition is dependent on the concept of homology. To make this definition operational, the conditions under which a trait has no homolog must be established.

Phylogenetic homology and biological homology

Müller and Wagner (1991) acknowledge the inadequacy of the view of homology used in systematics for their definition of novelty:

> "In systematics, any discernable (*sic*) structural difference may be homologized. In evolutionary biology it is more useful to restrict the homology concept to anatomical units. This excludes merely quantitative variation, changes of proportion, and topological relationships among body parts." (Müller & Wagner, 1991, p. 244)

Taxonomic characters are the attributes of organisms that are used in systematics to establish relations of homology and provide evidence of phylogenetic relationships. What Müller and Wagner (1991, cf. also Wagner, 1989) propose is to discard the "quantitative variation, changes of proportion, and topological relationships among body parts", which are the basis of distinctions between character states, and to retain only character identity.

Wagner (2014, p. 76) recently stressed again the distinction between his concept of homology and the one used in phylogenetics but argues for a relation of complementarity. Wagner's position could be interpreted as non-committal compared to, on one side, those who argue for a relationship of mutual dependence of the two concepts (Brigandt, 2007; Winther, 2009), and, on the other side, those who argue for their incompatibility (Cracraft, 2005; Scholtz, 2005).

> “The conceptual irrelevance of the distinction between characters and character states is true for systematics because of its pragmatic needs, and not because body parts with different character states do not exist. Anatomical, variational, and developmental evidence shows that they do exist and that the distinction is necessary to understand the pattern of biological diversity and disparity at the phenotypic level.“ (Wagner, 2014, p. 76)

This clear distinction of character and character state transfers the problem again to the notion of character as *anatomical unit*. Is there an agreement on how anatomical units are individuated?

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III – GUNTER WAGNER’S DEVELOPMENTAL APPROACH TO HOMOLOGY AND NOVELTY

The biological concept of homology

Günter Wagner relies on a biological concept of homology based on development mechanisms. Traits are homologous if they are produced by the same set of relatively autonomous developmental processes, or the same “character identity network” (Wagner, 2007, 2014), to use the concept he has developed in recent years. Thus a new homolog arises when a new independent character identity network arises. Now this developmental independence can arise a long time after the appearance of the new character.

Wagner’s theoretical elaborations on the developmental underpinnings of morphological characters and on the arising of novel characters span nearly thirty years from his formulation of the concept of biological homology (Wagner, 1989a, 1989b) to his recent theory of character identity networks (Wagner, 2007, 2014). The central principles of his more recent theory are already present in his early conception of biological homology.

An important problem is defining what makes traits the same and what makes traits in related species sufficiently different to not be homologs. The concept of biological homology developed by Wagner is an attempt to ground homology in its developmental underpinnings in order to answer the problem:

> “A biological homology concept is associated with a large number of empirical questions, most of them falling into the range between experimental embryology and comparative anatomy. How are ontogenetic networks of well-established homologs organized? How common are hierarchical and cyclical network structures? What is the pattern of interspecific variation of ontogenetic networks? How conservative are generative rules in comparison to character variation? *All of these questions suggest that a successful research program on the biological basis of homology should consider the evolution of morphological characters at two levels: 1) the level of character modification within a given framework of developmental constraints and 2) the level of the evolutionary modifications of constraints*.” (Wagner, 1989b, p. 1169, emphasis added)”

Wagner’s conception of homology and of evolutionary novelty is based on a sharp distinction between characters and character states. There are constraining developmental mechanisms producing and defining anatomical units or characters, and variation within these developmental frameworks is of a different nature than variation altering the framework itself or producing a new one. Wagner originally developed the notion of *epigenetic trap* (1989a, 1989b) to describe the developmental mechanisms that make evolutionary conservation more likely for some traits than for others, and those mechanisms that make anatomical units develop in a quasi-autonomous way. The hierarchical networks refer to cases where the development of some embryonic trait is dependent on the previous development of another embryonic trait. The more the functional traits are dependent on the formation of a previous trait, the more likely it is to be conserved through time. Cyclical networks refer to the mutual inductive relations between parts of a developing organ. This feedback mechanism makes the development of certain organs nearly independent of external inductive signals and explains how the phenomenon of ectopic organs is possible. The vertebrate eye and the fin-hook of Blenniids are examples of organs whose development relies on a cyclical network. The development of the vertebrate eye is characterised by a cycle of epigenetic interactions between the lens and the retina. The induction of new developmental stages is not triggered by external elements but by the parts of the eye themselves (McAvoy, 1980).

“Character identity networks”: the developmental solution to the problem of homology

Wagner (Wagner, 2007, 2014, 2015a) recently proposed a new formulation of his theory of character development, conservation and change: it is a three-stage model of character formation with at its centre the concept of Character identity network (ChIN), which is the developmental basis of homology. This formulation can be seen as a refined version of the definition of homology by Van Valen (1982) as continuity of information. Van Valen’s definition has been undermined by numerous cases of different developmental origins of homologous characters.

According to Wagner, the idea of continuity of information can be saved with a more fine-grained view of the development of character, which allows one to distinguish between variable and highly conserved stages. In the development of characters, Wagner distinguishes between the inductive signals, the character identity networks and the realizer genes. The variation of inductive signals and realizer genes is much less constrained than the variation of character identity networks. Examples of homologous characters forming from different precursors show the variability of the inductive signals but not of the gene networks determining the identity of the characters themselves. As Wagner writes: “inductive signals are not instructive (i.e., do not contain information about the final product), but are only permissive (i.e., they trigger a process intrinsic to the cells themselves)” (2014, p. 93).

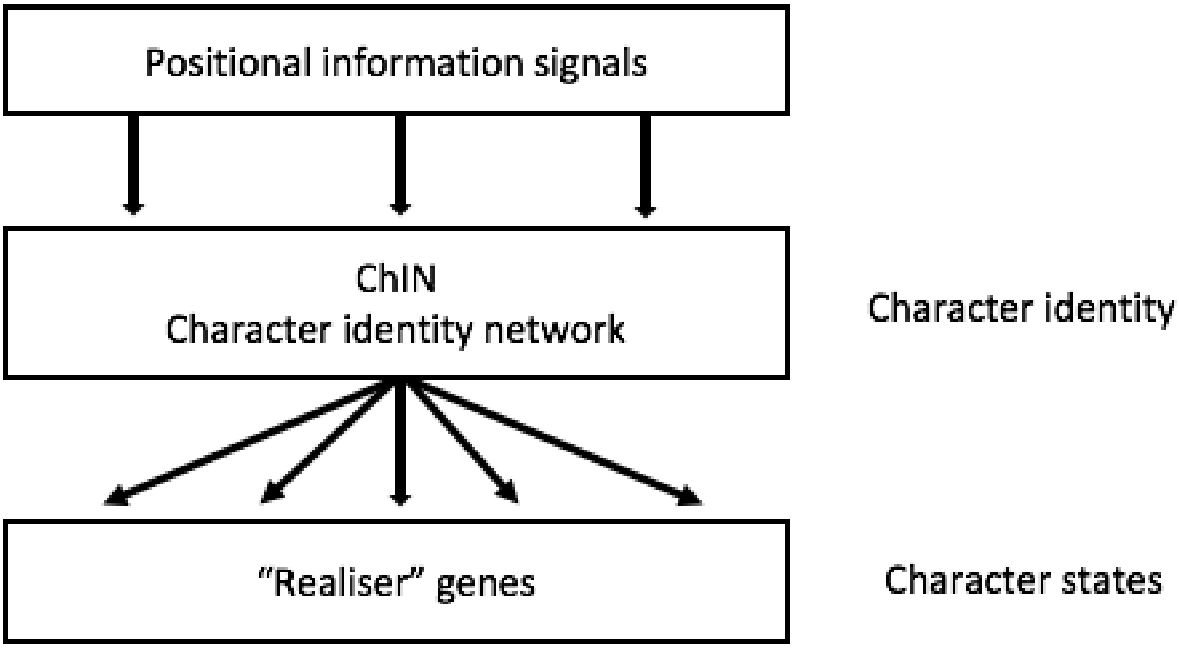

Fig. 12: Wagner's three-stage model of character development (redrawn after Wagner, 2014, p. 97)

The existence of a distinction between character identity genes and realizer genes, that is, genes governing the development of the details of the character, has been revealed by knockdown experiments. One significant example is the knockdown of the Ubx gene in the beetle *Tribolium* (Tomoyasu, Wheeler, & Denell, 2005). In *Drosophila*, which has wings at the forewings positions and haltere at the hindwings positions, the knockdown of Ubx leads to the formation of wings rather than halteres at the hindwings position. Thus, Ubx could either determine the formation of halteres or the hindwing identity. *Tribolium* has elytra at the forewings positions and wings at the hindwings positions. The knockdown of Ubx leads to the formation of elytra at the hindwings positions. This shows that Ubx determines hindwing identity and not a specific character state such as wing or haltere. When Ubx is knocked down, the forewing identity is expressed at the hindwing position.[127]

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[127] A similar idea is presented by Jean Deutsch (2005): "Hox genes have a critical role in differentiating serial homologues, whatever the precise morphology of these appendages could be. The present data lead us to adjust our point of view on Hox genes' function. It is common to say that the Hox genes determine the identity of body parts. What does identity mean? From our own human perspective,

ChINs and Kernels

What makes ChINs specific is their high degree of conservation. That property relates ChINs to the concept of kernel developed by Eric Davidson and Douglas Erwin. Kernels are highly conserved gene regulatory networks typically found in the patterning of body plans and the control of segment numbers in animals. Furthermore, the mode of origin of kernels and ChINs is also similar:

> "Critically, these kernels would have formed through the same processes of evolution as affect the other components, but once formed I they would have become refractory to subsequent change" (Davidson & Erwin, 2006, p. 761c)

The main difference between the two concepts is that kernels are defined by their formation in early metazoan evolution and their conservation across phyla or at the phylum level. On the contrary ChINs underpin a broader range of characters ancient as well as recently evolved.

Novelty: From the overcoming of developmental constraints to the creation of new homologues

The question of the mode of origin of ChINs invites us to look back and consider the conceptual change in Günter Wagner's theorisation of the evolution of novelty. There has been a significant change between Wagner's original formulation of the problem of novelty (Müller & Wagner, 1991; Wagner, 2000, 2001; Wagner, Chiu, & Laubichler, 2000) and his more recent formulation (Wagner, 2014). In chapter 1, I provided an analysis of the characterisation of the problem of novelty based on different articles dating from the turn of the century.

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most of us thought that it meant a precise morphology for a group of cells expressing a given Hox selector. Genetic analysis reveals the genome's point of view, that of the organism itself in its evolution. It now appears that the precise morphology of an organ or a segment does not matter, what matters for the Hox genes is relative morphology. In other words, identity, determined by Hox genes, means no more than difference between a certain body part and its neighbours along the AP axis. We can thus view the Hox genetic programme as a metaprogramme, versatile enough to accommodate changes in the underlying genetic programmes specifying the precise morphology of individual parts. In summary, the Hox genes do not make the difference between the three thoracic segments, after all. They might just ensure that they are (and maybe have to be) different from one another"(Deutsch, 2005).

The focus was on the developmental mechanisms responsible of the origin of a new morphological character. Attention was given:

_ To the possible difference between the original developmental mechanism responsible for the origin of the trait and the mechanism responsible of the development of the trait in extant species;

_ To identification of the type and degree of variation in developmental mechanism at the time of the origin of the character, that is, the measure of the developmental constraint that had been overcome.

Even though other mechanisms were considered, the assumption was that the origin was caused by a change in gene regulatory networks.

With the concept of the ChIN, the main focus is not directed at the origin of a morphological structure but at its acquisition of quasi-independence:

> ‘‘The origin of a morphological novelty is the evolutionary process through which a novel character identity arises. In other words, an evolutionary novelty originates when part of the body acquires individuality and quasi-independence’’ (Wagner, 2014, p. 125)

The original emergence of the structure is not the main explanandum anymore New ChIN do not appear in an abrupt way. Wagner admits that new ChINs are often absent in the incipient stages of evolutionary novelties. He acknowledges the role of Gerd Müller’s side-effect hypothesis for the origin of novelties (Müller, 1990) that states that the origin of morphological novelties is found not primarily in genetic changes but at higher levels in the reactions of cell populations to changes in mechanical pressures.

Thus, a new set of research question emerges:

> “_ How does the appropriate set of target genes come under the control of the gene regulatory network of the cell or the cell population?
>
> _ How is the expression of target genes linked to those signals that ensure differential expression within the appropriate spatial and temporal context?
>
> _ How does the gene regulatory network acquire the quasi-autonomy that is characteristic of individualized body parts and cell types?” (Wagner, 2014, p. 174)

The concept of ChIN is still related to the concepts of constraints and evolvability since the acquisition of a ChINs involves the acquisition of evolutionary independence that may enable further evolution. However, compared to the formulation of the problem of novelty analysed in chapter 1, there is more attention to developmental stability and adaptive consideration. The emergence of a ChIN may be favoured by selection because it brings *developmental robustness* to the new trait. ChIN may also have the adaptive role of preventing the expression of genes in spatial and temporal contexts where they would be harmful.

This dimension of ChINs is illustrated by Günter Wagner's comments on Müller's example of the origin of the syndesmoisis tibiofibularis presented in chapter 1 (section IV), and on Müller's organisational concept of homology, partly elaborated from a generalisation of this example.[128] Wagner himself distinguishes the epigenetic view of Müller from his own "more genetic view" (G.P. Wagner, 2014, p.172):

> "However, from the perspective of this book, Newman and Müller's (2005) perspective is incomplete because it does not explain the eventual developmental/genetic individualization of the new structure. There are at least two different hypotheses for the individuation of these structures:
> _ Selection pressure to make the development of the new structure more reliable, less dependent of the mechanical pressure. It would be a case of selection for developmental robustness.
> _ The structure is selected to assume a specific shape, which would increase its functional performance. This could lead to character-specific developmental program." (Wagner, 2014, p. 173)

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[128] "Homologues are autonomized elements of the morphological phenotype that are maintained in evolution due to their organizational roles in heritable, genetic, developmental, and structural assemblies." (Müller, 2003). Wagner thus considers Müller's position and his as complementary:"As such, the organizational homology concept is not concerned with explained how characters can be developmentally individualized and, thus, is complementary rather than competing with the ideas developed in this book." (Wagner, 2014, p.77)

The problem of the phylogenetic junctures at which novelties occur

Considering the late arising of ChIN, how should this affect the idea of a precise phylogenetic juncture for the appearance of a novelty? It seems that we should adopt a more encompassing view of novelty and accept that the process of origination can be spread out over long geological time. The example of the perianth in angiosperms illustrates how the process of origination of a novelty can have different stages and be spread out over long stretches of geological time (Endress, 2001, 2008; Specht & Bartlett, 2009; Warner, Rudall, & Frohlich, 2009). The differences in the approaches of Müller and Wagner indicate that while Müller would be focused on the emergence of the morphological characteristics of the perianth, Wagner is explicitly focused on the emergence of the ChIN for the whole flower, attributing distinct identities to sepals and petals.

As both researchers advocate, their views are not competing but complementary views on the evolution of homology and the origin of novelty. It thus appears that integration of approaches and explanations is the right path to follow. These ambiguities, or more accurately, these differences in focus and emphasis should be viewed as explanations of different aspects of the problem of novelty, or even, in certain cases like the perianth, explanations of different phases in the origin of a novelty. Now, this integrative approach seems only possible if the concept of the phylogenetic juncture at which novelty occurs is relaxed. Several cases are possible here:

a) All aspects or phases of the origin of a novelty can be located at the same phylogenetic juncture;
b) Different aspects or phases can be located at precise but distinct phylogenetic junctures;
c) The phylogenetic junctures of only some, but not all, phases or the origin of a novelty can be located;
d) No precise phylogenetic juncture can be located for any of the phases of the origin of a novelty.

IV- HOMOLOGY AND NOVELTY IN PLANTS

Before addressing recent development in research on the origin and evolution of the angiosperm flower and addressing Günter Wagner's application of his theory to this case, I will undertake a rapid review of differences between plants and animals that can potentially affect the problem of novelty and the generalisation of theories of novelty.

Differences between plants and animals relevant to the problem of novelty

Independent origins of plant and animal development

A common origin to plant and animal developments would give support to the transposition of theories from animal to plants. The data gathered by whole-genome sequencing and by developmental genetics point to independent origins of development in plants and in animals (Meyerowitz, 2002).[129] This means that we cannot rely on a relation of homology to transpose theories of novelty from animals to plants. That we cannot rely on common descent does not mean that there cannot be convergence between plant and animal development.

These two distinct emergences of development make possible a real comparative study of development that does not rely on common descent (Meyerowitz, 2002; Vervoort, 2014).[130] Plant and animal developments share important features, particularly in pattern formation, a fundamental mechanism in development (Meyerowitz, 2002). Regarding spatial pattern formation, homeotic genes acting in a similar manner can be found in animals and in plants. In animals, this role is in large part fulfilled by the HOX genes group whereas in plants it is the MADS-

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[129] "Although the logic underlying many developmental processes is similar, the molecules that carry out the logical plan are unrelated, or represent novel arrangements of ancient protein domains." (Meyerowitz, 2002, p. 1485)

[130] An important question however is how far reaching are the implications of this matter of origin. How informative is the fact of independent origins? This fact has to be confronted with the complexity of the phenomena of homology. The discovery of independent origins can be tempered by the phenomenon of deep homology (Shubin, Tabin, & Carroll, 2009).

box gene family that plays this role. The distinction between homology and homoplasy, or common descent and convergence, is actually not straightforward because of the phenomenon of deep homology. Plants and animals evolved development independently but they inherited the same genetic toolkit from their unicellular ancestor.

Plasticity, modularity and open development

The important level of developmental modularity and plasticity in plants entails a high level of tolerance to genetic mutations and recombinations. Thus the level of deleterious mutations and recombinations is in principle lower in plants than in animals.

Because most plants are not mobile and are thus highly dependent on the environment, environmentally induced variation is more frequent in plants than in animal. Evolution through phenotypic plasticity and genetic accommodation should then be more frequent in plants than in animals. Plants have an open system of development in which apical meristems continually produce new organs. There is a potential of genetic mosaicity when plant parts endure mutations. Because of the iterative production of sexual organs and of vegetative reproduction, the mutations have a higher probability of being transmitted than in animals.

Events of homeosis are probably more frequent in plants than in animals, because of the greater modularity of plant development (Baum & Donoghue, 2002). Some of these can lead to monogenic speciation. The evidence for single-step mutations that engender temporal or mechanical changes in reproductive organs is overwhelming, particularly in flowering plants. Outstanding example: simple one-step mutations that alter the number, position, symmetry and fusion of floral parts and even the sexuality of flowers. Because such features are used in taxonomy to characterize plants, this could lead to the sudden apparition of taxa at the genus level or above.

Hybridisation and polyploidy

The hybridisation and polyploidy in plant was already intensely studied during the Modern Synthesis (see chapter 2). However, Stebbins and other Modern Synthesis botanists only attributed a limited evolutionary potential to polyploidy (Soltis, Visger, & Soltis, 2014). Hybridization, both between subspecies and between species, is more frequent in plants than in animals. Production of extreme or novel characters by hybridization (Rieseberg, Archer, & Wayne, 2001; Yakimowski & Rieseberg, 2014)

General consequences for novelties in plants

This shows a variety of causes, mechanisms and paces and frequencies. The problem resides in weighing the respective importance of these phenomena. Some can be relatively well traced such as the number of polyploidy events in a lineage; others are still obscure such as the consequences of hybridization events for evolutionary rate and occurrence of novelties. Salient differences with animal novelties have however emerged.

_ Events of homeosis are probably more frequent in plants than in animals, because of the greater modularity of plant development (Baum & Donoghue, 2002). Some of these can lead to monogenic speciation. The evidence for single-step mutations that engender temporal or mechanical changes in reproductive organs is overwhelming, particularly in flowering plants. Outstanding example: simple one-step mutations that alter the number, position, symmetry and fusion of floral parts and even the sexuality of flowers. Because such features are used in taxonomy to characterize plants, this could lead to the sudden apparition of taxa at the genus level or above. This can occur though the production of apetalous fertile flowers; a change in the number of flowers in an inflorescence; a change in floral symmetry that can cause a potential alteration of the mode of pollination and thus a mechanical reproductive isolation; a change in temporal barriers to sexual reproduction, for example day-sensitive/day-neutral; a change in mechanical barriers: flower that do not open and therefore are self-pollinated.

_ A related fact is that he concept of “hopeful monster” is defended by more plant biologists than animal biologists (Bateman & DiMichele, 2002; Günter Theissen, 2006, 2009)

_ Homoploid hybrid speciation and allopolyploid speciation are much more common in plants than in animals (Abbott et al., 2013). Because they imply drastic genetic recombination and chromosomal changes, their probability or engendering drastic and rapid phenotypic novelties is much greater than that of small mutations and recombination through normal sexual reproduction.

The origin of the angiosperm flower

The origin of the angiosperm flower is still today considered as a very complex problem and there are maybe as many competing theories in the contemporary literature as there were in the Modern Synthesis era (Bateman, Hilton, & Rudall, 2006; David A. Baum & Hileman, 2006; Frohlich, 2003; Frohlich & Parker, 2000; Specht & Bartlett, 2009; Guenter Theissen & Melzer, 2007). However the speculative range of these theories has been narrowed a lot. Three main sources of evidence have given support to the strobilus theory of the origin of the flower and the homology of flower organs with leaves:

_ The advancement of phylogenetics systematics partly based on molecular phylogenies (Endress & Doyle, 2009; Judd, Campbell, Kellogg, Stevens, & Donoghue, 1999)
_ The discoveries of fossils (Donoghue, Doyle, Gauthier, Kluge, & Rowe, 1989)
_ Advances in plant developmental genetics (Causier, Schwarz-Sommer, & Davies, 2010; Coen & Meyerowitz, 1991; Jaramillo & Kramer, 2007; Kramer & Jaramillo, 2005; Meyerowitz, Smyth, & Bowman, 1989; Rosin & Kramer, 2009)

The ABC model of floral organ identity was developed through the study of genetic mutants with homeotic organ conversions. I was discovered that the identities of the different floral organs in *Arabidopsis* and *Antirrhinum* are determined by the interaction of transcription factors produced by different classes of MADS-box genes a type of homeobox containing genes that are involved in the developmental regulation of many plant organs. The expression of the gene controlling the production of the A-function transcription factor leads to the formation of sepals, expression of A-function and B-function produces petal, B-function and C-function produce stamens and C-function alone produces carpels. It was then discovered that the proteins of the A,B and C classes do not regulate organ identities alone but have to form dimers with another class of transcription factor proteins, called class E, in other to initiate organ formation (Theissen & Saedler, 2001).

The support of developmental genetics to the strobilus theory

If the strobilus theory of the origin of the flower is accepted, there are four main problems in the origin of the flower:

1) The transition from separate unisexual sporangiae to the bisexual condition.
2) The evolution of determination (limited growth) of the floral axis and the compression of the organs.
3) The origin of the perianth (the non-reproductive organs of the flower).
4) The differentiation of the perianth into petals and sepals.

An example of explanation of the four transitions is provided by Baum and Hileman (2006):

1) The evolution of the bisexual axis is conceived as an homeotic conversion of microsprophylls into megasporophylls in the ancestral male cone. This is explained by competition of the C-class and B-class transcription factors for their dimerization with E-class transcription factors. If there is an excess of C-class, a threshold can be reached when there is not enough E-class left for the dimerization necessary to initiate the male identity and a female cone develops.

2) The switch to determinacy is explained by the negative regulation by C-class transcription factor of the gene WUSCHEL responsible for the maintenance of the indeterminacy of the apical meristem.

3) The formation of the perianth, that is, non-reproductive organs, of the flower is explained by the sterilisation of stamens. The postulated scenario is that the co-regulation of WUSCHEL and C-class genes caused an spatial extension of the expression of B-class genes which allowed for the formation of petals.

4) The progression towards clear differentiation of the perianth into petals and sepals is explained by the increased dependence of B-class genes with co-regulators.

Character identity networks and the ABCE model of flower development

Is the sharp distinction between character and character state also justified in plants? Do we find in plant evolution the differential conservation of gene networks determining organ identity and realiser genes? Some of best case studies available to settle these questions are the flower organs of *Arabidopsis thaliana* (Brassicaceae) and *Antirrhinum majus* (Plantaginaceae) because their genetic and developmental underpinnings are widely studied. Günter Wagner interprets this example as an illustration of his theory of Character Identity Networks.

_ Wagner is interesting because he develops a general theory of novelty, mostly based on animal examples, but he also uses the example of the flower and applies his theory to the plant kingdom.

> "What is unique about flowers is how the deployment of the various parts became developmentally integrated into the flower. The developmental integration of the flower is implemented through the dependence on the expression and function of flower meristem genes (the E-class genes) of the organ identity genes (see above). This integration evolved through a derived dependency of the function of the organ identity transcription factors on protein-protein interactions with the flower meristem regulators. The notion of a developmental type, the angiosperm flower, can be grounded in the obligatory

> cooperativity among these transcription factor proteins.” (Wagner, 2014, pp. 414–415)

That is why Wagner is interested in the angiosperm flower, because it is one of the best known examples of the developmental control of organ identity. The advancement of research on novelty in plants is recognised by Günter Wagner:

> “The motivation is that research on character identity and character origination is much more advanced in plant biology than in any of the zoological model systems of which I am aware. [...] In contrast, much of the zoological literature focuses on other aspects of developmental evolution, such as the controversy regarding the relative importance of cis-regulatory and trans-regulatory evolutionary changes, the causes of organ loss (e.g., the loss of pelvic structures in freshwater stickleback populations), or the modifications of certain quantitative or meristic characters like the numbers and kinds of bristles in different parts of the insect larva or imago. Overall, the problem of organ identity origination has received much less attention in zoological devo-evo than in botany” (Wagner, 2014, p. 385)

From fading border to ABCE developmental programs, ecological explanation versus developmental explanation

The case of the evolutionary transition from flowers with a fuzzy morphology to the well-defined flower of core eudicots can illustrate the existence of different possible causes of robustness in developmental processes. The fading borders model interprets the gradual transition in floral morphology observed in basal angiosperms, magnoliids, and basal eudicots as reflecting a gradient in expression levels of floral organ identity genes across the developing floral meristem, where weak expression at the margin of the range of activity of a given gene overlaps with the expression of another regulator in adjacent organs (Chanderbali, Berger, Howarth, Soltis, & Soltis, 2016; Soltis, Chanderbali, Kim, Buzgo, & Soltis, 2007) . Gradually fading influence toward the periphery of broadly expressed organ identity functions, of B function in particular, imparts some features of one set of organs onto adjacent floral organs.

Ecological and selective factors

The gradual transition towards well-defined organs and the floral quartet as it is found in *Arabidopsis* is linked to the co-evolution of plants and their pollinators. The increased specialisation of plant-pollinator relations requires increased stability of phenotypic trait of the flower to properly attract the pollinator and be pollinated. Under this hypothesis, the flower structure would be kept constant by stabilizing selection. (Armbruster, 2016; Fenster, Armbruster, Wilson, Dudash, & Thomson, 2004).

Role of the developmental architecture (obligate heterodimerization)

Günter Wagner favours a hypothesis based on developmental properties:

> "The flexibility of the gymnosperm system results from the many possible interactions among transcription factor proteins, many of which are probably functionally redundant. By comparison, the rigidity of the angiosperm flower Bauplan results from the obligatory interaction among a number of transcription factors, all of which need to be co-expressed or reproductive organ development. This is unlikely to occur spontaneously outside of the flower context, as it would require multiple simultaneous changes. To my knowledge, this is the first example for which we have a mechanistically plausible explanation for the origin of a developmental type, the angiosperm flower. The integration of the developmental type results from the obligatory formation of a multimeric transcription factor complex, which necessitates the co-expression of multiple transcription factor genes with little or no functional redundancy. This situation arose from an ancestral situation in which numerous protein-protein interactions were possible and with many means for functional compensation. The derived canalized state was to a loss of possible physical protein-protein interactions among transcription factors, which made the activation of target genes dependent on a strictly determined set of factors." (Wagner, 2014, p. 405)

According to Wagner, the integration of the angiosperm flower resulted from the developmental genetic architecture. B- and C-class genes require the floral context to exert their role in the flower organ development. The phenotypic integration of the flower is a consequence of the molecular interaction of the floral organ transcription factors (B and C) and the floral meristem transcription factors

(E). B and C have to form tetrameric transcription factor complexes with E to be able to regulate organ development. This is not a necessary configuration. E-genes could only intervene to trigger the activation of B and C without being needed in the regulation of the target of B and C.

What is the relation between the two explanations? Are we faced with competing or complementary explanations?

a) Among the researchers studying the phenomenon experimentally, the alternative is framed as either selective advantage or the heterodimerization or genetic drift.

b) Wagner is less interested in what caused heterodimerization to be introduced and diffused in the first place (selection or drift), but more about what caused it to be conserved over a long evolutionary period. Here the alternative is between:

The example of the evolution of the flower raises several questions:

1) What the cause of the existence of this flower “Bauplan” or “type”?

   Wagner seems to draw an opposition in this case between the developmental explanation and the selective explanation. How can we articulate selection and developmental bias?

2) Is it representative of all the angiosperms? If not, how far can we extrapolate?

3) Is it representative of other plant characters?

   a. In terms of evolutionary trend (towards integrated ChINs).

   Can this observation of an evolutionary tendency towards more integrated and constraining developmental architecture be generalised?

   b. In terms of developmental underpinning of traits.

Homeosis, heterotopy and quasi-autonomous parts

The existence of heterotopic phenotypes, for example Eupomatia bennettii, which has stamens as the outermost whorl, does not contradict Wagner's theory of organ identity and of quasi autonomous parts. On the contrary the ABCE model of character identity in the flower, as an example of ChIN, can predict the occurrence of such phenotype with the shift of expression domains of the regulatory genes. But the pervasiveness of these heterotopic phenotypes (Baum & Donoghue, 2002; Rutishauser, Grob, & Pfeifer, 2008; Sattler, 1988, 2012)favors the hypothesis of the selection pressure on pollination rather the hypothesis of developmental constraints. They tend to show that it is a case where actual divergent variants have lower fitness rather than a case where divergent variants are made improbable by developmental constraints.

Fuzzy morphology

The existence of plants with more fuzzy morphologies is challenging Wagner's model more frontally. Rutishauser et al. (2008) talk of plant organ identity crisis. This questions the special status of ChINs (their high conservation). Considering open development and the need for plants to react to environment. The stability of the flower might be an exception due to the necessity of the attraction of specific pollinators.

V- PROMISES AND PITFALLS OF GENERALISATIONS IN EVO-DEVO

I want to argue here firstly that Wagner engages in different forms of typological thinking and that, despite classical objections, this method is perfectly justified in evo-devo. Secondly, I want to argue that a problem with Wagner comes not from the opposition between typological and population thinking, but from a tension between what Jenner (2008) has called the idiographic and nomothetic goals of evo-devo. In favouring the search for generalisations across higher taxa, especially the presence of ChINs across higher taxa, Wagner is not sensitive enough to diversity inside these higher taxa.

Wagner (2014) concludes his analysis of the case of the flower this way:

> “The tetrameric transcription factor complexes are, at least in this case, the very locus and root of the macroscopic integration of the *developmental type*, in this case the flower. This is a fundamental insight that raises hope for all of biology in that we may be close to a deep understanding of the vexing patterns and concepts of comparative anatomy, with names like body plan, developmental type, and homology, which have eluded experimental analysis and mechanistic understanding for centuries.” (Wagner, 2014, p. 398)

Wagner defines his type of reasoning as “homology thinking” (2014, p. 425) and not typological thinking because he focuses on examples of characters that are inherited from a common ancestor such as the tetrapod limb or the flower, and intends to uncover their developmental underpinnings to explain their evolutionary stability and what he calls their “variational properties”. Wagner does not hesitate to describe the flower as “a developmental type” because it is grounded in a shared evolutionary history of the angiosperms. But his approach goes beyond homology thinking when he develops the concept of character identity network and goes on to demonstrate that character identity networks with similar properties can be found across very distant taxa that did not inherit these similar networks from a common ancestor. The pervasiveness of character identity networks is not the product of homology, but is nonetheless a developmental regularity.

Jenner (2008) distinguishes between developmental type conceived as individual and developmental type conceived as class. In this framework, the flower developmental regulatory network is a developmental type of the individual form because it is supposed to have been inherited from a common ancestor. Thus each instance of this developmental mechanism is homologous with other instances. On the other hand, character identity networks are a developmental type of the class form, because they are found in many remotely related taxa and their widespread existence cannot be explained by common ancestry alone. Wagner does not talk of the category of character identity networks as a developmental type because it would be falling into typological thinking without any justifying ground (while homology justifies it in individual cases).

Nevertheless, it may be argued that his work is guided by an ambition of generalisation beyond individual developmental types. One of the main goals of his work is to show the pervasiveness of character identity networks and the reality of his three-stage model of development.

Typology versus population thinking

Is Wagner indulging in typological thinking? Is it the object of my analysis? Before I address my reservations regarding Wagner's approach, I want to distinguish my position from the common accusations against typological thinking that can be applied to practitioners of evo-devo like Wagner (see Witteveen, 2018, for a review). I am going to review the classical arguments against typological thinking to show that Wagner does not fall in these traps.

I will adopt the definition given by Tim Lewens:

> "The typological thinker believes there is some limited number of stable 'types' or 'forms', which explain the observed patterns of diversity in the biological world." (Lewens, 2009, p. 355)

Here are a few examples of use of typological concepts in evo-devo:

> "Diversity is not merely an inconvenience. It has also been regarded as a sort of epiphenomenon, the frills and digressions surrounding the real elements of development. To developmental biologists, there is a mechanistic universality in developmental processes despite any diversity of ultimate outcome." (Raff, 1996, p. 22)

> "If there is any *typological* concept that is alive and well, then it is the concept of an angiosperm flower.1 As we will see in the following sections, there are good reasons why the concept of "*flower type*" is a meaningful biological term. Flowers are developmentally tightly integrated and the extensive variation among extant angiosperms can be understood within the confines of a "*flower Bauplan*" or "*flower developmental type*." (Wagner, 2014, p. 386)

> "the different architectures of these wings [in bats, birds and pterosaurs] reflect different develop- mental modifications of a common tetrapod forelimb design" (Carroll, 2005, p.190)

The four arguments against typological thinking

Tiw Lewens (2009) has recently distinguished four arguments against typology:

a) Typological Thinking is committed to a platonic metaphysics.

b) Typological Thinking is antievolutionary.

c) Typologists are committed to the "Natural State" model.[131]

d) Typological Thinking is incompatible with the causes of population genetics.

Following Lewens, it is possible to adopt *a nominalist* understanding of developmental type. Such a view allows us to reject all four objections against typological thinking, especially the last one. The existence of developmental types is not incompatible with the concepts of population genetics. Natural selection can be the cause of their existence but is not the only possible one.

Nomothetic and idiographic approaches in evo-devo

There is thus no compelling reason to reject typological thinking in evo-devo. However, a problem might arise if the focus on developmental types favours generalisations over breath of the taxa studied. This can be best understood I the terms used by Jenner (2008) to define the goals of evo-devo:

> "Evo-devo is an ambitious young discipline with both idiographic and nomothetic

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[131] For the natural state model, the cause of deviation and the cause of stability are distinct.

> goals. Idiographically, evo-devo aims to document the unique effects of changes in evolutionary developmental mechanisms on the origin of novelties and the evolution of body plans. Nomothetically, evo-devo attempts to establish the general effects of evolutionary developmental mechanisms on determining the overall direction of phenotypic evolution." (Jenner, 2008, p. 114)

The idiographic and nomothetic tasks are complementary, the idiographic studies serve as evidence for generalisations. But there can be a tension between the two tasks, precisely because supplementary idiographic data can weaken preliminary generalisations. Günter Wagner's recent project developed in his 2014 book is arguably more nomothetically than ideographically oriented. In his demonstration of the pervasiveness of character identity networks, Wagner has looked for characters of plants that best illustrate the concept of ChIN. The question of how representative is the flower's ChIN of other plant characters' developmental underpinnings should not be separated of the search for ChIN across higher taxa because the evolutionary significance of ChINs is partly dependent on this question.

CONCLUSION

In chapter 1, after presenting and comparing the evo-devo and the functional-historical characterisations of the problem of novelty, I focused on two case studies, Walter Bock's research on the origin of the avian basitemporal articulation and Gerd Müller's research on the origin of the syndesmosis tibiofibularis, pertaining respectively to the functional-historical approach and to the evo-devo approach. I showed the existence of a dissonance between the great difference in expressed theoretical commitments and conceptual definitions on one side, and the proximity in the explanatory practices and the evidential sources used on the other side. A similar type of comparison can now be undertaken between Stebbins' research on plant novelties and Wagner's research on the origin and evolution of the flower.

As explained I chapter 3 (pp.158-161), Stebbins criticised Corner for conflating two conceptions of function in his definition and his examples of transference of function: proper cases of transference of function, according to Stebbins, involve the evolutionary transfer of the performance of an ecological function (such as protection of the embryo or dispersal) from one character to another; other cases involve what Stebbins calls a “reorganisation of the developmental pattern” (1974a, p.84), such as in the example of the transition from apocarpy to syncarpy. Interestingly, a related distinction has been recently developed by Baum and Donogue in their update of the theory of transference of function informed by developmental genetics (Baum and Donoghue, 2002). The first type of transference of function they identify, “non-homologous transference of function” refers to cases where the two structures involved (the one performing the function in the ancestral species and the other structure performing the same function in the descendant species) do not share, either totally or partially, developmental genetic programs. This is illustrated by the (hypothetical) example of the transference of the function of dispersal from fruit hairs to fruit wings. The second type, “homologous transference of function”, refers to cases where the two structures share some developmental genetic programs.[132]

Stebbins, like Baum and Donoghue, distinguished the two dimensions of ecological processes and developmental processes but attributed evolutionary significance to both of them; his attention to the latter is illustrated by his insistence on the role of intercalary meristems in morphological change. Günter Wagner operates the same distinction. In the case study that Wagner focuses on, the evolution of the flower, there is a potential competition between a developmental process, the evolution of obligate transcription factor interaction, and an ecological process, the co-evolution of plant hosts and pollinators leading to specialisation. There is, however, no major distinction in terms of conceptual

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[132] It should be noted that Baum and Donoghue adopt different concepts of homology and non-homology than Günter Wagner. For Wagner, if a character’s development is dependent on a new ChIN and if this new ChIN allows for the independent evolution of this character, then this character is non-homologous. For Baum and Donoghue, if a new structure shares some of its developmental genetic programs with a pre-existing structure, then this new structure is homologous to the pre-existing one. While Wagner focuses on the developmental and evolutionary autonomy of the ChIN to determine homology and non-homology, Baum and Donoghue focus on the genetic content of the ChIN.

framework between Stebbins and Wagner; both recognise and distinguish ecological and developmental factors in plant evolution. This comparison of Stebbins and Wagner is at odds with oppositions between Modern Synthesis and evo-devo as distinct and potentially irreconcilable theoretical frameworks. Or, more accurately, Stebbins' approach to plant evolution, at least as it is presented in his *Flowering plants*, does not match the alleged Modern Synthesis approach as described and criticised by some evo-devo proponents.

However, two important differences lie in the richness of the developmental data and concepts available to Wagner compared to those available to Stebbins and in the levels of analysis of development that each adopts. Although Stebbins uses the concept of regulatory genes and stresses their importance in evolution, in *Flowering plants*, this concept only has a programmatic status. When discussing the importance of developmental processes in evolution, Stebbins discusses the notion of meristematic capital and the role of intercalary meristems, thus adopting the levels of analysis of cells and tissues rather than the genetic and molecular levels. Other important evolutions distinguish the perspective of evo-devo from that of Stebbins, in particular the use of phylogenetics and the comparative methods to test hypotheses of adaptive radiations or morphological evolution. But however important, these conceptual and empirical evolutions do not amount to a transition from an omission of development to an integration of it.

Two central takeaway messages of chapters 2 and 3 of this thesis were that 1) the Modern Synthesis is indeed a moving target and the reductive view of its scope and dogmas offered by some evo-devo scientists and historians does not fully resist scrutiny; and 2) at least some scientists associated with the Modern Synthesis, such as Bock Rensch, Lerner and especially Stebbins, were sensitive to the role of development in evolution and participated in elaborating conceptual and empirical tools to study it. One important question that should now be addressed is: in what ways do these findings matter beyond historical accuracy? In chapter 1, I already attempted to show how reductive historical views of the Modern Synthesis were used to back the advocacy of a separation of research programs, especially of the study of novelty on one side and of adaptation on the other, and how this separation could be counterproductive. The history of research on novelty by Modern Synthesis scientists can also be related to contemporary calls for (Breuker et al., 2006; Brigandt and Love, 2012; Hallgrímsson et al., 2012) and practice of (e.g. Budd, 2006; Galis, 1996; Niklas, 2000; D.B. Wake, 2009) a functional evo-devo. The dominance of a structuralist perspective in evo-devo, focusing on changes in form without a concern for functional questions, is an uncontroversial fact (Brigandt and Love, 2012, p. 423). Criticisms of this bias and attempts at integrating structural and functional considerations in evo-devo have recently been formulated. This thesis can be viewed as a historical and philosophical contribution to this project by providing elements of an history of functional approaches to novelty and by showing continuities as well as evolutions between research projects of the Modern Synthesis era and some contemporary projects in constructional, evolutionary and functional morphology as well as evo-devo. As such, it stands as a counterpoint to historical accounts stressing the opposition between the structural and the functional perspectives (e.g. Amundson, 2005).

GENERAL SUMMARY AND CONCLUSIONS

I will summarise the insights and findings of each chapter, stressing the conclusions that can be drawn from my research.

Chapter 1

In this chapter I focused on two different characterisations of the problem of novelty, one from a gene-centred evo-devo perspective and another from a functional-historical perspective.

Some evo-devo practitioners claim that they have introduced the origin of novelty as a new research problem in evolutionary biology. This is justified in different ways depending on authors, either by distinguishing the problem of novelty from the problem of adaptation; by defining variation and innovation as distinct processes; or by relying on the epistemic concept of explanatory force. Evo-devo characterisations of the problem of novelty are centred around identifying the developmental mechanism responsible for the production of the phenotypic character investigated, determining whether the developmental mechanism originated at the same time as the phenotypic character, and determining the type of developmental change that occurred when the phenotypic character originated. For the majority of evo-devo researchers, the null hypothesis is that the change was genetic, but research for changes at other organisational levels is undertaken. Developmental biology alone is not sufficient for this endeavour and tackling these research questions requires the help of phylogenetic systematics, comparative anatomy, palaeontology and evolutionary genetics. The role of the last discipline seems however minimal, only present as a set of boundary conditions. The role of disciplines like functional morphology, biomechanics, physiology or ecology in solving the problem of novelty is rarely denied but the dominant idea seems to be that the developmental endeavour can be conducted separately.

The functional-historical approach to novelty can be compared to the evo-devo approach using the respectable form-function dichotomy. The latter can however be misleading because, while some evo-devo researchers or philosophers argue for a study of the evolution of form independently from function (Amundson, 2005; Raff, 1996), on the other hand the functional-historical approach is not a study of function independently of form, and instead partly relies on the idea that the evolution of form and function should not be studied separately.

The functional-historical approach, illustrated by Darwin's principle of conversion of functions, but not limited to it, is characterised by the use of different types of functions, activities and biological roles, and by the attention to different types of contingency, unpredictability and dependence on past conditions, which entails that the characters of organisms and their transformations cannot be explained solely either by their current function, nor past function, nor even the series past and present functions.

An important question emerging from the choice of considering and investigating the functional-historical perspective as an encompassing set of approaches on the evolution of organisms is that of the relation between the perspective of ecomorphology, oriented towards the relation of the organism to the specificities of its environment, and the perspective of constructional morphology, oriented towards the structural and functional organisation of living beings. Although some forms of structuralism focused on the idea of laws of structures and of their transformations (Webster & Goodwin, 1982) are incompatible with the functional-historical approach, I argued that common functional and historical principles and the relation between internal and external selection justify considering constructional morphology and ecomorphology as parts of a common functional-historical perspective. This contributes to nuancing the idea of a rupture between the Modern Synthesis and post Modern Synthesis periods.

A related question is that of a classification of types of characters and the appropriate approach to their study. While both internal and external selection are pertinent for the study of characters involved in locomotion or feeding for example, external selection seems more relevant for characters such as those involved in mating display, while internal selection is more relevant for general skeletal construction and performance of internal organs. This consideration can also be applied to the relations between developmental constraints and functional constraints. Developmental constraints arguably exist to the variation of most characters. For some types of characters, considerations of functional constraints and functional continuity are essential to the investigation of the evolution of the characters and more explanatory (for example, the shape that a heart can adopt is drastically limited by functional constraints). Other characters are much less functionally constrained, and little developmentally constrained, such as helmets on the pronotum of treehoppers, of which widely different forms are known in different species, and which often have a function of camouflage (Moczek, 2008). Yet other characters are both functionally and developmentally constrained such and limbs and digits (Smith et al., 1985).

Causes for the neglect of the functional were found in the conflation of the functional approach and the populational genetic approach. This conflation can be found for example in Amundson (2005). It is true that the Modern Synthesis introduced the population genetic approach, but a functional approach to evolution and novelty was also perpetuated by some during the Modern Synthesis era. An important factor was also the development of the concept of exaptation by Gould and Vrba, which was conceived as a critique of preadaptation. I argued, after others, that the exaptation did not bring a significant conceptual input compared to preadaptation. Furthermore, by conflating a defence of historical contingency and non-adaptation, Gould and Vrba wrongly assimilated the functional-historical approach to naïve adaptationism.

The comparison of Bock’s explanation of the origin of the avian basitemporal articulation and Müller ‘s and Streicher’s explanation of the avian syndesmosis tibiofibularis revealed very similar explanatory strategies, regardless of the latter’s far richer use of descriptive and experimental ontological evidence. This prompted a stress on a distinction between theoretical positions and debates one side and explanatory practices. However, this judgment about the proximity between the functional-historical approach of Bock and the epigenetic evo-devo approach of Müller should not be too quickly generalised. Because the epigenetic approach of Müller includes considerations of functional morphology, it is naturally closer to the functional-historical approach than genetic approaches to evo-devo.

I finally argued that, despite its limited effect on explanatory style, at least in the case study considered, the distinction between innovation and variation in terms of different process was conceptually unhelpful because it narrowed down a priori the possible processes of the origin of novelty, it attributed unjustified distinct properties to continuous and discontinuous variation, and confused the problem of the generation of variation with the problem of the generation of novelty.

The weaving together of novelty and adaptation by the functional-historical approach, especially by Modern Synthesis representatives of the approach, prompted a more general appraisal of the situation of the problem of novelty in the Modern Synthesis era.

Chapter 2

I undertook a historical investigation of the relation of different research programs and different concepts elaborated during the Modern Synthesis era to the problem of novelty. I was not guided by the search for precursors of evo-devo, nor more generally by a focus on development. Rather, inspired by the close relationship between novelty and adaptation and using a hermeneutic approach, I isolated five concepts potentially related to novelty.

There is a close relationship between novelty and mutationism and saltationism since these theories were formulated as explanations of novelty and provided a distinction between novelty and variation in terms of nature and process of origin. Beyond this association, two important distinctions were stressed regarding the relation of Modern Synthesis participants to mutationism: the distinction between different types of macromutations and the distinction between the problem of the occurrence of macromutations and the problem of their importance in evolution, particularly for the problem of the origin of higher taxa. The distinction between homeotic mutations, macromutations and systemic mutations has made clear that only the latter received widespread scepticism while homeotic mutations were acknowledged by Modern Synthesis biologists. The central debate, especially with Richard Goldschmidt and Otto Schindewolf, concerned the tempo and mode of the origin of higher taxa, between the Modern Synthesis "mosaic" view and the saltationists' taxonomic view of their evolution.

The development of speciation studies was marked by a conceptual distinction between speciation as reproductive isolation of populations and phenotypic change. There was then a conceptual movement of disconnection between speciation and the formation of new characters, whereas those processes were associated in Darwin's view, at least according to Dobzhansky's and Mayr's interpretation. The development of experimental taxonomy was a related illustration of this increased focus on speciation and intraspecific processes. However, experimental taxonomy in plants was specific in its degree of technical and experimental advancement. The strong focus on polyploidy and hybridisation, the recognition of its importance in evolution, associated with experimental techniques to induce polyploidy such as colchicine treatment allowed for attempt at experimentally testing hypotheses of plant evolution and experimentally producing novelties in plants.

The research problem of origin of higher taxa in plants was addressed from several different perspectives, some more closely related to the problem of novelty (e.g. character series) than others (e.g. biogeography). The Modern Synthesis perspective on macroevolution was probably more rejected or ignored by botanists than it was by animal paelontologists. The research goals of establishing taxonomic relations and explaining morphological evolution were often weaved together as illustrated by some of the research on the origin of the angiosperm flower.

The concepts of anagenesis, grades and levels of organisation reveal a focus on different notions of progress in evolution. They also reveal numerous ambiguities. The concept of an agenesis is particularly revealing. For Rensch, it refers to different types of improvement in structural organisation and complexity which he distinguishes from the concept of adaptation. For Simpson, anagenesis refers to progressive phenotypic evolution in a temporal rather than qualitative sense. A focus on the concept of preadaptation showed that it was put to different uses in different contexts. Simpson uses it with a focus on ecology. Some functional morphologists put it to use, among other explanatory concepts, in explanations of morphological novelties.

Chapter 3

In chapter 3, I confronted dominant views of the Modern Synthesis regarding the exclusion of development by showing Bernhard Rensch's and George Stebbins's attention to and involvement in developmental approaches to evolutionary novelty. I confronted the view of a consensual and hardening late Modern Synthesis by recovering debates related to Mayr's theory of genetic revolution and focusing on I. Michael Lerner as a missing link between Mayr and Dobzhansky on one side , and Waddington and Schmalhausen on the other.

The confusion regarding the position of (some) Modern Synthesis architects on novelty partly stems from a lack of attention to the contrast class. The main theories that were opposed to the Modern Synthesis views were saltationism, Lamarckism and orthogenesis. Although all three of these theories had many versions, prudence should be applied when extending the rejection of these theories by the Modern Synthesis to the idea of a rejection of any position that undermines selection. Rensch and Mayr can be taken as examples here. The position of the Modern Synthesis on novelty is often summarised by opponents in the terms of the extrapolation thesis: the factors of microevolution (natural selection, mutation, migration and drift) are sufficient to explain macroevolution. Applied more precisely to novelty, it means that new characters appear through the accumulation of microevolutionary events (e.g. Amundson, 2005; Bonner, 1982, pp. 279–280; Stoltzfus, 2017). Indeed, in *Evolution above the species level*, Rensch defends the thesis that natural selection and mutations are sufficient to explain macroevolution, including the emergence of novelties. However, a closer look at Rensch's work shows that he develops many hypotheses regarding the origin of novelties : material compensation, the action of hormones, heterochronies etc. These theories are all formulated at levels of organisation above the genes. Thus, it would not be accurate to summarise Rensch's view of novelty as the action of natural selection on mutations. This judgment can be applied to several approaches to novelty covered in this chapter and in chapter 2, to Stebbins's approach to angiosperm novelties and well as to the work of Walter Bock or parts of Ernst Mayr's.

Chapter 4

Chapter 4 first clarified the distinction between different concepts of homology, in particular the biological concept of homology as it is promoted by Günter Wagner and the phylogenetic concept of homology. Phylogenetic systematics uses a practice-based and pragmatic concept of homology based on contextual distinction between character and character states. Günter Wagner, in contrast, promotes a distinction of character and character states that carves nature at its joint, this is made possible by the developmental mechanism of character identity networks.

Wagner considers the angiosperm flower as an illustrious example where a character identity network is channeling evolutionary change. Indeed, research on the genetics of flower development has allowed the production of an elegant and refined model involving the regulation of organ identities by obligate association and correlated expression of transcription factors. This model has allowed the formulation of hypotheses on the origin of the angiosperm flower in developmental genetic terms via processes of homeotic conversion, thresholds of expression of transcription factor genes and progressive co-dependence between transcription factors. Despite this progress, multiple hypotheses are still competing and they still face problems of access to evidence that may never be solved. Wagner unapologetically uses the concept of type and, as the mechanism of obligate heterodimerisation suggests, the concept of type points to real mechanisms in nature. However, the flower is not representative of the great plasticity of plants and Wagner's focus may be interpreted as a bias towards types.

The integration of scientific disciplines to tackle research problems is a flourishing area of study in philosophy of science. More specifically, regarding the origin of novelties, it has already been stressed that different types of novelties can require different types of integration for their explanation (Brigandt and Love, 2012, p. 424). Connecting together materials presented in this thesis allows us to flesh out and expand on this programmatic insight. From the different case studies analysed in this thesis (Bock, Müller, Rensch, Stebbins, Wagner), it can be concluded that different types of organisms and of characters studied involve different types and degrees of integration. More precisely, the relationship between consideration of function and consideration of form is partly dependent on the type of organism or the type of character considered. The structural evo-devo approach has demonstrated its success for the study of theevolution of the flower; a synthesis centred on functional and evolutionary morphology may have more explanatory force for skeletal novelties in vertebrates or novelties in plant vascular systems. Furthermore, just as the elaboration of a structuralist evo-devo has benefited from historical perspectives on its conceptual and empirical roots, the historical and philosophical perspectives on functional approaches to novelty presented in this thesis should hopefully serve as materials for the elaboration of a functional evo-devo.

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